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Climate hindcasts: exploring the disjunct distribution of *Diopatra biscayensis*

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Abstract :

The ecosystem engineer onuphid polychaete *Diopatra biscayensis* has a continuous population in the Bay of Biscay from the Cantabria coast in Spain to southern Brittany in France. A group of disjunct populations also are found in the English Channel, separated from the Biscay population by more than 400 coastal kilometers. It remains unclear whether *D. biscayensis* is native to the Bay of Biscay; it is also debated whether the disjunct populations in the English Channel are relics of a formerly continuous population, or the product of recent introductions through aquaculture. Here, we use climate hindcasts to explore hypotheses about the *D. biscayensis* historical distribution in Europe. If *D. biscayensis* is native, its range would have been restricted to southern Iberia and the Mediterranean during the Last Glacial Maximum (21,000 BP). However, the species is completely absent from both regions today, further supporting its interpretation as a non-native species. If it was historically present in Europe, the climate hindcasts are congruent with range contraction in the Last Glacial Maximum (21,000 BP), expansion in the Mid-Holocene Warm Period (6000 BP), and contraction again in the past 1000 years (850–1850), prior to the first reports of *D. biscayensis* on the Spanish and French Atlantic coasts. However, the simulations do not support there being climatic refugia along the English Channel coast that would account for the existence of relic populations. Taken together, the evidence suggests that *D. biscayensis* has been introduced to the Bay of Biscay, and that disjunct populations in the English Channel are the result of recent transport through human activities, perhaps aquaculture.

Keywords : climate change, biogeography, metapopulation, Diopatra, historical projections

Careful exploration of habitats and their associated fauna often reveals that taxa once thought to represent a single species are, in fact, several, and that distributions of species once thought to be continuous are, in fact, disjunct. Assuming that disjunct populations are real (and not sampling artefacts), they raise the fundamental question of whether the distributional extremes represent historical biogeographic processes or new introductions. The distribution of the ecosystem engineer *Diopatra biscayensis* FAUCHALD ET AL. 2012 on the Atlantic coast of Europe is a poster child for such questions. This onuphid polychaete was among the last species described by Kristian Fauchald (Fauchald et al. 2012). Individuals build emergent tubes decorated with shell fragments and other debris, and reach densities as high as 360 m^{-2} (Woodin et al. 2014). The geographic distribution of the species is restricted to the Atlantic coasts of Spain and France (Fig. 1). In the Bay of Biscay it is distributed from San Vicente de la Barquera in Spain (43°23'N, 4°23'W) (Arias & Paxton 2015) to La Trinité-sur-Mer in France (47°35'N, 3°1.5'W)(Woodin et al. 2014). Several disjunct populations exist along the English Channel from Saint-Géran in the Bay of La Fresnaye (48°38.8'N, 2°17.8'W) to Champeaux in the Bay of Mont-Saint-Michel (48°43.9'N, 1°33.1'W), separated from the Bay of Biscay populations by more than 400 coastal kilometers (Woodin et al. 2014).

These disjunct populations in the English Channel have been interpreted either as recent introductions through mussel aquaculture (Woodin et al. 2014), or as relics of a historically continuous population (Arias & Paxton 2015). We know that *D. biscayensis* populations on the north coast of Spain date from at least the late 19th century, based on the collections of Augusto González de Linares. These collections contain specimens of both *D. neapolitana* DELLE CHIAJE 1841 and *D. biscayensis,* with *D. neapolitana* ten times more common than *D. biscayensis* (Arias & Paxton 2015). From published descriptions and specimens in the Musée National d'Histoire Naturelle, Paris, *Diopatra* specimens collected near Arcachon in France (44°39.6'N, 1°8.5'W) from 1865 through the 1930s were *D. neapolitana* (Fauchald et al. 2012). *Diopatra biscayensis* appears to have expanded more than 300 km along the Biscay coast of France since the late 19th century, most likely in response to long-term global warming and short-term climate fluctuations (Wethey & Woodin 2008, Berke et al. 2010, Wethey et al. 2011). The range expansions occurred during periods of regional ocean warming (Berke et al. 2010), coincident both with expansions of other subtropical species (e.g., Philippart et al. 2011) and with contractions of boreal species along this coast (e.g., Wethey & Woodin 2008, Wethey et al. 2011). The rate of expansion is consistent with the short (less than one week) planktonic larval period of the species (Woodin et al. 2014, Arias & Paxton 2015). Given this limited dispersal ability, Woodin et al. (2014) proposed that the establishment of the disjunct populations in the English Channel recently occurred due to the transport of aquaculture materials, especially mussel seed ropes, from Marennes-Oléron Bay (45°55'N, 1°10'W) in the central Bay of Biscay. These authors argued that when mussel seed collection ropes fall on the sediment surface, potentially remaining there for days, juvenile *D. biscayensis* may attach their tubes to the ropes, and then be transported with the ropes from the Bay of Biscay to mussel grow-out areas in the English Channel. Mussel rearing in France was expanded from the Bay of Biscay to Northern Brittany in 1954 and to the Bay of Mont-Saint-Michel in 1965 (Goulletquer & Héral 1997). As a result of this expansion, transport of mussel seed ropes has now occurred for 50 years along the coast of France. The primary collection areas for mussel seed are Marennes-Oléron Bay where since the 1970s there have been very dense populations of *D. biscayensis.* The primary grow-out areas for mussels are those where we now find *D. biscayensis* in the Bay of Mont-Saint-Michel. Arias and Paxton

(2015) on the other hand, hypothesize that *D. biscayensis* was once broadly distributed along the coast of Europe, and that the English Channel populations are remnants of a previously continuous distribution. They also suspect, on the basis of reproductive details, that some individuals described from Naples in the late 19th Century (Lo Bianco 1899) were *D. biscayensis*. This would be indicative of a historically broad distribution including the English Channel, the Bay of Biscay, and the Mediterranean.

Historical climate data can help to resolve these competing hypotheses. In this paper we use age-structured metapopulation models in conjunction with climate hindcasts and forecasts from the IPCC Coupled Model Intercomparison Project (CMIP5, Taylor et al. 2012) to test several hypotheses:

1) The current *D. biscayensis* distribution is consistent with its long occupation of European waters as a native species.

2) *Diopatra biscayensis* was broadly distributed throughout the Atlantic coast of Europe during past climate optima like the Mid-Holocene Warm Period.

3) If *D. biscayensis* had been broadly distributed in the Mid-Holocene Warm Period, its current disjunct distribution could have evolved during the past 1000 years as a result of changes in climate.

4) In the next 100 years, *D. biscayensis* will expand its range into the Irish Sea and North Sea.

Methods

Field Identification Characteristics

To ascertain the likelihood that investigators collecting specimens in the field would notice the difference between tube caps of the two common intertidal species, we compared tube cap position and decoration. Field photographs of tube caps from 143 individuals of *Diopatra neapolitana* and 98 individuals of *D. biscayensis* were available from sites in Portugal, Spain, and France. Thirty of each species were chosen randomly, and categorized for degree of decoration (high, medium, low, none), direction of the aperture opening (down, sideways, up), and height above the sediment [flush with the sediment surface, slight (emerging less than one tube diameter), or high (emerging one or more tube diameters)]. Equality of category distribution between species was tested using G-tests.

Subtidal surveys

To supplement existing biogeographic information from the intertidal zone (e.g., Wethey & Woodin 2008; Berke et al. 2010; Wethey et al. 2011; Woodin et al. 2014; Arias & Paxton 2015), we examined subtidal samples from the French coast in the region of the geographic limit on the Bay of Biscay. Subtidal samples were collected with box cores as part of the REBENT surveys by IFREMER in the Bay of Vilaine (47.45°N, 2.6°W), the Bay of Quiberon (47.5°N, 3°W), the Bay of Concarneau (47.87°N, 3.95°W), the Archipeligo of Glénan (47.7°N, 4°W), and the Bay of Audierne (47.9°N, 4.5°W). A total of eight individuals of *Diopatra* were found in the samples.

Metapopulation Models

Diopatra biscayensis reproduction was assumed to fail if August monthly sea surface temperature (SST) was less than 18°C (Berke et al. 2010, Wethey et al. 2011). This is consistent with the relationship between August SST and population density in field surveys, which shows that populations are only found in regions with average August SST above 17.9°C (Figs. 1, 2). Age-structured metapopulation models were used to analyze changes in biogeographic distributions based on changes in SST. Populations were placed on all ocean pixels of 0.25° × 0.25° longitude × latitude SST maps of the European shelf. Consistent with field estimates of a 3–5 year lifespan (Woodin et al. 2014), each population had three age classes of 1-year duration each, and 50% yearly mortality in each age class. If August SST was permissive, SST $\geq$ 18°C, each 2- or 3-year-old individual produced 1000 larvae, 1% of which dispersed in each of the cardinal directions, consistent with Lagrangian transport estimates of *Diopatra* 1- to 6-day larval dispersal from high resolution (250-m grid scale, 15-min time scale) ocean model velocities (Woodin et al. 2014). Each population had a maximum density of 10,000 individuals. This method makes the simplifying assumption that larval transport rates are the same each year, and that there is geographic symmetry (Wethey et al. 2011). Direct Lagrangian dispersal simulations were not possible because the CMIP5 models only save monthly ocean velocities, and the spatial scale of the models is too large to resolve the dispersal process.

Environmental Data

We used SST maps from several climate modeling experiments from Phase 5 of the Coupled Model Intercomparison Project (CMIP5, Taylor et al. 2012) for these analyses (Table 1). The Mid-Holocene Warm Period ~6000 BP was characterized by warmer summers than today, so it is a candidate for conditions that would lead to a broadscale European distribution of *D. biscayensis* since reproductive success in this species appears to be limited by cool summer conditions (Berke et al. 2010, Wethey et al. 2011). The CMIP5 Past 1000 year experiments cover the period 850–1850, which include the Medieval Warm Period (850–1300) and the Little Ice Age (1600–1850). The cooling during the Little Ice Age could lead to remnant populations if only small refugia remained in northern areas; alternatively, it might lead to total retraction from the northern range if no refugia existed. The historical period (1850–2005) covers the time for which historical records of geographic distribution exist and allows validation of the metapopulation models by comparing historical changes to hindcasts of changes (e.g., Wethey et al. 2011). The RCP 8.5 scenario, which assumes a global energy imbalance of 8.5 Wm^{-2} by 2100, was used for future projections.

CMIP5 model SST data were downloaded from the Earth System Grid Federation data archives (http://pcmdi.llnl.gov) and from the World Data Center for Climate (http://cera-www.dkrz.de/WDCC/ui/). We used models for which SST data were available from Historical (1850–2005), the Past Millennium (850–1850), the Mid-Holocene (6000 BP), the Last Glacial Maximum (21,000 BP), and the RCP8.5 future (2005–2099) simulations. Yearly maps of August SST from the CMIP5 models were bilinearly interpolated to a 0.25° × 0.25° grid using the akima package (Akima & Gebhardt 2015) in R. Calendars were converted from the native formats of the CMIP5 data to the Gregorian leap-year calendar using the PCICt package (Bronaugh 2013) in R. Daily Optimally Interpolated SST data on a 0.25° × 0.25° grid (OISST, Reynolds et al. 2007) were downloaded from the National Climatic Data Center (http://www.ncdc.noaa.gov/oisst).

The CMIP5 Last Glacial Maximum simulations imposed ice sheets in northern Europe, while Mid-Holocene simulations imposed earth-orbit parameters consistent with the period. Both simulations provided well-mixed greenhouse gas concentrations for each time period (Taylor et al. 2011). The CMIP5 Past Millennium (850-1850) simulations imposed evolving solar intensity variations and volcanic aerosols whose timing was based on the historical climate proxy record, along with pre-industrial concentrations of greenhouse gases (Taylor et al. 2011). The Historical (1851–2005) simulations imposed changing conditions of land use, solar forcing, atmospheric composition, and volcanic aerosols, all consistent with observations (Taylor et al. 2011). The RCP8.5 simulations imposed changing greenhouse gas concentrations and aerosols such that the earth's radiation imbalance reached 8.5Wm^{-2} in 2100 (Taylor et al. 2011). The CMIP5 simulations all use coupled ocean–atmosphere models, so that the ocean model is influenced by the atmosphere and atmospheric model is influenced by the ocean.

Because of differences in their approximations of physical processes in the atmosphere and oceans, some models run hot or cold (e.g., Wang et al. 2014), and this can potentially influence the results of the metapopulation models. In addition, the spatial scale of many of the models is too large to resolve local phenomena like upwelling, which can strongly influence biogeographic patterns. To reduce the influence of these problems, we carried out a spatial bias correction of the data, using the spatial differences between historical runs and OISST observations (e.g., Bruyère et al. 2014). This correction assumes that the spatial pattern of the bias will not change over time, and that the models are internally consistent in their deviations from observation during the reference period. CMIP5 modeling groups sometimes did an ensemble of runs for each experiment; we restricted our analyses to the same ensemble member (r1i1p1) whenever possible. Spatial bias maps were created by subtracting the OISST August 1986–2005 mean map from the CMIP5 model August 1986–2005 mean map for each of the historical runs. Bias-correction of CMIP5 model runs was done by subtracting the model-specific August bias map from each of the yearly August SST maps.

Biogeographic Projections

Metapopulation models were initialized with a Europe-wide population of *D. biscayensis* at the beginning of each Last Glacial Maximum (21,000 BP), Mid-Holocene (6000 BP), and Past Millennium (850) simulation. We ran 850–2100 continuous simulations by joining together the bias-corrected SST time series from Past Millennium, Historical (1851), and RCP8.5 simulations from the same model and same ensemble member (usually r1i1p1). Thus the population distribution in 1850 from the Past Millennium run was the initial condition for the Historical (1851–2005) simulation, and the 2005 distribution from the Historical run was the initial condition for the RCP8.5 simulation (2006–2100). A separate metapopulation simulation was run using each of the available CMIP5 datasets for which Past Millennium, Historical, and RCP8.5 runs existed, providing an ensemble of biogeographic predictions and hindcasts. We used a summary of the ensemble of predictions of biogeographic distribution: the fraction of models that agreed that the population was present.

Results

Field Identification Characteristics

Tube caps of *D. biscayensis* were much more highly decorated ($p<0.0001$) (Fig. 3), much more often facing down ($p<0.0001$), and much more often highly emergent from the sediment ($p<0.0001$) (Fig. 3, 4). These are differences that are quite obvious in the field (Fig. 3), making it unlikely that previous workers would have overlooked populations of *D. biscayensis* at locations where they were historically present and abundant.

Subtidal Populations

Diopatra biscayensis and *D. neapolitana* are known to live in the shallow subtidal as well as the intertidal. One possibility is that there are subtidal populations north of the intertidal range limit in the Bay of Biscay providing continuity with the populations in the English Channel. The REBENT monitoring network at IFREMER at Brest extensively sampled the shallow subtidal of ten bays in Brittany between 2003 and 2009. The samples contained a total of eight individuals of *Diopatra.* They were exclusively from the Bay of Vilaine (47.45°N, 2.6°W) which corresponds to the northern intertidal limit of *D. biscayensis* in the Bay of Biscay (Fig. 1). All individuals were small but could be identified from their chaetae. They were from samples in 5–10 m of water in muddy sands. Three were *D. biscayensis* and five were *D. neapolitana.* Samples from subtidal locations north of the intertidal limit of *D. biscayensis* in the Bay of Quiberon (47.5°N, 3°W), the Bay of Concarneau (47.87°N, 3.95°W), the Archipeligo of Glénan (47.7°N, 4°W), and the Bay of Audierne (47.9°N, 4.5°W) contained zero specimens of *Diopatra.* The intertidal and subtidal limits thus appear to be congruent.

Metapopulation Models of Biogeographic Range

In all simulations that started with broadscale distributions of *D. biscayensis*, populations died back within 3 years to a smaller geographic range that was close to the August 18°C isotherm at the time. The populations always spread slightly beyond the 18°C isotherm due to larval dispersal. The Last Glacial Maximum and Mid-Holocene simulations had only year to year variations, but no temperature trend, so the geographic boundary of the species fluctuated but did not markedly expand beyond its fourth-year margin during either period. The boundary remained at the 18°C isotherm for that period. The Past Millennium, Historical, and RCP8.5 simulations all had temporal trends in net global energy balance (Taylor et al. 2011, 2012), so there were long-term changes in the geographic boundary. The Past Millennium simulations included the changes in radiative forcing that led to the Medieval Warm Period and the Little Ice Age, so first expansion and later contraction of the species range occurred in most metapopulation runs. The historical simulations included the 19th–20th Century warming with isolated cooling events due to volcanic eruptions like Mt. Pinatubo, so there were species range expansions punctuated by contractions. The RCP8.5 simulations included warming due to increasing net global energy imbalance, so populations expanded.

In the Last Glacial Maximum cold period (21,000 BP), *D. biscayensis* would most likely have been restricted to southern Portugal and the southern Mediterranean. Sixty to seventy percent of the models agree that the northern limit of the species in the Atlantic would have been at Sagres, Portugal, far south of its current known northern limit (Fig. 5A).

In the Mid-Holocene Warm Period (6000 BP), conditions were warm enough that *D. biscayensis* could have been present as far north as 53°N in the North Sea and throughout the English Channel, far north of its current known northern limit (Fig. 5B).

In the past millennium, even if *D. biscayensis* had been broadly distributed in 850, all models agree that it would not have persisted in the English Channel and north by 1890 (Fig. 6C). Since the spatial scale of the CMIP5 models is greater than 100 km, it is possible that a small refuge in the English Channel could have existed, but was undetectable in the models. The models do not replicate the expansion of the population from Arcachon to southern Brittany in the 20th Century, but they predict that populations would have reached the current distribution limit by 2005 (Fig. 6C–E). In all models the southern limit is in the Mediterranean, far south of the observed southern limit in northern Spain.

By 2100, under the RCP8.5 scenario, *D. biscayensis* should expand into the English Channel and the Irish Sea, with four out of seven models predicting invasion of the North Sea (Fig. 6F). The predicted distribution in 2100 is generally consistent with that hindcast from the Mid-Holocene simulation (Fig. 5B).

Discussion

The geographic distribution of the ecosystem engineering polychaete *Diopatra biscayensis* on the European coast has raised questions about the origin of the species and its pre-historical geographic range. Currently it is found from San Vicente de la Barquera in Spain (43°23’N, 4°23’W) (Arias & Paxton 2015) to La Trinité-sur-Mer in France (47°35’N, 3°1.5’W) (Woodin et al. 2014), and there are isolated populations along the English Channel in Brittany and Normandy (Woodin et al. 2014) (Fig.1). Woodin et al. (2014) proposed that the disjunct populations on the Channel coast were the result of recent transport by the mussel industry. Arias and Paxton (2015) by contrast, postulated that the species was broadly distributed in the past, including the English Channel, and that the disjunct populations on the Channel coast are remnants of a broadly distributed species that survived in refuge areas.

We used metapopulation models to test historical biogeographic hypotheses regarding the distribution of *D. biscayensis*. To have confidence in these tests, it is necessary to validate the metapopulation models themselves. The models assumed that conditions were permissive for reproduction if August SST was greater than 18°C (Fig. 2) (Berke et al. 2010, Wethey et al. 2011). The metapopulation models worked very well in a qualitative sense. The 850–2100 simulations were initialized with a broadly distributed population in 850, and by 2005 the northern limit of *D. biscayensis* on the Bay of Biscay was close to the observed geographic limit (Fig. 6E). Therefore, we believe that the metapopulation models should provide a qualitatively accurate estimate of biogeographic distribution in the Last Glacial Maximum, Mid-Holocene, and RCP8.5 runs. The metapopulation models did not however duplicate the 20th century population expansion because the underlying CMIP5 climate models do not attempt to replicate the true historical climate pattern; rather, they are free-running and simulate hypothetical long term trajectories due to the changes in radiative forcing by greenhouse gases (Taylor et al. 2012). Thus, the observed waves of population expansion separated by periods of hiatus are not seen in the 20th century metapopulation dynamics. Our metapopulation analysis in Wethey et al. (2011) used climate models prescribed with boundary conditions set by meteorological observations for the historical period (1950–2000), so they followed the observed trajectory more closely than did the CMIP5 models, and the population dynamics were closer to historical records. Of course we have no such meteorological observations for the distant past so such boundary conditions are not possible.

Tests of Biogeographic Hypotheses

First we tested the hypothesis that the current *D. biscayensis* distribution is consistent with its having a long history in Europe. During the Last Glacial Maximum (21,000 BP) many species were restricted to refugia in southern Europe since the ice sheets covered Wales, Ireland, and half of the North Sea (Böse et al. 2012). Glacial refugia in the English Channel that were occupied by cold water species during the Last Glacial Maximum (e.g., Campo et al. 2010, Huarao et al. 2007), were too cold for *D. biscayensis* (Fig. 5A). Hindcasting results suggest that, if *D. biscayensis* had been in Europe during the Last Glacial Maximum, it would have been able to persist only in refugia on the south coast of the Iberian Peninsula and in the southern

Mediterranean (Fig. 5A), similar to what has been postulated for the seagrass *Zostera noltii* (Coyer et al. 2004). If this were true, one would expect to find remnant populations today in southern Iberia and the Mediterranean. However, there is currently no evidence of *D. biscayensis* to the west and south of San Vicente de la Barquera, on the north coast of Spain (Berke et al. 2010, Fauchald et al. 2012, Arias & Paxton 2015). Two southern locations have been sampled especially thoroughly where there are very large populations of other species of *Diopatra*, yet no *D. biscayensis* were found. Importantly, one is in the Mediterranean on the Turkish coast in Izmir Bay in the Aegean Sea (38°26.34'N, 26°59.07'E) (Dağli et al. 2005) and the other is the Ria de Aveiro on the north coast of Portugal (40°38.49N, 8°44.08E) (Rodrigues et al. 2009, Pires et al. 2010). The hindcast simulations all indicate that populations in these locales (Izmir Bay and the Ria de Aveiro) would have persisted until the present (Fig. 6). Their absence is inconsistent with the hypothesis that *D. biscayensis* is native to Europe but now exists in only a portion of its original range, a range which *D. neapolitana* (with similar temperature requirements) continues to occupy.

Second, we tested the hypothesis that *D. biscayensis* could be broadly distributed in past warm periods like the mid-Holocene (6000 BP). Results of the simulation indicate that during warm periods like the mid-Holocene (6000 BP), conditions were permissive for *D. biscayensis* in the English Channel and southern North Sea (Fig. 5B). If *D. biscayensis* was broadly distributed in the mid-Holocene, then it is possible that it could have persisted over the past 6000 years in small refuges in otherwise inhospitable areas like the English Channel. Mont-Saint-Michel Bay in the English Channel is one such possibility because it is the warmest area in the region in summer (Fig. 1). We looked for such refuge populations in millennial simulations, but found no evidence of them.

Third, we tested the hypothesis that *D. biscayensis* could have evolved from a broadscale distribution in the Medieval Warm Period (850–1100) and persisted in refuges north of the Bay of Biscay during the Little Ice Age (1550–1800), leading to the modern disjunct biogeographic distribution. The millennial simulations, however, indicate that conditions were not permissive in the English Channel at any time between the Medieval Warm Period (900–1200) and the present (Fig. 6).

Our original hypothesis stated that if *D. biscayensis* had been broadly distributed in the Mid-Holocene Warm Period as the simulations suggest, changes in climate during the past 1000 years might significantly alter its distribution resulting in its current disjunct distribution. The distribution is clearly altered, but the simulations do not suggest that any areas in the English Channel would have been permissive to the continued existence of *D. biscayensis* (Fig. 6). Based on this result we believe that the broad distribution hypothesis of Arias & Paxton (2015) is not adequate to explain the disjunct populations in the English Channel, unless areas like Mont-Saint-Michel Bay are thermal refugia that cannot be resolved by the simulations.

Fourth, we hypothesized that the population would expand during the next century of climate warming (e.g., Wethey et al. 2011). The RCP8.5 simulations show expansion into the Irish Sea, the English Channel, and the southern North Sea, consistent with this hypothesis (Fig. 6). The predictions of the CMIP5 models are similar to those from our previous metapopulation simulations that were based on the CMIP3 A1B scenario (Wethey et al. 2011).

Origin of *D. biscayensis*

Several questions still remain regarding *D. biscayensis*, including whether it is a native or an imported species. The tube of *D. biscayensis* is quite large and, if anything, more obvious than that of *D. neapolitana*, being more highly decorated and extending further above the sediment surface. This makes it unlikely that 19th and early 20th century scientists simply overlooked its presence in France, especially given that they reported on *D. neapolitana* from other regions (Berke et al. 2010, Wethey & Woodin 2008). Taken together, the totality of evidence suggests that *D. biscayensis* is non-native. But what, then, is its origin? Genetically, *D. biscayensis* and *D. neapolitana* diverge by 15–22% in nucleotide sequence at cytochrome c oxidase subunit I (COI), cytochrome b (CytB), and 16S RNA loci (Berke et al 2010, Pires et al 2010), which seems inconsistent with a close evolutionary relationship. Morphologically, *D. biscayensis* is quite distinct from the other species both in Europe and elsewhere in the Atlantic in having two postchaetal lobes, a trait shared with only five other species of *Diopatra,* out of 55 species in the genus (Budaeva et al. 2016). With the exception of *D. biscayensis,* all species with double postchaetal lobes are from the Pacific (*D. chiliensis,* Chile and Peru; *D. dexiognatha,* Hawaii; *D. gesae,* Chile and Ecuador; *D. kristiani,* Panama; *D. sugokai,* Indo-Pacific) (Arias & Paxton 2015). *Diopatra biscayensis* differs from all five of these species in various ways including reproductive mode. However, given that all other species with two postchaetal lobes are from the Pacific, one suspects that *D. biscayensis* may also be Pacific in origin.

There are several periods during the past few hundred years when *D. biscayensis* could have been imported to Europe from the northwest Pacific. The Asian oyster *Crassostrea gigas* (also known in Europe as *C. angulata,* the Portuguese oyster) was introduced into Portugal from Taiwan (Boudry et al. 1998, Ó Foighil et al. 1995), some time between 1500 and 1800, perhaps on ship hulls (Wolff 2005). It seems unlikely that *D. biscayensis* could have survived on a ship hull during the transit from Taiwan. However, if oysters were intentionally transported in barrels below the waterline of ships, there is a slight possibility of survival. In the mid 19th century, steamships like the SS Ajax, Achilles, and Agamemnon could make the trip from China to the UK in 58 days (Clark 1910), raising the possibility that live oysters and associated fauna could have survived the trip.

Transport by ship with oysters does not seem likely for a large infaunal tube-builder like *Diopatra* but remains a possibility, especially for juvenile individuals. Given that *D. biscayensis* was on the north coast of Spain in San Vicente de la Barquera and Santander in the late 1800s (Arias & Paxton 2015), and that the oyster industry in 19th century Spain was concentrated in Santander and La Coruña in the northwest (Dean 1891), the oyster transport hypothesis seems plausible.

The historical simulations do not support the existence of northern refugia permitting the existence of remnant populations in the English Channel. Importantly, the historical simulations also do not provide an explanation for the disappearance of *D. biscayensis* from the Mediterranean and southern Iberia. If *D. biscayensis* is indeed native to the region, it should have been broadly distributed during climatic optima (Fig. 5B), so the disappearance of southern populations needs to be explained. Instead, the historical simulations are consistent with the idea that *D. biscayensis* is non-native in Europe, and that the disjunct populations in the English Channel are secondary introductions from the Bay of Biscay (Woodin et al. 2014). This hypothesis is consistent with genetic and morphological evidence that *D. biscayensis* populations have limited diversity. Pires et al. (2010) examined the relative variance among morphological characters for four species of *Diopatra.* The morphological variance among *D. biscayensis* was strikingly smaller than all other species. Similarly, the genetic diversity of *D. biscayensis* is strikingly smaller than that of *D. neapolitana* based on haplotype networks for COI and CytB (Berke et al. 2010). Both the morphological diversity and the haplotype diversity indicate a species with little variance, consistent with a relatively recent founder event. A more extensive genetic analysis is planned in the near future to examine the phylogeography of this species more closely.

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Figures

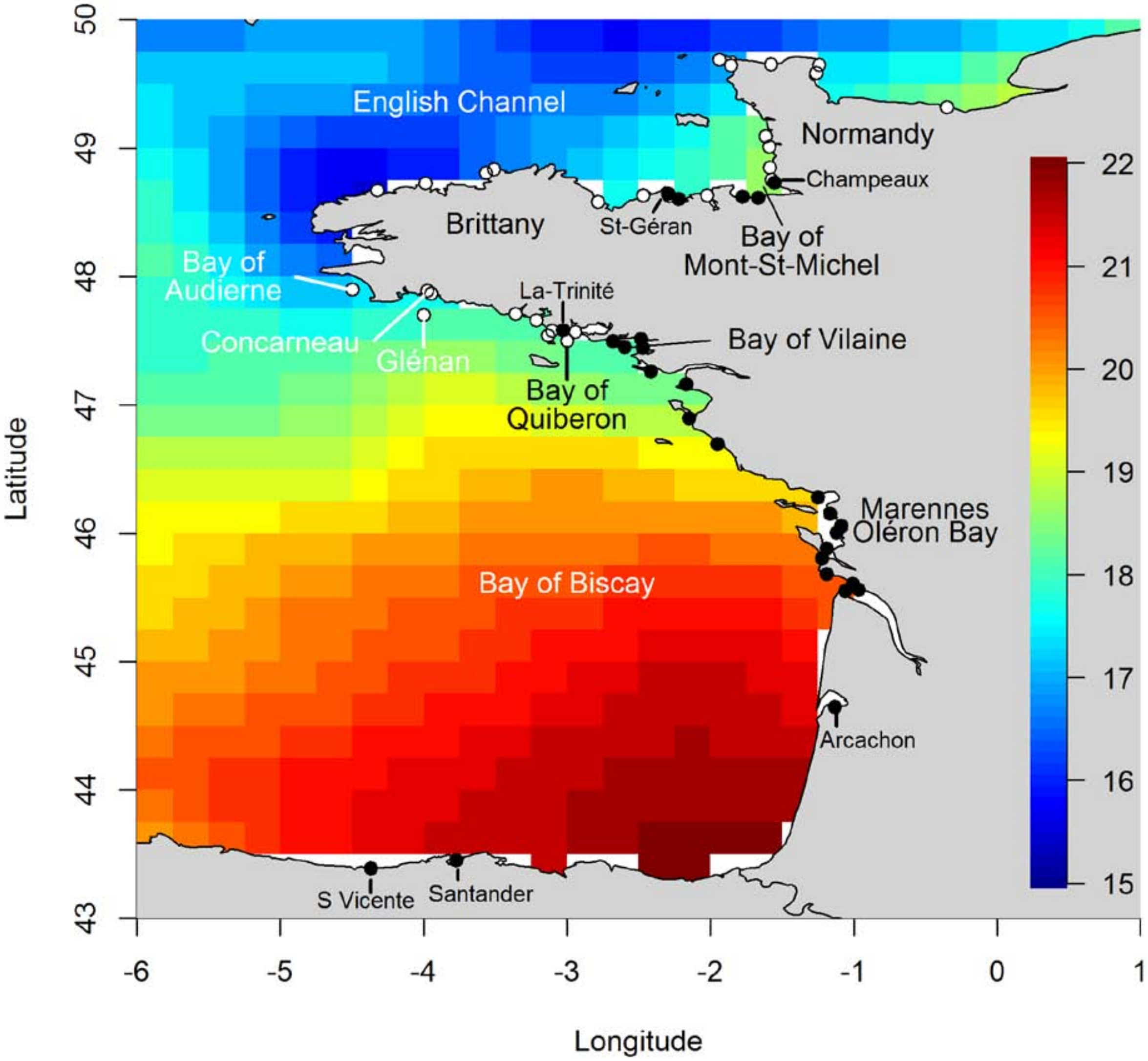

Fig. 1. Distribution of *Diopatra biscayensis* (2006–2015) with map of mean August SST (1986–2005). SST is from NOAA OISST (Reynolds et al. 2007). Distribution data from Wethey & Woodin 2008, Berke et al. 2010, Wethey et al. 2011, Woodin et al. 2014, Arias & Paxton 2015, Dubois (unpubl. data), Woodin et al. (unpubl. data). Black circles are sites where *D. biscayensis* was found, and open circles are sites where it was not found.

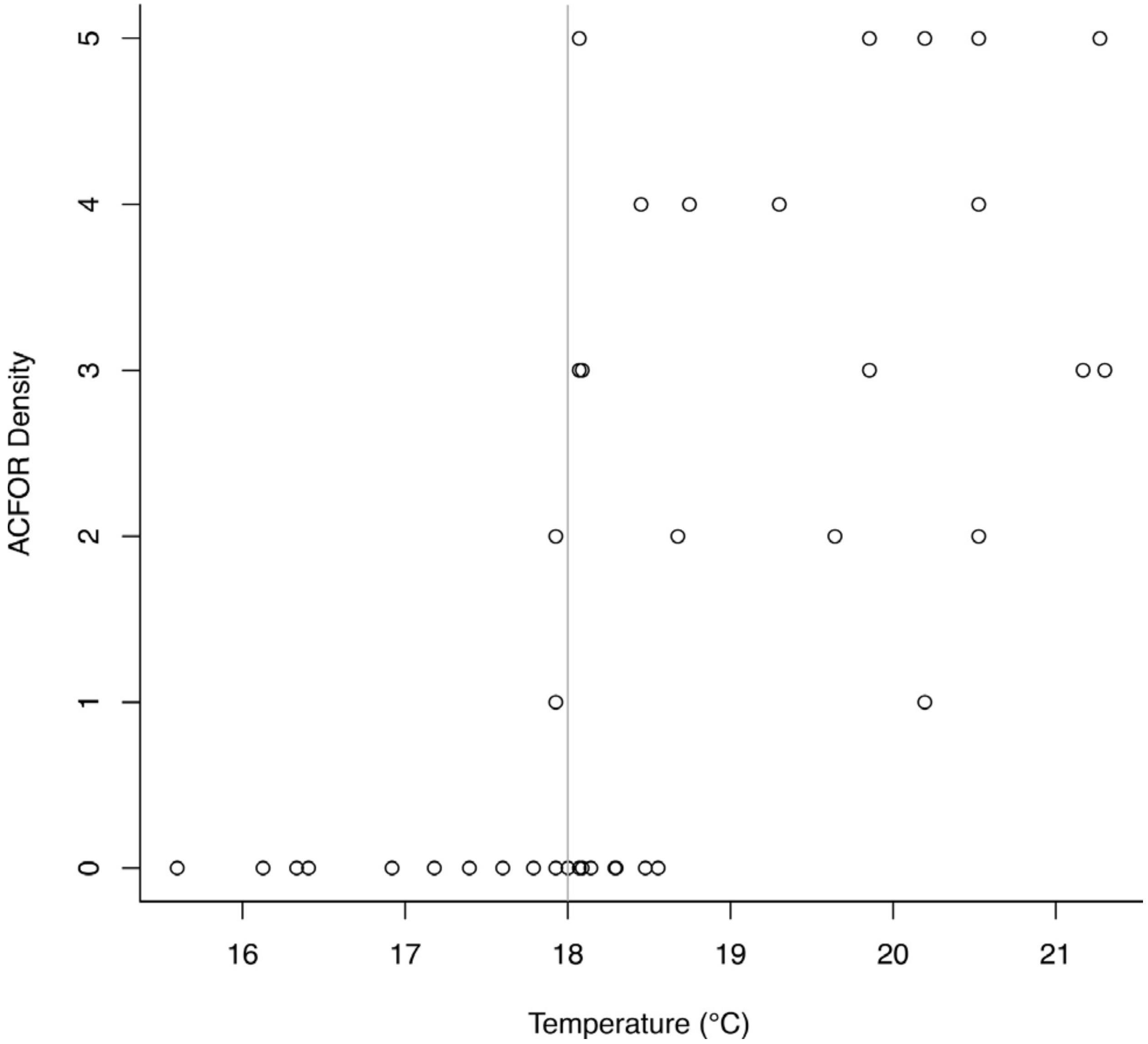

Fig. 2. Density of *D. biscayensis* in relation to mean August SST (1986–2005). SST is from NOAA daily OISST (Reynolds et al. 2007). Density is on ACFOR logarithmic scale: 5, Abundant (>24 m^{-2}); 4, Common (10–24 m^{-2}); 3, Frequent (1–10 m^{-2}); 2, Occasional (0.1–1 m^{-2}); 1, Rare (<0.1 m^{-2}); 0, None. (Wethey &Woodin, 2008; Crisp & Southward, 1958). Vertical line is at 18°C.

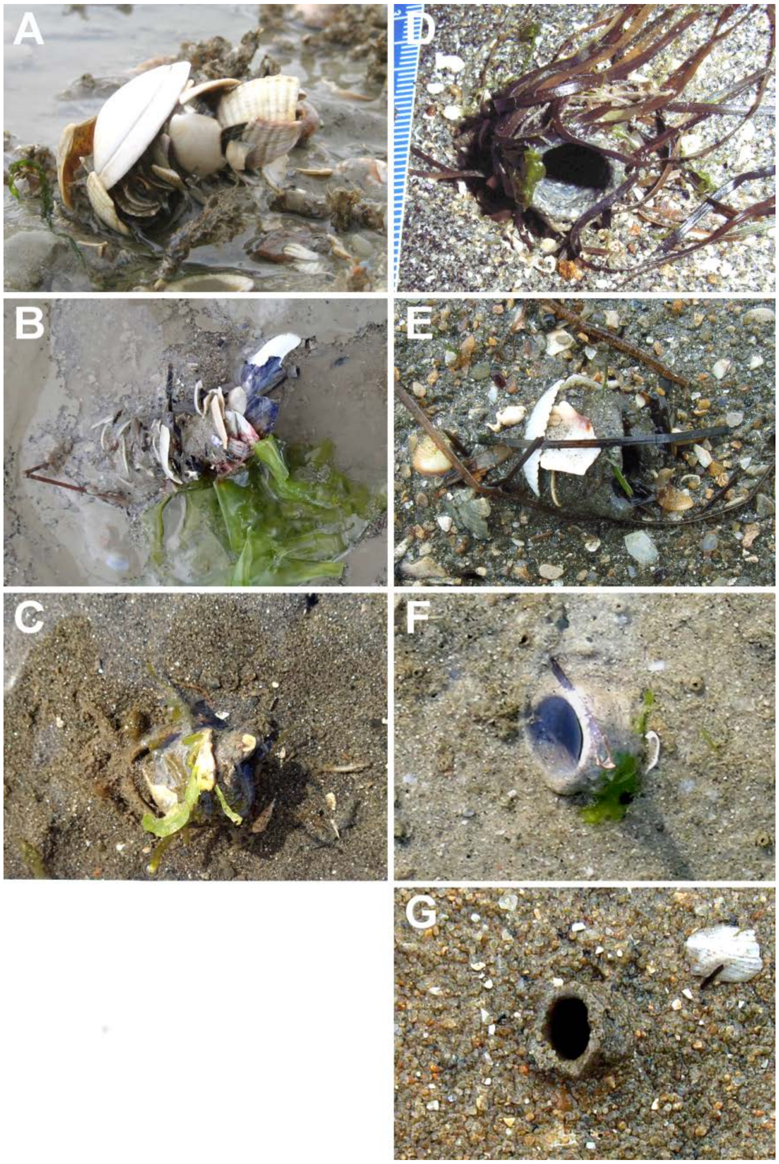

Fig. 3. Levels of decoration in *D. biscayensis* (**A, B, C**) and *D. neapolitana* (**D, E, F, G**). High decoration (A, D), medium decoration (B, E), low decoration (C, F), no decoration (G).

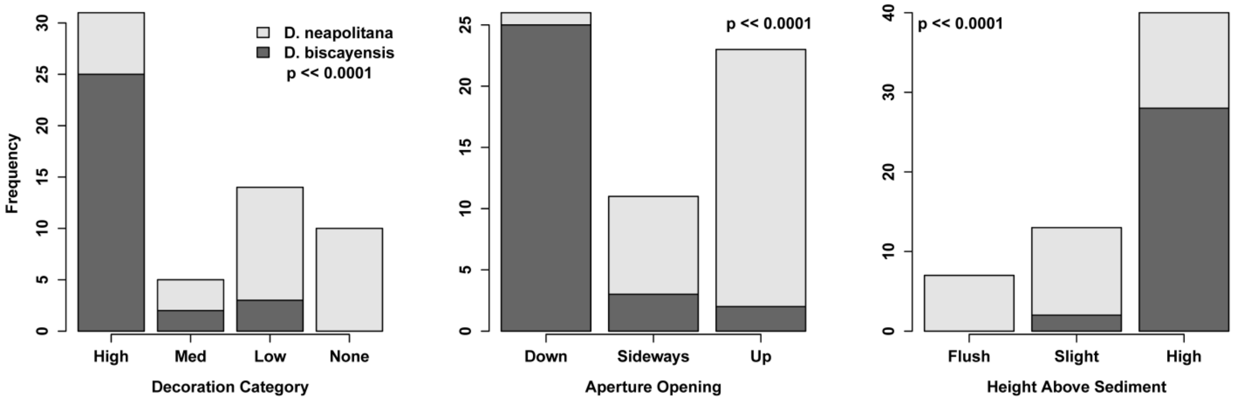

Fig. 4. Tubes of *D. biscayensis* are distinct from those of *D. neapolitana*. Individuals of *D. biscayensis* decorate more, are more likely to point their apertures down towards the sediment surface, and build more emergent tubes. Data were collected from field photographs.

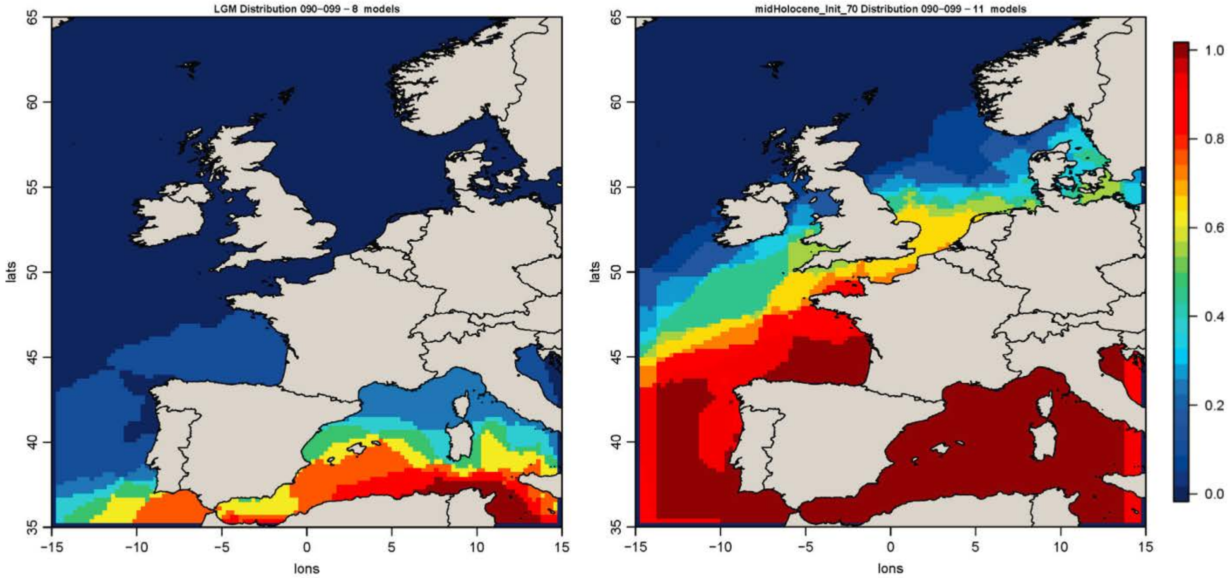

Fig. 5. Distributions of *D. biscayensis* in Last Glacial Maximum simulations (left) and Mid-Holocene Warm Period (right). Map colors indicate the fraction of models agreeing that *D. biscayensis* is present (scale on right).

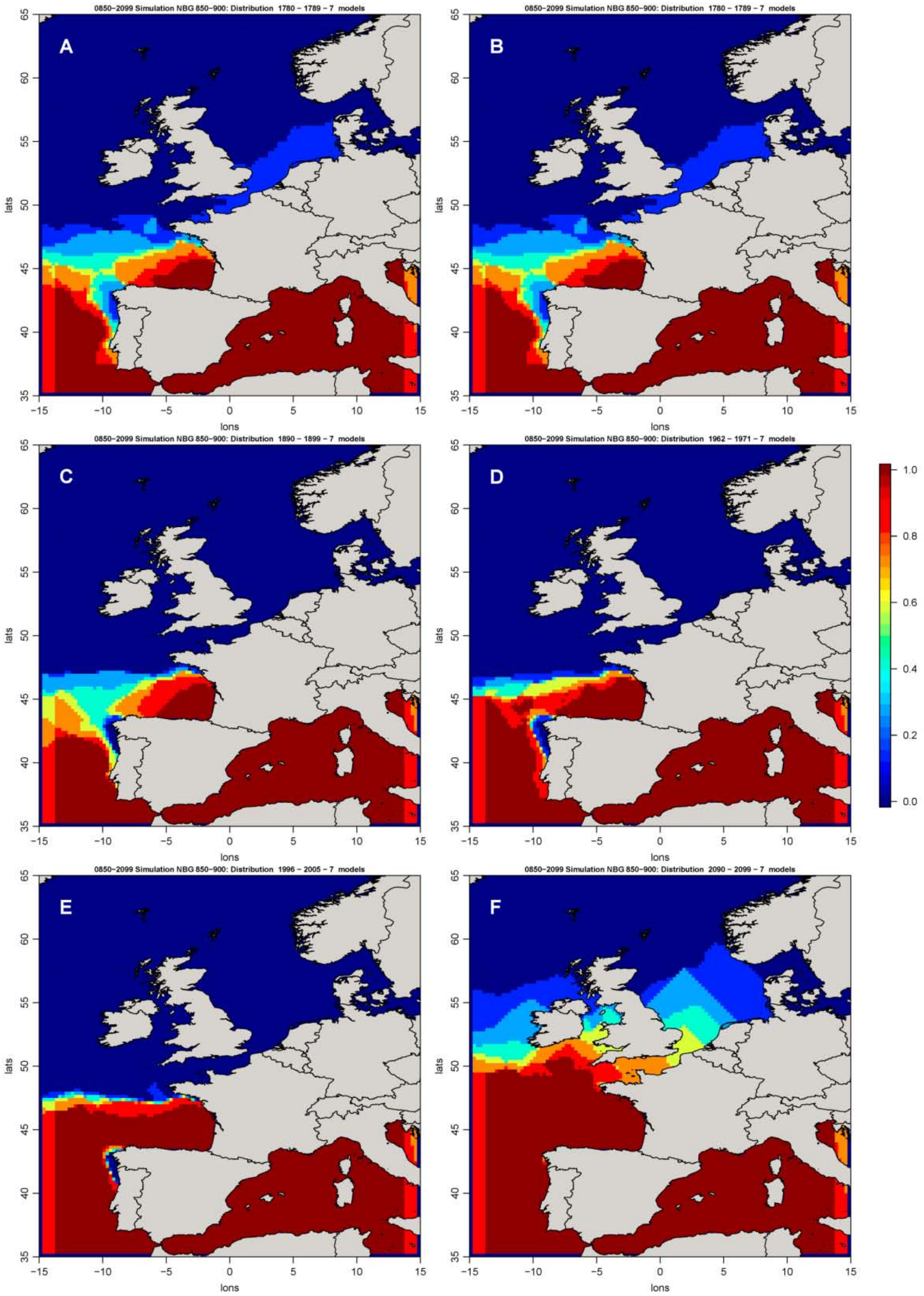

Fig. 6. Distributions of *D. biscayensis* in combined metapopulation simulations for the years 850–2100. The simulations used SST fields from Past 1000 (850–1850), Historical (1851–2005), and RCP8.5 (2006–2099) simulations. Maps show decadal averages of the fraction of models agreeing *D. biscayensis* is present, color scale on right. **A:** 1100–1109, **B:** 1780–1789, **C:** 1890–1899, **D:** 1962–1971, **E:** 1996–2005, **F:** 2090–2099.

Table 1. Climate models used in metapopulation modeling and summary of results.

Experiment	CMIP5 Model[a]	Dates	Summary of Results
Last Glacial Maximum	CNRM-CM5 IPSL-CM5A-LR LASG-FGOALS-g2 MIROC-ESM MPI-ESM-P NASA-GISS-E2-R MRI-CGCM3 NCAR-CCSM4	21,000 BP	Restricted to southern Portugal and Mediterranean
Mid-Holocene Warm Period	BCC-CSM1-1 CNRM-CM5 CSIRO-Mk3-6-0 IPSL-CM5A-LR LASG-FGOALS-s2 MetOffice-HadGEM2-CC MIROC-ESM MPI-ESM-P MRI-CGCM3 NASA-GISS-E2-R NCAR-CCSM4	6000 BP	Expansion north to Wadden Sea and southern UK
Combined run Past 1000 years + Historical + RCP8.5	BCC-CSM1-1 LASG-FGOALS-s2 MIROC-ESM MPI-ESM-P MRI-CGCM3 NASA-GISS-E2-R NCAR-CCSM4	850–1850 1851–2005 2006–2100	Contraction to Bay of Biscay, refugia not evident in English Channel Expansion to North Sea

[a] BCC: Beijing Climate Center, China Meteorological Administration, China
CNRM: Centre National de Recherches Météorologiques, Météo-France, Toulouse, France
CSIRO: Commonwealth Scientific and Industrial Research Organization Marine & Atmospheric Research and Queensland Climate Change Centre of Excellence, Australia
IPSL: Institut Pierre Simon Laplace, Paris, France
LASG: Institute of Atmospheric Physics, Chinese Academy of Sciences, Beijing, and Center for Earth System Science,Tsinghua University, Beijing
MetOffice: Met Office Hadley Centre, Exeter, UK
MIROC: Japan Agency for Marine-Earth Science and Technology and Atmosphere and Ocean Research Institute, University of Tokyo
MPI: Max Planck Institute for Meteorology, Hamburg, Germany
NASA-GISS: NASA Goddard Institute for Space Studies, New York, New York, USA
NCAR: National Center for Atmospheric Research, Boulder, Colorado, USA