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

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, 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
1. Introduction

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

Wethey and Woodin (2008) and Wethey et al. (2011) built metapopulation models for *Diopatra* and Berke et al. (2010) used regression tree analysis and in all cases their models indicated that the distribution is limited by cool summer temperatures (SST < 18 or 18.8°C). Their models suggest that the thermal conditions of the distal half of the Brittany Peninsula are currently not permissive for *Diopatra* reproduction and thus prohibit expansion along the coast from the Bay of Biscay into the Normano-Breton Gulf. Their models also predicted that the entire Brittany
peninsula would only become permissive in the late 21st century, which would then allow
expansion into the English Channel and north. Based on these analyses, it is very surprising that
Diopatra has already colonized the Normano-Breton Gulf. Here we examine the distribution of
Diopatra biscayensis, and make comparisons between the contiguous populations of the Bay of
Biscay and the disjunct populations of the Normano-Breton Gulf, populations over 450 km
beyond the end of the Bay of Biscay populations. The questions of interest are as follows: 1. are
the population characteristics of these disjunct northern populations different from those of the
French coast of the Bay of Biscay; 2. could planktonic larval dispersal be the source of these
disjunct populations and if not, what other source is likely? To address these questions we (1)
measured the density and size structure of eight populations in the Bay of Biscay from Arcachon
to La Trinité-sur-Mer and those of the four populations in the Normano-Breton Gulf from 2011
to 2013, (2) looked for spatial associations of Diopatra with aquaculture structures, and (3) ran
larval dispersal simulations to address the connectivity of the populations within each region and
across regions.

2. Materials and Methods

2.1. Diopatra

On the Atlantic coast of Europe there are at least five species of Diopatra that occur in shallow
subtidal to intertidal waters (Berke et al. 2010; Fauchald et al. 2012; Pires et al. 2010; Rodrigues
et al. 2009). South of Arcachon, France (44.6585° N, 1.1423° W), D. neapolitana appears to
predominate in most intertidal areas. However, the distribution of D. marocensis is expanding, is
already common in parts of the Portuguese coast (Rodrigues et al. 2009), and is known to have
been present in northern Spain from as early as 1976 (Arias et al. 2010). From Arcachon, France
to La Trinité-sur-Mer (47.5830° N, 3.0242° W), D. biscayensis is the predominant species in the
intertidal (Berke et al. 2010), though D. neapolitana is still present in the intertidal at Arcachon
(Pires et al. 2010) and in the subtidal further north (S. Dubois unpub.). Individuals in
populations from the English Channel are morphologically identical to D. biscayensis and were
used in the description of the species (Fauchald et al. 2012).

2.2. Census

Population densities were estimated from June to mid-July at some sites in 2010 and at more
sites in each year in 2011, 2012, and 2013. At each census, densities of Diopatra were estimated
from counts of 0.25 m$^2$ quadrats taken every 5 m along a 50 to 100 m transect line parallel to
shore within the Diopatra zone at that location. Diopatra are often continuous in their
distribution, given appropriate habitat, and the transect approach works well in such locations
(Woodin 1978). The sizes of the Diopatra zone vary with location. Generally individuals of
Diopatra are found from the shelf break and below. In a location with a very shallow slope such
as at Châtelaillon-Plage, the intertidal zone of occurrence might be several hundred meters wide.
If large areas of inappropriate habitat such as reef or rock or mud slurries resulted in discrete
patches of Diopatra, then total counts within a known area within the patch were used; typically
all individuals were measured within 10 × 10 m areas.
Alternatively, if densities were so low that few quadrats contained any individuals so that most transects of 10 m or more would contain 1 or 0 individuals, densities were estimated from nearest neighbour distances (Diggle 1975) using Universal Transverse Mercator (UTM) coordinates of individuals. In such sparse populations transect data yields little information on distances between individuals. Given that reproduction for such species is a function of separation between adults, knowledge of inter-individual distances is important in assessing the viability of a population. With higher densities, transects yield this information when multiple individuals are found within 0.25m$^2$ quadrats. Coordinates were measured with a Garmin Foretrex 101 GPS (2010 to 2012) and with a Spectra Precision Mobile Mapper 10 (2013), both with real-time differential corrections. Mobile Mapper coordinates were postprocessed using data from nearby public reference stations to increase precision (std. error ~0.5 m). Population density was estimated from N individual nearest neighbour distances (NND) using the Diggle (1975) relationship for randomly dispersed individuals:

$$Density = \frac{N}{\pi \sum NND^2}$$  

(1)

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

2.3. Bouchot Census

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

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

Tube-cap aperture diameters were measured in the field by delicate insertion into the tube-cap aperture of a brass tapered cone marked with rings at millimetre increments in diameter. The regression of width of the 10th chaetiger (x)(body only, not including parapodia) versus tube-cap mouth (aperture) (y) was $y = 1.202x + 0.0375$ ($R^2 = 0.79$, N = 17, aperture sizes 1.5 to 7 mm, 10th chaetiger widths 1.34 to 5.08 mm) (Fig. 1). Tube-cap aperture diameter thus can be used as a proxy for body size in the field. The smallest individuals recorded had tube-cap apertures of approximately 1 mm. Even those individuals had established tubes with imbricate decoration.
and often a shell over the aperture, typical of *Diopatra*. Individuals with tubes 3 to 4.5 mm in
diameter appeared to be six to nine months old, therefore individuals with aperture diameters less
than 5 mm were designated as young of the year or recruits (see section 3.4.1 for confirmation of
this designation). We use the term ‘recruitment’ to refer to these individuals, which of course we
are recording several months after actual settlement (Bachelet 1990).

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

2.5. Size Frequency Analysis

The size frequency data for each year and site were examined using the FiSAT II cohort
identification software (FiSAT II, Gayanilo et al. 2005). Bhattacharya’s method was used to
generate initial estimates of means and standard deviations of potential component normal
distributions i.e. presumptive cohorts. It assigns a separation index to the presumptive cohorts.
Separation indices of < 2 are typically unreliable, not statistically supported, and thus those
presumptive cohorts were rejected (see FiSAT II, Gayanilo et al. 2005). These initial estimates
were then used as inputs into the NORMSEP routine which uses a maximum likelihood iteration routine to generate estimates of means, standard deviations and number of individuals per cohort.

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

The maximum size of *D. biscayensis* was set to 13 mm aperture diameter.

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

2.6. Dispersal Distance

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

Two-dimensional velocity fields on a 250 m grid scale were available in 15-minute increments over the period 2009-2012. Since most bays and peninsulas on this coast are 1 km or greater in size, flow within and around those features is resolved at this scale. The 250 m scale MARS2D models are nested inside a 700 m scale 2D model, which is nested inside a 4 km scale 3D model of the European shelf (Franck Dumas, pers. comm.). The 4 km scale 3D model used 8 tidal constituents at the open ocean boundary, and all models use meteorological forcing from the ARPEGE forecasts of Meteo-France (Lazure and Dumas 2008). The MARS models have been validated using oceanographic data (Lazure et al. 2009) and radionuclide plumes (Bailly du Bois and Dumas 2005). In our Lagrangian simulations, cohorts of 500 passive particles (proxies for larvae) were released each hour during the 7-hour period centered on high tides during three days around the new and full moon during the months of September to December in each of the years 2009 to 2012. Larvae were released from sites of known populations of *D. biscayensis*, were followed for 6 days, and were assumed to be competent to settle after the first day. Dispersal simulations were carried out in the Lagrangian transport simulator Ichthyop Version 3 (Lett et al. 2008), using Euler’s method with an integration time step of 1 minute. Dispersal potential was estimated by determining the fraction of larvae in each cohort from each release location that passed within 500 m radius of points along the coastline, spaced 1 km apart and 1 km offshore during the period of larval competency (days 2-6 after release). These sampling locations were
chosen in order to avoid possible artefacts associated with land boundaries of the numerical ocean models. Since the larvae in the simulation were proxies for potentially much larger cohorts of real larvae, they were allowed to continue dispersing for the entire 6-day period, even if they passed through one or more of the “capture” locations. Dispersal potential calculations were carried out in the R statistical language (Ihaka and Gentleman 1996, R Development Core Team 2007, Chambers 2008), using the spatial statistics library “spatstat” (Baddeley and Turner 2005); latitude /longitude to UTM conversion was carried out using the “clim.pact” library (Benestad 2004).

3. Results

3.1. Population Densities

3.1.1. Bay of Biscay Populations

Densities were greatest in Arcachon (44.6585° N, 1.1423° W), Châtelaillon-Plage (46.0597° N, 1.0907° W), and the Baie du Bile (47.4454° N, 2.4756° W) in all years, although the Plage de Gatseau (45.80411° N, 1.22172° W) which we sampled only in 2013, had the highest overall density (111 m$^{-2}$) and the highest quadrat density (360 m$^{-2}$)(Fig. 2). With the exception of La Trinité-sur-Mer (47.5830° N, 3.0242° W), all populations censused in the Bay of Biscay had mean densities of greater than 1.7 m$^{-2}$. Individuals separated by < 10 cm were common in all years implying that successful reproduction could occur in at least some cases. The population at La Trinité-sur-Mer had no young of the year in any of our censuses and with a mean nearest
neighbor distance greater than 4 m, the likelihood of successful reproduction is small (Table 1, Figs. 2, 3).

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

3.1.2. Normano-Breton Gulf Populations

Unlike the Bay of Biscay populations, except for the terminal population at La Trinité-sur-Mer, all four populations in the Normano-Breton Gulf had mean densities per meter square of less than one and mean nearest neighbor distances > 1 m (Fig. 2). These distances among adults may greatly reduce the probability of fertilization success, depending upon sperm transfer (Levitan
and Petersen 1995). The only population in which we saw any individual smaller than 5 mm in aperture diameter was at Sainte-Anne near Cherrueix in 2010 and 2012, where we found one young of the year in each year (< 5 mm aperture) (Fig. 3, Table 1). Mean nearest neighbor distances at Saint-Anne were between 1.1 m and 1.8 m (Fig. 2). All four Normano-Breton Gulf populations had mean aperture diameters as large or larger than those of the populations in the Bay of Biscay (Table 1). The population at Saint-Géran in the Baie de la Fresnaye was very small: in three hours of searching only 12 individuals were found. Mean nearest neighbour distances at Saint-Géran were > 4m (density < 0.001 m$^{-2}$), and all individuals were large (Table 1).

3.2. Size Frequency Distributions

3.2.1. Bay of Biscay Populations

The most southern populations, Arcachon, Verdon-sur-Mer (45.55123° N, 1.05893° W), and Plage de Gatseau on Île d’Oléron, are characterized by a high percentage of individuals < 5 mm tube aperture diameter (young of the year) and by no individuals over 10 mm tube aperture diameter (Fig. 3, Table 1). The more northern populations from Châtelaillon-Plage to the Dolmen du Crapaud near Billiers (47.51528° N, 2.48445° W) rarely had more than 5% of the censused individuals in the < 5 mm tube aperture category and in one case no young of the year were found in a sample of over 100 individuals (Tharon Plage at Saint-Michel-Chef-Chef (47.1647° N, 2.17° W) 2011, n=131). Individuals of 10 mm or more tube aperture diameter can be common in these more northern populations in contrast to those further south where few large individuals were found in three years (Fig. 3). Mean sizes were smaller at the southern sites, reflecting both a smaller upper size and a larger proportion of young of the year (Table 1, Fig. 3).
The northernmost population in the continuous distribution is at La Trinité-sur-Mer and its population was dramatically different from all others in that no individuals < 8 mm tube aperture diameter were found in our surveys of 2010-2013, most individuals are $\geq 9$ mm tube aperture diameter, and the population has decreased by almost two orders of magnitude since 2010 (Table 1, Figs. 2, 3).

3.2.2. Normano-Breton Gulf Populations

The populations of the Normano-Breton Gulf are more than 450 km from those of the Bay of Biscay. The coast between these two regions has areas of suitable habitat and we have searched intertidal locations north from La Trinité-sur-Mer in the Vilaine/Loire region of the Bay of Biscay to Jospinet in Saint-Brieuc Bay (48.5515° N, 2.6066° W) on the English Channel side of the Brittany Peninsula, but we have found no Diopatra (Fig. 4). Additionally we have searched both the east and west sides of the Cotentin Peninsula in Normandy and again have found no Diopatra (Fig. 4). The four populations discovered to date in the Normano-Breton Gulf between Champeaux (48.7327° N, 1.5521° W) and Saint-Géran (48.6467° N, 2.2966° W) in the Baie de la Fresnaye are all dominated by large individuals and at only one site have we seen any young of the year or any individuals < 7 mm tube aperture diameter (Table 1, Fig. 3: Sainte-Anne).

3.3. Cohort Analysis

Cohort analysis of size frequency distributions differed between the two southernmost populations and those further north in the Bay of Biscay, but in neither case did it prove to be very informative. Only at Arcachon could more than one cohort be resolved in all three years.
In the case of Arcachon, with good densities of small individuals in all years sampled (Fig. 3), a peak centered on 3.4 mm with upper and lower 95% confidence limits of 4.6 and 2.2 mm could be resolved, which crudely corresponds to what we have designated as young of the year i.e. worms with tube apertures of < 5 mm. As is clear from the size distributions of the populations (Fig. 3), in only a few cases is any coherent cohort size structure apparent; so, we restrict ourselves to merely recognizing individuals with very small apertures (< 5 mm) as young of the year.

### 3.4. Growth Rate and Lifespan Estimates

#### 3.4.1. Estimates from FiSAT II ELEPHAN I

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

All census observations were made in June to mid-July depending on year and site. Assuming reproduction and recruitment from September through December (see Materials and Methods: ...
2.5), the young of the year would be 5 to 10.5 months old at the time of census. Based on our calculated growth parameters these individuals would be expected to have aperture diameters between 2.0 and 4.3 mm. This again corresponds to those we are designating as young of the year (Tables 1 and 2, Fig. 3).

3.4.2. Field Data on Growth Increments and Lifespan

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

3.5. Connectivity

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

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

4. Discussion

*Diopatra biscayensis* belongs to a genus of important ecosystem engineers (Woodin 1978, Berke et al. 2010, Woodin et al. 2010). At densities of 5 or more per 0.01 m² the tube clumps of *Diopatra* alter both the biotic and physical characteristics of the habitat, acting as an ecosystem engineer (Bailey-Brock 1984; Luckenbach 1986; Woodin 1978, 1981). The populations along the French coast of the Bay of Biscay commonly exceed such densities (Fig. 2). *D. biscayensis* is common from Arcachon in southern France to the southern edge of Brittany and has disjunct populations without intermediate stepping stones in the Normano-Breton Gulf (Fig. 4). We asked two sets of questions. First, are the disjunct populations in the Normano-Breton Gulf self-
sustainable? How is this reflected in their densities and size frequency distributions? What does this imply about the likelihood of the distribution of *D. biscayensis* in the eastern English Channel? Second, given the larval dispersal capabilities, how connected are the disjunct and continuous populations? If they are not connected by planktonic dispersal, are other sources of transport such as human assistance via aquaculture likely?

4.1. Census and Geographic Distribution

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

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

The populations of *Diopatra biscayensis* along the French coast in the Bay of Biscay differ in the frequency of young of the year each year. The most southern populations (Arcachon and Verdon-sur-Mer) have a higher proportion of young of the year than those further north (Fig. 3). In all years during this study, 2010 to 2013, within the populations in the Bay of Biscay,
complete absence of young of the year was extremely rare, seen only once at Tharon Plage in 2011 (Fig. 3, Table 1). The one exception to this pattern of recruitment success in the Bay of Biscay was the terminal population at La Trinité-sur-Mer where no individuals smaller than 8 mm tube aperture have been recorded (Fig. 3). Densities at La Trinité-sur-Mer are decreasing rapidly; over 75% of the adults seen in 2011 were gone by 2012 and the density in 2011 was one-tenth that of 2010 (Fig. 2). Our estimates of growth suggest that individuals 8 mm in aperture diameter are 1.5 to 2 years old (Table 2); so, the population we found in 2010 may reflect a recruitment event in 2009 or earlier. Based on our previously published metapopulation models of *D. biscayensis* (Berke et al. 2010, Wethey et al. 2011), the failure of this population does not appear to be due to either winter mortalities of juveniles or failure of reproduction in cool summers since populations 40 km to the east are highly successful with consistent presence of young of the year (Table 1, Fig. 3) and much higher densities (Fig. 2). A more likely explanation is that the local population density is too low for successful reproduction and dispersal distances are too great for recruitment from the larger populations to the east and south (Levitan and Petersen 1995) (Fig. 4, 5). For example, in both 2012 and 2013 no individual at La Trinité-sur-Mer was as close as 4 m to another. Given a lifespan of 3 to 5 years or more (Table 2), the population will display a demographic storage effect of adults present but no successful local reproduction. With short distance dispersal distances such a population may derive from a rare recruitment event with much higher than normal dispersal distances or survivorships (Wethey et al. 2011). We did not see any larval transport from nearby reproductive populations to La Trinité-sur-Mer in our simulations of the years 2009-2012 (Fig. 4 and 5), so the event likely occurred before 2009.
The distribution of sizes also differs across the populations in the Bay of Biscay with the southern populations at Arcachon and Verdon-sur-Mer having both smaller mean apertures and smaller maximum size than in populations further north (Table 1, Fig. 3). The mean size difference is expected because the southern populations have larger proportions of young of the year, 0.10 to 0.27 in 2011 to 2013 versus 0.01 to 0.075 at Châtelaillon-Plage to Dolmen du Crapaud (ignoring the 0.0 in 2011 at Tharon-Plage). The difference in maximum size (Table 1) may well reflect a difference in disturbance or predation in the southern populations and thus more frequent episodes of regeneration. We have no data to support or refute this proposition but it seems most likely given the frequency with which this genus is known to lose tissue (Berke and Woodin 2008, Berke et al. 2009, Pires et al. 2012a).

4.3. Dispersal and Connectivity

Our dispersal simulations suggest that dispersal is likely to be less than 50 km in scale but varies with both wind and tidal conditions as seen in other simulation studies (Ayata et al. 2009, 2010; Dubois et al. 2007; Gilg and Hilbish 2002). Within the Bay of Biscay, populations are sufficiently close that some larval input from adjacent populations is likely (Fig. 4, 5). This is also true for the populations within the Normano-Breton Gulf (Fig. 4, 5). However the simulations indicate that populations within the Bay of Biscay have no larval exchange with those of the Normano-Breton Gulf. The lack of connectivity that we observed between the Vilaine/Loire region of the Bay of Biscay and the Normano-Breton Gulf is consistent with larval simulations by Ayata et al. (2010). Their simulations were for different seasons from ours (January – August), their larval durations were longer (2 – 4 weeks), and they observed no connectivity between the Vilaine/Loire region of the Bay of Biscay and the Normano-Breton
Gulf in 5 years of simulations, 2001-2005 (Ayata et al. 2010). The average north-south dispersal
distance observed in their 2-week simulations was 50 km, consistent with our estimates from the
decline in connectivity with distance (Fig. 5). Therefore we believe that planktonic larval
dispersal cannot account for the origin of the Normano-Breton Gulf populations

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

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

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

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

4.5.1. Association with Mussel Seed Ropes

If the scenario of human-assisted-transport from mussel seed collection areas in the Vendée / Charente-Maritime regions in the Bay of Biscay to mussel grow-out areas in the Normano-
Breton Gulf is correct, then one would expect the population of *D. biscayensis* to be spatially associated with the mussel seed ropes and not to other portions of the mussel culture installations. Consistent with the human-assisted-transport hypothesis, over 83% of the individuals found were within 5 m of mussel seed ropes in the population at Quatre Vaux in the Bay of Arguenon (see Results: 3.6).

4.5.2. Normano-Breton Gulf Populations

The population of *Diopatra biscayensis* near the Sainte-Anne sabellariid reef at Cherrueix was already well-established when Dubois discovered it in 2001-2. It is near to mussel culture areas with bouchots; so, presumably it originated via human-assisted-transport associated with aquaculture. At this site, it is common to find two or more individuals within 0.25 m² so it seems likely that this population has sufficient density for fertilization success; over 38% of the 194 individuals measured in 2013 for example shared a 0.25 m² with another individual and the average nearest neighbor distance was 1.1 m. This is a higher population density and more frequent occurrence of multiple individuals within 0.25 m² than any of the other populations in the Normano-Breton Gulf (Fig. 2). Like the population at Sainte-Anne, the populations at Quatre Vaux and at St-Géran are near mussel culture areas; the population at Champeaux is not. Our dispersal simulations indicate that the Champeaux population may have been established as a result of larval dispersal from the Sainte-Anne population which is less than 5 km distant (Fig. 4). Ayata et al. (2009) also showed extensive larval exchanges between Sainte-Anne and Champeaux *Sabellaria alveolata* populations, consistent with our results.
The dispersal simulations indicate that there was no connectivity between the two populations in the western Normano-Breton Gulf (Saint-Géran and Quatre Vaux) and the two eastern populations (Sainte-Anne and Champeaux) during the period 2009-2012 (Fig. 4). This result implies that the western populations represent a colonization event independent of the establishment of the eastern populations. Since there are extensive bouchots and chantiers at Saint-Géran and Quatre Vaux, and since the *D. biscayensis* at Quatre Vaux are clustered near to the chantiers (see Results 3.6), we believe that direct transport to this region is more likely than recruitment of larvae from the Sainte-Anne and Champeaux populations.

### 4.6. Conclusions

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

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

5. Acknowledgements

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

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

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<tbody>
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<td>Arcachon</td>
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<td>5.95</td>
<td>Saint-Géran</td>
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<tr>
<td></td>
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<td>(1 to 10)</td>
<td>(2 to 8.5)</td>
<td></td>
<td>(9 to 10.5)</td>
<td></td>
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</tr>
<tr>
<td>Verdon-sur-Mer</td>
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<td>5.8</td>
<td>6.2</td>
<td>Quatre Vaux</td>
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<td>10.3</td>
<td>9.6</td>
</tr>
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<td></td>
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<td>(2 to 10)</td>
<td>(3 to 8.5)</td>
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<td>(8 to 12)</td>
<td>(8 to 12)</td>
</tr>
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<td>Plage de Gateau</td>
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<td>na</td>
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<td>Sainte-Anne</td>
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<td>9.2</td>
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<td>(6 to 11)</td>
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<td>8.6</td>
<td>7.3</td>
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<td></td>
<td>(7 to 12)</td>
<td>(9 to 12)</td>
<td>(8 to 12)</td>
</tr>
<tr>
<td>Tharon Plage</td>
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<td>7.9</td>
<td>7.6</td>
<td></td>
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<td>(5 to 9)</td>
<td>(3 to 12)</td>
<td>(2 to 10.5)</td>
<td></td>
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<td></td>
<td></td>
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<td>Le Poulguen</td>
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<td>8.1</td>
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<td>(4 to 11)</td>
<td></td>
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<td>Baie du Bile</td>
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<td>8.1</td>
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<td>(3 to 11)</td>
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<td>8.1</td>
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<td>(3 to 11)</td>
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<tr>
<td>La Trinité-sur-Mer</td>
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<td>9.8</td>
<td>9.3</td>
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<td>(8 to 11)</td>
<td>(8 to 11)</td>
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Table 2. Growth estimates from FiSAT ELEPHAN I algorithm. Estimated means and standard deviations in millimetres of aperture diameters at yearly intervals calculated from growth constants (K and D) for populations at Arcachon and Verdon-sur-Mer using ELEPHAN I. Mean calculated K is 0.8 per year, ranging from 0.77 to 0.92. Calculated D is 0.77.

<table>
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<tr>
<th>Estimated Age</th>
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<tr>
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<td>Mean (std dev)</td>
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<tr>
<td>12 months</td>
<td>4.9 (0.4)</td>
</tr>
<tr>
<td>24 months</td>
<td>8.5 (0.4)</td>
</tr>
<tr>
<td>36 months</td>
<td>10.6 (0.3)</td>
</tr>
<tr>
<td>48 months</td>
<td>11.7 (0.2)</td>
</tr>
<tr>
<td>60 months</td>
<td>12.3 (0.2)</td>
</tr>
<tr>
<td>72 months</td>
<td>12.6 (0.1)</td>
</tr>
</tbody>
</table>
Table 3. Sizes in aperture diameter (mm) of known individuals at the northernmost site in the Bay of Biscay, La Trinité-sur-Mer, from 2011 to 2013. Values in 2013 labelled as ‘missing’ indicate that the individual was not found even after two days of searching and presumed dead; value in 2011 labelled ‘NA’ reflects expansion of census search area in 2012 to include additional individuals due to disappearance of over 75% of the individuals seen in 2011.

<table>
<thead>
<tr>
<th>Known Individuals</th>
<th>Aperture Diameter (mm) by Year of Observation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2011</td>
</tr>
<tr>
<td>Ind 1</td>
<td>8</td>
</tr>
<tr>
<td>Ind 2</td>
<td>NA</td>
</tr>
<tr>
<td>Ind 3</td>
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<tr>
<td>Ind 7</td>
<td>10</td>
</tr>
<tr>
<td>Ind 8</td>
<td>10.5</td>
</tr>
<tr>
<td>Ind 9</td>
<td>NA</td>
</tr>
<tr>
<td>Ind 10</td>
<td>NA</td>
</tr>
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</table>
Figure 1. Measurements of body width (mm) (minus parapodia and chaetae) at the 10th chaetiger versus measurements of tube-cap aperture diameter (mm) in small *Diopatra biscayensis*. Linear regression relationship: $y = 1.202x + 0.0375$, $R^2 = 0.79$, $N = 17$, aperture sizes 1.5 to 7 mm, 10th chaetiger widths 1.34 to 5.08 mm.

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

Figure 3. Size frequency distributions of *Diopatra biscayensis* for 2011, 2012, and 2013. Proportions by aperture diameter are shown for each population as well as number of individuals (‘N’) in the census. The census size in most cases represents three hours or more of searching. The populations from the Bay of Biscay are arranged from south to north: Arcachon, Verdon-sur-Mer, Châtelaillon-Plage, Tharon Plage, Le Pouliguen, Baie du Bile, Dolmen du Crapaud, and La Trinité-sur-Mer. Those from the Normano-Breton Gulf are arrayed west to east: Quatre Vaux, Sainte-Anne reef at Cherrueix, and Champeaux. The vertical dotted line separates the likely young of the year (< 5 mm aperture inner diameter) from presumptive adults. Solid dark bars are from 2011, grey bars from 2012, open bars from 2013. The populations at Saint-Géran and Gatseau were discovered in 2013 so have only one year of data and are not displayed; see Table 1 for size ranges. The 2013 census for the population at Le Dolmen du Crapaud is small due to a mud deposition event that killed the lower intertidal portion of the population.
Figure 4. Locations of survey sites in France, with regional estimates of larval connectivity.

Background map: black symbols in Brittany are sites surveyed between La Trinité-sur-Mer and the central English Channel where we did not find *Diopatra* (o = appropriate habitat; × = inappropriate habitat); red circles (online color map) or black circles (print map) in the southern Bay of Biscay are *Diopatra* population sites: CP=Châtelaillon-Plage, GA=Plage de Gatseau, VD=Verdon-sur-Mer, AR=Arcachon. Upper inset map: Normano-Breton Gulf region: CH=Champeaux, SA= Sainte-Anne, QV=Quatre Vaux, SG=Saint- Géran, JO=Jospinet. Lower inset map: upper Bay of Biscay in the Vilaine/Loire region: LT=La Trinité-sur-Mer, DC=Dolmen du Crapaud, BB=Baie du Bile, PG=Le Pouliguen, TP=Tharon Plage. Shading colors (online) or greyscale (print) in inset maps indicate larval connectivity estimates after 6 days of dispersal, from Lagrangian particle modeling of releases from the survey sites, using velocity fields from MARS2D models. Color scale or greyscale on right in log_{10} units; thus, ‘-1’ represents the recruitment zone of 10% of the larvae while ‘-6’ is the recruitment zone of 0.0001% of the larvae. The rapidity of the change indicates that dispersal is extremely local.

Figure 5. Larval connectivity as a function of distance from release point, after 6 days of dispersal. Data are from Lagrangian transport simulations with passive particles, using velocity fields from 250 meter scale MARS2D models. Each line represents the decline in connectivity as a function of distance from an individual release location. Releases in the Normano-Breton Gulf were from adult population locations at Champeaux (CH), Sainte-Anne (SA), and Quatre Vaux (QV). Releases in the Vilaine/Loire region within the upper Bay of Biscay were from the Dolmen du Crapaud (DC), the Baie du Bile (BB), Le Pouliguen (PG), and Tharon Plage (TP).
See Fig. 4 for map locations. Average slope of the lines: Normano-Breton Gulf -0.0996, Bay of Biscay Vilaine/Loire -0.1000.

Figure 6. Mussel culture at Quatre Vaux, Baie de l’Arguenon (QV) within the Normano-Breton Gulf. Bouchots are the vertical pilings which are wrapped with mussel ropes for final grow-out. Chantiers are the racks in the foreground with the horizontal seed ropes draped between them. A second row of chantiers and bouchots is visible in the background, parallel to the row in the foreground.
$y = 1.202x + 0.0375$
$R^2 = 0.7926$
Brittany

Normano-Breton Gulf

Bay of Biscay

Vilaine / Loire

-8  -6  -4  -2

44 46 48

−6  −5  −4  −3  −2  −1  0
Normano–Breton Gulf

Vilaine / Loire

log10(Connectivity)

Distance (km)

Distance (km)