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Physiology and biogeography: The response of European mussels (*Mytilus* spp.) to climate change*

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Abstract: To understand how ecological communities may respond to climate change we have adopted the approach of determining the response of major ecosystem engineers that determine community composition and function. We utilize two approaches, correlative and mechanistic, to understand the current and future distributions of the marine mussels *Mytilus edulis* Linnaeus, 1758 and *M. galloprovincialis* Lamarck, 1819 in Europe. Both are dominant space-occupying species that control biodiversity in many coastal ecosystems and are the basis of the largest aquaculture production in Europe. A mechanistic analysis of physiological energetic response to temperature of the two species indicates that *M. edulis* cannot sustain a positive energy balance for sustained periods when sea surface temperature (SST) is greater than 23 °C, while *M. galloprovincialis* can maintain a positive energy balance at SST up to 30 °C. There is no difference in energetic response of the two species at cold temperatures (5–10 °C). The upper temperature threshold of positive energy balance in each species corresponds closely to the distribution of SST at their respective southern range limits in Europe. Alternatively, the northern range limit of *M. galloprovincialis* coincides with areas where winter SST is less than 9 °C, but there is no evidence of an energetic limit to this species at the cold end of its geographic range. Presently there is no mechanistic explanation for the difference between species in their northern range limits; however, as indicated by Random Forest modeling, *M. galloprovincialis* appears to be limited by cold temperatures during winter, suggesting the hypothesis of failure in reproductive development. These approaches allow for the ability to forecast changes in the distributions of these two species in Europe as SST continues to increase.

Key words: Species distribution modeling, Random Forest, blue mussel, ecological forecasting

It is now well established that organisms are responding to the unprecedented rate of climate warming, including changes in the timing of biological activities (Philippart *et al.* 2003, Edwards and Richardson 2004, Burrows *et al.* 2011) and biogeography (Burrows *et al.* 2011, Hilbish *et al.* 2012, Jones *et al.* 2012). To understand current and potential distributions of species, many biologists rely on species distribution models (SDMs) that use spatial environmental data relevant to a species to predict its distribution (Guisan and Thuiller 2005, Elith and Leathwick 2009, Peterson *et al.* 2011). There are two types of SDMs: correlative and mechanistic, though the two are not mutually exclusive. Correlative SDMs create predictions based on correlations between species distribution records and environmental variables (Robertson *et al.* 2003, Buckley *et al.* 2010). These types of models can be generated fairly quickly and can often, particularly for a species for which little is known, provide more information on what specific environmental variables may be important for the distribution of that species (Robertson *et al.* 2003, Elith and Leathwick 2009). Mechanistic SDMs create predictions based on knowledge of underlying physiological and/or life history responses to environmental variables (Robertson *et al.* 2003, Kearney and Porter 2009, Buckley *et al.* 2010, Woodin *et al.* 2013). Mechanistic SDMs are more time-consuming to develop, since the important physiological mechanisms that potentially regulate the species distribution must first be determined (Kearney and Porter 2009), but may provide greater insight into the factors limiting a species' distribution than a purely correlative model.

The current challenge is to move beyond modeling changes in the range limits of single species to develop an understanding of the biological mechanisms responsible for these changes and, importantly, the responses of communities and the functions of ecosystems. We have taken the

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approach of focusing on the response of key ecosystem engineers that both control the composition and diversity of ecological communities and are primary determinants of the “function” of ecosystems with respect to the goods and services provided to human societies, using both correlative and mechanistic methods. Mechanistic SDMs have been suggested as a more responsive model to climate change and invasive species scenarios (Kearney and Porter 2009) as they are better able to extrapolate to novel environmental conditions due to an understanding of the causative mechanisms behind species distributions (Helmuth *et al*. 2005, Kearney and Porter 2009, Woodin *et al*. 2013). However, these two types of approaches are not mutually exclusive and we show that incorporating both may provide a more robust model of a species’ complete biogeographic range (Lawler *et al.* 2006, Elith and Leathwick 2009, Sará *et al.* 2011).

In this study our focal system is marine mussels in the genus *Mytilus* across Linnaeus, 1758 a European scale. We selected mussels because they are major determinants of space and, therefore, biodiversity within rocky intertidal marine communities (Suchanek 1992). Also, mussels are farmed commercially, and mussel aquaculture is a multibillion dollar industry (FAO 2012). *Mytilus edulis* Linnaeus, 1758 and *M. galloprovincialis* Lamarck, 1819 are sister species that inhabit the coastal waters of Europe. *Mytilus edulis* is a cold-temperate species, inhabiting northern European waters to the French/Spanish border in the Bay of Biscay (Hilbish *et al*. 2012). *Mytilus galloprovincialis* is native to the Mediterranean and is found as far north as the British Isles (Skibinski *et al*. 1983, McDonald *et al*. 1991, Seed 1992). The overlap of these species has created a mosaic hybrid zone, with alternating patches of hybrids and pure parental populations from the Bay of Biscay to northern Scotland (Skibinski *et al*. 1983, Coustau *et al*. 1991, Bierne *et al*. 2003, Gosling *et al*. 2008, Hilbish *et al.* 2012). We sought to understand what controls the biogeographic distributions of these economically and ecologically important species in Europe, and how their functional performance differs within their ranges. This work provides a basis for forecasting future changes in the distribution of these species as the climate continues to change.

MATERIALS AND METHODS

European *Mytilus* distributions

Mytilus spp. have been well studied for many decades in Europe (Skibinski *et al.* 1983, Coustau *et al.* 1991, Gardner and Skibinski 1991, Rawson and Hilbish 1998, Daguin *et al.* 2001, Bierne *et al.* 2003), and their distribution in the past decade in various regions has been documented quite thoroughly. Much of this distribution was reported in Hilbish *et al.* (2012), who sampled 97 locations along the Atlantic coast of Spain and France. However, we developed an even more extensive range database by collating data from several studies (Lionetto *et al*. 2003, Gosling *et al.* 2008, Pisanelli *et al*. 2009, Banni *et al*. 2011, Kijewski *et al.* 2011, Hilbish *et al.* 2012, Wethey unpubl. data, Appendix A) as well as sampling in certain regions that were missing recent data (particularly the United Kingdom). Although these species do hybridize, for the purposes of this study we focused on “pure” species populations (populations that contained ≥ 95% allele frequency of one species) because the physiological studies of Fly and Hilbish (2013), described below, focused on “pure” species rather than hybrids. In 2008 and 2009, we sampled mussel populations at 43 sites in England, Scotland, and Wales that were originally sampled in 1976 and 1977 by Skibinski *et al*. (1983). To gain higher spatial resolution of the hybrid zone in southwest England, we sampled an additional 24 sites in 2010 that were previously sampled in 1996 by Hilbish *et al.* (2002). DNA extraction and genotyping at the Glu-5′ locus followed the protocols in Hilbish *et al.* (2012).

Modeling

We used two separate, yet complementary, modeling approaches to identify key variables determining the range limits of *Mytilus edulis* and *M. galloprovincialis*. The correlative approach was used primarily to classify known sites of “pure” populations of one of the two species, and then identify temperature variables that could be used to differentiate between *M. edulis* sites and *M. galloprovincialis* sites. The mechanistic approach used laboratory estimates of scope for growth of the two species to compare regions where scope for growth is estimated to be zero with the geographic limits of the two species.

Correlative approach

To estimate the importance of sea surface temperature (SST) on the distribution of *Mytilus* spp. in Europe, we analyzed the distribution of “pure” *Mytilus* populations using Random Forest (RF) modeling, which is becoming increasingly popular in ecological studies (Cutler *et al*. 2007). This machine learning model generates a summary of many classification trees to determine the best predictor variables for a dataset (Breiman 2001). To build the model, we classified sites from both our field studies and the literature (see Appendix A) as either *M. galloprovincialis* or *M. edulis* based on allele frequency with a 95% threshold; sites with ≥ 95% of alleles for a particular species were classified as a population of that species. We used the temperature parameters of yearly mean SST, monthly mean SST (for each month), and seasonal mean SST, as in Hilbish *et al.* (2012). These parameters were calculated using National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation ¼ Degree

Daily SST (OISST) data derived from Advanced Very High Resolution Radiometer (AVHRR) satellite sensors (Reynolds *et al*. 2007), acquired from the National Climatic Data Center archive at http://www.ncdc.noaa.gov/thredds/catalog/oisst/NetCDF/AVHRR/catalog.html. The SST value for each sample site was estimated by finding the pixel on each SST grid nearest to the sampling location. We determined SST means listed above for each population for the five years prior to each mussel sample date. This time period of five years was chosen to encompass on average the life span of the mussels (Hilbish *et al*. 2012).

The RF model was built using the randomForest package (Liaw and Wiener 2002) in R version 2.7.1 (R Development Core Team 2010) with 250,000 individual trees, in which one-third of the cases were left out of each tree to be used as an estimate of classification error as the trees were added to the forest. Classification error is the frequency of test cases (those not included in model generation) incorrectly classified by the final model and was used to evaluate the ability of the model to differentiate between *M. galloprovincialis* and *M. edulis* sites. The relative importance of each temperature variable was determined for the RF model to identify which variables were most useful for classifying the sites, thus, identifying temperature differences between the ranges of the two species. The importance of the predictor temperature variables was determined using the mean decrease in accuracy calculated during the RF analysis. This metric is calculated by identifying the decrease in the accuracy of the model when the values of a single predictor variable are randomly permuted. Thus, variables with the larger mean decrease in accuracy are more important for data classification.

Mechanistic approach

The physiological energetics of *Mytilus edulis* and *M. galloprovincialis* were measured by Fly and Hilbish (2013). They integrated measurements of filtration rate, absorption efficiency, and metabolic rate to derive an estimate of the scope for growth (SFG) (sensu Widdows and Bayne 1971 the SFG measures the energy above maintenance available for growth and reproduction) of mussels at water temperatures ranging from 5 °C to 30 °C. We used their estimate of the critical SST at which SFG = 0 to determine the geographic regions in Europe in which each species can potentially maintain a permanent population. In regions that exceed the critical SST at which SFG = 0, populations of each species are expected to be absent or ephemeral (Sokolova *et al.* 2012, Woodin *et al.* 2013). We compared the distribution of *M. edulis* and *M. galloprovincialis* to the monthly SST along the European coastline and to the critical temperature at which SFG = 0 (Fly and Hilbish 2013). SFG data were collected from one population of each species (Fly and Hilbish 2013). While local adaptation may be possible, *Mytilus* populations have the potential for very high gene flow, with dispersal distances of up to 100 km (Gilg and Hilbish 2003). The data presented below suggest that there is not local adaptation occurring in genes relevant to setting *Mytilus* range limits, since the physiological energetics measured using animals from one population appear to well explain the southern range edge of both *M. edulis* and *M. galloprovincialis*. If there were local adaptation occurring, we would expect to see these data fail to explain distribution limits.

Ecological forecasting

Forecasts of future environmental conditions were made using model output from the EURO-CORDEX project (Jacob *et al.* 2014). This project uses regional circulation models (RCM) to downscale global circulation models (GCM) in order to predict monthly average SST on a 44 km grid. We chose to use the 4.5 Wm^{-2} (rcp4.5) global energy imbalance scenario of the IPCC 5th Assessment Report, which simulates moderate future warming and is similar to the IPCC 4th Assessment Report scenario A1B. To date, 8 GCMs have been downscaled with one RCM (Appendix B), and the results have been posted on the Earth System Grid (http://esgf-data.dkrz.de/esgf-web-fe/). EURO-CORDEX 44-km data were on a curvilinear grid, so they were interpolated to a 25 km Mercator grid, using the R package "akima" (Akima *et al.* 2013). Since there is disagreement among the models in terms of the spatial distribution of sea surface temperatures, we made maps of the fraction of models that predicted SST of at least 20 °C in summer (August) and at least 9 °C in winter (February). The temperature of 20 °C in summer is a proxy for the southern geographic limit of *M. edulis (*Fly and Hilbish 2013) and the temperature of 9 °C is a proxy for the northern geographic limit of *M. galloprovincialis* (Hilbish *et al.* 2012), as indicated by the mechanistic and correlative models. We used the median of the model predictions as our estimate of the expected geographic distribution of the *Mytilus* species over the periods 2046–2050 and 2096–2100. For comparison to the present, we used the daily NOAA OISST product (Reynolds *et al.* 2007) to make maps of monthly average SST over the period 2002–2009. We then determined for each pixel in the map, the fraction of years (2002–2009) with temperatures higher than 9 °C in winter and 20 °C in summer.

RESULTS

The distribution of *Mytilus* spp. in Europe ranges from northern Africa, through the Mediterranean, along the Atlantic coastline into Scandinavia and on the British Isles (Fig. 1). Contiguous populations of *M. galloprovincialis* extend from the Mediterranean north to the border between Spain and France in the Bay of Biscay (Fig. 1). Two disjunct

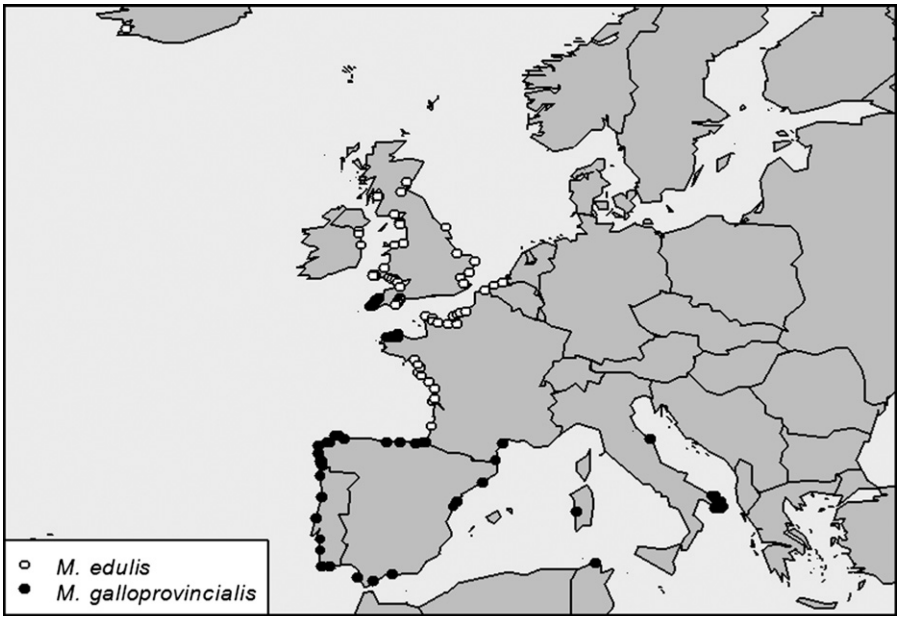

Figure 1. Sample locations used for biogeographic modeling of *Mytilus* spp. in Europe. These data were collated from several published studies (see Appendix A) as well as additional sampling in certain regions that were missing data (in particular the United Kingdom). For the purposes of this study we focused on "pure" species populations, and we defined "pure" as populations that contained ≥ 95% genotype of either *M. edulis* or *M. galloprovincialis*. Although the data points are sparse in the Mediterranean and North Sea, these areas are nearly exclusively *M. galloprovincialis* and *M. edulis*, respectively. The current southern limit of *M. edulis* occurs at the France/Spain border in the Bay of Biscay, while the current northern limit of *M. galloprovincialis* is on France's Brittany coast on Europe's mainland and in southwest England.

populations of *M. galloprovincialis* occur in Brittany, France, and in Cornwall, England (Fig. 1). Thus, there are three northern limits of *M. galloprovincialis* in Europe. The North Sea, Irish Sea, and the eastern English Channel are composed almost exclusively of populations of *M. edulis*. A disjunct population of *M. edulis* occurs in a certain area of the Bay of Biscay in France (Fig. 1) where SST is generally cooler than the rest of the bay (Fig. 5A). We plotted these populations with respect to winter and summer SST, using February and August SST, respectively, to see how the distributions were related to the warmest and coldest environmental temperatures these populations experienced (Fig. 2). Populations of *M. galloprovincialis* in Europe never occur in areas where mean monthly SST falls below 9 °C in the winter, while populations of *M. edulis* occur in areas down to 6 °C (Fig. 2). In the summer, most populations of *M. edulis* occur where summer temperatures are below 20 °C, and no populations persist where summer SST is greater than 23 °C. Conversely, populations of *M. galloprovincialis* inhabit much warmer locations (Figure 2) including sites where summer SST regularly exceeds 23 °C. The warmest average summer temperature experienced by *M. galloprovincialis* in our dataset was 26.4 °C; however, the distribution of this species in northern Africa is not well-documented, so populations likely experience even warmer temperatures.

The Random Forest classification model, a correlative model, performed well, correctly classifying the out of bag samples (30% of data excluded when building the model) 97.14% of the time. Relative importance evaluation identified winter and spring variables (mean winter temperature, mean spring temperature, mean January temperature, mean March temperature, and mean April temperature) as the most important variables (ranked by mean decrease in model accuracy) for correctly classifying a site as *Mytilus edulis* or *M. galloprovincialis*. These results align nicely with a smaller-scale RF model based on *M. galloprovincialis* distribution in France and Spain, and explain historical changes in the distribution of *M. galloprovincialis* along the Normandy coast in France (Hilbish *et al.* 2012). Based on this correlative model and the known distribution of *M. galloprovincialis* with respect to SST, *M. galloprovincialis* is likely precluded from inhabiting areas where winter SST is routinely below 9 °C, while *M. edulis* is more cold-adapted (Fig. 2). However, this correlative approach provides no explanation for the mechanism involved in this northern range limit of *M. galloprovincialis*. Previous work discerning the energetics of these two species (Fly and Hilbish 2013) provides evidence that the mechanism is not adult mussel energetics, as there are no significant differences at cold temperatures (Fig. 3).

Differences in energetics can, however, be ascertained as the mechanism for the differences in the species' southern limits. As stated previously, populations of *Mytilus edulis* do not inhabit areas where summer temperatures routinely exceed ~23 °C (Fig. 2). Fly and Hilbish (2013) determined the critical temperature at which SFG = 0 for *M. edulis* and *M. galloprovincialis*. While there were seasonal differences, the critical temperature for *M. edulis* was regularly around 23 °C (Fig. 3, Fly and Hilbish 2013), which corresponds with the environmental temperatures at the southern range edge of this species (Fig. 2, Fig. 4). The critical temperature for *M. galloprovincialis* was between 29–30 °C (Fig. 3, Fly and Hilbish 2013), and *M. galloprovincialis* inhabits regions in Europe with SST that does not exceed this threshold (Fig. 2, Fig. 4).

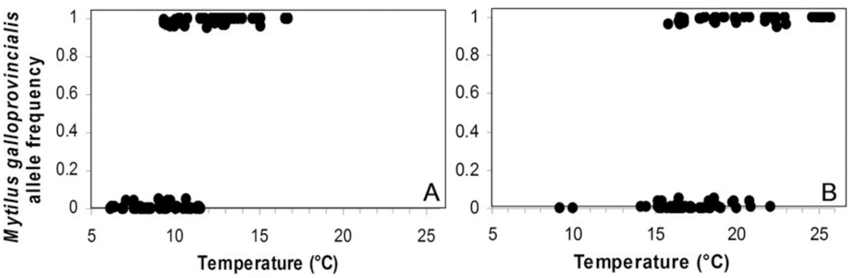

Figure 2. Distribution of European *Mytilus* populations with respect to winter and summer sea surface temperatures (SST). We plotted the populations shown in Figure 1 with respect to winter and summer SST, using **A,** February and **B,** August SST, respectively, to see how the distributions were related to environmental temperatures. **A,** Populations of *M. galloprovincialis* never occur in areas where mean monthly SST falls below 9 °C in the winter, while populations of *M. edulis* occur in areas down to 6 °C. **B,** In the summer, most populations of *M. edulis* occur where summer temperatures are below 20 °C, and no populations persist where summer SST is greater than 23 °C. Conversely, populations of *M. galloprovincialis* inhabit much warmer locations.

both winter and summer warming (Fig. 5C–F). The result of this warming is the northward movement of the conditions for survival of *M. edulis* and *M. galloprovincialis*. The median of the EURO-CORDEX rcp4.5 forecasts predicts that summer maximum monthly SST of 20 °C will move northward to just south of the Brittany peninsula in France by 2050 (Fig. 5D), and move into the western English Channel and southern North Sea to 53°N by 2100 (Fig. 5F). This 20 °C isotherm is a proxy for the expected southern geographic limit of *M. edulis*, and predicts that the only region of the English Channel that will be habitable by *M. edulis* by 2100 will be along the Normandy coast of France (between Cherbourg and Calais). While a similar

In the past decade, the 9 °C winter isotherm has been in the western part of the English Channel in the south (Fig. 5A). During the same period, the 20 °C summer isotherm has traversed the Bay of Biscay from just south of the mouth of the Gironde (45 °N) to NW Spain (Fig. 5B). This pattern is consistent with the exclusion of *Mytilus edulis* from the lower Bay of Biscay (Fig. 1). The EURO-CORDEX forecast predicts

permissible area appears on England's side of the English Channel (between Bournemouth and Dover), mussels are not readily found in this area due to a predominance of sandy beaches rather than hard substrates. The median of the rcp4.5 forecasts suggest that winter monthly SST higher than 9 °C will move eastward into the English Channel and northward into the Irish Sea by 2050 (Fig. 5C),

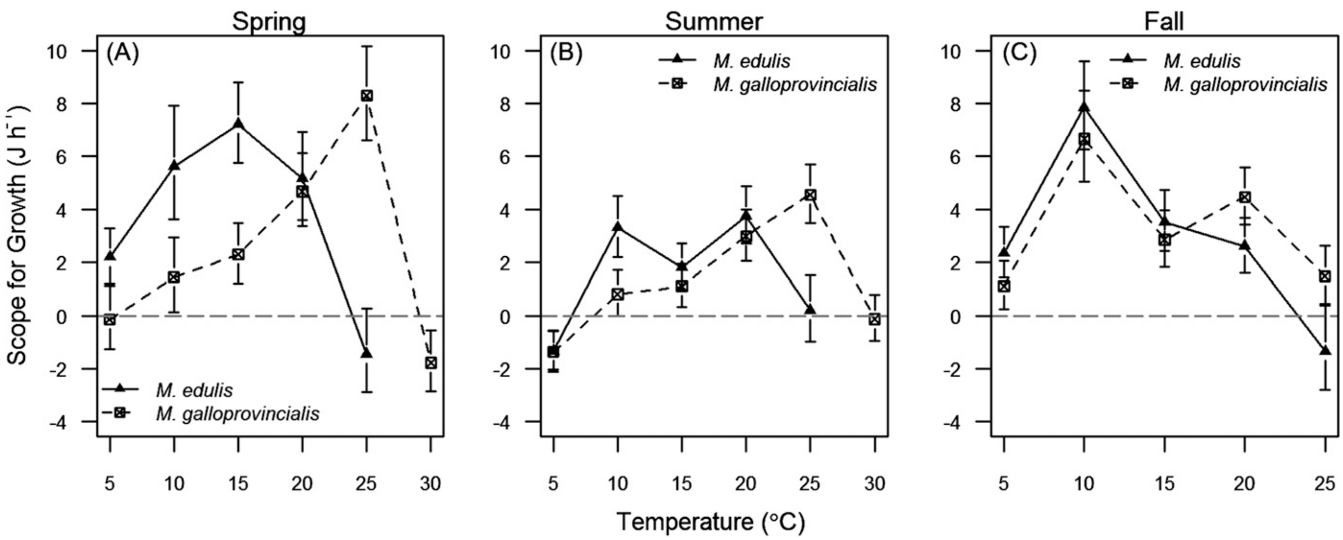

Figure 3. Physiological energetics of *Mytilus edulis* and *M. galloprovincialis***.** Measurements of filtration rate, absorption efficiency and metabolic rate were used to derive an estimate of scope for growth (SFG) (sensu Widdows and Bayne 1971 the SFG measures the energy above maintenance available for growth and reproduction) of mussels at water temperatures ranging from 5 °C to 30 °C in **A,** spring, **B,** summer, and **C,** fall. No mussels survived at 30 °C in the fall. Estimates of the critical temperatures at which SFG = 0 (dashed line) were used to determine the geographic regions in Europe in which each species can potentially maintain a permanent population. This figure was adapted from Fly and Hilbish (2013).

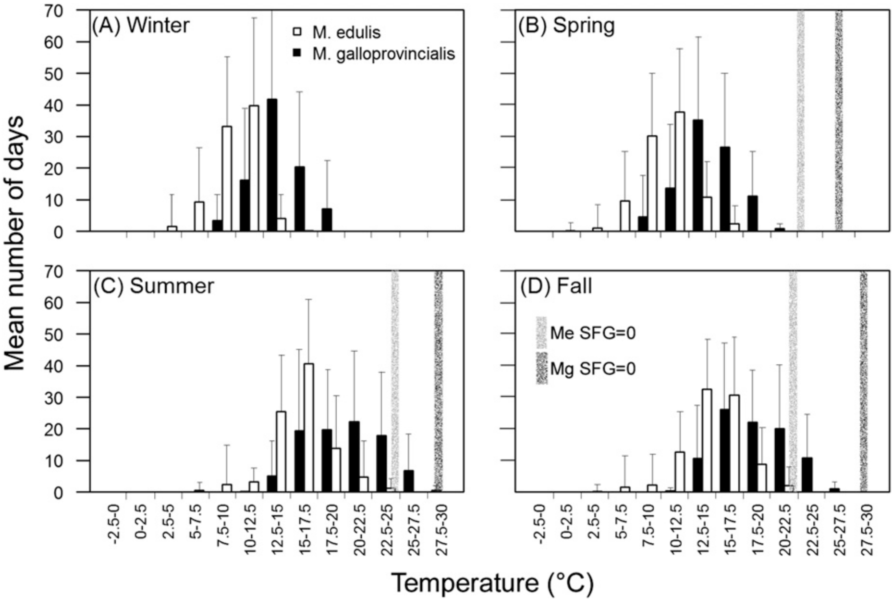

Figure 4. Average temperature profile of European *Mytilus edulis* (gray) and *M. galloprovincialis* (black) populations in each season**.** The transparent rectangles (gray for *M. edulis* and black for *M. galloprovincialis*) indicate the critical temperature at which SFG = 0 in spring, summer, and fall, as determined by Fly and Hilbish (2013). SFG data were not collected for winter (**A**). In regions that exceed this critical temperature, populations of mussels are expected to be ephemeral or absent and, indeed, very few populations experience temperatures higher than that critical temperature. Summer (**C**) and fall (**D**) appear to be more physiologically-limiting than spring (**B**). This figure was adapted from Fly and Hilbish (2013).

with only slightly further movement into the northern North Sea by 2100 (Fig. 5E). This prediction suggests that *M. galloprovincialis* will be much more prevalent in the British Isles and English Channel than it currently is.

DISCUSSION

Species distribution models are useful in understanding current and potential distributions of species; however, oftentimes one type of SDM is incapable of accurately predicting all of a species' range limits (*e.g.*, north and south, east and west) (Woodin *et al.* 2013). This is because a given SDM applies a single mechanism or environmental profile across an entire species' range, when, it is often the case that different mechanisms or stressors control different portions of a species' geographic range or its distribution in different geographic regions (Sokolova *et al.* 2012, Woodin *et al.* 2013). This appears to be the case with *Mytilus edulis* and *M. galloprovincialis*. As suggested by mechanistic modeling, the southern limit of *M. edulis* is likely controlled by physiological constraints on the adult populations: specifically, populations cannot persist in areas where summer SST routinely exceeds 20 °C, due to rapidly declining SFG above this temperature. It is likely that the southern limit of *M. galloprovincialis* is also controlled by energetic limitation; however, the southern limit of this species on the northwest African coast is not well-documented, so we cannot currently determine temperatures experienced at the very southern range edge of this species. Interestingly, while the southern limits of *Mytilus* spp. in Europe appear to be controlled by sublethal temperature effects of adult energetics, the southern limit of *M. edulis* on the east coast of the U.S. is controlled by lethal temperature effects on adult populations (Jones *et al.* 2010). This is likely because the east coast of the U.S. has a more continental climate (and, therefore, greater temperature extremes) than the west coast of Europe, which has a more coastal climate (Wethey 1985, Jenkins *et al.* 2008, Bailey 2009). Thus, mechanisms can differ within the same species in different regions.

The mechanism limiting the northern range of *Mytilus galloprovincialis* in Europe is still unknown; however, limitations due to adult energetics are very unlikely. Blue mussels are physiologically quiescent during winter (Bayne 1976), and there are no major differences in the SFG of *M. edulis* and *M. galloprovincialis* at cold temperatures in other seasons that would explain the inability of *M. galloprovincialis* populations to persist where winter temperatures are below 9 °C (Fly and Hilbish 2013). This cold-water limitation has been noted previously for European *M. galloprovincialis* populations (Hilbish *et al.* 2012), as well as populations on the west coast of the U.S. (Hilbish *et al.* 2010). There are several hypotheses on the mechanism of this limitation that warrant further investigation, including tolerance to cold-shock and reproductive abilities.

The tolerance of species to cold temperatures depends on a variety of factors, including the thermal regimes and acclimation times experienced (Renault *et al.* 2004, Terblanche *et al.* 2011). Jansen *et al.* (2007) found that *Mytilus galloprovincialis* populations were much more sensitive to cold shock than *M. edulis* populations. This suggests that *M. galloprovincialis* might not have the same capability to recover from cumulative cold damage as *M. edulis*. Another possibility is that the reproductive capabilities of *M. galloprovincialis* are impeded at temperatures below 9 °C (Hilbish *et al.* 2010,

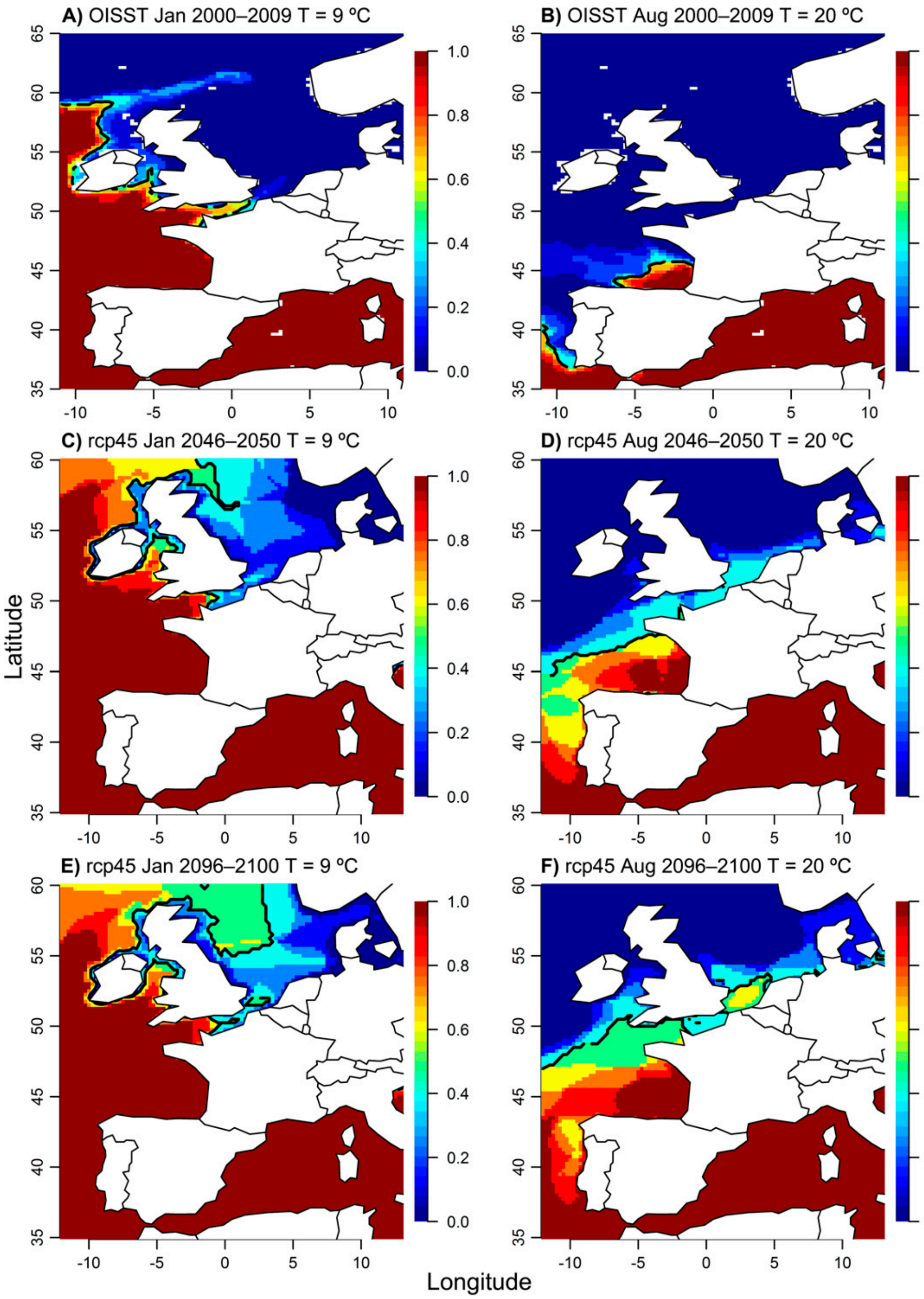

Figure 5. A, Fraction of winters 2002–2009 with temperatures above 9 ºC in winter (February) and **B,** above 20 ºC in summer (August), derived from NOAA Optimally Interpolated Sea Surface Temperature data. The contour line is the 50th percentile of the values throughout the figure. **C,** Fraction of EURO-CORDEX rcp4.5 models indicating temperatures above 9 ºC in winter (February) and **D,** 20 ºC in summer (August) in the period 2046–2050. **E,** Fraction of EURO-CORDEX rcp4.5 models indicating temperatures above 9 ºC in winter (February) and **F,** 20 ºC in summer (August) in the period 2096–2100. The temperature of 20 ºC in summer is a proxy for the southern geographic limit of *Mytilus edulis* and the temperature of 9 ºC is a proxy for the northern geographic limit of *M. galloprovincialis*. The contour lines for the forecasts (C–F) indicate the median of the model predictions. (Color shown in electronic version only).

Hilbish *et al.* 2012). Most populations of mussels spawn in the spring after having undergone gametogenesis over the winter (Bayne 1976). The fact that the RF model indicated winter or early spring as a key time for determining the distribution of these mussels suggests a hypothesis that some aspect of gametogenesis and/or spawning is temperature dependent and different between species.

Understanding the mechanism controlling this northern limit will be useful in making better predictions for the expansion of these populations as winter SSTs warm. The RF correlative model used monthly mean SST, while the mechanistic model considered distributions on a daily scale. Hilbish et al. (2012) ran a similar model using maximum entropy modeling (Maxent, http://www.cs.princeton.edu/~schapire/maxent/), that considered the number of days below temperature thresholds as variables. The two variables contributing most to mussel distribution were days below 9 °C and days below 10 °C (Hilbish *et al.* 2012). As hypotheses for mechanisms explaining this temperature distribution are examined, the temporal scale of the temperature distribution should be considered.

Warming of the ocean is not expected to occur uniformly (Xie *et al.* 2010), which suggests that the northern range limit of *Mytilus galloprovincialis* and the southern range limit of *M. edulis* will likely change at heterogeneous rates over the remainder of the 21st century. During the first half of the current century (present to 2050) the northern range limit of *M. galloprovincialis* is expected to shift substantially into the English Channel and into the Irish Sea and North Atlantic Ocean (Fig. 5C). However, during the second half of the century further range expansion is expected to be comparatively small (Fig. 5E). Conversely, the anticipated contraction of the southern range edge of *M. edulis* is expected to remain south of France's Brittany coast in the Bay of Biscay through 2050 (Fig. 5D), but shift dramatically north to 53°N by 2100, leaving only a small portion of French coastline, mainly the Normandy coast, suitable for *M. edulis* (Fig. 5F). France produces about 73,000 tons of mussels each year, 22% of which are produced in Normandy (Eurostat 2009). These potential future SST shifts indicate the bulk of the commercial mussel farms on the rest of the French coastline may no longer be able to cultivate *M. edulis* by the end of the century.

Mytilus edulis and *M. galloprovincialis* hybridize extensively, and the differing rates in their range expansions and contractions have implications for the hybrid zones formed between them. With a rapid northward expansion of *M. galloprovincialis* and minimal contraction of *M. edulis* by 2050, the hybrid zones between these two species could expand substantially. However, by 2099, many current regions of hybridization should be displaced by *M. galloprovincialis* and new hybrid zones may form in the Irish and North Atlantic Seas, regions currently inhabited primarily by *M. edulis*. This brings to light the vulnerability of *M. edulis* to warming environmental conditions: those populations exposed to summer SSTs greater than 20 °C are highly vulnerable to being unable to persist.

Although we understand an important mechanism controlling the southern range edge of *Mytilus edulis* in Europe, we currently have still used 20 °C as our proxy for the physiological limit of this species. While the temperature at which SFG = 0 for *M. edulis* is ~23 °C, the southern range edge of this species maps more closely to a 20 °C SST isotherm, with only several populations persisting where summer temperatures range between 20–23 °C. It is likely that the populations living in this summer temperature range are physiologically stressed (Sokolova *et al.* 2012) and heavily dependent on other factors such as food availability. We should be able to develop an even stronger model to predict not only the range edge of this species with changing SST based on where SFG = 0, but to begin to quantify the productivity of these mussel beds based on the physiological rates measured (Fly and Hilbish 2013). These mechanistic models, as stated earlier, require much more input and background knowledge than correlative models. Thus, several issues must be resolved to produce a meaningful mechanistic model based on physiological productivity. A more detailed model will better take into account any differences between submerged and intertidal mussels. *Mytilus edulis* and *M. galloprovincialis* reduce their aerial rate of oxygen consumption to 4–17% that of their rate of aquatic oxygen consumption (Widdows *et al.* 1979), and incur only a small cost in terms of oxygen debt recovery (Widdows and Shick 1985). However, intertidal mussels can only feed while submerged, thus, affecting food availability and energy intake. A robust mechanistic model will take into account food availability and duration of exposure at low tide conditions.

The most outstanding question is how to incorporate food availability into projections of secondary production. Mussels consume food particles in the size range of 2–20 µm (Bayne 1976), but algal biomass within this size range is only, at best, weakly correlated with chlorophyll *a* or other pigments that can be assessed with remote sensing (Alpine and Cloern 1985, Han and Furuya 2000, Arin *et al.* 2002). Additionally remote sensing products are often unreliable in near-shore coastal environments where materials of terrestrial origin and reflection off of the ocean bottom interfere with sensor readings (Hellweger *et al.* 2004, Moses *et al.* 2009). The result is that it is very difficult to predict present day secondary production of mussels (and many other marine species) on a regional scale. It will be even more difficult to forecast changes in primary production, specifically of the nanoplankton as a consequence of climate change and to incorporate these changes into models of secondary production of mussels and other coastal species (Sommer and

Lengfellner 2008). Until meaningful projections of changes in coastal primary production become available the most productive approach may be to forecast changes in local and regional potential for secondary production and provide mechanistic models that will allow the incorporation of local primary production to assess the management of coastal species with respect to climate change.

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Appendix A Data used for Europe-wide Random Forest model using distributions of "pure" populations of *Mytilus galloprovincialis* and *M. edulis* based on published accounts or genetic analyses done for this study where *M. galloprovincialis* allele frequencies were greater than 95% or less than 5%, respectively. The sample sites are listed by latitude from North to South.

Year sampled	Site	Latitude	Longitude	Frequency of *Mg* allele	Source
2003	White Sea, Russia	66.00	39.37	0.00	Kijewski *et al.* 2011
2003	Reykjavik, Iceland	64.17	-22.02	0.00	Kijewski *et al.* 2011
2008	Tayport, Scotland	56.44	-2.94	0.01	current study
2008	Cramond, Scotland	55.98	-3.30	0.01	current study
2009	Fairlie, Scotland	55.76	-4.86	0.04	current study
2009	Millport, Scotland	55.75	-4.93	0.01	current study
2009	Rockcliffe, England	54.85	-3.79	0.00	current study
2009	Seascale, England	54.40	-3.49	0.00	current study
2009	Ravenglass, England	54.36	-3.41	0.00	current study
2008	Filey Brigg South, England	54.22	-0.27	0.04	current study
2005	Carlingford, Ireland	54.04	-6.18	0.00	Gosling *et al.* 2008
2005	Dunany, Ireland	53.86	-6.24	0.00	Gosling *et al.* 2008
2009	Thurstaston, England	53.34	-3.15	0.00	current study
2005	Dublin, Ireland	53.30	-6.15	0.00	Gosling *et al.* 2008
2009	Conwy, Wales	53.29	-3.83	0.00	current study
2008	Heacham, England	52.91	0.47	0.00	current study
2008	Lowestoft, England	52.45	1.74	0.01	current study
2008	Llangranog, Wales	52.16	-4.47	0.01	current study
2008	Harwich, England	51.93	1.27	0.00	current study
2008	Solva, Wales	51.87	-5.20	0.00	current study
2008	Milford Haven, Wales	51.72	-5.10	0.02	current study
2008	Dales, Wales	51.71	-5.17	0.00	current study
2008	Burry Port, Wales	51.68	-4.25	0.00	current study
2008	South Woodham Ferrers, England	51.63	0.61	0.00	current study
2008	Port Talbot, Wales	51.59	-3.81	0.00	current study
2008	Mumbles, Wales	51.57	-3.99	0.00	current study
2008	Porthcawl, Wales	51.50	-3.74	0.00	current study
2008	Atlantic College, England	51.40	-3.53	0.00	current study
2008	Swale, England	51.35	0.88	0.00	current study
2008	Minehead, England	51.21	-3.46	0.00	current study
2009	Exmouth, England	50.61	-3.41	0.00	current study
2009	Teignmouth, England	50.54	-3.49	0.00	current study
2009	Maidencombe, England	50.51	-3.51	0.00	current study
2009	Torbay, England	50.45	-3.54	0.00	current study
2009	Dartmouth, England	50.34	-3.57	0.00	current study
2009	Torcross, England	50.26	-3.65	0.00	current study
2003	Vlissengen, Netherlands	51.44	3.56	0.05	Kijewski *et al.* 2011
2003	Oostende, Belgium	51.24	2.92	0.00	Kijewski *et al.* 2011
2005	Dunkirk, France	51.05	2.38	0.00	Hilbish *et al.* 2012
2005	Dieppe, France	49.94	1.09	0.00	Hilbish *et al.* 2012
2005	Saint-Vaast-la-Hougue, France	49.58	-1.26	0.00	Hilbish *et al.* 2012
2003	Seine, France	49.42	0.08	0.00	Kijewski *et al.* 2011
2007	Merville-Franceville, France	49.29	-0.20	0.00	Hilbish *et al.* 2012
2006	Billiers, France	47.52	-2.48	0.04	Hilbish *et al.* 2012
2006	Barbatre, France	46.89	-2.15	0.01	Hilbish *et al.* 2012
2005	Saint-Gilles-Croix-de-Vie, France	46.69	-1.95	0.04	Hilbish *et al.* 2012
2006	La Tranche-sur-Mer, France	46.34	-1.46	0.03	Hilbish *et al.* 2012
2006	Vieux Châtelaillon, France	46.06	-1.09	0.00	Hilbish *et al.* 2012
2006	Montalivet-les-Bains, France	45.38	-1.16	0.01	Hilbish *et al.* 2012
2006	Mimizan-Plage, France	44.21	-1.29	0.01	Hilbish *et al.* 2012
2006	Pointe de Grave, France	45.57	-1.06	0.04	Hilbish *et al.* 2012
2006	Pornic, France	47.11	-2.11	0.05	Hilbish *et al.* 2012

Appendix A. (Continued)

Year sampled	Site	Latitude	Longitude	Frequency of *Mg* allele	Source
2006	Saint-Brevin-les-Pins, France	47.27	-2.17	0.03	Hilbish *et al.* 2012
2006	Nacqueville, France	49.68	-1.72	0.01	Hilbish *et al.* 2012
2006	Pointe du Moulard, France	49.64	-1.23	0.00	Hilbish *et al.* 2012
2006	Ravenoville, France	49.47	-1.24	0.00	Hilbish *et al.* 2012
2006	Sainte-Honorine-des-Pertes, France	49.36	-0.80	0.00	Hilbish *et al.* 2012
2006	Luc-sur-Mer, France	49.32	0.47	0.00	Hilbish *et al.* 2012
2006	Saint-Jouin-Bruneval, France	49.65	0.15	0.00	Hilbish *et al.* 2012
2006	Étretat, France	49.71	0.20	0.00	Hilbish *et al.* 2012
2006	Saint-Pierre-en-Port, France	49.81	0.49	0.01	Hilbish *et al.* 2012
2006	Saint-Valéry-en-Caux, France	49.87	0.71	0.00	Hilbish *et al.* 2012
2006	Pourville, France	49.92	1.03	0.00	Hilbish *et al.* 2012
2009	Port Quin, England	50.59	-4.87	0.99	current study
2009	Rock, England	50.54	-4.92	0.98	current study
2009	Porthcothan, England	50.51	-5.03	0.97	current study
2009	Newquay, England	50.42	-5.07	0.96	current study
2009	Trevaunance Cove, England	50.32	-5.20	0.98	current study
2009	Portreath, England	50.26	-5.30	0.98	current study
2009	Saint Ives, England	50.22	-5.49	0.96	current study
2005	Île Callot, France	48.68	-3.92	0.98	Hilbish *et al.* 2011
2005	Roscoff, France	48.73	-3.99	1.00	Hilbish *et al.* 2012
2005	Île Grande, France	48.81	-3.57	0.99	Hilbish *et al.* 2013
2007	Locquirec, France	48.69	-3.64	0.99	Hilbish *et al.* 2012
2007	Brignogan-Plage, France	48.67	-4.32	0.96	Hilbish *et al.* 2012
2006	Saint-Jean-de-Luz, France	43.39	-1.67	1.00	Hilbish *et al.* 2012
2005	Viveiro, Spain	43.72	-7.62	0.97	Hilbish *et al.* 2012
2005	Ortigueira, Spain	43.71	-7.85	0.99	Hilbish *et al.* 2012
2005	Foz, Spain	43.57	-7.25	0.98	Hilbish *et al.* 2012
2006	Laredo, Spain	43.41	-3.42	1.00	Hilbish *et al.* 2012
2005	Cabanas, Spain	43.41	-8.17	0.99	Hilbish *et al.* 2012
2006	San Vincente de la Barquera, Spain	43.39	-4.37	0.98	Hilbish *et al.* 2012
2006	Hondarribia, Spain	43.37	-1.79	0.95	Hilbish *et al.* 2012
2005	A Coruña, Spain	43.37	-8.38	0.98	Hilbish *et al.* 2012
2006	Deba, Spain	43.30	-2.35	0.98	Hilbish *et al.* 2012
2005	Laxe, Spain	43.22	-9.00	0.97	Hilbish *et al.* 2012
2005	Esteiro, Spain	42.79	-8.98	0.99	Hilbish *et al.* 2012
2005	Marin, Spain	42.40	-8.69	0.99	Hilbish *et al.* 2012
2005	San Xenxo, Spain	42.38	-8.85	0.99	Hilbish *et al.* 2012
2005	Bueu, Spain	42.23	-8.79	0.99	Hilbish *et al.* 2012
2005	Viana do Castelo, Portugal	41.70	-8.86	1.00	Hilbish *et al.* 2012
2005	Ílhavo, Portugal	40.62	-8.75	1.00	Hilbish *et al.* 2012
2005	São Martinho do Porto, Portugal	39.52	-9.15	1.00	Hilbish *et al.* 2012
2005	Tróia, Portugal	38.49	-8.90	1.00	Hilbish *et al.* 2012
2006	Sines, Portugal	37.91	-8.80	1.00	Hilbish *et al.* 2012
2005	Albufeira, Portugal	37.08	-8.23	1.00	Hilbish *et al.* 2012
2006	Burgau, Portugal	37.07	-8.77	1.00	Hilbish *et al.* 2012
2003	Cádiz, Spain	36.55	-6.37	0.96	Kijewski *et al.* 2011
2006	Ancona, Italy	43.56	13.59	1.00	Pisanelli *et al.* 2009
2006	Cap d'Agde, France	43.27	3.52	1.00	Wethey, unpubl. data
2003	Banyuls-sur-Mer, France	42.48	3.13	1.00	Kijewski *et al.* 2011
2003	Barcelona, Spain	41.37	2.20	1.00	Kijewski *et al.* 2011
2000	Carovigno, Italy	40.72	17.80	1.00	Lionetto *et al.* 2003
2000	Brindisi, Italy	40.65	17.98	1.00	Lionetto *et al.* 2003
2000	Torchiarolo, Italy	40.54	18.08	1.00	Lionetto *et al.* 2003
2006	Peñíscola, Spain	40.36	0.40	1.00	Wethey, unpubl. data

Appendix A. (Continued)

Year sampled	Site	Latitude	Longitude	Frequency of *Mg* allele	Source
2000	Lecce, Italy	40.34	18.37	1.00	Lionetto *et al.* 2003
2000	Otranto, Italy	40.15	18.49	1.00	Lionetto *et al.* 2003
2000	Santa Maria al Bagno, Italy	40.13	17.99	1.00	Lionetto *et al.* 2003
2006	Oropesa del Mar, Spain	40.08	0.14	1.00	Wethey, unpubl. data
2000	Gallipoli, Italy	40.05	17.97	1.00	Lionetto *et al.* 2003
2000	Castro, Italy	40.00	18.43	1.00	Lionetto *et al.* 2003
2003	Oristano, Sardinia	39.86	8.55	1.00	Kijewski *et al.* 2011
2008	Bizerte, Tunisia	37.27	9.89	1.00	Banni *et al.* 2011
2006	Torrox, Spain	36.73	-3.96	1.00	Wethey, unpubl. data
2006	Estepona, Spain	36.41	-5.17	1.00	Wethey, unpubl. data

Appendix B. Combinations of global and regional circulation models used in ensemble predictions of ocean climate change. **C4I,** Community Climate Change Consortium for Ireland, **CNRM,** Météo France, **DMI,** Danish Meteorological Institute, **ETHZ,** Swiss Institute of Technology Zurich, **GKSS,** Helmholz Center Geesthacht Institute for Coastal Research, **ICTP, KNMI,** Royal Netherlands Meteorological Institute, **HC,** UK Met Office Hadley Centre, **MPI,** Max Planck Institute, **OURANOS,** Consortium on Regional Climatology and Adaptation to Climate Change, **SMHI,** Swedish Meteorological and Hydrological Institute, **UCLM,** Universidad Castilla, La Mancha, **VMGO,** Voeikov Main Geophysical Observatory.

Modeling Group	Global Model	Regional Model
C4I	ECHAM5	RCA3
CNRM	ARPEGE	Aladin4.5
CNRM	ARPEGE	Aladin5.1
DMI	ARPEGE	HIRHAM5
DMI	ECHAM5	HIRHAM5
DMI	BCM	HIRHAM5
ETHZ	HadCM3Q0	CLM
GKSS	IPSL	CLM
KNMI	ECHAM5-r3	RACMO2
HC	HadCM3Q0	HadRM3Q0
HC	HadCM3Q3	HadRM3Q3
HC	HadCM3Q16	HadRM3Q16
MPI	ECHAM5	M-REMO
OURANOS	CGCM3	CRCM
SMI	BCM	RCA
SMI	ECHAM5-r3	RCA
SMI	HadCM3Q3	RCA
UCLM	HadCM3Q0	PROMES
VMGO	HadCM3Q0	RRCM