
Population structure and spread of the Polychaete *Diopatra biscayensis* along the French Atlantic Coast: Human-assisted transport by-passes larval dispersal

Sarah Ann Woodin^{a,*}, David S. Wethey^a, Stanislas F. Dubois^b

^a Department of Biological Sciences, University of South Carolina, 715 Sumter Street, Columbia, South Carolina 29208, USA

^b IFREMER, DYNECO Laboratoire d'Ecologie Benthique, F-29280 Plouzané, France

*: Corresponding author : Sarah Ann Woodin, tel.: +1 803 777 4254 or 1 803 782 9727 ;
email address : woodin@biol.sc.edu
wethey@biol.sc.edu ; Stanislas.Dubois@ifremer.fr

Abstract:

Intertidal populations of the ecosystem engineering polychaete, *Diopatra biscayensis*, were analyzed on the French Atlantic coast for three years with individual size estimated from tube-cap aperture. All but the northernmost population along the Bay of Biscay have yearly recruitment. Individuals live 3-5 years and are likely reproductive as one year olds. Simulations indicate dispersal distances are < 50 km; yet, populations also exist within the Normano-Breton Gulf in the western English Channel, more than 450 km from the northernmost Bay of Biscay population at La Trinité-sur-Mer. Three of the four populations in the Normano-Breton Gulf have no young of the year, but are near to active mussel culture where mussel seed is transported on ropes from dense *D. biscayensis* areas in the Vendée-Charente region in the Bay of Biscay. The majority of *D. biscayensis* were adjacent to the likely source, mussel seed ropes. Transport assisted by aquaculture is the likely explanation for the populations in the Normano-Breton Gulf.

Highlights

► Bay of Biscay populations show yearly recruitment except in northernmost. ► recruitment in only one of four Normano-Breton Gulf populations. ► Normano-Breton Gulf populations stem from aquaculture-assisted transport. ► dispersal simulations used to estimate connectivity. ► populations have demographic storage effect and short distance dispersal.

Keywords : *Diopatra biscayensis* ; ecosystem engineer ; larval dispersal ; aquaculture ; life history ; human-assisted-transport ; connectivity

34

35 **1. Introduction**

36

37 The polychaete genus *Diopatra* is well-known as an ecosystem engineer in marine sediments,
38 affecting both sediment and community characteristics in a density dependent manner (Bailey-
39 Brock 1984; Luckenbach 1986; Myers 1972; Woodin 1978). From the perspective of its effects
40 on the dynamics of sedimentary assemblages and their physical properties, the distribution and
41 abundance of *Diopatra* is of significance (Berke et al. 2010). The range of *Diopatra biscayensis*
42 has been expanding northward in the Bay of Biscay since the late 1960s (Glemarec 1979) and
43 now ranges from Arcachon France (44.6585° N, 1.1423° W) near the border with Spain to La
44 Trinité-sur-Mer (47.5830° N, 3.0242° W) in southern Brittany in France. Surprisingly, *D.*
45 *biscayensis* then reappears in the English Channel at the head of the Normano-Breton Gulf, over
46 450 km from its last known location and has a final northern limit within the Bay of Mont-Saint-
47 Michel in France (Berke et al. 2010; Fauchald et al. 2012; Wethey and Woodin 2008; Wethey et
48 al. 2011).

49

50 Wethey and Woodin (2008) and Wethey et al. (2011) built metapopulation models for *Diopatra*
51 and Berke et al. (2010) used regression tree analysis and in all cases their models indicated that
52 the distribution is limited by cool summer temperatures (SST < 18 or 18.8°C). Their models
53 suggest that the thermal conditions of the distal half of the Brittany Peninsula are currently not
54 permissive for *Diopatra* reproduction and thus prohibit expansion along the coast from the Bay
55 of Biscay into the Normano-Breton Gulf. Their models also predicted that the entire Brittany

56 peninsula would only become permissive in the late 21st century, which would then allow
57 expansion into the English Channel and north. Based on these analyses, it is very surprising that
58 *Diopatra* has already colonized the Normano-Breton Gulf. Here we examine the distribution of
59 *Diopatra biscayensis*, and make comparisons between the contiguous populations of the Bay of
60 Biscay and the disjunct populations of the Normano-Breton Gulf, populations over 450 km
61 beyond the end of the Bay of Biscay populations. The questions of interest are as follows: 1. are
62 the population characteristics of these disjunct northern populations different from those of the
63 French coast of the Bay of Biscay; 2. could planktonic larval dispersal be the source of these
64 disjunct populations and if not, what other source is likely? To address these questions we (1)
65 measured the density and size structure of eight populations in the Bay of Biscay from Arcachon
66 to La Trinité-sur-Mer and those of the four populations in the Normano-Breton Gulf from 2011
67 to 2013, (2) looked for spatial associations of *Diopatra* with aquaculture structures, and (3) ran
68 larval dispersal simulations to address the connectivity of the populations within each region and
69 across regions.

70

71 **2. Materials and Methods**

72

73 *2.1. Diopatra*

74 On the Atlantic coast of Europe there are at least five species of *Diopatra* that occur in shallow
75 subtidal to intertidal waters (Berke et al. 2010; Fauchald et al. 2012; Pires et al. 2010; Rodrigues
76 et al. 2009). South of Arcachon, France (44.6585° N, 1.1423° W), *D. neapolitana* appears to
77 predominate in most intertidal areas. However, the distribution of *D. marocensis* is expanding, is

78 already common in parts of the Portuguese coast (Rodrigues et al. 2009), and is known to have
79 been present in northern Spain from as early as 1976 (Arias et al. 2010). From Arcachon, France
80 to La Trinité-sur-Mer (47.5830° N, 3.0242° W), *D. biscayensis* is the predominant species in the
81 intertidal (Berke et al. 2010), though *D. neapolitana* is still present in the intertidal at Arcachon
82 (Pires et al. 2010) and in the subtidal further north (S. Dubois unpub.). Individuals in
83 populations from the English Channel are morphologically identical to *D. biscayensis* and were
84 used in the description of the species (Fauchald et al. 2012).

85

86 2.2. Census

87 Population densities were estimated from June to mid-July at some sites in 2010 and at more
88 sites in each year in 2011, 2012, and 2013. At each census, densities of *Diopatra* were estimated
89 from counts of 0.25 m² quadrats taken every 5 m along a 50 to 100 m transect line parallel to
90 shore within the *Diopatra* zone at that location. *Diopatra* are often continuous in their
91 distribution, given appropriate habitat, and the transect approach works well in such locations
92 (Woodin 1978). The sizes of the *Diopatra* zone vary with location. Generally individuals of
93 *Diopatra* are found from the shelf break and below. In a location with a very shallow slope such
94 as at Châtelailon-Plage, the intertidal zone of occurrence might be several hundred meters wide.
95 If large areas of inappropriate habitat such as reef or rock or mud slurries resulted in discrete
96 patches of *Diopatra*, then total counts within a known area within the patch were used; typically
97 all individuals were measured within 10 × 10 m areas.

98

99 Alternatively, if densities were so low that few quadrats contained any individuals so that most
100 transects of 10 m or more would contain 1 or 0 individuals, densities were estimated from
101 nearest neighbour distances (Diggle 1975) using Universal Transverse Mercator (UTM)
102 coordinates of individuals. In such sparse populations transect data yields little information on
103 distances between individuals. Given that reproduction for such species is a function of
104 separation between adults, knowledge of inter-individual distances is important in assessing the
105 viability of a population. With higher densities, transects yield this information when multiple
106 individuals are found within 0.25m² quadrats. Coordinates were measured with a Garmin
107 Foretrex 101 GPS (2010 to 2012) and with a Spectra Precision Mobile Mapper 10 (2013), both
108 with real-time differential corrections. Mobile Mapper coordinates were postprocessed using
109 data from nearby public reference stations to increase precision (std. error ~0.5 m). Population
110 density was estimated from N individual nearest neighbour distances (NND) using the Diggle
111 (1975) relationship for randomly dispersed individuals:

$$112 \quad \text{Density} = \frac{N}{\pi \sum NND^2} \quad (1)$$

113 Total search area was estimated from the convex hull of the UTM coordinates. Population
114 densities were calculated using Eq. 1, and the 95% confidence limits were calculated from the
115 nearest neighbour values using the Diggle (1975) estimate of the standard error of the reciprocal
116 of density.

117

118 2.3. Bouchot Census

119 The original sites where *Diopatra* was first discovered within the Normano-Breton Gulf were
120 near *Sabellaria* reefs with nearby bouchot mussel culture sites: Sainte-Anne reef near Cherrueix

121 (48.6459° N, 1.6459° W) and reef near Champeaux (48.7327° N, 1.5521° W). We surveyed
122 those areas as well as others associated with bouchot mussel culture alone: Quatre Vaux
123 (48.6065° N, 2.2235° W) in the Baie de l'Arguenon and Saint-Géran (48.6467° N, 2.2966° W) in
124 the Baie de la Fresnaye and Jospinet (48.5515° N, 2.6066° W) in the Baie de Saint-Brieuc. We
125 found that *D. biscayensis* at the *Sabellaria* reef sites were usually near the reefs, at the edges but
126 rarely within the reef. At mussel culture sites, there were extensive rows of bouchots, which are
127 vertical wooden pilings, 30 cm in diameter and 3 m high, typically separated by ~1 m (Prou and
128 Gouletquer 2002). Bouchots are set up in parallel rows 100 m long, often in pairs of rows
129 separated by ~5 m with the next set of bouchots ~20 m away. Also at these sites were chantiers,
130 which are racks for the seed recruitment ropes. These racks hold rows of seed ropes parallel to
131 the sediment surface, approximately 1 m above the sediment. Chantiers are 3 to 5 m wide, and
132 are placed 1 to 3 m from each bouchot row in more sheltered (western) regions of bays. We
133 surveyed throughout the spaces between the bouchot rows, including areas adjacent to bouchots,
134 in the chantier areas, and in the 20 m wide open areas between the sets of bouchot/chantier rows.
135

136 2.4. Size Measurements – Tube-Cap Aperture Diameter and Age Estimation

137 Tube-cap aperture diameters were measured in the field by delicate insertion into the tube-cap
138 aperture of a brass tapered cone marked with rings at millimetre increments in diameter. The
139 regression of width of the 10th chaetiger (x)(body only, not including parapodia) versus tube-cap
140 mouth (aperture) (y) was $y = 1.202x + 0.0375$ ($R^2 = 0.79$, $N = 17$, aperture sizes 1.5 to 7 mm, 10th
141 chaetiger widths 1.34 to 5.08 mm) (Fig. 1). Tube-cap aperture diameter thus can be used as a
142 proxy for body size in the field. The smallest individuals recorded had tube-cap apertures of
143 approximately 1 mm. Even those individuals had established tubes with imbricate decoration

144 and often a shell over the aperture, typical of *Diopatra*. Individuals with tubes 3 to 4.5 mm in
145 diameter appeared to be six to nine months old, therefore individuals with aperture diameters less
146 than 5 mm were designated as young of the year or recruits (see section 3.4.1 for confirmation of
147 this designation). We use the term 'recruitment' to refer to these individuals, which of course we
148 are recording several months after actual settlement (Bachelet 1990).

149
150 Small tube diameters do not mean that the worms are small. Individuals called young of the year
151 (aperture < 5 mm) may have total body lengths > 8 cm based on the regression of 10th chaetiger
152 width and body length of Pires et al. (2012b) for the similar species *D. neapolitana*. The
153 smallest individual of *D. neapolitana* found to have gametes was ~14 cm long (Pires et al.
154 2012b). This corresponds crudely to a worm with a 10th chaetiger width of 4 mm according to
155 their regression of body length on 10th chaetiger width, and by our regression of 10th chaetiger
156 width on tube aperture for *D. biscayensis*, this would be a worm with a tube aperture of ~5 mm.
157 Hence we consider animals with tube aperture diameters ≥ 5 mm to be adults.

158

159 2.5. Size Frequency Analysis

160 The size frequency data for each year and site were examined using the FiSAT II cohort
161 identification software (FiSAT II, Gayanilo et al. 2005). Bhattacharya's method was used to
162 generate initial estimates of means and standard deviations of potential component normal
163 distributions i.e. presumptive cohorts. It assigns a separation index to the presumptive cohorts.
164 Separation indices of < 2 are typically unreliable, not statistically supported, and thus those
165 presumptive cohorts were rejected (see FiSAT II, Gayanilo et al. 2005). These initial estimates

166 were then used as inputs into the NORMSEP routine which uses a maximum likelihood iteration
167 routine to generate estimates of means, standard deviations and number of individuals per cohort.

168

169 The ELEPHAN I program for estimating growth parameters from size distributions (FiSAT II,
170 Gayanilo et al. 2005) was used to assess growth rates. In only two populations, Arcachon and
171 Verdon-sur-Mer, were there sufficiently large samples (>130 each year) with numbers of young
172 of the year to do the analysis in all three years with aperture diameter measurements, 2011 to
173 2013. The ELEPHAN I program recognizes that in habitats with distinct seasonal differences in
174 temperature, growth rates may vary with season (Pauley 1987). Given that *Diopatra* is a sub-
175 tropical genus and members of the genus are known to cease activities such as feeding and tube-
176 building under cold conditions (Mangum and Cox 1971, Myers 1972), reductions in growth
177 during winter months are likely. The relevant parameters are the seasonal growth oscillation
178 parameter C and the month of lowest growth due to low temperature ('WP' in ELEPHAN I) and
179 as suggested, they were set to 0.8 and 0.1 respectively (Pauley 1987; de Graaf and Dekker 2006).
180 The maximum size of *D. biscayensis* was set to 13 mm aperture diameter.

181

182 We view the growth rate estimates with caution because soft-bodied organisms can shrink as
183 well as grow over time. *Diopatra* as a genus is known to lose its anterior and its posterior to
184 predators (Berke et al. 2009, Pires et al. 2012a). During regeneration of lost body parts,
185 depending on conditions, the worm may shrink, i.e. degrow. This also may occur with stress.
186 Size thus is not a good measure of age for such soft-bodied organisms. This may be particularly
187 true for older individuals which may have lost tissue to predators or experienced multiple periods
188 of stress. The smaller the individual, the higher the probability may be of death rather than tissue

189 loss with predation, so very small individuals may be more reliably assigned to age classes than
190 larger individuals.

191

192 2.6. Dispersal Distance

193 To estimate dispersal capabilities of *Diopatra biscayensis* both within the contiguous range in
194 the Bay of Biscay and their potential dispersal from the Bay of Biscay to the Normano-Breton
195 Gulf in the English Channel, we carried out Lagrangian transport simulations using velocity
196 fields from the IFREMER MARS2D models (Bailly du Bois and Dumas 2005; Lazure and
197 Dumas 2008). Simulated larvae were released from known population locations and treated as
198 passive particles. The larval duration and release period were based on our best estimate derived
199 from the literature on *D. neapolitana*. We used information from the congener because the
200 reproductive season of *D. biscayensis* is unknown, the species only having been described in
201 2012 (Fauchald et al. 2012). The older literature, particularly for the Atlantic coast of France,
202 may contain observations ascribed to *D. neapolitana* that really are for *D. biscayensis*, because
203 the two species are very similar in size and life habits, and the appearance of *D. biscayensis* is
204 unresolved except to be after the 1920s and probably before the 1960s for at least the area of
205 Arcachon, France (Berke et al. 2010). *D. neapolitana* reproduces from May to September in
206 Portugal (Pires et al. 2012b) and the sperm microstructure is consistent with broadcast spawning
207 (Conti et al. 2005). Cazaux (1973) working in Arcachon found larvae of *Diopatra* which he
208 called *D. neapolitana* in the water column only from September to December. These may well
209 have been larvae of *D. biscayensis*. The initial growth descriptions by all authors (Cazaux 1973,
210 Conti and Massa 1998, Pires et al. 2012b) are congruent; larvae are lecithotrophic, spend 4 to 6
211 days in the water column, then are benthic with a tube, and by 3 months are 1.5 cm in length.

212 Thus in the dispersal simulations we used a reproductive release period of September through
213 December with a maximum larval life of 6 days. These simulations provide a maximum
214 estimate of planktonic larval transport because they assume the larvae spend all of their time in
215 the surface layers of the ocean.

216

217 Two-dimensional velocity fields on a 250 m grid scale were available in 15-minute increments
218 over the period 2009-2012. Since most bays and peninsulas on this coast are 1 km or greater in
219 size, flow within and around those features is resolved at this scale. The 250 m scale MARS2D
220 models are nested inside a 700 m scale 2D model, which is nested inside a 4 km scale 3D model
221 of the European shelf (Franck Dumas, pers. comm.). The 4 km scale 3D model used 8 tidal
222 constituents at the open ocean boundary, and all models use meteorological forcing from the
223 ARPEGE forecasts of Meteo-France (Lazure and Dumas 2008). The MARS models have been
224 validated using oceanographic data (Lazure et al. 2009) and radionuclide plumes (Bailly du Bois
225 and Dumas 2005). In our Lagrangian simulations, cohorts of 500 passive particles (proxies for
226 larvae) were released each hour during the 7-hour period centered on high tides during three days
227 around the new and full moon during the months of September to December in each of the years
228 2009 to 2012. Larvae were released from sites of known populations of *D. biscayensis*, were
229 followed for 6 days, and were assumed to be competent to settle after the first day. Dispersal
230 simulations were carried out in the Lagrangian transport simulator Ichthyop Version 3 (Lett et al.
231 2008), using Euler's method with an integration time step of 1 minute. Dispersal potential was
232 estimated by determining the fraction of larvae in each cohort from each release location that
233 passed within 500 m radius of points along the coastline, spaced 1 km apart and 1 km offshore
234 during the period of larval competency (days 2-6 after release). These sampling locations were

235 chosen in order to avoid possible artefacts associated with land boundaries of the numerical
236 ocean models. Since the larvae in the simulation were proxies for potentially much larger cohorts
237 of real larvae, they were allowed to continue dispersing for the entire 6-day period, even if they
238 passed through one or more of the “capture” locations. Dispersal potential calculations were
239 carried out in the R statistical language (Ihaka and Gentleman 1996, R Development Core Team
240 2007, Chambers 2008), using the spatial statistics library “spatstat” (Baddeley and Turner 2005);
241 latitude /longitude to UTM conversion was carried out using the “clim.pact” library (Benestad
242 2004).

243

244

245 **3. Results**

246

247 *3.1. Population Densities*

248 *3.1.1. Bay of Biscay Populations*

249 Densities were greatest in Arcachon (44.6585° N, 1.1423° W), Châtelailon-Plage (46.0597° N,
250 1.0907° W), and the Baie du Bile (47.4454° N, 2.4756° W) in all years, although the Plage de
251 Gatseau (45.80411° N, 1.22172° W) which we sampled only in 2013, had the highest overall
252 density (111 m⁻²) and the highest quadrat density (360 m⁻²)(Fig. 2). With the exception of La
253 Trinité-sur-Mer (47.5830° N, 3.0242° W), all populations censused in the Bay of Biscay had
254 mean densities of greater than 1.7 m⁻². Individuals separated by < 10 cm were common in all
255 years implying that successful reproduction could occur in at least some cases. The population at
256 La Trinité-sur-Mer had no young of the year in any of our censuses and with a mean nearest

257 neighbor distance greater than 4 m, the likelihood of successful reproduction is small (Table 1,
258 Figs. 2, 3).

259
260 Most populations showed density changes of two to three fold between years, but none appeared
261 to be declining by 5 fold or more except for the population at La Trinité-sur-Mer (Fig. 2).
262 Densities at La Trinité-sur-Mer declined by an order of magnitude in 2011 relative to 2010 and
263 by a factor of 8 in 2012 relative to 2011 so that mean nearest neighbor distances rose
264 dramatically from 0.4 m in 2010 to 4.3 m in 2013 as densities declined (Fig. 2). The populations
265 at Arcachon and perhaps at Dolmen du Crapaud have decreasing mean densities but the
266 magnitudes of the declines are less than three fold between years. Regressions of density versus
267 time were significant for the populations at Arcachon, Dolmen du Crapaud and La Trinité-sur-
268 Mer (respective p values: 3.8×10^{-6} , 4.3×10^{-3} , 3.4×10^{-15}). However, for the populations at
269 Arcachon and Dolmen du Crapaud, the R^2 values were very small, 0.11 and 0.07 respectively;
270 thus, the regressions explained only a small proportion of the variance. In contrast, the
271 regression of density versus time for the population at La Trinité-sur-Mer had an R^2 value of
272 0.39.

273

274 *3.1.2. Normano-Breton Gulf Populations*

275 Unlike the Bay of Biscay populations, except for the terminal population at La Trinité-sur-Mer,
276 all four populations in the Normano-Breton Gulf had mean densities per meter square of less
277 than one and mean nearest neighbor distances > 1 m (Fig. 2). These distances among adults may
278 greatly reduce the probability of fertilization success, depending upon sperm transfer (Levitan

279 and Petersen 1995). The only population in which we saw any individual smaller than 5 mm in
280 aperture diameter was at Sainte-Anne near Cherrueix in 2010 and 2012, where we found one
281 young of the year in each year (< 5 mm aperture) (Fig. 3, Table 1). Mean nearest neighbor
282 distances at Saint-Anne were between 1.1 m and 1.8 m (Fig. 2). All four Normano-Breton Gulf
283 populations had mean aperture diameters as large or larger than those of the populations in the
284 Bay of Biscay (Table 1). The population at Saint-Géran in the Baie de la Fresnaye was very
285 small: in three hours of searching only 12 individuals were found. Mean nearest neighbour
286 distances at Saint-Géran were > 4 m (density < 0.001 m⁻²), and all individuals were large (Table
287 1).

288

289 3.2. Size Frequency Distributions

290 3.2.1. Bay of Biscay Populations

291 The most southern populations, Arcachon, Verdon-sur-Mer (45.55123° N, 1.05893° W), and
292 Plage de Gatseau on Île d'Oléron, are characterized by a high percentage of individuals < 5 mm
293 tube aperture diameter (young of the year) and by no individuals over 10 mm tube aperture
294 diameter (Fig. 3, Table 1). The more northern populations from Châtelailon-Plage to the
295 Dolmen du Crapaud near Billiers (47.51528° N, 2.48445° W) rarely had more than 5% of the
296 censused individuals in the < 5 mm tube aperture category and in one case no young of the year
297 were found in a sample of over 100 individuals (Tharon Plage at Saint-Michel-Chef-Chef
298 (47.1647° N, 2.17° W) 2011, n=131). Individuals of 10 mm or more tube aperture diameter can
299 be common in these more northern populations in contrast to those further south where few large
300 individuals were found in three years (Fig. 3). Mean sizes were smaller at the southern sites,
301 reflecting both a smaller upper size and a larger proportion of young of the year (Table 1, Fig. 3).

302 The northernmost population in the continuous distribution is at La Trinité-sur-Mer and its
303 population was dramatically different from all others in that no individuals < 8 mm tube aperture
304 diameter were found in our surveys of 2010-2013, most individuals are ≥ 9 mm tube aperture
305 diameter, and the population has decreased by almost two orders of magnitude since 2010 (Table
306 1, Figs. 2, 3).

307

308 3.2.2. Normano-Breton Gulf Populations

309 The populations of the Normano-Breton Gulf are more than 450 km from those of the Bay of
310 Biscay. The coast between these two regions has areas of suitable habitat and we have searched
311 intertidal locations north from La Trinité-sur-Mer in the Vilaine/Loire region of the Bay of
312 Biscay to Jospinet in Saint-Brieuc Bay (48.5515° N, 2.6066° W) on the English Channel side of
313 the Brittany Peninsula, but we have found no *Diopatra* (Fig. 4). Additionally we have searched
314 both the east and west sides of the Cotentin Peninsula in Normandy and again have found no
315 *Diopatra* (Fig. 4). The four populations discovered to date in the Normano-Breton Gulf between
316 Champeaux (48.7327° N, 1.5521° W) and Saint-Géran (48.6467° N, 2.2966° W) in the Baie de
317 la Fresnaye are all dominated by large individuals and at only one site have we seen any young
318 of the year or any individuals < 7 mm tube aperture diameter (Table1, Fig. 3: Sainte-Anne).

319

320 3.3. Cohort Analysis

321 Cohort analysis of size frequency distributions differed between the two southernmost
322 populations and those further north in the Bay of Biscay, but in neither case did it prove to be
323 very informative. Only at Arcachon could more than one cohort be resolved in all three years.

324 In the case of Arcachon, with good densities of small individuals in all years sampled (Fig. 3), a
325 peak centered on 3.4 mm with upper and lower 95% confidence limits of 4.6 and 2.2 mm could
326 be resolved, which crudely corresponds to what we have designated as young of the year i.e.
327 worms with tube apertures of < 5 mm. As is clear from the size distributions of the populations
328 (Fig. 3), in only a few cases is any coherent cohort size structure apparent; so, we restrict
329 ourselves to merely recognizing individuals with very small apertures (< 5 mm) as young of the
330 year.

331

332 3.4. Growth Rate and Lifespan Estimates

333 3.4.1. Estimates from FiSAT II ELEPHAN I

334 The populations at Arcachon and Verdon-sur-Mer had numerous young of the year in all census
335 years (Fig. 3) and thus could be used to estimate growth parameters. Growth parameters
336 estimated from the FiSAT II ELEPHAN I algorithm for these populations suggest that by 12
337 months of age individuals would have an aperture diameter of ~ 5 mm (Table 2). Size data
338 relative to the presence of developing gametes exist for *D. neapolitana*, a very similar worm in
339 terms of size (Pires et al. 2012b). In *D. neapolitana*, animals of 5 mm aperture diameter are ~ 14
340 cm long and are of reproductive size (Pires et al. 2012b, section 2.3). Choe (1960) reported very
341 similar growth rates for a Japanese species of *Diopatra*, individuals reaching lengths of 12.4 to
342 13.9 cm in one year.

343

344 All census observations were made in June to mid-July depending on year and site. Assuming
345 reproduction and recruitment from September through December (see Materials and Methods:

346 2.5), the young of the year would be 5 to 10.5 months old at the time of census. Based on our
347 calculated growth parameters these individuals would be expected to have aperture diameters
348 between 2.0 and 4.3 mm. This again corresponds to those we are designating as young of the
349 year (Tables 1 and 2, Fig. 3).

350

351 3.4.2. *Field Data on Growth Increments and Lifespan*

352 Densities at most locales are too great to allow worms to be individually followed through time;
353 so, neither lifespan nor growth rate can be estimated from known individuals. The densities at
354 La Trinité-sur-Mer are sufficiently small that this could be done for 10 individuals recorded in
355 2011, 2012 and 2013 (Table 3). Members of this genus with sediment tubes rarely move; thus, if
356 the individual is still alive, it should be at the previous year's coordinates \pm the GPS error
357 (Brenchley 1975, Myers 1972). We therefore can use the data on this very limited number of
358 individuals to ask whether the measured growth increments and lifespans are consistent with the
359 estimates derived from FiSAT II. In 5 of the 10 cases, worms grew at rates crudely conforming
360 to those estimated from ELEPHAN I assuming the animals were 1.5 to 2 years old when we first
361 started tracking them in 2011 (Table 3). In the other 5 cases the worms either did not grow or
362 shrank between years, which is consistent with soft-bodied organisms which often degrow. Note
363 that 21 of the 28 individuals total seen in 2011 were never seen again. In 2012 and again in
364 2013, we searched without success areas 20 to 40 m in diameter centered on the coordinates of
365 individuals found in 2011. We presume they are dead. Two of the seven individuals from 2011
366 that were seen in 2012 were not found in two days of searching in 2013, and again are presumed
367 dead. Five survived the three year observation period (Table 3). These data also are consistent

368 with a lifespan for *D. biscayensis* of 3 to 5 or more years which is also the estimate from FiSAT
369 II (Table 2).

370

371 3.5. Connectivity

372 The results of the larval transport simulations are consistent with short-distance dispersal,
373 typically < 50 km (Figs. 4, 5). Larvae released from sites adjacent to the northern geographic
374 limit of *D. biscayensis* in the Vilaine/Loire region dispersed only within the local region during
375 the 1 to 6 day larval period as is reflected in the rapidity of decrease in connectivity with distance
376 (Figs. 4, 5). Larval connectivity was high close to the sites of origin, and declined by one order
377 of magnitude for each 10 km of distance from the source (Fig. 5). No larvae escaped the
378 Vilaine/Loire region (see the inset map on Fig. 4) in our simulations over the period 2009-2012.
379 It is therefore highly unlikely that larvae from the Vilaine/Loire populations are the source of the
380 populations in the Normano-Breton Gulf unless some additional mechanism of transport is
381 involved. Within the Normano-Breton Gulf, dispersal was possible between the Sainte-Anne
382 and Champeaux populations, and between the Quatre Vaux population in the Baie de l'Arguenon
383 and the Saint-Géran population in the Baie de la Fresnaye. However the Sainte-Anne and
384 Champeaux populations never exchanged larvae with Quatre Vaux or Saint-Géran in our
385 simulations (Fig. 4). Therefore it is likely that the western two populations in the Normano-
386 Breton Gulf were seeded independently from the eastern two populations. The decline of
387 connectivity with distance in the Normano-Breton Gulf was 1 order of magnitude per 10 km,
388 indistinguishable from the rate of decline measured in the Vilaine/Loire region (Fig. 5).

389

390 3.6. Human-Assisted Transport via Aquaculture

391 The Normano-Breton Gulf is an area of intense aquaculture activity, both of oysters and mussels.
392 Several of the populations of *D. biscayensis* are seemingly spatially discrete and associated with
393 bouchots. The population in the Baie de l'Arguenon at Quatre Vaux was used to test this
394 association. Two of us searched for three hours, looking for individuals of *D. biscayensis* at
395 three types of locales: (1) within 5 m of mussel seed rope deployments (chantiers) (Fig. 6), (2)
396 within 5 to 15 m of mussel seed ropes, (3) further away from mussel seed ropes such as within 5
397 m of bouchots or in 20 m wide zones between rows of bouchots or in areas without bouchots. 96
398 individuals of *D. biscayensis* were found; 83% (80 individuals) were within 5 m of mussel seed
399 ropes, 13.5% (13 individuals) were within 5 to 15 m of mussel seed ropes, and 3.5% (3
400 individuals) were found elsewhere.

401

402 4. Discussion

403

404 *Diopatra biscayensis* belongs to a genus of important ecosystem engineers (Woodin 1978, Berke
405 et al. 2010, Woodin et al. 2010). At densities of 5 or more per 0.01 m² the tube clumps of
406 *Diopatra* alter both the biotic and physical characteristics of the habitat, acting as an ecosystem
407 engineer (Bailey-Brock 1984; Luckenbach 1986; Woodin 1978, 1981). The populations along
408 the French coast of the Bay of Biscay commonly exceed such densities (Fig. 2). *D. biscayensis*
409 is common from Arcachon in southern France to the southern edge of Brittany and has disjunct
410 populations without intermediate stepping stones in the Normano-Breton Gulf (Fig. 4). We
411 asked two sets of questions. First, are the disjunct populations in the Normano-Breton Gulf self-

412 sustainable? How is this reflected in their densities and size frequency distributions? What does
413 this imply about the likelihood of the distribution of *D. biscayensis* in the eastern English
414 Channel? Second, given the larval dispersal capabilities, how connected are the disjunct and
415 continuous populations? If they are not connected by planktonic dispersal, are other sources of
416 transport such as human assistance via aquaculture likely?

417

418 4.1. Census and Geographic Distribution

419 It is very difficult to dig intact individuals of *Diopatra* (Quatrefages 1866) but the tube-cap is
420 distinctive and the diameter of the aperture is related to worm size (Fig. 1) so both densities and
421 size distributions can be surveyed in the field. The continuous biogeographic range of *D.*
422 *biscayensis* is from Arcachon (44.65° N, 1.13333° W) in the south of France on the Bay of
423 Biscay to La Trinité-sur-Mer (47.5826° N, 3.02677° W) in southern Brittany. Populations
424 disjunct from those of the Bay of Biscay exist at four sites in the western English Channel in the
425 Normano-Breton Gulf (Fig. 4). Individuals identified as *D. biscayensis* from the Bay of Biscay
426 and Normano-Breton Gulf are morphologically identical (Fauchald et al. 2012), so we consider
427 them all to be one species.

428

429 4.2. Density, Recruitment, and Size Structure in the Bay of Biscay

430 The populations of *Diopatra biscayensis* along the French coast in the Bay of Biscay differ in the
431 frequency of young of the year each year. The most southern populations (Arcachon and
432 Verdon-sur-Mer) have a higher proportion of young of the year than those further north (Fig. 3).
433 In all years during this study, 2010 to 2013, within the populations in the Bay of Biscay,

434 complete absence of young of the year was extremely rare, seen only once at Tharon Plage in
435 2011 (Fig. 3, Table 1). The one exception to this pattern of recruitment success in the Bay of
436 Biscay was the terminal population at La Trinité-sur-Mer where no individuals smaller than 8
437 mm tube aperture have been recorded (Fig. 3). Densities at La Trinité-sur-Mer are decreasing
438 rapidly; over 75% of the adults seen in 2011 were gone by 2012 and the density in 2011 was
439 one-tenth that of 2010 (Fig. 2). Our estimates of growth suggest that individuals 8 mm in
440 aperture diameter are 1.5 to 2 years old (Table 2); so, the population we found in 2010 may
441 reflect a recruitment event in 2009 or earlier. Based on our previously published metapopulation
442 models of *D. biscayensis* (Berke et al. 2010, Wethey et al. 2011), the failure of this population
443 does not appear to be due to either winter mortalities of juveniles or failure of reproduction in
444 cool summers since populations 40 km to the east are highly successful with consistent presence
445 of young of the year (Table 1, Fig. 3) and much higher densities (Fig. 2). A more likely
446 explanation is that the local population density is too low for successful reproduction and
447 dispersal distances are too great for recruitment from the larger populations to the east and south
448 (Levitan and Petersen 1995) (Fig. 4, 5). For example, in both 2012 and 2013 no individual at La
449 Trinité-sur-Mer was as close as 4 m to another. Given a lifespan of 3 to 5 years or more (Table
450 2), the population will display a demographic storage effect of adults present but no successful
451 local reproduction. With short distance dispersal distances such a population may derive from a
452 rare recruitment event with much higher than normal dispersal distances or survivorships
453 (Wethey et al. 2011). We did not see any larval transport from nearby reproductive populations
454 to La Trinité-sur-Mer in our simulations of the years 2009-2012 (Fig. 4 and 5), so the event
455 likely occurred before 2009.

456

457 The distribution of sizes also differs across the populations in the Bay of Biscay with the
458 southern populations at Arcachon and Verdon-sur-Mer having both smaller mean apertures and
459 smaller maximum size than in populations further north (Table 1, Fig. 3). The mean size
460 difference is expected because the southern populations have larger proportions of young of the
461 year, 0.10 to 0.27 in 2011 to 2013 versus 0.01 to 0.075 at Châtelailon-Plage to Dolmen du
462 Crapaud (ignoring the 0.0 in 2011 at Tharon-Plage). The difference in maximum size (Table 1)
463 may well reflect a difference in disturbance or predation in the southern populations and thus
464 more frequent episodes of regeneration. We have no data to support or refute this proposition
465 but it seems most likely given the frequency with which this genus is known to lose tissue (Berke
466 and Woodin 2008, Berke et al. 2009, Pires et al. 2012a).

467

468 *4.3. Dispersal and Connectivity*

469 Our dispersal simulations suggest that dispersal is likely to be less than 50 km in scale but varies
470 with both wind and tidal conditions as seen in other simulation studies (Ayata et al. 2009, 2010;
471 Dubois et al. 2007; Gilg and Hilbish 2002). Within the Bay of Biscay, populations are
472 sufficiently close that some larval input from adjacent populations is likely (Fig. 4, 5). This is
473 also true for the populations within the Normano-Breton Gulf (Fig. 4, 5). However the
474 simulations indicate that populations within the Bay of Biscay have no larval exchange with
475 those of the Normano-Breton Gulf. The lack of connectivity that we observed between the
476 Vilaine/Loire region of the Bay of Biscay and the Normano-Breton Gulf is consistent with larval
477 simulations by Ayata et al. (2010). Their simulations were for different seasons from ours
478 (January – August), their larval durations were longer (2 – 4 weeks), and they observed no
479 connectivity between the Vilaine/Loire region of the Bay of Biscay and the Normano-Breton

480 Gulf in 5 years of simulations, 2001-2005 (Ayata et al. 2010). The average north-south dispersal
481 distance observed in their 2-week simulations was 50 km, consistent with our estimates from the
482 decline in connectivity with distance (Fig. 5). Therefore we believe that planktonic larval
483 dispersal cannot account for the origin of the Normano-Breton Gulf populations

484

485 *4.4. Normano-Breton Gulf Populations versus the Bay of Biscay Populations*

486 Along most of the French Bay of Biscay coast there is abundant suitable habitat for *Diopatra*.
487 We had previously projected a northward expansion, facilitated by larval dispersal as
488 temperature conditions became more permissive, leading to possible expansion into the
489 Normano-Breton Gulf by perhaps 2050 and certainly by 2099 (Berke et al. 2010, Wethey et al.
490 2011). However *Diopatra* is already present in the Normano-Breton Gulf. Based on our
491 connectivity analysis and the lack of stepping stone populations around the Brittany peninsula,
492 one cannot invoke larval dispersal to bridge the over 450 km distance from the Bay of Biscay
493 (Fig. 4 and 5). One of the four Normano-Breton Gulf populations (Sainte-Anne) appears to be
494 sustainable since it has existed since 2001-2 (S. Dubois, unpub.), and we have twice seen young
495 of the year (2010 and 2012), although the densities are very low (0.2 m^{-2}) with mean nearest
496 neighbor distance of 1.1 m in 2013 (Fig. 2). In spring 2014 Dubois again found young of the
497 year at Sainte-Anne. The other three populations resemble that of La Trinité-sur-Mer since no
498 young of the year have been seen, densities are low ($< 0.1 \text{ ind. m}^{-2}$) with nearest neighbor
499 distances often 2 meters or larger greatly reducing the probability of sperm transfer (Levitan and
500 Petersen 1995), and in two of the three populations we found relatively few individuals despite
501 long searches (Quatre Vaux: $N=107$; Saint-Géran: $N=12$) (Figs. 2, 3). The population densities
502 and proportion of young of the year are thus strikingly different from the Bay of Biscay, with

503 those of the Normano-Breton Gulf appearing to be not or only marginally self-sustainable (Fig.
504 2, 3).

505

506 4.5. Mussel Culture and Biogeography of *Diopatra biscayensis*: Normano-Breton Gulf

507 The Normano-Breton Gulf is one of the most important mussel grow-out areas of France but
508 limited natural recruitment has led to the use of imported seed to support the industry in this
509 region. Transplantation of seed from distant grow-out areas is common in Europe (FAO 2013,
510 Maguire et al. 2007). Over 90% of the seed used in mussel culture in Brittany comes from the
511 Marennes-Oléron Bay in the Bay of Biscay where the densities of *D. biscayensis* can exceed 300
512 ind. m⁻² and mean density in 2013 was 111 ind. m⁻² (Figs. 2, 4: Gatseau site GA). Mussels in the
513 Bay of Mont-Saint-Michel have an AOC designation which requires that the mussel seed ropes
514 be only from the region between Île d'Oléron and Le Pointe de l'Aiguillon (Marteil 1979). This
515 very restricted area includes the Gatseau site and has abundant *Diopatra*. In both the seed
516 collection areas and in the grow out areas, it is common to see seed collection ropes lying on the
517 ground after becoming detached from the rack and it is equally common to see older seed ropes
518 in the grow-out areas which also have become detached. Transport of juvenile or older *D.*
519 *biscayensis* on ropes is easily possible since *D. biscayensis* attaches debris, including ropes, to its
520 tube-cap and will extend its tube onto such structures.

521

522 4.5.1. Association with Mussel Seed Ropes

523 If the scenario of human-assisted-transport from mussel seed collection areas in the Vendée /
524 Charente-Maritime regions in the Bay of Biscay to mussel grow-out areas in the Normano-

525 Breton Gulf is correct, then one would expect the population of *D. biscayensis* to be spatially
526 associated with the mussel seed ropes and not to other portions of the mussel culture
527 installations. Consistent with the human-assisted-transport hypothesis, over 83% of the
528 individuals found were within 5 m of mussel seed ropes in the population at Quatre Vaux in the
529 Bay of Arguenon (see Results: 3.6).

530

531 4.5.2. Normano-Breton Gulf Populations

532 The population of *Diopatra biscayensis* near the Sainte-Anne sabellariid reef at Cherrueix was
533 already well-established when Dubois discovered it in 2001-2. It is near to mussel culture areas
534 with bouchots; so, presumably it originated via human-assisted-transport associated with
535 aquaculture. At this site, it is common to find two or more individuals within 0.25 m² so it seems
536 likely that this population has sufficient density for fertilization success; over 38% of the 194
537 individuals measured in 2013 for example shared a 0.25 m² with another individual and the
538 average nearest neighbor distance was 1.1 m. This is a higher population density and more
539 frequent occurrence of multiple individuals within 0.25 m² than any of the other populations in
540 the Normano-Breton Gulf (Fig. 2). Like the population at Sainte-Anne, the populations at
541 Quatre Vaux and at St-Géran are near mussel culture areas; the population at Champeaux is not.
542 Our dispersal simulations indicate that the Champeaux population may have been established as
543 a result of larval dispersal from the Sainte-Anne population which is less than 5 km distant (Fig.
544 4). Ayata et al. (2009) also showed extensive larval exchanges between Sainte-Anne and
545 Champeaux *Sabellaria alveolata* populations, consistent with our results.

546

547 The dispersal simulations indicate that there was no connectivity between the two populations in
548 the western Normano-Breton Gulf (Saint-Géran and Quatre Vaux) and the two eastern
549 populations (Sainte-Anne and Champeaux) during the period 2009-2012 (Fig. 4). This result
550 implies that the western populations represent a colonization event independent of the
551 establishment of the eastern populations. Since there are extensive bouchots and chantiers at
552 Saint-Géran and Quatre Vaux, and since the *D. biscayensis* at Quatre Vaux are clustered near to
553 the chantiers (see Results 3.6), we believe that direct transport to this region is more likely than
554 recruitment of larvae from the Sainte-Anne and Champeaux populations.

555

556 4.6. Conclusions

557 The importance of human intervention in marine biogeography has been increasing as a result of
558 larval transport by ballast water (Carlton 1985), adult transport on ballast rock (Brawley et al.
559 2009), introduction of structures that can be used as stepping stones (Johannesson and Warmoes
560 1990, Moschella et al. 2005, and Firth et al. 2013), and introduction of commercially harvested
561 species in new regions: Japanese oysters in British Columbia in Canada and Europe (Quayle
562 1964, Grizel and Héral 1991), the mussel *Mytilus galloprovincialis* in California (Rawson et al.
563 1999) and South Africa (Griffiths et al. 1992), the carpet clam *Tapes philippinarum* worldwide
564 (Flassch and Leborgne 1994, Quayle 1964). As a consequence, there have been unanticipated
565 introductions of associated species: e.g. gastropods *Rapana venosa* and *Ocenebrellus inornatus*
566 in the bay of Quiberon, South Brittany (Bouget et al. 2001, Joly et al. 2002) or *Cyclope neritea*
567 (Bachelet et al. 2004) in the whole Bay of Biscay, *Crepidula fornicata* into Great Britain and
568 subsequently into France (Blanchard 1997), all introduced because of oyster and mussel cultures.
569 Here we have shown that disjunct populations of *Diopatra* beyond a regional biogeographic

570 boundary are in sites where there is yearly trans-regional transport of aquaculture materials. Thus
571 aquaculture provides a mechanism for the bridging of a regional biogeographic boundary.
572 Upwelling zones form biogeographic boundaries of many warm-water species, and penetration
573 of those boundaries usually occurs only after extreme events (e.g. Lima et al. 2006, Sousa et al.
574 2012). However, as we have shown here, continuous human- assisted transport of aquaculture
575 materials across oceanographic boundaries has the potential to alter fundamentally the
576 biogeographic structure of our coastlines. The transport of aquaculture materials is a
577 fundamentally different process from the introduction of stepping-stone structures (e.g.
578 Johannesson and Warmoes 1990, Moschella et al. 2005, and Firth et al. 2013) because the
579 necessary sedimentary habitat for infauna like *Diopatra* already exists, however a natural mechanism
580 of larval transport does not (e.g. Fig 4). Our metapopulation models of the effects of future
581 climates on biogeography indicated that *Diopatra* would invade the English Channel by the mid
582 21st century (Berke et al. 2010, Wethey et al. 2011), but this time scale has been cut in half by
583 human-assisted transport.

584

585 **5. Acknowledgements**

586 This research was supported by grants from NSF (OCE1039513), NOAA (NA04NOS4780264),
587 NASA (NNX07AF20G and NNX11AP77G). We thank the MARS modeling group and the
588 PREVIMER Project staff at IFREMER for their hospitality and in particular F. Dumas and F.
589 Lecornu for making available model runs and the developmental version of Ichthyop. We also
590 thank D. Gerla for pointing out the *Diopatra* populations in les Quatre Vaux.

591

592 Author contributions: DSW, SAW, and SFD conceived the idea. DSW and SAW carried out the
593 majority of the field surveys. SFD located several of the populations and did the initial surveys
594 at those locations. DSW wrote and ran the dispersal simulations. SAW did the size analysis and
595 led the writing.

596

597

598 **6. Literature Cited**

599

600 Arias, A., N. Anadón, and H. Paxton. 2010. New records of *Diopatra marocensis* (Annelida:
601 Onuphidae) from northern Spain. *Zootaxa* 2691: 67-68.

602

603 Ayata, S.-D., C. Ellien, F. Dumas, S. Dubois, and E. Thiébaud. 2009. Modelling larval dispersal
604 and settlement of the reef-building polychaete *Sabellaria alveolata*: Continental Shelf Research
605 29: 1605-1623.

606

607 Ayata, S.-D., P. Lazure, and E. Thiébaud. 2010. How does the connectivity between populations
608 mediate range limits of marine invertebrates? A case study of larval dispersal between the Bay of
609 Biscay and the English Channel (North-East Atlantic). *Progress in Oceanography* 87: 18-36.

610

611 Bachelet, G. 1990. Recruitment of soft-sediment infaunal invertebrates: the importance of
612 juvenile benthic stages. *La mer* 28: 199-210.

613

- 614 Bachelet, G., B. Simon-Bouhet, C. Desclaux, P. Garcia-Meunier, G. Mairesse, X. de
615 Montaudouin, H. Raigné, K. Randriambao, P.G. Sauriau, and F. Viard. 2004. Invasion of the
616 eastern Bay of Biscay by the nassariid gastropod *Cyclope neritea*: origin and effects on
617 resident fauna. *Marine Ecology Progress Series* 276: 147-169.
- 618
- 619 Baddeley, A. and R. Turner. 2005. Spatstat: an R package for analyzing spatial point patterns.
620 *Journal of Statistical Software* 12(6): 1-42.
- 621
- 622 Bailey-Brock, J. 1984. Ecology of the tube-building polychaete *Diopatra leuckarti* Kinberg,
623 1865 (Onuphidae) in Hawaii: community structure, and sediment stabilizing properties.
624 *Zoological Journal of the Linnean Society, London* 80: 191-199.
- 625
- 626 Bailly du Bois, P. and F. Dumas. 2005. Fast hydrodynamic model for medium- and long-term
627 dispersion in seawater in the English Channel and southern North Sea, qualitative and
628 quantitative validation by radionuclide tracers. *Ocean Modelling* 9: 169-210.
- 629
- 630 Benestad, R. E. 2004. Empirical-statistical downscaling in climate modeling. *Eos* 85: 417.
- 631
- 632 Berke, S. K., and S. A. Woodin. 2008. Tube decoration may not be cryptic for *Diopatra cuprea*
633 (Polychaeta: Onuphidae). *Biological Bulletin* 214: 50-56.
- 634

- 635 Berke, S. K., V. Cruz, and R. W. Osman. 2009. Sublethal predation and regeneration in two
636 onuphid polychaetes: patterns and implications. *Biological Bulletin* 217: 242-252.
- 637
- 638 Berke, S. K., A. R. Mahon, F. P. Lima, K. M. Halanych, D. S. Wetthey, and S. A. Woodin. 2010.
639 Range shifts and species diversity in marine ecosystem engineers: patterns and predictions for
640 European sedimentary habitats. *Global Ecology & Biogeography* 19: 223-232.
- 641
- 642 Blanchard, M. 1997. Spread of the slipper limpet *Crepidula fornicata* (L. 1758) in Europe.
643 Current state and consequences. *Scientia Marina* 61 (Supplement 2): 109-118.
- 644
- 645 Bouget J.-F., P. Camus, J.-P. Joly. 2001. *Ocenebrellus inornatus* (Recluz, 1851), *Rapana venosa*
646 (Valenciennes, 1846) : deux nouveaux gastéropodes introduits dans la Baie de Quiberon.
647 <http://archimer.ifremer.fr/doc/00092/20360/>, accessed 2013 October 28.
- 648
- 649 Brawley, S. H., J. A. Coyer, A. M. H. Blakeslee, G. Hoarau, L. E. Johnson, J. E. Byers, W. T.
650 Stam, and J. L. Olsen. 2009. Historical invasions of the intertidal zone of Atlantic North
651 America associated with distinctive patterns of trade and emigration. *Proceedings of the*
652 *National Academy of Sciences* 106: 8239-8244.
- 653
- 654 Brenchley, G.A. 1975. Competition, disturbance, and community structure: the importance of
655 physical structure in a marine epifaunal assemblage. Masters thesis, University of Maryland,
656 College Park, MD, 69pp.

657

658 Carlton, J. T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the
659 biology of ballast water. *Oceanography and Marine Biology Annual Review* 23: 313-371.

660

661 Cazaux, C. 1973. Cycle et distribution des larves de polychetes; caracteres du meroplancton des
662 differents types de masses d'eaux du bassin d'Arcachon. *Bull. Ecol.* IV: 257-275.

663

664 Chambers, J. M. 2008. *Software for Data Analysis*. Springer, NY.

665

666 Choe, S. 1960. On the life history of the polychaete worm *Diopatra neapolitana* Delle Chiaje.
667 *Bulletin of the Japanese Society for Scientific Fisheries* 26: 430-437.

668

669 Conti, G. and F. Massa. 1998. Esperienze di allevamento del polichete *Diopatra neapolitana*
670 Delle Chiaje, 1841 Nella Laguna di S. Gilla (Sardegna Meridionale). *Biol. Mar. Medit.* 5: 1473-
671 1480.

672

673 Conti, G., F. Loffredo, and M. S. Lantini. 2005. Fine structure of the spermatozoon of *Diopatra*
674 *neapolitana* (Polychaeta, Onuphidae). *Zoomorphology* 124: 155-160.

675

676 Diggle, P. J. 1975. Robust density estimation using distance methods. *Biometrika* 62: 39-48.

677

- 678 Dubois, S., T. Comtet, C. Retière, and E. Thiébaud. 2007. Distribution and retention of
679 *Sabellaria alveolata* larvae (Polychaeta: Sabellariidae) in the Bay of Mont-Saint-Michel,
680 France. *Marine Ecology Progress Series* 346: 243-254.
- 681
- 682 Fauchald, K., S. K. Berke, and S. A. Woodin. 2012. *Diopatra* (Onuphidae: Polychaeta) from
683 intertidal sediments in southwestern Europe. *Zootaxa* 3395: 47-58.
- 684
- 685 FAO Fisheries & Aquaculture – Cultured Aquatic Species Information Programme – *Mytilus*
686 *edulis* (Linnaeus, 1758). www.fao.org/fishery/culturedspecies/Mytilus_edulis/en#tcNA00FE,
687 accessed 2013 August 7.
- 688
- 689 Firth et al. 2013. Climate change and adaptational impacts in coastal systems: the
690 case of sea defences. *Environmental Science: Processes and Impacts* 15: 1665-1670.
- 691
- 692 Flassch, J. P. and Y. Leborgne. 1994. Introduction in Europe, from 1972 to 1980, of the
693 Japanese Manila clam (*Tapes philippinarum*) and the effects on aquaculture production and
694 natural settlement. *ICES Marine Science Symposium* 194: 92-96.
- 695
- 696 Gayanilo, F.C., Jr, P. Sparre, and D. Pauly. 2005. FAO-ICLARM Stock Assessment Tools II
697 (FiSAT II). Revised verion. FAO Computerized Information Series (Fisheries). No. 8, Rome,
698 FAO, 168 p.
- 699

700 Gilg, M. R. and T. J. Hilbish. 2002. The geography of marine larval dispersal: coupling genetics
701 with fine-scale physical oceanography. *Ecology* 84: 2989-2998.

702

703 Glemarec, M. 1979. Les fluctuations temporelles des peuplements benthiques liees aux
704 fluctuations climatiques. *Oceanologica Acta* 2: 365-371.

705

706 de Graaf, G. J. and P. Dekker. 2006. A simple spreadsheet model to incorporate seasonal growth
707 into length-based stock assessment methods. *NAGA WorldFish Center Quarterly* 29: 46-54.

708

709 Griffiths, C. L., P. A. R. Hockey, C. Van Erkom Shurink, and P. J. Le Roux. 1992. Marine
710 invasive aliens on South African shores: implications for community structure and trophic
711 functioning. *South African Journal of Marine Science* 12: 713-722.

712

713 Grizel, H. and M. Héral. 1991. Introduction into France of the Japanese oyster (*Crassostrea*
714 *gigas*). *J. Cons. int. Explor. Mer* 47: 399-403.

715

716 Ikaha, R. and R. Gentleman. 1996. R: a language for data analysis and graphics. *Journal of*
717 *Computational and Graphical Statistics* 5: 299-314.

718

- 719 Johannesson and Warmoes. 1990. Rapid colonization of Belgian breakwaters by the
720 direct developer, *Littorina saxatilis* (Olivi) (Prosobranchia, Mollusca). *Hydrobiologia*
721 193: 99-108.
722
- 723 Joly J.-P., J.-F. Bouget and T. Hirata. 2002. Le gastéropode prédateur *Rapana venosa*: point sur
724 les connaissances et expérimentations au laboratoire.
725 <http://archimer.ifremer.fr/doc/00016/12699/>, accessed 2013 October 28.
726
- 727 Lazure, P. and F. Dumas. 2008. An external-internal mode coupling for a 3D hydrodynamical
728 model for applications at regional scale (MARS). *Advances in Water Resources* 31: 233-250.
729
- 730 Lazure, P., V. Garnier, F. Dumas, C. Herry, and M. Chifflet. 2009. Development of a
731 hydrodynamic model of the Bay of Biscay. Validation of hydrology. *Continental Shelf Research*
732 29: 985-997.
733
- 734 Lett, C., P. Verley, C. Mullon, C. Parada, T. Brochier, P. Penven, and B. Blanke. 2008. A
735 Lagrangian tool for modelling ichthyoplankton dynamics. *Environmental Modelling and*
736 *Software* 23: 1210-1214.
737
- 738 Levitan, D. R. and C. Petersen. 1995. Sperm limitation in the sea. *Trends in Ecology and*
739 *Evolution* 10: 228-231.
740

- 741 Lima, F. P., N. Queiroz, P. A. Ribeiro, S. J. Hawkins, and A. M. Santos. 2006. Recent changes in
742 the distribution of a marine gastropod, *Patella rustica* Linnaeus, 1758, and their relationship to
743 unusual climatic events. *Journal of Biogeography* 33: 812-822.
- 744
- 745 Luckenbach, M. W. 1986. Sediment stability around animal tubes: the roles of hydrodynamic
746 processes and biotic activity. *Limnology and Oceanography* 31: 779-787.
- 747
- 748 Maguire, J. A., T. Knights, G. Burnell, T. P. Crowe, F. O'Beirn, D. McGrath, M. Ferns, N.
749 McDonough, N. McQuaid, B. O'Connor, R. Doyle, C. Newell, R. Seed, A. Smaal, T. O'Carroll,
750 L. Watson, J. Dennis, and M. O'Cinneide. 2007. Management recommendations for the
751 sustainable exploitation of mussel seed in the Irish Sea. *Marine Environment and Health Series*
752 no. 31, 83pp.
- 753
- 754 Mangum, C. P. and C. D. Cox. 1971. Analysis of the feeding response in the onuphid polychaete
755 *Diopatra cuprea* (Bosc). *Biological Bulletin* 140: 215-229.
- 756
- 757 Marteil, L. 1979. La conchyliculture française. 3. L'ostreiculture et la mytiliculture. *Revue des*
758 *Travaux de l'Institut des Pêches Maritimes* 43(1): 10-130.
- 759
- 760 Moschella et al. 2005. Low-crested coastal defence structures as artificial habitats
761 for marine life: using ecological criteria in design. *Coastal Engineering* 52: 1053-
762 1071.

- 763
- 764 Myers, A. 1972. Tube-Worm-Sediment relationships of *Diopatra cuprea*
765 (Polychaeta:Onuphidae). *Marine Biology* 17: 350-356.
- 766
- 767 Pauley, D. 1987. A review of the ELEFAN system for analysis of length-frequency data in fish
768 and aquatic invertebrates. In D. Pauly and G. R. Morgan (eds.) *Length-based methods in*
769 *fisheries research*. ICLARM Conference Proceedings 13, 468 p. International Center for Living
770 *Aquatic Resources Management*, Manila, Philippines, and Kuwait Institute for Scientific
771 *Research*, Safat, Kuwait, pp. 7-34.
- 772
- 773 Pires, A., H. Paxton, V. Quintino, and A. M. Rodrigues. 2010. *Diopatra* (Annelida: Onuphidae)
774 diversity in European waters with the description of *Diopatra micrura*, new species. *Zootaxa*
775 2395: 17-33.
- 776
- 777 Pires, A., R. Freitas, V. Quintino, and A. M. Rodrigues. 2012a. Can *Diopatra neapolitana*
778 (Annelida: Onuphidae) regenerate body damage caused by bait digging or predation? *Estuarine,*
779 *Coastal and Shelf Science* 110: 36-42.
- 780
- 781 Pires, A., F. Gentil, V. Quintino, and A. M. Rodrigues. 2012b. Reproductive biology of *Diopatra*
782 *neapolitana* (Annelida, Onuphidae), an exploited natural resource in Ria de Aveiro
783 (Northwestern Portugal). *Marine Ecology* 33: 56-65.

784

785 Prou, J. and P. Gouletquer. 2002. The French mussel industry: present status and perspectives.
786 Proceedings of the First International Mussel Forum Aquaculture Canada super(OM) 2002,
787 Charlottetown, PEI, 17-20 September 2002 102: 17-23.

788

789 Quatrefages, A. d. 1866. Histoire naturelle des Annelés marins et d'eau douce. Annélides et
790 Géphyriens. Librairie Encyclopédique de Roret, Paris.

791

792 Quayle, D. B. 1964. Distribution of introduced marine Mollusca in British Columbia waters.
793 Journal of the Fisheries Research Board of Canada 21: 1155-1181.

794

795 R development Core Team. 2007. R: A language and environment for statistical computing. R
796 Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>, accessed 2013
797 October 28.

798

799 Rawson, P. D., V. Agrawal, and T. J. Hilbish. 1999. Hybridization between the blue mussels
800 *Mytilus galloprovincialis* and *M. trossulus* along the Pacific coast of North America: evidence
801 for limited introgression. Marine Biology 134: 201-211.

802

- 803 Rodrigues, A. M., A. Pires, S. Mendo, and V. Quintino. 2009. *Diopatra neapolitana* and
804 *Diopatra marocensis* from the Portuguese coast: Morphological and genetic comparison.
805 Estuarine, Coastal and Shelf Science 85: 609-617.
- 806
- 807 Sousa, L. L., R. Seabra, D. S. Wethey, R. Xavier, N. Queiroz, S. Zenboudji, and F. P. Lima.
808 2012. Fate of a climate-driven colonisation: Demography of newly established populations of the
809 limpet *Patella rustica* Linnaeus, 1758, in northern Portugal. Journal of Experimental Marine
810 Biology and Ecology 438: 68-75.
- 811
- 812 Wethey, D. S. and S. A. Woodin. 2008. Ecological hindcasting of biogeographic responses to
813 climate change in the European intertidal zone. Hydrobiologia 606: 139-151.
- 814
- 815 Wethey, D. S., S. A. Woodin, T. J. Hilbish, S. J. Jones, F. P. Lima, and P. M. Brannock. 2011.
816 Response of intertidal populations to climate: Effects of extreme events versus long term change.
817 Journal of Experimental Marine Biology and Ecology 400: 132-144.
- 818
- 819 Woodin, S. A. 1978. Refuges, disturbance, and community structure: a marine soft-bottom
820 example. Ecology 59: 275-284.
- 821
- 822 Woodin, S. A. 1981. Disturbance and community structure in a shallow water sand flat. Ecology
823 62: 1052-1066.
- 824

825 Woodin, S. A., D. S. Wethey, and N. Volkenborn. 2010. Infaunal hydraulic ecosystem engineers:
826 cast of characters and impacts. *Integrative and Comparative Biology* 50: 176-187.

827

828

ACCEPTED MANUSCRIPT

829 Table 1. Tube-cap aperture diameters (mm) (2011 to 2013) (means and ranges) of *Diopatra*
 830 *biscayensis* along the Atlantic coast of France. 'na' no data for that site for that year. Sites
 831 within the Bay of Biscay are arranged from south (Arcachon) to north (La Trinité-sur-Mer),
 832 while those in the Normano-Breton Gulf are west (Saint-Géran) to east (Champeaux).
 833

Aperture Diameters: Means and Ranges (mm)							
Bay of Biscay	2011	2012	2013	Normano-Breton Gulf	2011	2012	2013
Arcachon	5.4 (2 to 9)	5.6 (1 to 10)	5.95 (2 to 8.5)	Saint-Géran	na	na	9.7 (9 to 10.5)
Verdon-sur-Mer	6.4 (3 to 9)	5.8 (2 to 10)	6.2 (3 to 8.5)	Quatre Vaux	na	10.3 (8 to 12)	9.6 (8 to 12)
Plage de Gatseau	na	na	4.8 (1.5 to 10)	Sainte-Anne	na	9.6 (3.5 to 12)	9.2 (6 to 11)
Châtelailon-Plage	7.1 (3 to 10)	8.6 (3 to 12)	7.3 (2 to 11)	Champeaux	8.9 (7 to 12)	10.3 (9 to 12)	9.75 (8 to 12)
Tharon Plage	7.5 (5 to 9)	7.9 (3 to 12)	7.6 (2 to 10.5)				
Le Pouliguen	na	9.7 (2 to 11.5)	8.1 (4 to 11)				
Baie du Bile	8 (2 to 10)	8.5 (4 to 12)	8.1 (3 to 11)				
Dolmen du Crapaud	7.3 (3 to 11)	8.6 (2 to 11)	8.1 (1.5 to 11)				
La Trinité-sur-Mer	8.9 (8 to 11)	9.8 (8 to 11)	9.3 (8 to 11)				

834

835

836 Table 2. Growth estimates from FiSAT ELEPHAN I algorithm. Estimated means and standard
837 deviations in millimetres of aperture diameters at yearly intervals calculated from growth
838 constants (K and D) for populations at Arcachon and Verdon-sur-Mer using ELEPHAN I. Mean
839 calculated K is 0.8 per year, ranging from 0.77 to 0.92. Calculated D is 0.77.

Estimated Age	Estimated Aperture Diameter Mean (std dev)
12 months	4.9 (0.4)
24 months	8.5 (0.4)
36 months	10.6 (0.3)
48 months	11.7 (0.2)
60 months	12.3 (0.2)
72 months	12.6 (0.1)

840

841 Table 3. Sizes in aperture diameter (mm) of known individuals at the northernmost site in the
 842 Bay of Biscay, La Trinité-sur-Mer, from 2011 to 2013. Values in 2013 labelled as ‘missing’
 843 indicate that the individual was not found even after two days of searching and presumed dead;
 844 value in 2011 labelled ‘NA’ reflects expansion of census search area in 2012 to include
 845 additional individuals due to disappearance of over 75% of the individuals seen in 2011.

846

Known Individuals	Aperture Diameter (mm) by Year of Observation		
	2011	2012	2013
Ind 1	8	9.5	11
Ind 2	NA	9.5	10
Ind 3	8	11	10
Ind 4	8.5	10	missing
Ind 5	8	9.5	9
Ind 6	9	9	missing
Ind 7	10	8.5	8
Ind 8	10.5	10	9
Ind 9	NA	10	10
Ind 10	NA	10	9

847

848 Figure 1. Measurements of body width (mm) (minus parapodia and chaetae) at the 10th chaetiger
849 versus measurements of tube-cap aperture diameter (mm) in small *Diopatra biscayensis*. Linear
850 regression relationship: $y = 1.202x + 0.0375$, $R^2 = 0.79$, $N = 17$, aperture sizes 1.5 to 7 mm, 10th
851 chaetiger widths 1.34 to 5.08 mm.

852

853 Figure 2. Mean density per m² with 95% confidence limits. The nine sites in the Bay of Biscay
854 are in rows one and two and are arranged from south (Arcachon) to north (La Trinité-sur-Mer),
855 while those of the Normano-Breton Gulf are in row three and are west to east. Note to allow
856 visual comparison the vertical scale of density per meter square is a logarithmic scale and is
857 constant for all sites.

858

859 Figure 3. Size frequency distributions of *Diopatra biscayensis* for 2011, 2012, and 2013.
860 Proportions by aperture diameter are shown for each population as well as number of individuals
861 ('N') in the census. The census size in most cases represents three hours or more of searching.
862 The populations from the Bay of Biscay are arranged from south to north: Arcachon, Verdon-
863 sur-Mer, Châtelailon-Plage, Tharon Plage, Le Pouliguen, Baie du Bile, Dolmen du Crapaud, and
864 La Trinité-sur-Mer. Those from the Normano-Breton Gulf are arrayed west to east: Quatre
865 Vaux, Sainte-Anne reef at Cherrueix, and Champeaux. The vertical dotted line separates the
866 likely young of the year (< 5 mm aperture inner diameter) from presumptive adults. Solid dark
867 bars are from 2011, grey bars from 2012, open bars from 2013. The populations at Saint-Géran
868 and Gatseau were discovered in 2013 so have only one year of data and are not displayed; see
869 Table 1 for size ranges. The 2013 census for the population at Le Dolmen du Crapaud is small
870 due to a mud deposition event that killed the lower intertidal portion of the population.

871

872 Figure 4. Locations of survey sites in France, with regional estimates of larval connectivity.

873 Background map: black symbols in Brittany are sites surveyed between La Trinité-sur-Mer and

874 the central English Channel where we did not find *Diopatra* (o = appropriate habitat; × =

875 inappropriate habitat); red circles (online color map) or black circles (print map) in the southern

876 Bay of Biscay are *Diopatra* population sites: CP=Châtelailon-Plage, GA=Plage de Gatseau,

877 VD=Verdon-sur-Mer, AR=Arcachon. Upper inset map: Normano-Breton Gulf region:

878 CH=Champeaux, SA= Sainte-Anne, QV=Quatre Vaux, SG=Saint- G éran, JO=Jospinet. Lower

879 inset map: upper Bay of Biscay in the Vilaine/Loire region: LT=La Trinité-sur-Mer,

880 DC=Dolmen du Crapaud, BB=Baie du Bile, PG=Le Pouliguen, TP=Tharon Plage. Shading

881 colors (online) or greyscale (print) in inset maps indicate larval connectivity estimates after 6

882 days of dispersal, from Lagrangian particle modeling of releases from the survey sites, using

883 velocity fields from MARS2D models. Color scale or greyscale on right in \log_{10} units; thus, '-1'

884 represents the recruitment zone of 10% of the larvae while '-6' is the recruitment zone of

885 0.0001% of the larvae. The rapidity of the change indicates that dispersal is extremely local.

886

887 Figure 5. Larval connectivity as a function of distance from release point, after 6 days of

888 dispersal. Data are from Lagrangian transport simulations with passive particles, using velocity

889 fields from 250 meter scale MARS2D models. Each line represents the decline in connectivity

890 as a function of distance from an individual release location. Releases in the Normano-Breton

891 Gulf were from adult population locations at Champeaux (CH), Sainte-Anne (SA), and Quatre

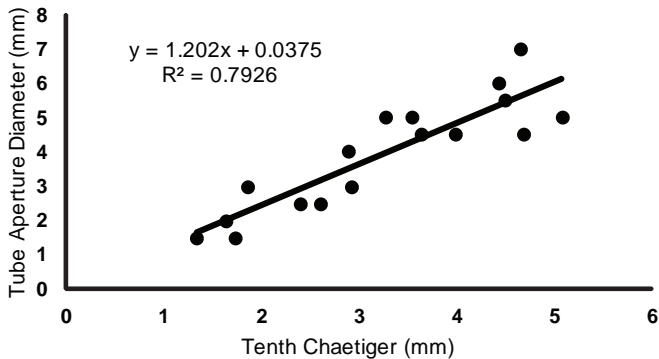
892 Vaux (QV). Releases in the Vilaine/Loire region within the upper Bay of Biscay were from the

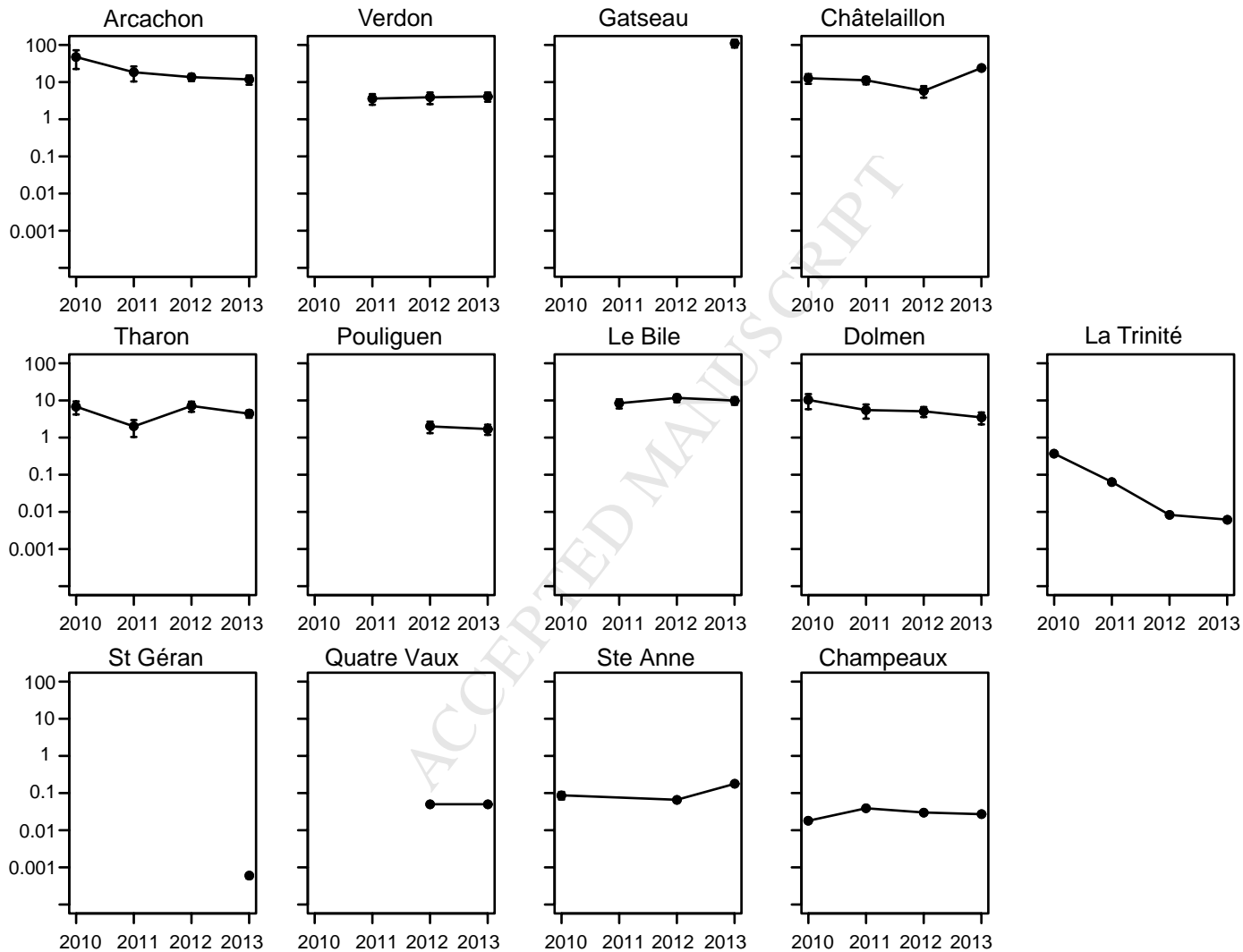
893 Dolmen du Crapaud (DC), the Baie du Bile (BB), Le Pouliguen (PG), and Tharon Plage (TP).

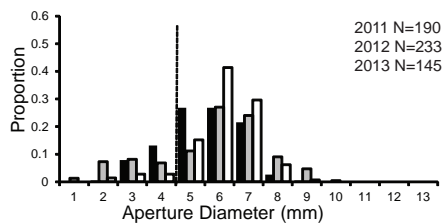
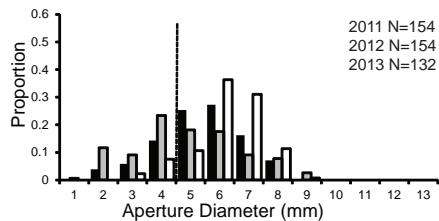
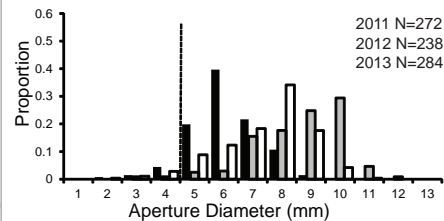
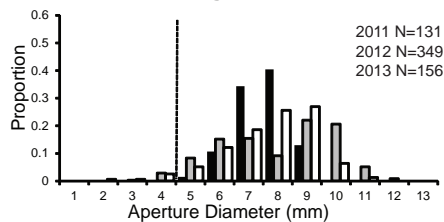
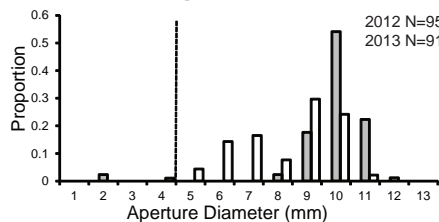
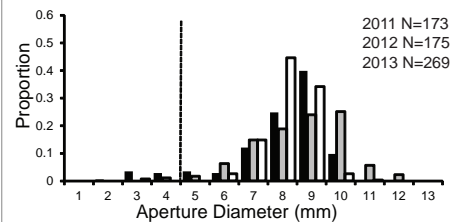
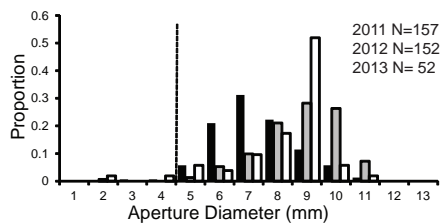
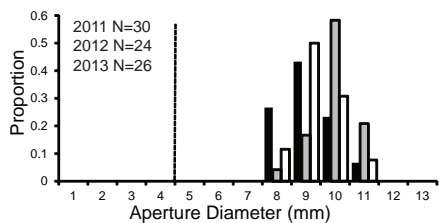
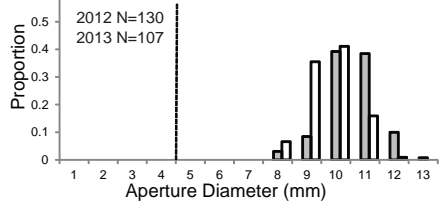
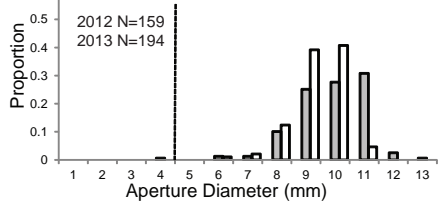
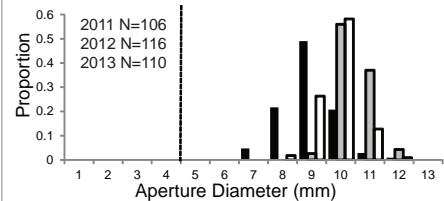
894 See Fig. 4 for map locations. Average slope of the lines: Normano-Breton Gulf -0.0996, Bay of
895 Biscay Vilaine/Loire -0.1000.

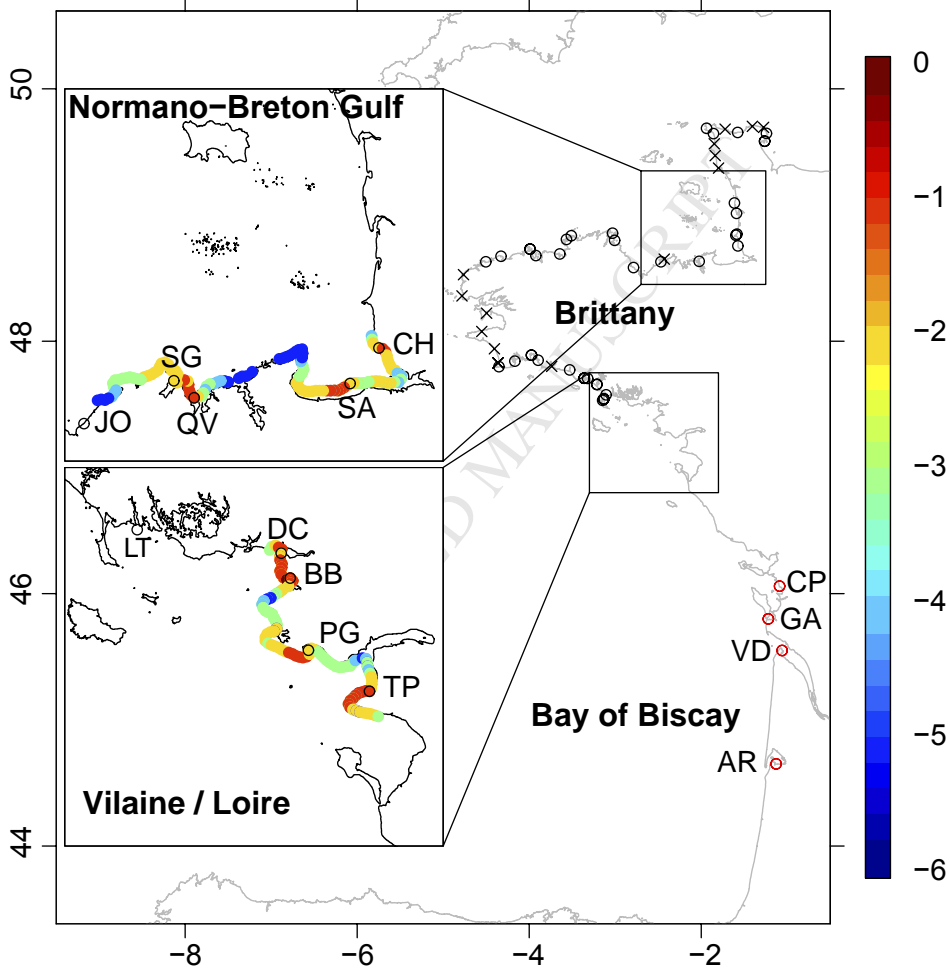
896

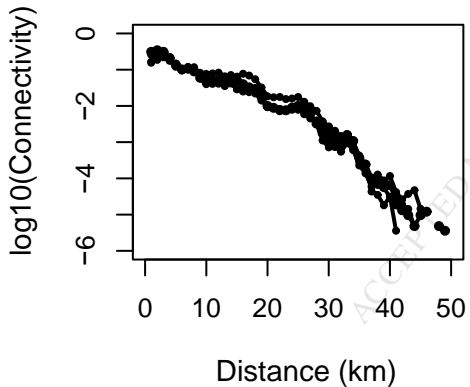
897 Figure 6. Mussel culture at Quatre Vaux, Baie de l'Arguenon (QV) within the Normano-Breton
898 Gulf. Bouchots are the vertical pilings which are wrapped with mussel ropes for final grow-out.
899 Chantiers are the racks in the foreground with the horizontal seed ropes draped between them. A
900 second row of chantiers and bouchots is visible in the background, parallel to the row in the
901 foreground.

D. biscayensis



Arcachon 2011 - 2013**Verdon - sur - Mer 2011 - 2013****Châtelailon - Plage 2011 - 2013****Tharon Plage 2011 - 2013****Le Pouliguen 2012 - 2013****Baie du Bile 2011 - 2013****Dolmen du Crapaud 2011 - 2013****La Trinité - sur - Mer 2011 - 2013****Quatre Vaux, Baie de l'Arguenon
2012 - 2013****Ste Anne, Cherruix, Baie du Mont-Saint-Michel
2012 - 2013****Champeaux, Baie du Mont-Saint-Michel
2011 - 2013**



Normano-Breton Gulf**Vilaine / Loire**