Linking life-history traits, spatial distribution and abundance of two species of 2 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.

Keywords

Arenicola marina, *Arenicola defodiens*, spawning, population structure, size at first maturity, recreational fisheries, conservation, English Channel

Introduction

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

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

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

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

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

Besides, these management measures are merely restrictions, often taken without any considerations of the life history traits of the local populations (Watson et al., 2017a). Studies linking bait collection data to abundance, spatial distribution and life history traits of lugworm are scarce. Xenarios et al. (2018) assessed the sustainable levels of some polychaetes species (*Diopatra neapolitana*), only taking into account the harvest effort, and Blake (1979) combined the harvest effort to population data (e.g. density and size structure). Nevertheless, the only study of this kind dealing with lugworms (Blake, 1979) was performed before the knowledge of the co-occurrence of two potential species of the genus *Arenicola* inhabiting the intertidal area (Cadman, 1997).

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

1. Material and Methods

1.1. Study Area

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

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

1.2.1. Sampling strategy

Spatial distributions of lugworms were investigated on the sandy shore in April-Mai 2016 at the four sites (Wx, LT, FM and Au) during spring tide periods. Formerly, lugworms distributions were assessed by samplings on uniformly distributed points along transects (Beukema and De Vlas, 1979; Beukema, 1995). However, on the studied sites, distributions of lugworms were highly aggregative (with spots of faecal casts and spaces without faecal casts next to them). Therefore, a stratified random sampling approach was chosen (Fagan and Nelson, 2017), in order to improve the performance of the spatial interpolation methods (Li and Heap, 2008). At each site, the area was subdivided into a grid of equally-sized rectangle 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 70 m divided into 24 boxes at LT and at FM (Fig. 1). In each box, a random sampling point was computed (Fig.1), where the abundance of lugworms (both species combined) was assessed by counting the number of faecal casts in three quadrates placed randomly, of 0.0625 m^2 (when densities were higher than 10 faecal casts), or of 1 m^2 (when densities were lower than 10 faecal casts). Every 3 to 5 sampling points, lugworms were dug using either an Alvey bait pump (Decathlon ltd, extracting the worm by suction), a fork or a shovel, and the proportion of each species was calculated at the different bathymetries to correct the number of individuals belonging to each species.

1.2.2. Species identification

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

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

1.2.3 Data analyses

To assess the spatial distribution and abundance of *Arenicola spp*., first, the total number of lugworms at each point was estimated by the number of faecal casts (Farke et al., 1979), assuming that one worm produced 0.84 cast.tide^{-1} in *A. marina* (Supplementary Material: Fig. C). We assumed that both species produce approximately the same amount of casts per tide. The relative proportions of *A. marina* and *A. defodiens* were recorded for each collection point taking into account the bathymetry (height above chart datum). Since only few individuals could be collected in spring 2016, the data from autumn and winter 2015 was also used (Table 1). Bathymetries were obtained from the interregional project "CLAREC, INSU – CNRS M2C-UNICAEN" (http://www.unicaen.fr/dataclarec/home/elevations.html). When no bathymetry record was available (FM), we used the distance from the shoreline as a proxy. The shoreline HISTOLITT® was taken from the SHOM, the hydrographic and oceanographic service of the French navy (http://diffusion.shom.fr/loisirs/trait-de-cote-histolittr.html). The existence of a correlation between the proportions of the two species and the bathymetry or the shoreline distance was investigated (Spearman correlation test) at each site separately. When a correlation between the proportion of *A. marina* and *A. defodiens* and bathymetry could be established (Wx), a fitting model was adjusted on Matlab R2015b using the Curve Fitting Toolbox and a sigmoid model inspired by Cadman (1997) (Supplementary Material: Fig. D). The number of individuals of each species was then calculated following the fitted model at each collection point's bathymetry. When no particular correlation was noticed (LT, FM) (Supplementary Material: Fig. E), the number of individuals of each species was calculated from the overall proportion of the individuals of both species from autumn 2015 to spring 2016. Eventually, when the number of individuals of *A. marina* and *A. defodiens* was assessed in every point of the grid, it was then interpolated on QGis 2.18.0 (QGIS development team, 2016) using the inverse distance weight (IDW) method. Interpolations were superimposed to EUNIS habitat communities maps obtained from Rolet et al. (2014) and from additional samplings performed according to Rolet et al. (2014) at FM and Au in Spring 2016, which is based on species identification of the macrofauna and on the particle size analysis (Supplementary Material: Table F). The number of individuals of each species was obtained on the whole grid from the interpolation and then reduced to 1 m² to get the mean density. The significance of the difference of densities between sites was then estimated with a chi-squared test for each species separately, performed on R (R Core Team, 2017).

1.3. Life-history traits of the lugworm populations

1.3.1. Sampling strategy

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

1.3.2. Laboratory measurements

After each sampling, all worms were put in separated containers filled with seawater. Worms were maintained in the laboratory during 24 h to 48 h at 15°C in a cold room to allow gut contents to devoid prior to observations (Watson et al., 2000). After identification, worms were anesthetized in three successive solutions of twice-filtered sea water (TFSW, 0.45 µm and 0.2 µm) at 1%, 2.5% and 5% of ethanol (Gaudron and Bentley, 2002). Each individual was measured (total length and trunk length) and weighted (wet weight). To assess their reproductive status, biopsies of the coelomic fluid were performed on individuals of *Arenicola marina* and *A. defodiens* (Table 1) with a sterile hypodermic syringe. The gametes were then rinsed twice in TFSW and kept in ethanol (96%) at 4°C. Fifty random oocytes of each female were measured under the microscope assisted by the software Motic Image Plus 2.0. Reproductive structures of males (rosettes, morulae and spermatozoids) were analyzed using the same method. To assess the size at first maturity, the occurrence of gametes was searched in coelomic fluids of 106 individuals of *A. marina.*

1.3.3. Data Analysis

Spawning dates

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

Population and age structures of Arenicola marina

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

First size and age at maturity of Arenicola marina

The first size at maturity is the size at which more than 50% of the individuals are 'mature' (i.e. able to produce gametes, thus adult stage). Since reproductive organs are difficult to observe in *Arenicola* spp. (Cassier et al., 1997), the presence/absence of gametes in the coelomic fluid was checked at the end of the gametogenesis period (September). These observations allowed to estimate the number of individuals containing gametes (adults), and that without gametes (juveniles). The cumulated frequency of the proportion of 'mature' individuals per trunk length (TL) class was then calculated and the size at first maturity was considered the size at which the cumulated frequency equaled to 0.5 (or 50 %). The differences in TL between adult males and females of *A. marina* at Wx, and between adults and juveniles (at the same site) were assessed using a non-parametric Kruskal-Wallis (K-W) test as distributions were not normal (Shapiro test, $p < 0.05$, performed on R (R Core Team, 2017)).

1.4. Survey of bait collection within the MPA

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

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

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

2. Results

2.1. Species identification, spatial distribution and abundance

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

2.2. Life history traits of lugworms

2.2.1. Spawning dates

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

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

2.2.2. Population structure and age

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

2.2.3. First size at maturity of A. marina

Adult lugworms ranged from 2.5 to 6.3 cm (TL). The first size at maturity of *Arenicola marina* at Wx was assessed at 3.8 cm of TL (Fig. 5), which corresponds approximately to 1 g of wet weight (Fig. 4c). No significant difference was found between the lengths of males and females (K-W: 0.63, $p > 0.05$), then all the data were analysed together. A highly significant difference between the size of juveniles (2.29 ± 0.97 cm) and adults (3.92 ± 0.91 cm) was observed (K-W: 0.96, $p < 0.001$) (Fig. 5). According to the population structure of *A. marina* from Wx, lugworms become adult between 1.5 and 2.5 years-old (Fig. 4a, Table 2).

2.3. Bait collection data and retail value

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

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

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

3. Discussion

3.1. Species identification, abundances and spatial distribution

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

The maximum abundance of *Arenicola marina* found in this study at Wx (61 individuals. m^{-2}) was comparable to those found in other studies in the Wadden Sea and Portugal (~ 40 to 70 individuals. m^{-2} max) (Beukema and De Vlas, 1979; Flach and Beukema, 1994; Pires et al., 2015) but did not reach the highest abundance recorded by Farke et al. (1979) (more than 150 individuals. m^{-2}). In comparison, the values found at LT and FM for this species (2.7 and 0.6 individuals. m^{-2} max respectively) appeared relatively low. This discrepancy may be linked to physical disturbances within the higher shore at these two sites caused by mechanical engines that remove debris deposited by the tide. Beukema (1995) showed that repeated mechanical harvest of lugworms using digging machines similar to what is present at LT and FM, could decrease the overall densities of worms. In these two sites no recruits were observed during the spring period and only few individuals were collected on the higher shore during the autumn. Some individuals of *A. marina* may have migrated on the lower shore, on the EUNIS habitat A2.23 (medium to fine sands with amphipods and *Scolelepis* sp.) or even on the EUNIS habitat A5.231 (medium to fine sands with *Donax vittatus*), as lugworms may do during cold winters (Wolff and de Wolf, 1977). The trade-off made by sharing the same ecological niche with *A. defodiens* on the lower shore at FM and LT involves interspecific competition for food and habitat, higher predation rate by birds and flatfish. This would make the survival rate of *A. marina* lower, and consequently decrease its abundance in comparison with sites where *A. marina* could live not in sympatry with *A. defodiens* such as at Wx. For *A. defodiens*, the maximum abundance at all sites ranged from 1.6 to 2.9 individuals. m^{-2}. This is higher to what Pires et al. (2015) found in Portugal (between 0.25 and 1 individual. m^{-2}). The similar abundance of *A. defodiens* observed at all sites might be linked to the presence of a subtidal population of this species: when, for some reason, densities of population from the foreshore decrease, the subtidal individuals could colonize the empty spaces and reload the intertidal *A. defodiens* population. Indeed, the subtidal presence of *A. defodiens* was recorded in Portugal by Pires et al. (2015) and in France on the Eastern English Channel by the present authors (unpublished data). However, the density estimation for *A. defodiens* was made from data of cast production obtained for *A. marina*, and further investigation on the cast production of *A. defodiens* is needed to conclude more accurately on the abundance of this species.

3.2. Life-history traits of lugworm

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

The size at first maturity found for *Arenicola marina* at Wx (3.8 cm) corresponds to an individual of approximately 1 g, which is close to the weight at which individuals of *A. marina* started developing gametes in the laboratory experiment performed by De Wilde and Berghuis (1979). Recruits of *A. marina* were only spotted at Wx and recruitment happened between the end of spring and the beginning of summer, which mirrored recruitment period recorded by Flach and Beukema (1994). No recruits of *A. marina* were detected on the other sites. Since sampling for spatial distribution pattern was performed at the beginning of spring at LT and FM, we might have come too early to detect recruitment of the first cohort of *A. marina* on these sites and further investigation will be needed since some small individuals were then detected on the upper shore in autumn 2016 at both sites. However, another possible explanation to the uneven distribution and abundance of *A. marina* recorded at the different sites might be explained by a particularly low survival rate of the recruits at LT, FM, and Au compared to Wx, due to physical disturbance as mentioned earlier. Another hypothesis is linked to the lifecycle of *A. marina* that involves a post-larval nursery grounds composed of sheltered soft sediments, macro-algae and/or mussel beds (Farke and Berghuis, 1979b; Reise, 1985). These transitory colonization habitats might have been degraded by anthropogenic disturbance at Au (Paute, 2015) or naturally absent close to LT and FM (as suggested by the subtidal macrobenthic community map for the area designed by Croguennec et al. (2011)), enhancing a post-larval mortality and subsequently a low recruitment of juveniles on the beach after the second larval dispersal phase. The low recruitment of *A. marina* at LT, FM and Au might also be linked again to the two phases of dispersal during its lifecycle, where, under certain weather conditions, a strong current may be directed up North (Bailly Du Bois et al., 2002; Ellien et al., 2000; Nicolle et al., 2017) during the second dispersal phase prior to the settlement of juveniles on the higher shore, favoring recruitment to North sites such as Wx (which could be considered as a sink of propagules) compared to the three others sites that are more south on the MPA (which could rather be considered as sources of propagules). Further studies on larval dispersal using a modeling approach based on biophysical model or population genetics should be applied to support this hypothesis.

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

At Wx, LT and FM, according to the survey carried out in 2015 on recreational fishermen, extraction levels of lugworms appeared quite low compared to the lugworm abundances calculated in this study (less than 5% of the population harvested). Moreover, the presence of numerous young individuals of *A. marina* at Wx seems to ensure a rapid renewal of the part of the population allocated to bait digging. However, 104 professional licenses have been delivered to some fishermen specialized in lugworm digging within the MPA and some of them are able to extract more than 400 worms per tide (anonymous fisherman communication). The lugworm extraction may have been underestimated in this study as the survey was done only on recreational fishermen. Besides, the proportion of the lugworm population dug at Au was already quite high (13.7 % of the total number of individuals and 13.9 % of the individuals heavier than 3 g). If we consider that the maximum age of *Arenicola defodiens* is close to the one of *A. marina*, which is around 5 to 6 years old, it means that every year, around one sixth to one fifth (e.g. 17% to 20%) of the population is renewed (Beukema and De Vlas, 1979). In this case, maybe the managers of the MPA should consider following up the population's density of this species to make sure that its abundance does not decrease over time. If so, some preventive management measures should be implemented such as forbidding or restricting the bait collection during the spawning periods and giving a minimum size limit of worm collection. Again, the numbers of *A. marina* were really low at Au compared to the total number of dug individuals, and actions should be taken to follow up and manage this species in order to allow its recovery. The species was found to be able to produce gametes (adult) between the cohort 2 and 3 (1.5 to 2.5 years old and approximately 1 g) and managers should encourage local fishermen to harvest only lugworms from cohorts 4 or 5 (i.e. worms that spawned at least once, older than 3 years old), where worms are larger to 6.15 cm long (TL) and getting close to 3 g (Fig. 3c). Although, further study of the dynamics of population of this studied site is needed to determine the best "size limit" management strategy (Gwinn et al., 2015), especially since the weight/size/age relationships of *A. marina* were only studied at Wx, where the growth of the individuals of this species might be different from the one of the individuals of the same species at Au. However, as mentioned before, Au might not be a sink of larvae of *A. marina*. A second hypothesis is due to the natural mussels' beds of this site that is not in a good status and may lead to a mortality of the first settlers during their lifecycle (Reise, 1985; Paute, 2015). These last considerations enlighten the need for an integrated management of the different activities, species and habitats in the area.

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

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

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

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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 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	*Arenicola marina*	186	A2.223	May and July 2017
Species distribution	Wx	*A. marina*	24	A2.223 + A2.23	March 2016
		A. defodiens	5	A2.223 + A2.23	
	LT	*A. marina*	4	A2.223 + A2.23	April 2016
		A. defodiens	1	A2.223 + A2.23	
	FM	*A. marina*	4	A2.223 + A2.23	April 2016
		A. defodiens	3	A2.223 + A2.23	
	Au	*A. marina*	1	A2.23	May and June 2016
		A. defodiens	11	A2.23	
Spawning period	Wx	*A. marina*	51 86	A2.223	Sept - Nov 2015 Sept - Oct 2016
		A. defodiens	34 16	A2.23	Sept 2015 – Jan 2016 Oct 2016 – Dec 2016
	LT	*A. marina*	17 8	A2.23 + A2.223	Oct – Dec 2015 Oct 2016
		A. defodiens	16 12	A2.23	Oct – Dec 2015 Nov 2016
	FM	*A. marina*	5 19	A2.23 + A2.223	Sept – Nov 2015 Oct 2016
		A. defodiens	17 11	A2.23	Sept – Nov 2015 Nov 2016
	Au	*A. defodiens*	26	A2.23	Oct – Nov 2015
Size at first maturity	Wx	*A. marina*	106	A2.223	Sept 2017

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

	Mean trunk length (cm)	Number of individuals	SI
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	-

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 (km²)**	**Estimated number of fishing sessions / year (*)**	**Mean estimated catch / fishing session (*)**	**Estimated removed number**	**Estimated removed weight (kg)**	**Retail Price**	**Total retail value (€)**	**References**
Studied sites (*Arenicola* spp.)	Wx	0.9	1246 ± 40	39.8 ± 32.1	49 590 ± 19 755	198 kg to 744	4.19 € / 10 worms	20 778 ± 8 277	https://www.decathlon.fr/catalogue-sport-appats-vivants-peche-mer.html https://estamp.afbiodiversite.fr/donnees
	LT	1.5	692 ± 39	34.0 ± 15.2	23 528 ± 5 626	353 kg to 541		9 858 ± 2 357	
	FM	1.8	311 ± 32	21.3 ± 20.5	6 624 ± 6 702	86 kg to 179		2 775 ± 2 808	
	Au	1.8	3862 ± 173	30.5 ± 25.4	117 791 ± 98 203	1.885		49 354 ± 41 147	
Whole MPA	*Arenicola* 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	https://www.decathlon.fr/catalogue-sport-appats-vivants-peche-mer.html
	Mytilus edulis	-	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 http://www.manger-la-mer.org
	Crangon crangon	-	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

Figure captions

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

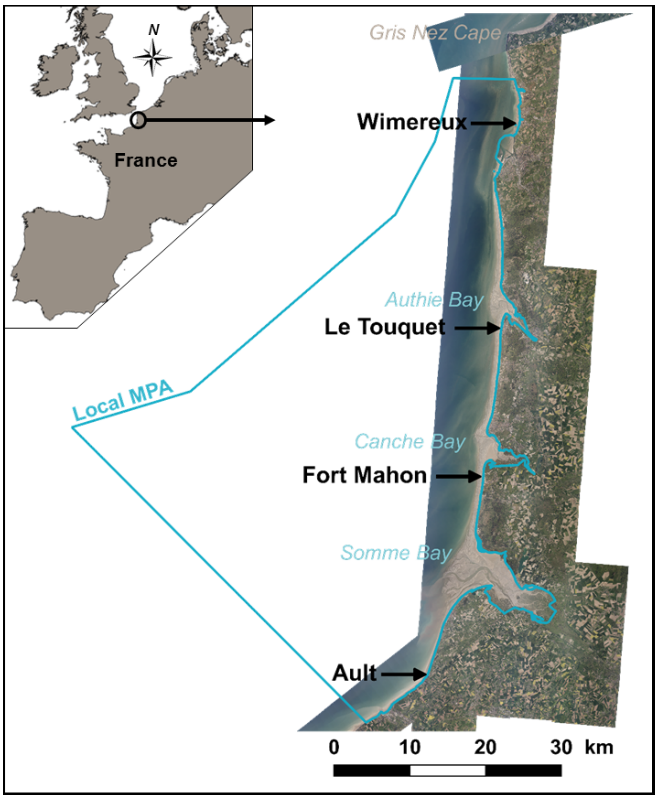
Figure 2. Spatial distributions of the two species *Arenicola marina* and *A. defodiens* at the four studied sites: Wimereux (Wx), Le Touquet (LT), Fort Mahon (FM) and Ault (Au), and associated bathymetries (height above chart datum) or distance from the shoreline and EUNIS habitats.

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

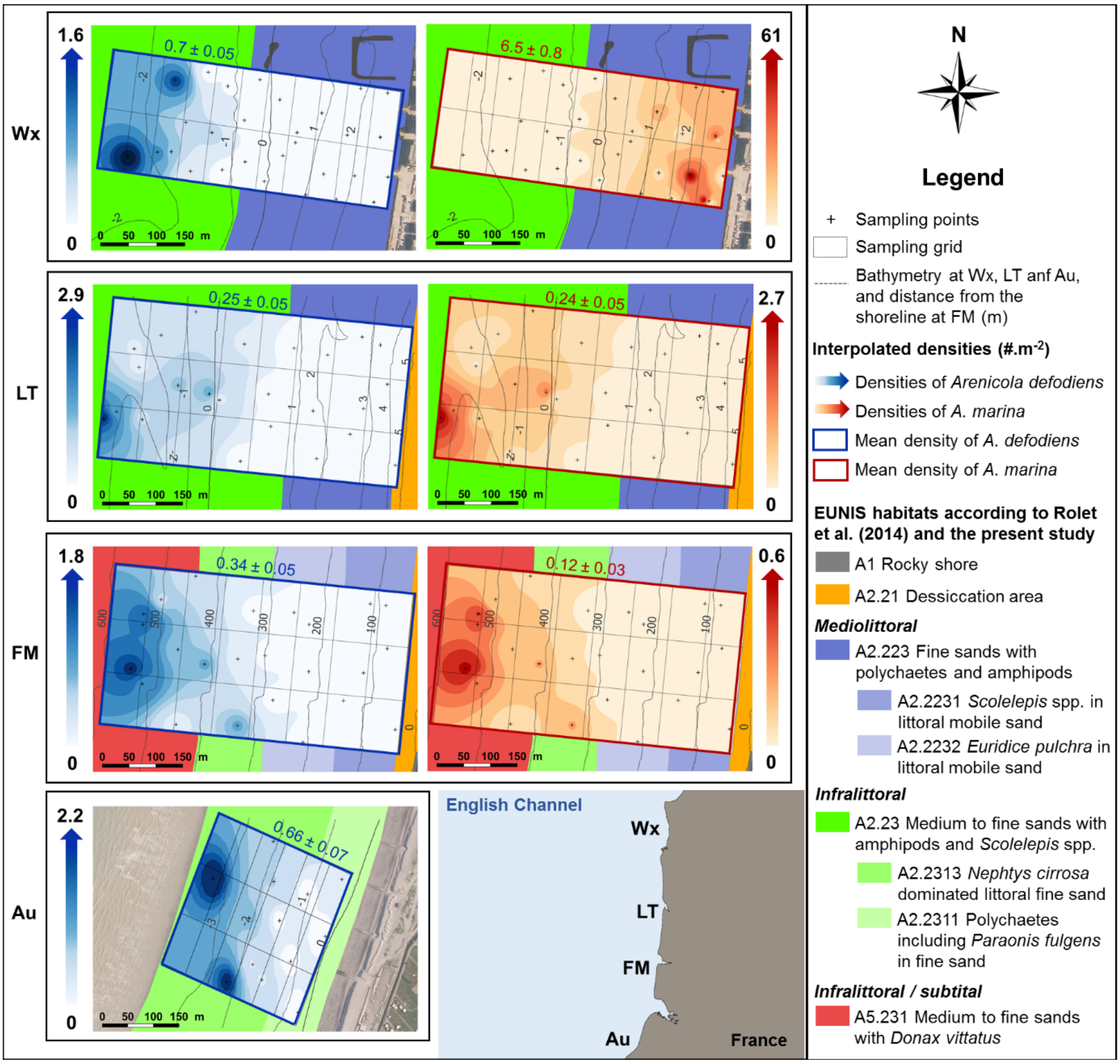
Figure 4. Length-frequency distributions of the trunk lengths of all specimens of *Arenicola marina* obtained from Wimereux in summer 2017 analysed using FISAT II. Normal curves represent each detected cohort (C.1 to C.5) (A), spatial distribution of the different sizes along the shore level (low = 0.1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

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

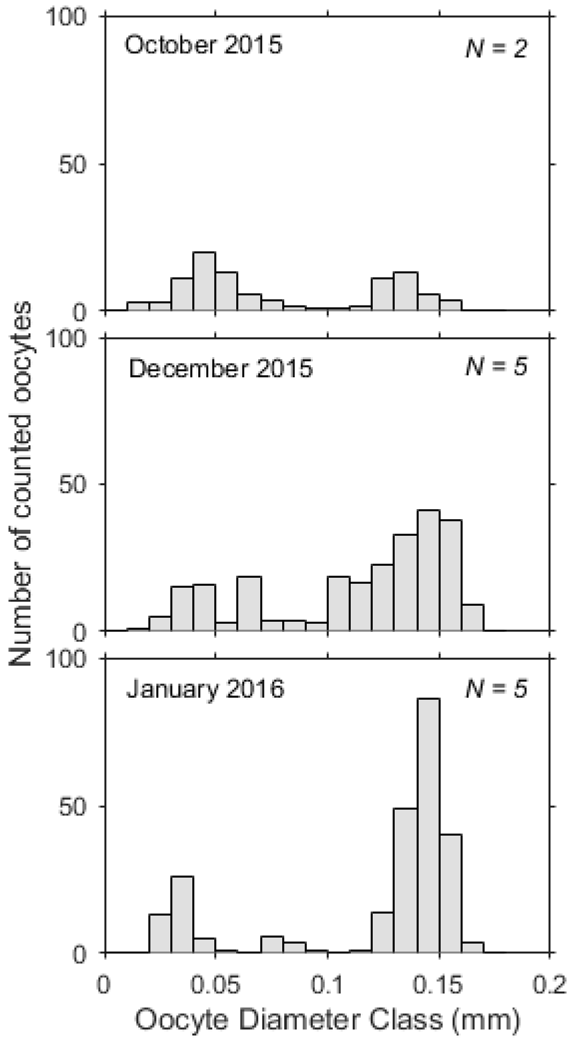
Figure 6. Comparison of the total number of individuals, number of individuals above 3 g and number of lugworms harvested in 2015 by recreational fishermen respectively for *Arenicola marina*, *A. defodiens*, and both species combined at Wimereux (Wx), Le Touquet (LT), Fort Mahon (FM) and Ault (Au).

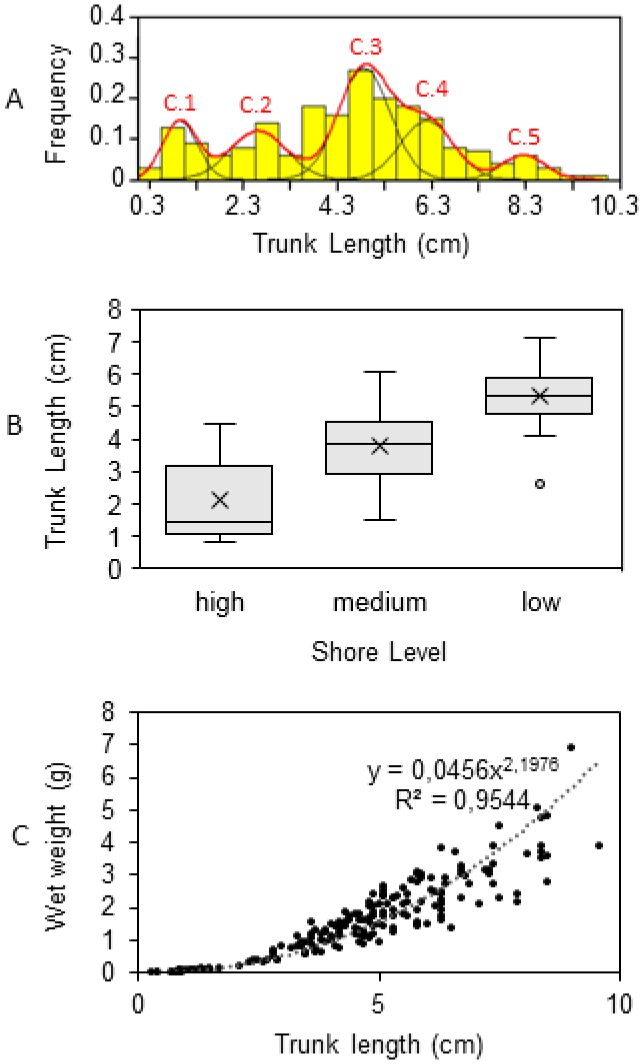


Gris Nez Cape
N
France
Wimereux
Authie Bay
Le Touquet
Local MPA
Canche Bay
Fort Mahon
Somme Bay
Ault
0
10
20
30 km

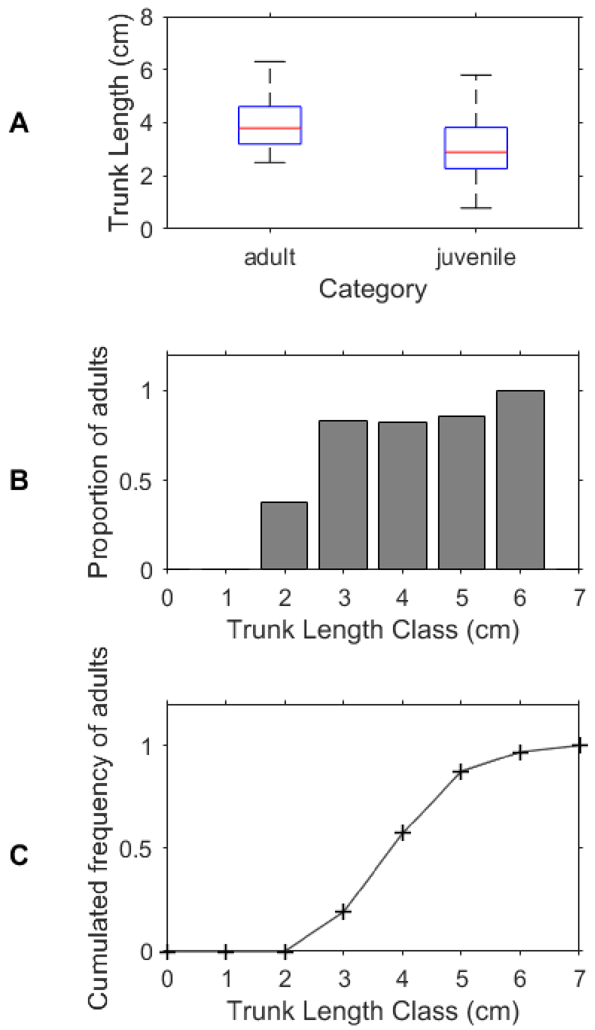


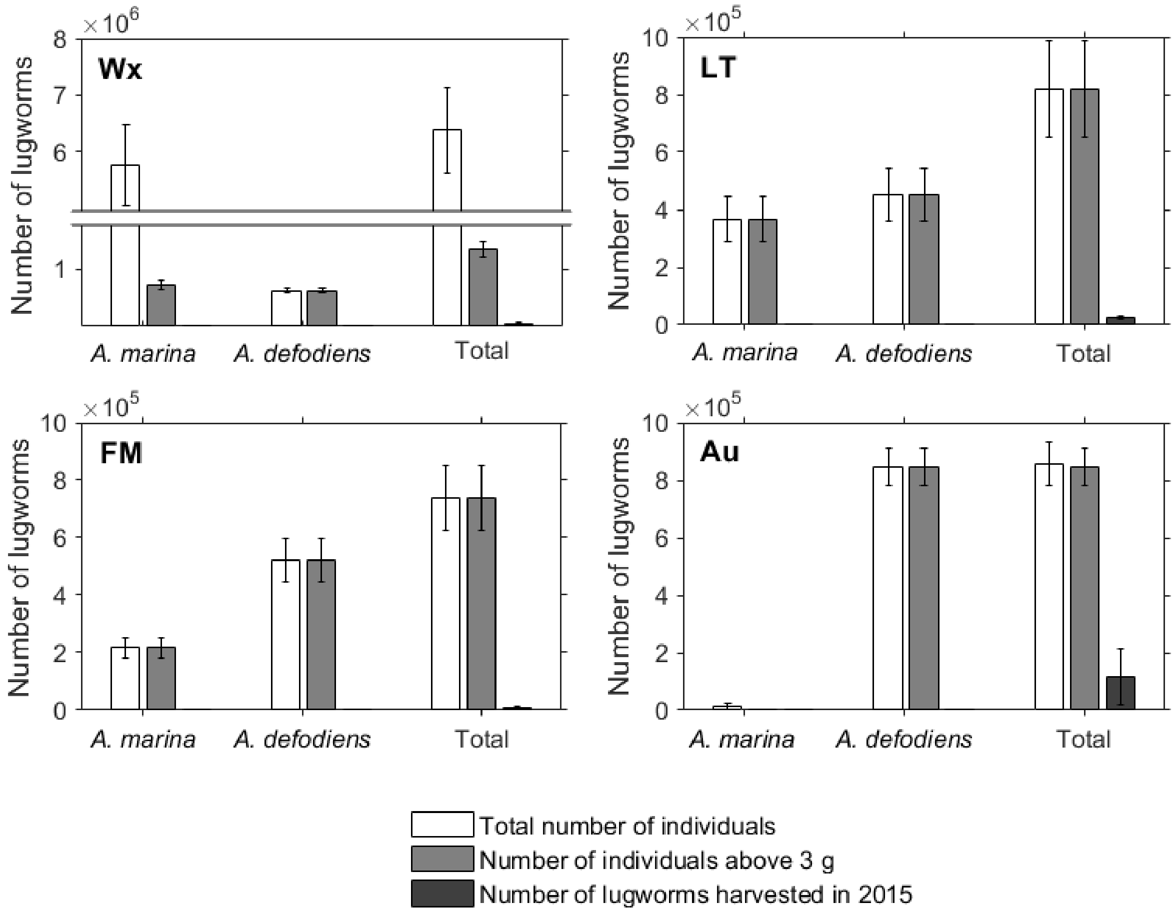
Wx
1.6
0
0.7 ± 0.05
6.5 ± 0.8
61
0
LT
2.9
0
0.25 ± 0.05
0.24 ± 0.05
2.7
0
FM
1.8
0
0.34 ± 0.05
0.12 ± 0.03
0.6
0
Au
2.2
0
0.66 ± 0.07
0 50 100 150 m
English Channel
Wx
LT
FM
Au
France
N
Legend
Sampling points
Sampling grid
Bathymetry at Wx, LT anf Au, and distance from the shoreline at FM (m)
Interpolated densities (#.m-2)
Densities of Arenicola defodiens
Densities of A. marina
Mean density of A. defodiens
Mean density of A. marina
EUNIS habitats according to Rolet et al. (2014) and the present study
A1 Rocky shore
A2.21 Dessiccation area
Mediolittoral
A2.223 Fine sands with polychaetes and amphipods
A2.2231 Scolelepis spp. in littoral mobile sand
A2.2232 Euridice pulchra in littoral mobile sand
Infralittoral
A2.23 Medium to fine sands with amphipods and Scolelepis spp.
A2.2313 Nephtys cirrosa dominated littoral fine sand
A2.2311 Polychaetes including Paraonis fulgens in fine sand
Infralittoral / subtital
A5.231 Medium to fine sands with Donax vittatus


October 2015
N = 2
December 2015
N = 5
January 2016
N = 5
Number of counted oocytes
Oocyte Diameter Class (mm)
0
50
100
0.05
0.1
0.15
0.2



A
Frequency
0.4
0.3
0.2
0.1
0
C.1
C.2
C.3
C.4
C.5
0.3
2.3
4.3
6.3
8.3
10.3
Trunk Length (cm)
B
Trunk Length (cm)
8
7
6
5
4
3
2
1
0
high
medium
low
Shore Level
C
Wet weight (g)
8
7
6
5
4
3
2
1
0
y = 0,0456x^2,1976
R² = 0,9544
0
5
10
Trunk length (cm)


A
Trunk Length (cm)
0
2
4
6
8
adult
juvenile
Category
B
Proportion of adults
0
0.5
1
0
1
2
3
4
5
6
7
Trunk Length Class (cm)
C
Cumulated frequency of adults
0
0.5
1
0
1
2
3
4
5
6
7
Trunk Length Class (cm)


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

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

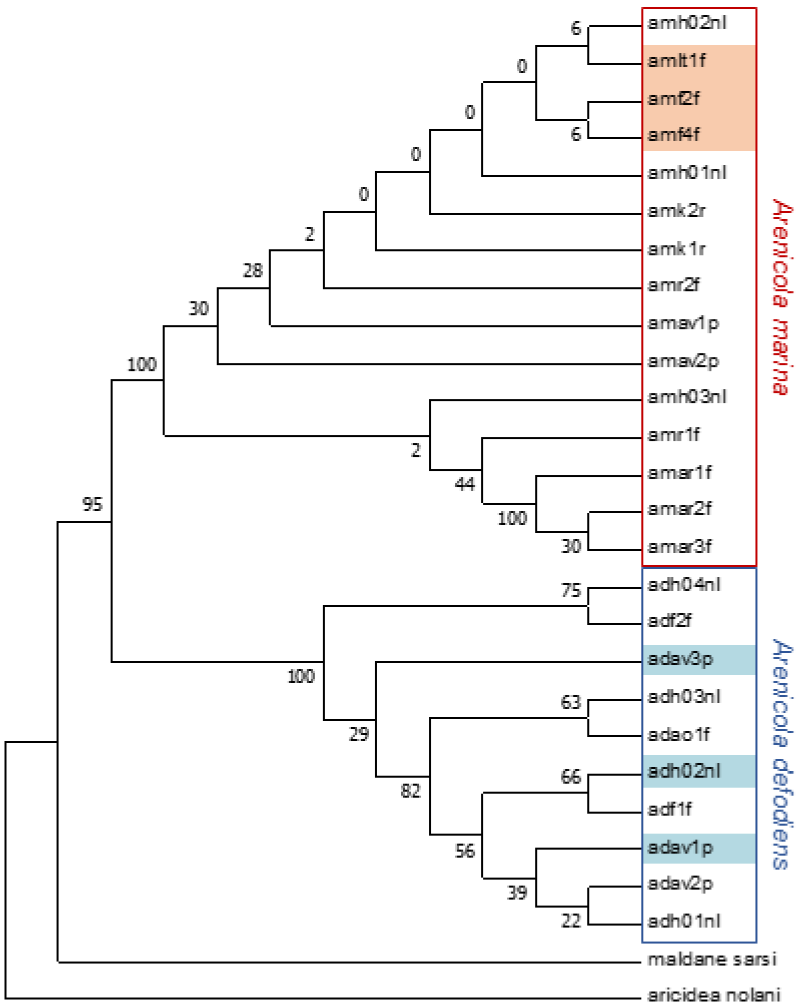


Figure C. Linear relation between the number of faecal casts produced and the number of individuals of *Arenicola marina.*

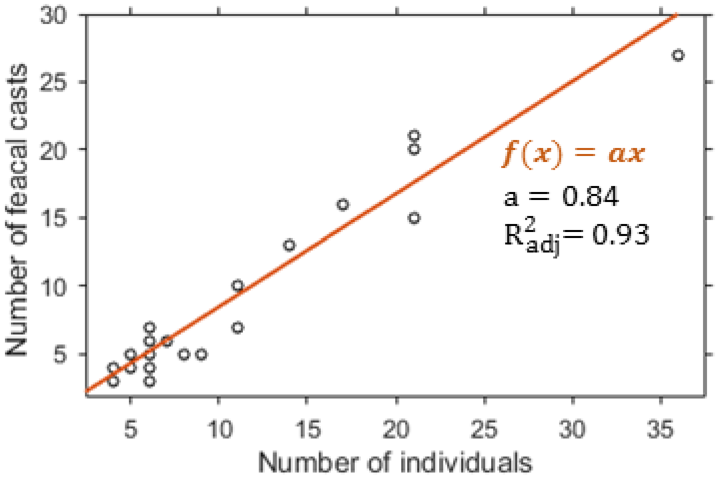


Figure D. Proportion of *Arenicola marina* (red dots) and *A. defodiens* (blue dots) according to bathymetry at Wimereux and the associated fitting transition curves and functions, as well as the number of lugworms collected at each point to calculate the proportion (weight of the different proportion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

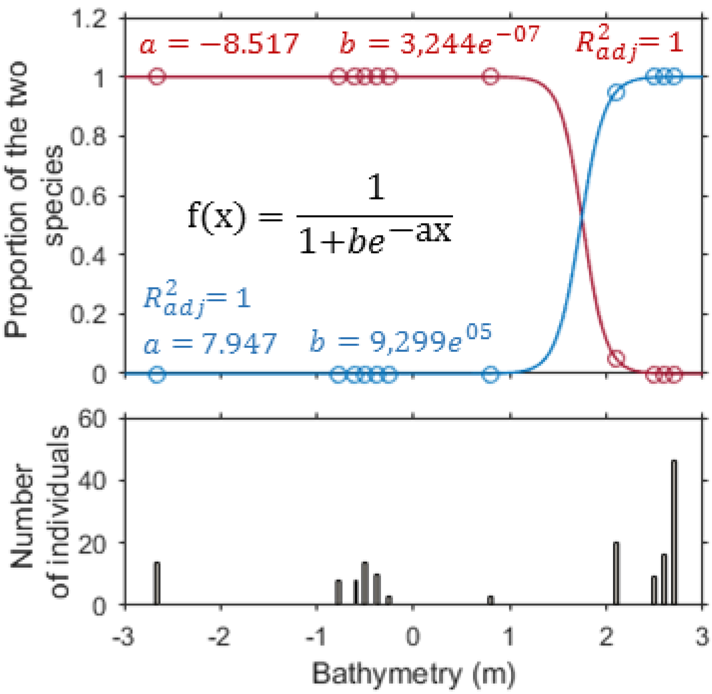


Figure E. Proportion of *Arenicola marina* (red dots) and *A. defodiens* (blue dots) according to bathymetry or distance from the shoreline and the related number of individuals used to calculate the proportion at Le Touquet (LT) and Fort Mahon (FM).

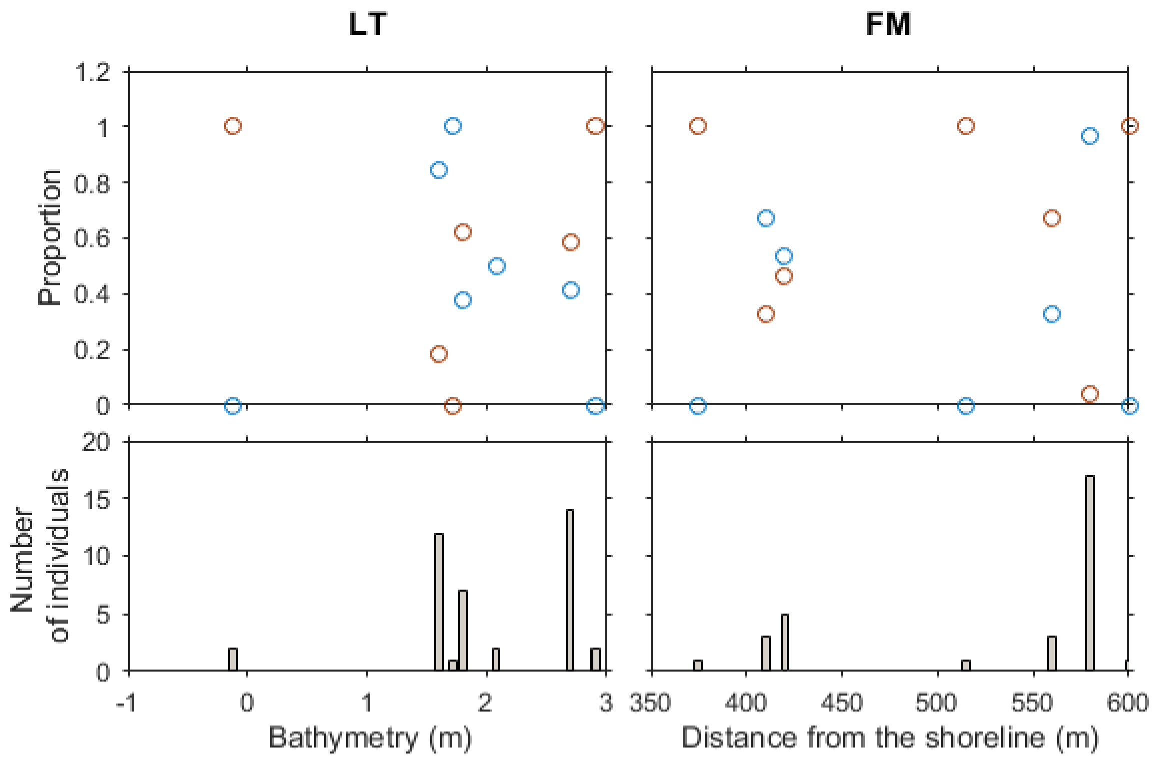


Table F. EUNIS habitats found at Fort Mahon and Ault based on particle size analysis and species identification at these sites

Site	GPS location	Species abundancy (%)		Particle size analysis (%)		Corresponding EUNIS habitat
Fort Mahon (FM)	1°32'31.68'' E 50°20'24.89'' N	*Donax vittatus*	73	mudstones	0	A5.231 Medium to fine sands with *Donax vittatus*
		Urothoe poseidonis	10	fine sands	70.7	
		Nephtys cirrosa	8	medium sands	23.6	
		Spio martinensis	5	coarse sands	1.9	
		Urothoe brevicornis	5	fine gravels	1.8	
		Notrotopis falcatus	4	coarse gravels	2.1	
		Lanice conchilega (juveniles)	4			
		Eurydice pulchra	3			
		Vaunthompsonia cristata	2			
		Gastrosaccus spinifer	1			
		Spio sp.	1			
		Nephtys hombergii	1			
		Eteone picta	1			
	1°32'39.03'' E 50°20'24.36'' N	*Nephtys cirrosa*	57	mudstones	0	A2.2313 *Nephtys cirrosa* dominated littoral fine sands
		Eurydice pulchra	21	fine sands	53.1	
		Portumnus latipes	14	medium sands	43.6	
		Nephtys hombergii	7	coarse sands	1.8	
				fine gravels	1	
				coarse gravels	0.5	
	1°32'47.60'' E 50°20'23.32'' N	*Eurydice pulchra*	60	mudstones	0	A2.2232 *Eurydice pulchra* in littoral mobile sand
		Scolelepis squamata	39	fine sands	34.2	
		Haustorius arenarius	0.3	medium sands	63.5	
		Urothoe poseidonis	0.3	coarse sands	1.6	
		Bathyporeia pilosa	0.3	fine gravels	0.5	
		Nemertean	0.3	coarse gravels	0.2	
	1°32'54.07'' E 50°20'22.79'' N	*Scolelepis squamata*	81	mudstones	0	A2.2231 *Scolelepis* spp. in littoral mobile sand
		Bathyporeia pilosa	13	fine sands	35.4	
		Carcinus maenas	2	medium sands	62.1	
		Ophelia rathkei	2	coarse sands	1.4	
		Haustorius arenarius	2	fine gravels	0.3	
				coarse gravels	0.7	
Ault (Au)	1°27'09.49'' E 50°06'43.13'' N and 1°27'04.04'' E 50°06'44.05'' N	*Nephtys cirrosa*	50	mudstones	0.1	A2.2313 *Nephtys cirrosa* dominated littoral fine sand
		Bathyporeia pelagica	19	fine sands	58.0	
		Portumnus latipes	6	medium sands	38.3	
		Haustorius arenarius	6	coarse sands	1.9	
		Nephtys hombergii	6	fine gravels	0.9	
		Lanice conchilega	6	coarse gravels	0.9	
		Oligochaete	6			
	1°27'15.07'' E 50°06'42.31'' N	*Paraonis fulgens*	31	mudstones	0.1	A2.2311 Polychaetes, including *Paraonis fulgens*, in littoral fine sand
		Gastrosaccus spinifer	19	fine sands	30.8	
		Eurydice pulchra	19	medium sands	66.3	
		Nephtys hombergii	13	coarse sands	0.8	
		Bathyporeia pelagica	13	fine gravels	0.4	
		Bathyporeia pilosa	6	coarse gravels	1.6	

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

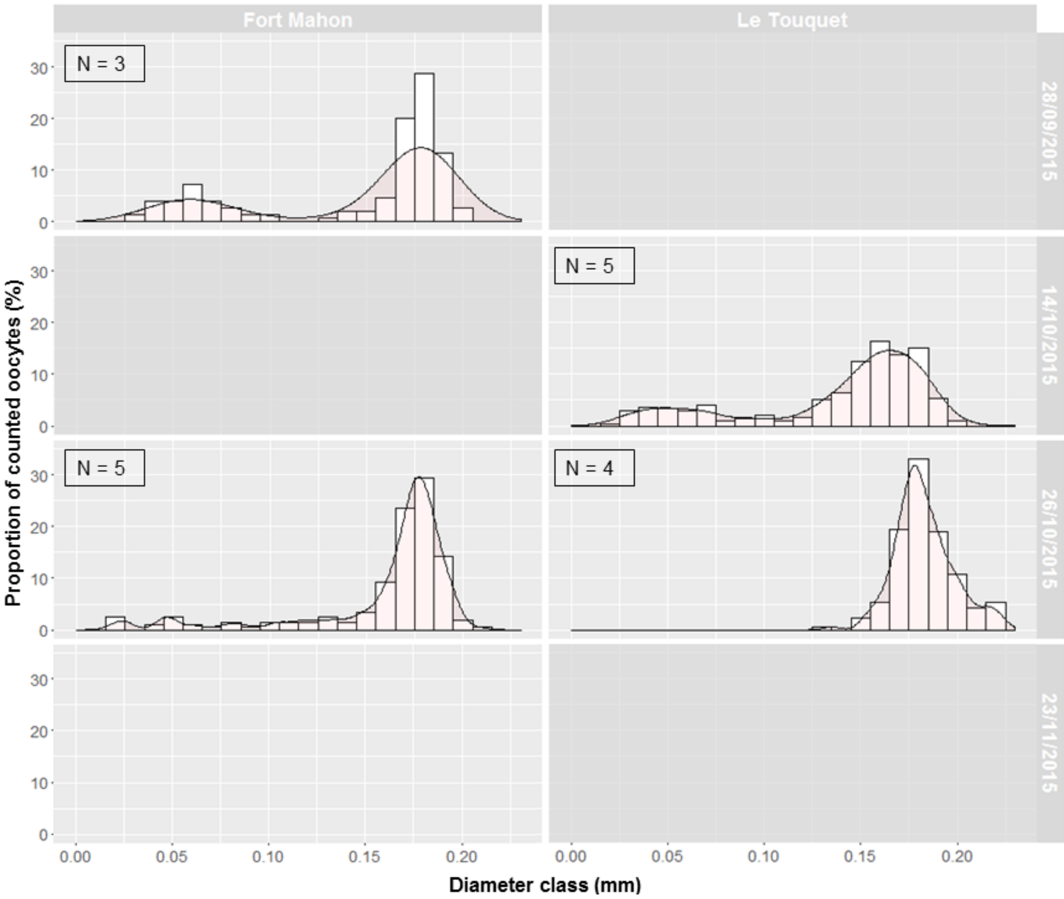


Figure G.2. Oocyte diameter distributions of the collected females (N is the number of females) of *Arenicola marina* at Fort Mahon, Le Touquet and Wimereux in autumn 2016**.** When boxes appear, darker the sites were not sampled at the corresponding date.

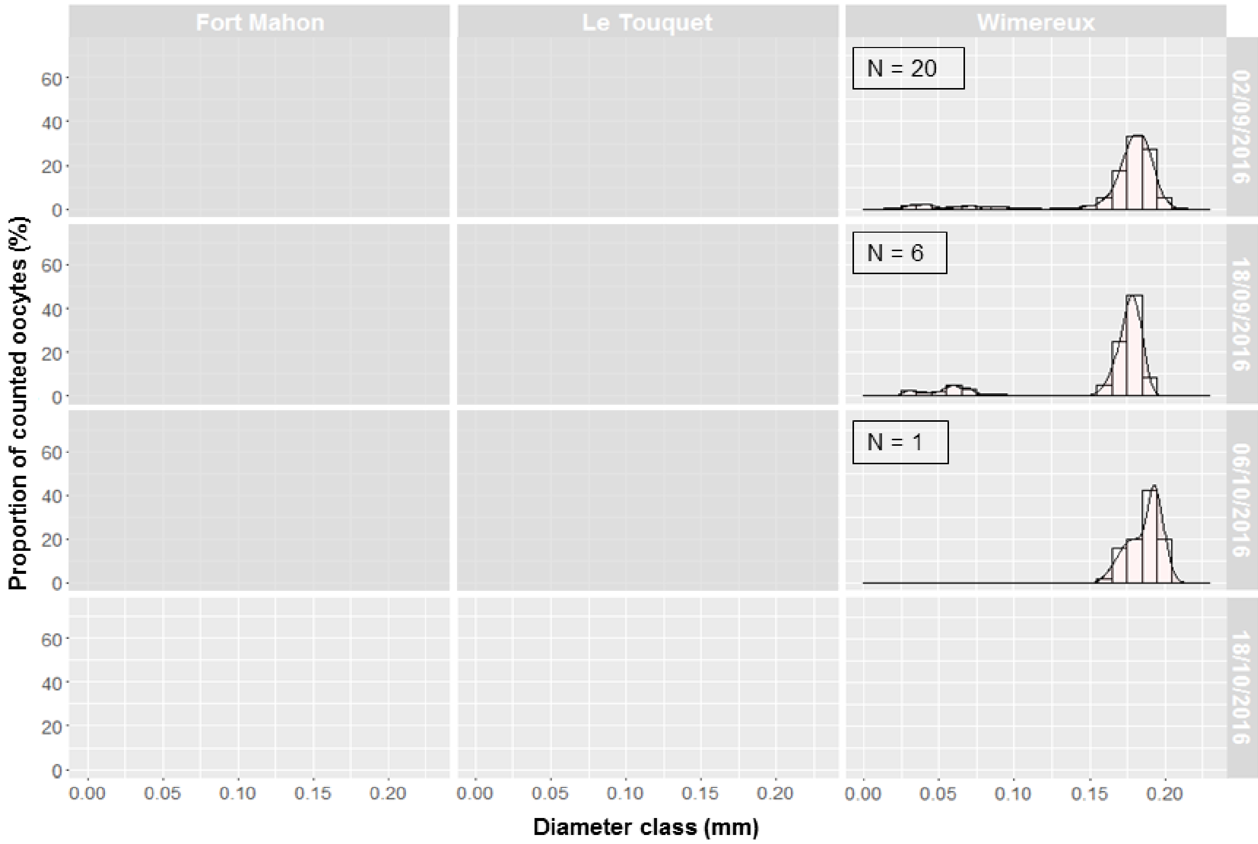


Figure G.3. Oocyte diameter distributions of the collected females (N is the number of females) of *Arenicola defodiens* at all sites in autumn and winter 2015/2016. When boxes appear darker, the sites were not sampled at the corresponding date.

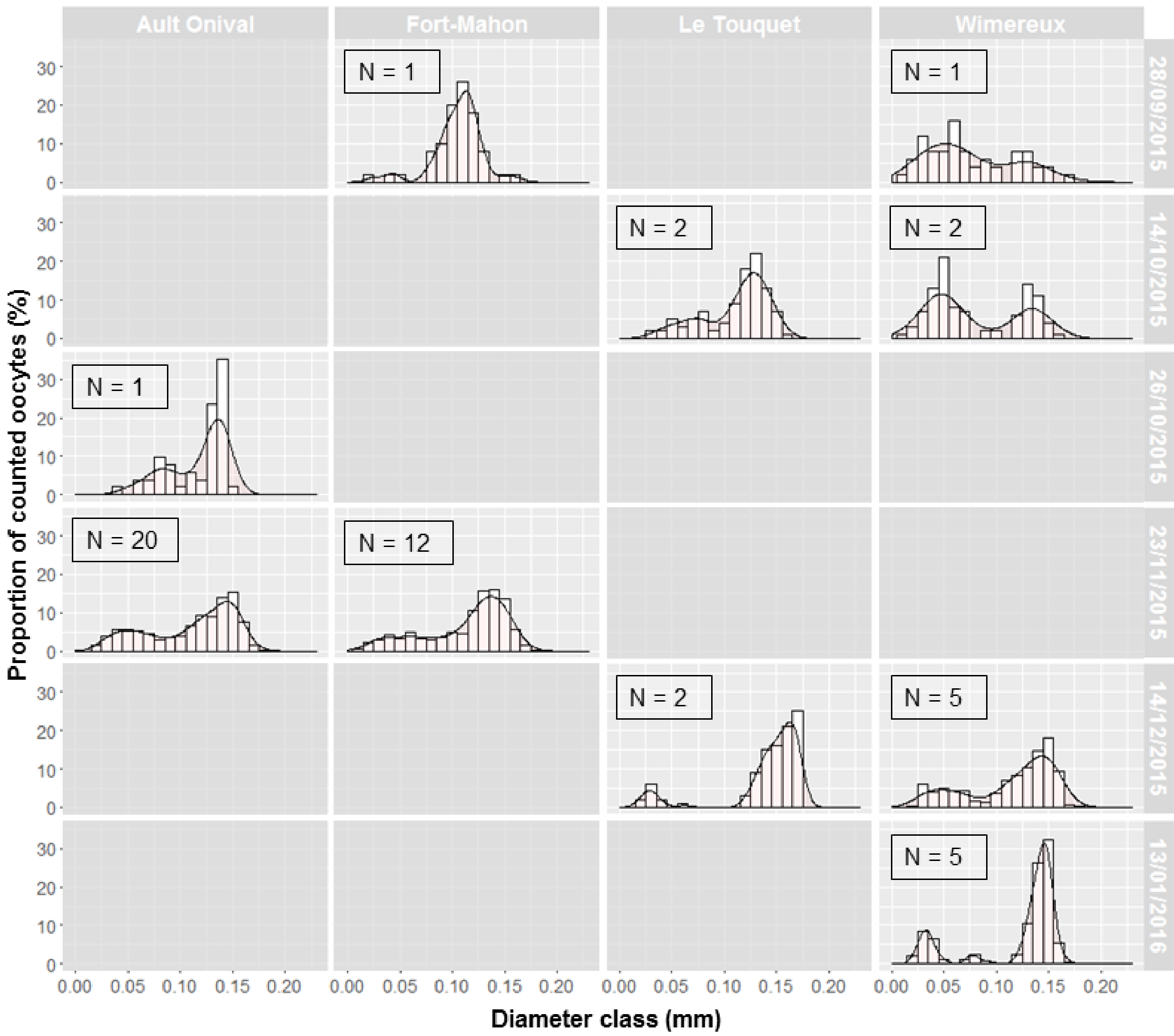


Figure G.4. Oocyte diameter distributions of the collected females (N is the number of females) of *Arenicola defodiens* at Wimereux, Le Touquet and Fort Mahon in autumn and winter 2016/2017. When boxes appear darker, the sites were not sampled at the corresponding date.

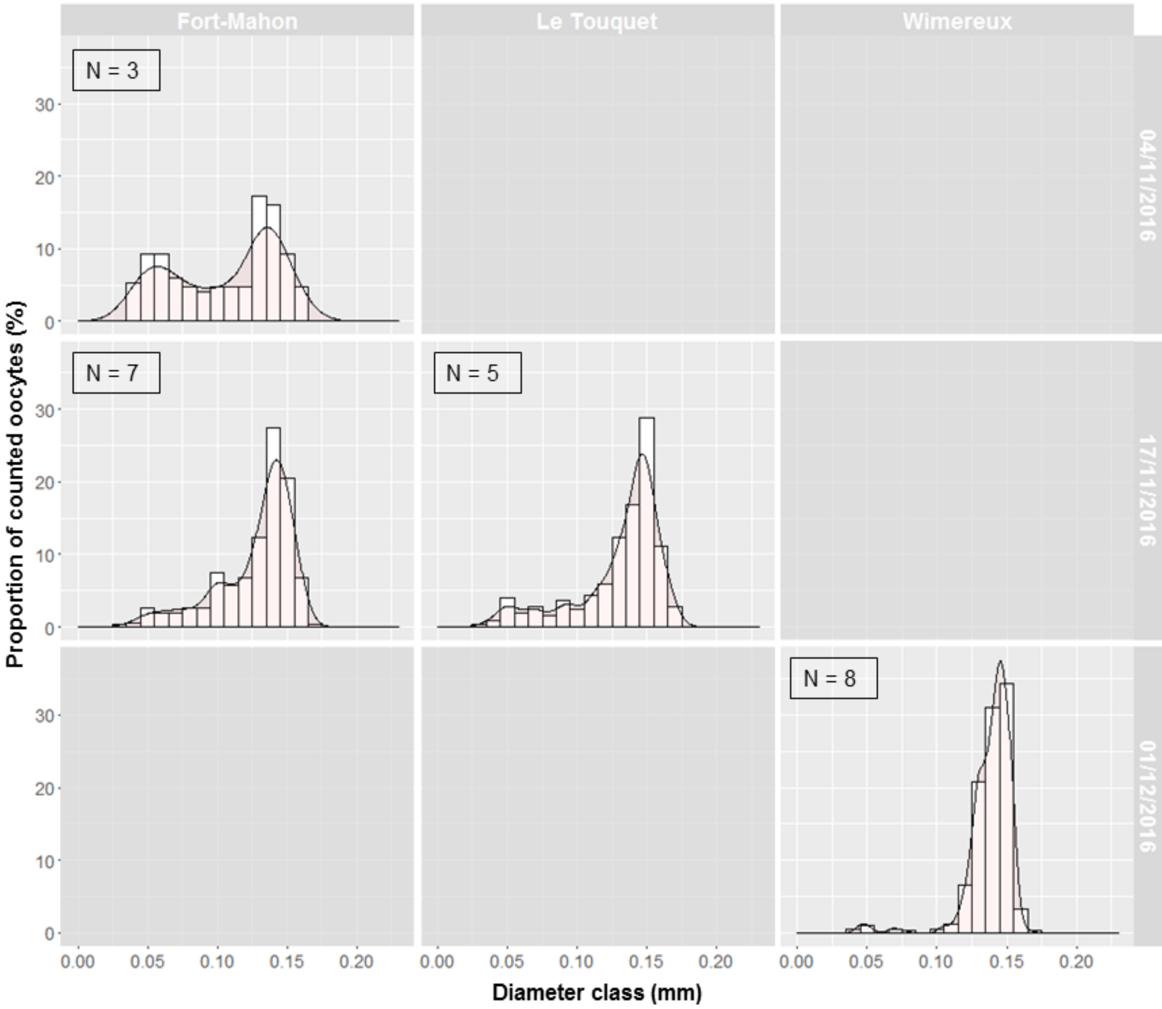


Figure H. Inferred spawning dates of *Arenicola marina* (red) and *A. defodiens* (blue) at all sampled sites in 2015 (darker) and 2016 (lighter) and associated tide coefficients (in black) and water temperatures (in green).