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The location, strength, and mechanisms behind marine biogeographic boundaries of the east coast of North America

Paula Pappalardo, James M. Pringle, John P. Wares and James E. Byers

P. Pappalardo (paulapappalardo@gmail.com) and J. E. Byers, Odum School of Ecology, Univ. of Georgia, Athens, GA 30602, USA. – J. M. Pringle, Dept of Earth Sciences, and the Inst. of Earth, Oceans, and Space, 142 Morse Hall, 8 College Road, Univ. of New Hampshire, Durham, NH 03824, USA. – J. P. Wares, Dept of Genetics, Univ. of Georgia, Athens, GA 30602, USA.

Classic biogeographic studies emphasized differences in species composition between regions to define biogeographic provinces and delimit biogeographic boundaries. Here we analyze the permeability of biogeographic boundaries to different species to gain mechanistic insight into the processes that maintain species boundaries in the coastal ocean. We identify sites with high frequencies of range boundaries using almost 1800 benthic marine invertebrates along the northwestern Atlantic coast and address whether their magnitude and location vary as a function of species' taxonomy, pelagic larval duration and depth distribution. We observed clusters of species boundaries at Cape Hatteras, Cape Cod and the Bay of Fundy that are largely independent of taxonomic group. However, the boundaries were permeable and asymmetric, with a higher percentage of species shared across boundaries in the equatorward direction (82%) than in the reverse direction (59%). This pattern was particularly strong for shallow species (median occurrence depth < 20 m). Pelagic larval duration was more important to explain distributions of boundaries for deep species (median occurrence depth > 20 m), where species with long larval dispersal had significantly higher occurrence of boundaries than species with short larval dispersal. When they do exist, species boundaries seem to be set by the interaction of currents, depth distribution and pelagic larval duration. Importantly, species boundaries tend to be pinned to regions of reduced water transport, which might explain why species boundaries are concentrated in narrow geographical areas.

The processes that affect the location of biogeographic boundaries are important to predictions of how the distribution and codistribution of species might change in response to climate change (Parmesan et al. 2005) or to predict the spread of invasive species (Byers and Pringle 2006, Pringle et al. 2011). Species boundaries can be determined by changes in environmental factors that affect physiology and dictate the optimal niche for a particular species (Lee et al. 2009), but also by biotic interactions such as competition (Wethey 2002) or predation (Holt and Barfield 2009). However, in regions where many species boundaries coincide, it is more likely that abrupt changes in environmental conditions or direct barriers to dispersal can explain species distributions. The literature on the mechanisms that control species boundaries has been growing in recent decades (Holt and Keitt 2005, Gaston 2009), but there is a bias toward studies in the terrestrial environment (Parmesan et al. 2005). Even though similar mechanisms may produce boundaries in terrestrial or aquatic systems, there are important differences for species that exhibit passive dispersal by means of propagules (such as seeds, spores, eggs or larvae). Because the directional component of dispersal can be stronger in marine or riverine systems and the dispersal distances are larger, it is more likely that fluid dynamics can generate range boundaries in these systems (Gaylord and Gaines 2000, Kinlan and Gaines 2003).

In the case of marine biogeographic boundaries, the effects of temperature and currents are hard to separate because changes in the ocean circulation are often associated with abrupt changes in temperature. New insights to separate the effects of correlated environmental factors on species distributions can be gained by analyzing the permeability of biogeographic boundaries to species with different characteristics (Wares et al. 2001, Gaines et al. 2009). Species traits that are more likely to be affected by currents can help to distinguish whether currents or temperature could be more important (Wares et al. 2001, Gaines et al. 2009). An important trait that can influence the location, as well as permeability, of boundaries is larval duration. In many marine species that have a pelagic larva in their life cycle, the larvae can be in the water weeks or months; and due to this long larval duration, the distribution of larvae in these species can be affected by currents.

Theoretical models demonstrate the potential of ocean currents to create range boundaries by affecting larval transport and the importance of larval duration in determining the fate of populations and the location of range boundaries (Gaylord and Gaines 2000, Byers and Pringle 2006, Gaines et al. 2009). These models, developed for species with pelagic larva along a linear coastline, showed that range boundaries can occur when there are two convergent or two diverging currents at a point on the coast, when a current diverges offshore, or when there is a retention zone (Gaylord and Gaines 2000, Byers and Pringle 2006). Currents may generate a boundary by exporting larvae offshore and reducing the alongshore transport of larvae, while a retention zone generates a boundary because it is a region with reduced currents and reduced larval transport of potential competitors from upstream. In each case it is the effective reduction of larval input from upstream that allows a boundary to form, and these boundaries should be more evident in species with long larval duration. Thus, if a biogeographic boundary is imposed primarily by currents, we would expect a higher proportion of range boundaries for species with pelagic larva and long larval durations.

Another significant, yet poorly explored attribute that may influence boundaries in marine organisms is depth distribution. The factors that limit distributions of intertidal or very shallow water species may be different than those that limit organisms in deeper water (Jackson 1974, Roy et al. 1995, Jones and Quattro 1999, Marko 2004). Since different water conditions (e.g. temperature, salinity) can be found at different depths, individual tolerances that drive changes in the location of species boundaries along the coast will also be affected by depth distribution (Roy et al. 1995). Additionally, depth distribution could affect the alongshore dispersal of larvae when the strength of currents changes with depth (Lentz 2008). Conversely, the processes that drive inner shelf transport, such as tides or cross-shelf wind stress (Lentz and Fewings 2012) may be more important for shallow species. In this context, we could predict that species inhabiting different depths of the continental shelf that release pelagic larva could show different distribution of range boundaries.

The increase in the availability of georeferenced data in recent years has the potential to help in the analysis of range boundaries for a vast number of species. In this study, we use occurrence data from the Global Biodiversity Information Facility (GBIF) to determine species distributions and to identify sites with a high frequency of range boundaries of marine benthic invertebrates along the northwestern Atlantic coast. We address whether the magnitude and location of range boundaries vary as a function of species' taxonomy, pelagic larval duration and depth distribution to widen our understanding of the factors regulating distribution of species. The northwestern Atlantic coast includes different oceanographic regimes that will allow us to explore some of the hypotheses proposed to explain the spatial distribution of species boundaries. Along this region there are also important differences in the width of the shelf, which could reflect habitat availability for benthic invertebrates.

Since range size and range boundaries have been shown to exhibit phylogenetic conservatism in marine mollusks (Jablonski and Hunt 2006, Roy et al. 2009), it is important to consider our questions in different taxonomic groups with some attempt at phylogenetic independence among data. Consequently, we compared the distribution of boundaries for five phyla: mollusks, arthropods (crustaceans), annelids, cnidarians and echinoderms. If we find similar patterns of range boundaries across different taxonomic groups, it is likely that current environmental pressures are an important force to maintain species boundaries.

We show that locations at two major (and classically recognized) biogeographic breaks along the northwestern Atlantic coast act as strong asymmetric boundaries, with a higher percentage of species distributed across the observed boundaries going from the poles to the equator than in the reverse direction. Furthermore, we show that species that differ in their depth distribution and type of larval dispersal are differentially affected by the boundaries. The variation between groups suggests the potential mechanisms that can explain the distribution of boundaries in each group.

Methods

Study area

The general pattern of circulation along the northwestern Atlantic coast is schematized in Fig. 1.The flow in the Gulf of Maine (Fig. 1) is basically southwest-ward, with an estimated transit time of 55 d between the Bay of Fundy and the Great South Channel in Cape Cod (Manning et al. 2009). The Bay of Fundy and Nantucket shoals (Fig. 1) are zones of increased retention and thus reduced larval input from upstream (Aretxabaleta et al. 2008, Manning et al. 2009); these areas thus have a higher probability of retaining locally produced larvae (Byers and Pringle 2006, Pringle and Wares 2007). From Cape Cod to Cape Hatteras the flow in the Mid Atlantic Bight region (Fig. 1) is uniformly towards the south, weaker towards the coast and near the bottom, and fastest at the shelf break (Lentz 2008). The water of the Mid Atlantic Bight region converges with the water of the South Atlantic Bight region at Cape Hatteras generating the 'Hatteras Front' (Fig. 1), driving offshore transport in the Cape Hatteras region and creating a strong alongshore gradient in temperature, salinity and density. In the South Atlantic Bight region (Fig. 1) the Gulf current flows northward before deflecting to the northeast at Cape Hatteras (Lee et al. 2009). The width of the shelf decreases from north to south (Fig. 1). However, north of Cape Cod in the Gulf of Maine, there is a large area with depths between 100 and 300 m inshore of the shelf break, but the width of the shelf shallower than 50 m is very small (light blue in Fig. 1). South of Cape Cod the shelf break is at about 100 m, and the shelf break shallows to about 50 m at Cape Hatteras (Fig. 1). As a result, availability of shelf habitat deeper than 50 m decreases to the south (blue in Fig. 1).

Species distribution database

To compile a database with geographic ranges of benthic marine invertebrates along the east coast of North America we used occurrence data to estimate each species' alongshore range. Species occurrence data were extracted from the Global Biodiversity Information Facility in July 2013 (GBIF, < http://data.gbif.org/welcome.htm >). GBIF is an international open data infrastructure that provides a single point of access to different databases in a network of more than five hundred institutions all over the world. This generates a large but heterogeneous database that combines all the reported occurrences for a particular species, collected by different

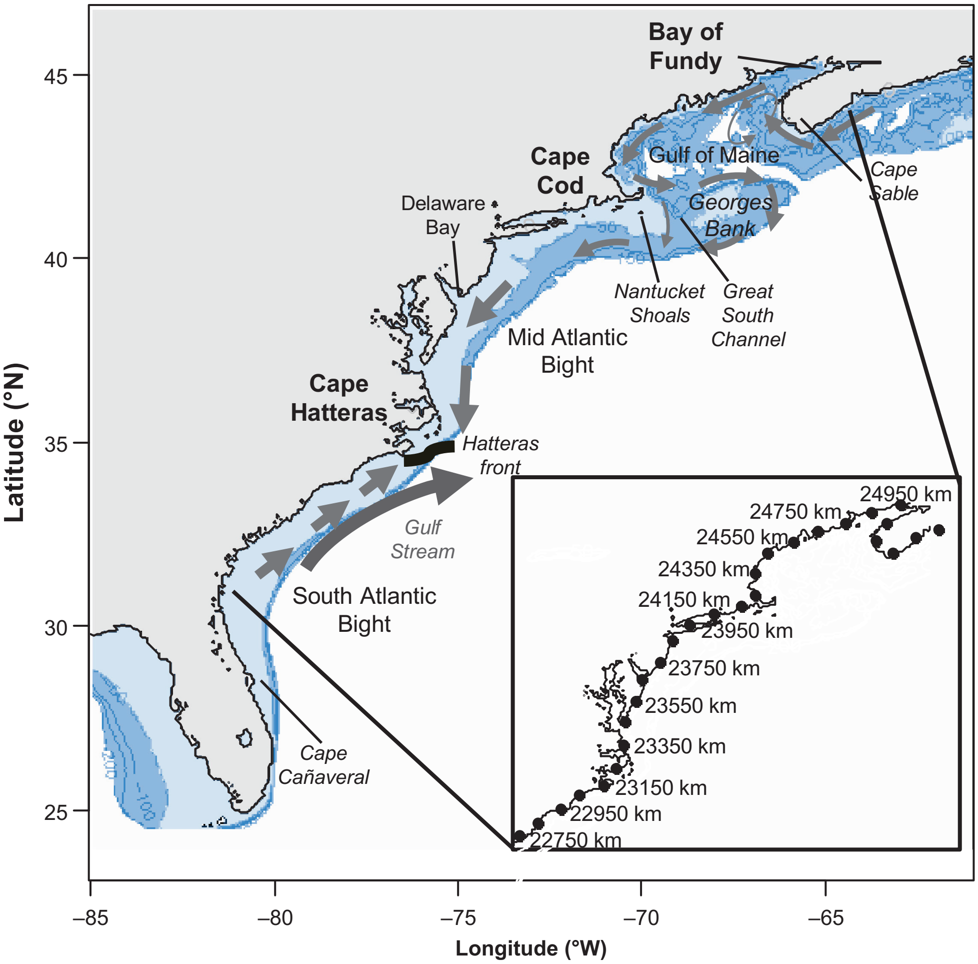

Figure 1. Pattern of circulation in the study area; the arrows schematize the mean flow. Light blue indicates shelf area shallower than 50 m, blue indicates the shelf area between depths of 50 and 200 m. Colored lines represent the isobaths every 50 m. The insert shows the points that were used for the estimation of range boundaries and the associated distance in km along the coastline.

institutions, using different methods. Despite the heterogeneous sources, this type of data can be useful to estimate area of distribution of a species. The records span from 1900 to recent years, and are constantly updated. Because there are small problems (like any other heterogeneous large database) we verified and filtered the occurrences downloaded from GBIF, and also compared a subsample with distribution from another source, but overall we believe that this type of large scale data provides valuable information.

We initially downloaded occurrence data for the entire western Atlantic coast drawing a path along the coastline using ETOPO1 1 arc-minute global relief model of Earth's surface (Amante and Eakings 2009, <www.ngdc.noaa.gov/mgg/global/>). This path consisted of a vector of distances (in km) with a zero starting point in Tierra del Fuego (54.67°S–65.17°W, Argentina) at the southern tip of South America to Lacy Island in North America (60.67°N–64.58°W, Canada). All occurrence data in GBIF cells over ocean depths <2000 m were downloaded and assigned to the nearest point in the path. Each occurrence was assigned an alongshore location based on the closest coastline point. We estimated depth of the occurrences from the ETOPO1 1 arc-minute bathymetry and calculated the minimum, maximum and median depth for each species. We used taxonomic filters to exclude pelagic species, birds, microorganisms, algae and components of the holoplankton (e.g. fish, cephalopods). We also double checked species with $>50\%$ of occurrences above sea level to discover if they were intertidal species or freshwater or terrestrial species not detected by the taxonomic filters that we could then manually exclude. Marine occurrence data can appear to be on land due to the finite resolution of the occurrence and bathymetric data.

Taxonomic information for all the species included in the occurrences database was downloaded from GBIF and verified with ITIS (Integrated Taxonomic Information System, < www.itis.gov/ >). After applying the initial taxonomic and sea level filters we ended up with 2543 species inside the study area (described below). Of these species, 240 were synonyms, not currently valid, and were reassigned to the accepted name of the species as of July 2013 following WoRMS (World Register of Marine Species, Appeltans et al. 2012). Synonyms were resolved using ITIS, WoRMS (Appeltans et al. 2012) and Malacolog (Rosenberg 2009) databases. After another thorough revision, we dropped 407 more species because they were terrestrial, freshwater or deep-sea species. The final number of species ($n = 1896$) detailed by taxonomic composition are presented in Table 1.

Table 1. Taxonomic groups considered in this study and information of occurrences and data available within the study area: number of species, total number of occurrences (range per species within parenthesis), mean number of occurrences per species, and the number and percentage of species with information on type of larval dispersal for each group.

Phylum	Number of species	Number of occurrences	Mean number of occurrences	Information on type of larval dispersal (%)
Mollusca	625	115 119 (25–2475)	184.3	227 (36.3%)
Arthropoda (crustaceans)	492	86 432 (25–4969)	175.7	382 (77.6%)
Annelida	456	114 748 (25–3140)	251.6	56 (12.3%)
Echinodermata	90	17 504 (25–1695)	194.5	39 (43.3%)
Cnidaria (anthozoans)	107	11 483 (25–713)	107.3	4 (3.7%)
Chordata (ascidians)	44	5328 (25–536)	121.1	8 (18.1%)
Porifera	45	30 238 (25–489)	67.18	1 (2.2%)
Bryozoa	37	5027 (26–594)	135.9	1 (2.7%)
Totals	1896	358 714		718 (37.8%)

Information on larval development and time of pelagic larval duration for each of 718 species was compiled from the literature (Table 1). All peracarid crustaceans included (orders Amphipoda, Cumacea, Isopoda, Mysida and Tanaidacea) exhibit direct development; for the rest of the species the references used to infer larval development are detailed in the Supplementary material Appendix 1, Table A1. In most cases, information was collected to the level of species (92.3%), with a small number of cases where information was assumed to genus (4.3%) or family (3.4%) level (Supplementary material Appendix 1, Table A1).

We found an extremely low amount of data reported in GBIF along the western Atlantic coast for South and Central America (Supplementary material Appendix 1, Fig. A1A); the Caribbean islands and the Bahamas were excluded in our search. Since the region from the Texas/Mexico border to Cape Breton (Canada) is well sampled we only included the occurrences within that region for the estimation of range boundaries. That means that one or both (if a species is present throughout the region) of a species' boundaries can coincide with the limits of this Texas/Mexico and Cape Breton area. Since this truncation introduced spurious boundaries at Texas/Mexico and Cape Breton, we did not analyze those boundaries and restricted the results and discussion to a smaller, central region extending from the north of Cape Canaveral to Cape Sable (Fig. 1).

Each GBIF occurrence was weighted by the density of all occurrences of marine species in our database, 1/(occurrences/km along the path), to obtain an unbiased estimator that compensates for sampling effort; we assumed this density is a proxy for sampling effort. More details on how we estimated sampling density are given in the Supplementary Information (Supplementary material Appendix 1, Fig. A1). We included only species with a minimum number of 25 occurrences for the estimation of range, and truncated 1.5% of the weighted-occurrences from each end of the range to avoid extreme reports that may not represent the extent of the viable population. Thus, the species range was computed as the alongshore distance which encompasses the central 97% of the weighted-occurrences for each species within our study area. The poleward and the equatorward limit of distribution estimated for each species was included in the database (expressed in km along the path). We show in the supplementary material how changing these assumptions regarding sampling density functions, minimum number of occurrences, and the level of tail truncation produces qualitatively similar results (Supplementary material Appendix 1, Fig. A2). We also compared the alongshore ranges estimated from the occurrence data with published latitudinal ranges and found a good match with our analysis (Supplementary material Appendix 1, Fig. A3).

Data analysis

We calculated the spatial distribution of poleward (northern) range boundaries and equatorward (southern) range boundaries every 100 km along the coast for all the species with a boundary in the study area (inset in Fig. 1). For each (100 km) segment we calculated the frequency of range boundaries by dividing the number of species with boundaries by the total number of species present in that segment. The analysis was repeated within depth and larval dispersal subgroups; the frequency reported is the frequency within the subgroup.

Species were classified as shallow (< 20 m) or deep (> 20 m) based on the median depth of occurrences inside the study area. Given the focus on coastal species, we did not include a species if $> 25\%$ of its occurrences were deeper than 200 m. The median depth of species was bimodal, with most species' distribution median deeper than 50 m or shallower than 20 m (Supplementary material Appendix 1, Fig. A4). Thus our results were not sensitive to the exact threshold separating shallow and deep.

'Short' dispersal includes those species with no pelagic larval phase (direct development), or species with a pelagic larval duration ≤ 3 d. 'Long' dispersal includes species with a pelagic larval duration > 3 d. We choose the boundary at 3 d because this is a typical value of the Lagrangian decorrelation time scale in the coastal ocean (Brink et al. 2003, Siegel et al. 2003) but our results are not sensitive to the exact choice because most larvae have either relatively short or long dispersal modes (Shanks 2009, more details in the Supplementary material Appendix 1). Because depth classification (shallow or deep) had an important effect on location of range boundaries we conducted the analysis of type of larval dispersal separately for each depth group.

To compare the distribution of range boundaries between taxonomic groups we calculated Pearson's correlation coefficients between the frequency of boundaries and the alongshore distance vector separately for northern and southern limits, for each taxonomic group. To compare between the frequency of northern and southern boundaries and between the different categories of larval dispersal and depth, we calculated the binomial confidence interval for each sampling point using the function binom.confint in the package binom (Dorai-Raj 2009) of the R program (R Core Team). Peaks in frequency of boundaries along the coast were defined as where the 1 STD error bar at a particular location does not overlap those at locations on each side. The occurrence of peaks at identical locations in different taxonomic groups strongly suggests that the observed peaks are not due to statistical subsampling effects. We tested if two frequencies at a given location are significantly different with $p < 0.05$ using a Chi Square test implemented in R (R Core Team).

Results

Taxonomic group

The final database included information on range boundaries for 8 phyla and 1896 species within our study area (Table 1). As the number of occurrences and number of species was low for ascidians, poriferans and bryozoans (Table 1), we performed the full analysis only for molluscs, crustaceans, annelids, echinoderms and cnidarians (1770 species). The frequency of both the northern and southern boundaries did not differ by the taxonomic group with the exception of annelids, which had very low correlations with the other groups (Supplementary material Appendix 1, Table A2, Fig. A5). For that reason, in the following sections we report all species pooled together; in the Supplementary material we reported the distribution of range boundaries deconstructed by median depth (Supplementary material Appendix 1, Fig. A6) and by type of dispersal (Supplementary material Appendix 1, Fig. A7) for the different taxonomic groups.

Species boundaries

The location and frequency of range boundaries differed depending on whether the boundary was setting a northern or southern limit for a species (Fig. 2A) or whether the species were classified by depth distribution or type of dispersal (Fig. 3). For all the species pooled together, the frequency of northern boundaries along the coast exhibited peaks near Cape Hatteras, Cape Cod and Bay of Fundy, while the frequency of southern boundaries only exhibits a peak at Cape Cod (Fig. 2A). The frequency of northern boundaries was significantly higher than the frequency of southern boundaries in all the mentioned locations. The number of species included in our study increased towards the equator, mirroring larger patterns of species diversity (Hillebrand 2004) (Fig. 2B).

Depth distribution

The distribution of range boundaries deconstructed by median depth differed between shallow and deep shelf species (Fig. 3 left panel), but was similar between taxonomic groups with the exception of annelids (Supplementary material Appendix 1, Fig. A6). Both shallow and deep species exhibited high frequency of northern boundaries (Fig. 3A), but only deep species showed multiple peaks of southern boundaries (Fig. 3B). The region south of Cape Hatteras showed a significantly higher frequency of northern boundaries for deep species, while Cape Cod and Bay of Fundy showed the opposite pattern, with a higher frequency of northern boundaries for shallow species (Fig. 3A). Southern boundaries of deep species were concentrated north of Cape Hatteras, Delaware Bay and Cape Cod (Fig. 3B). The number of shallow species decreased from south to north, while the number of deep shelf species decreased from the tropics to Cape Hatteras, increased slowly towards Cape Cod, and decreased north of Cape Cod (Fig. 3C). Species ratios between shallow and deep species switched south of Cape Cod (Fig. 3C).

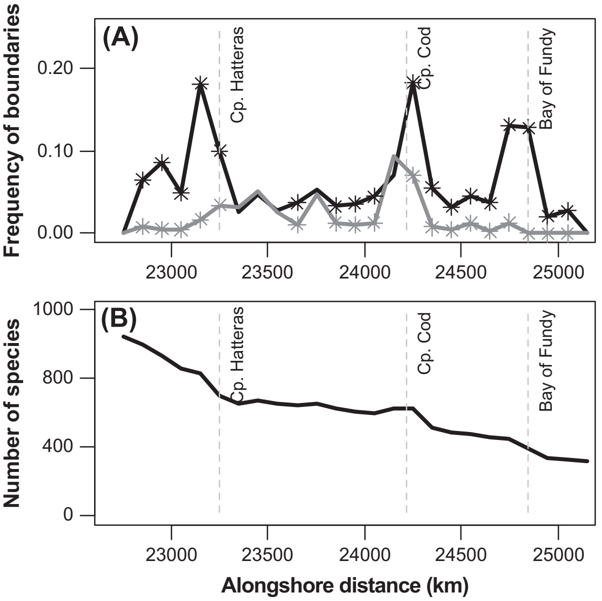

Figure 2. Distribution of range boundaries and number of species included in this study. (A) Frequency of northern (black) and southern (gray) range boundaries for all the species within the study area; the asterisks indicate the locations in which northern and southern boundaries differ significantly ($p < 0.05$). (B) Number of species along the study area. Alongshore distance increases in a poleward direction. Vertical dashed lines indicate geographic references; Cape Hatteras and Cape Cod are recognized biogeographic boundaries (as per Wilkinson et al. 2009).

Type of larval dispersal

We were able to classify 37.8% of the species in our database according to the duration of the pelagic phase; since crustaceans, echinoderms and molluscs had more information we limited the larval dispersal analysis to those groups (Table 1). There were significant differences in the frequency of boundaries between species with short or long dispersal in both the shallow and deep species (Fig. 3 right panel). The frequency of northern boundaries was higher for species with long dispersal compared to species with short dispersal at Cape

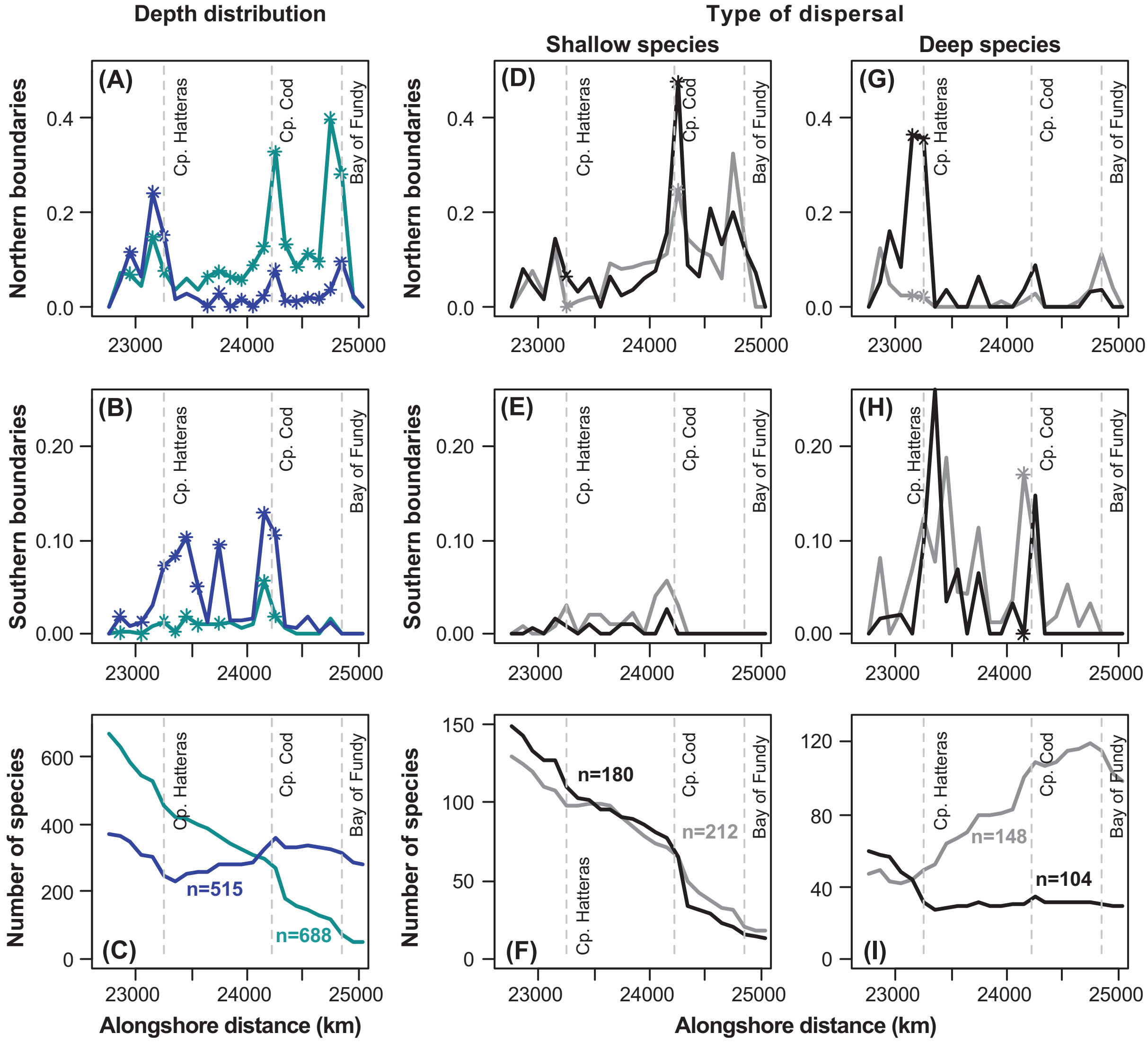

Figure 3. Distribution of range boundaries and change in number of species along the study area for species classified by depth distribution and type of dispersal. Left panel: frequency of northern (A) and southern (B) boundaries and the number of species (C) for shallow (cyan, median depth < 20 m) and deep (blue, median depth > 20 m) species. Note the different scaling of panels (A) and (B). Right panel: frequency of northern (D, G) and southern (E, H) boundaries and number of species (F, I) for species with short (gray) and long (black) dispersal. The frequency of boundaries for short (pelagic duration ≤ 3 d) and long dispersal (pelagic duration > 3 d) was calculated separately for shallow and deep species. The asterisks indicate the locations in which the frequency of boundaries of each group differs significantly ($p < 0.05$). Number of species in each group is indicated in the plot of the number of species (C, F, and I). Alongshore distance increases in a poleward direction. Vertical dashed lines indicate geographic references.

Cod for shallow species (Fig. 3D) and at Cape Hatteras for deep species (Fig. 3G). The frequency of southern boundaries for deep species (Fig. 3H) at Cape Hatteras showed a higher frequency of range boundaries for species with long dispersal than for species with short dispersal (the difference was not significant, $p = 0.06$). We observed changes in the number of species along the coast between the two types of larval dispersal. Within the shallow species, the number of species with long and short dispersal showed a similar increase in the number of species towards the tropics (Fig. 3F). However, within the deep species, the number of species with short dispersal increased toward the pole, while the number of species with long dispersal decreases towards Cape Hatteras and then remained fairly constant (Fig. 3I).

Discussion

Patterns

In a comprehensive study of almost 1800 benthic invertebrates along the northwestern Atlantic coast, we observed clusters of species boundaries at Cape Hatteras, Cape Cod and the Bay of Fundy that are, for the most part, indistinguishable between taxonomic groups. This suggests that these boundaries are shaped by underlying environmental and biological dynamics that are independent of the phylogenetic history of each taxon. This is not to deny that phylogenetic conservatism of range boundaries can be important on larger scales (Roy et al. 2009); however, at the smaller scale that defines the location of individual boundaries in advective systems like the coastal ocean, it seems that contemporary conditions dominate. This leads us to examine what contemporary mechanisms shape the boundaries of species ranges and biogeographic provinces.

In the vast majority of biogeographic boundaries shown in Fig. 2A and 3, there is a larger fraction of poleward boundaries (i.e. the northern-most extent of a species range in our study area) than equatorward boundaries (i.e. the southern-most extent of a species range in our study area). This pattern has been observed previously on the Californian coast of the eastern Pacific (Roy et al. 1995, Gaines et al. 2009) and at Cape Cod in estuarine communities (Engle and Summers 1999). The asymmetry of the boundaries is quite high in our study with 82% of the species that exist poleward of the boundaries persisting equatorward of the boundaries and 59% the other way around. This difference could be explained by a mechanism able to generate asymmetric boundaries, such as currents (discussed below in 'Pattern of circulation'), but is in part the result of the latitudinal gradient of species richness. Because the number of species decreases going towards the poles, one must find more poleward range boundaries than equatorward range boundaries. The origin of increased species diversity in lower latitudes has been much discussed, for both terrestrial and marine systems (Willig et al. 2003, Krug et al. 2009, Wiens 2011), but is outside the scope of this work.

The biogeographic boundaries are not only asymmetric, they are highly permeable. In Fig. 2A and 3 only a few tens of percent of the species have boundaries at any one location. Our largest-magnitude boundary was 48% (for the northern boundary at Cape Cod in shallow species with long dispersal, Fig. 3), meaning that 52% of species in this region move through this boundary apparently unimpeded. This is consistent with the findings of Gaines et al. 2009 along the Californian coast. Yet, in the studies that report the frequency of total boundaries without differentiating between northern and southern boundaries, the number of species stopped at a particular boundary may be between 40 and 80% (Newell 1948, Roy et al. 1998, Macpherson 2003), obscuring that many species cross the boundaries. Importantly, the permeability of boundaries differs depending on the ecological attributes of the species, as we can see by the differences in the frequency of boundaries along the coast between groups (Fig. 3). This variation provides insight into how physics and biology interact to set species boundaries, and below we discuss the relative importance of temperature, currents and habitat to determine the location of range boundaries.

Mechanisms

Temperature

Species boundaries have often been assumed to be the location where a species can no longer tolerate the environmental conditions (Gaston 2003); however, terrestrial species have often been shown to under-fill the potential latitudinal niches that would be expected from their temperature tolerances. In marine systems, changes in water temperature associated with the limited window of thermal tolerance in marine ectotherms – whether affecting survival or reproductive capacity – have been used to explain large-scale patterns of species distribution (Hutchins 1947, Briggs 1974, Pörtner 2002, Sunday et al. 2012). If we assume that the spatial variation in boundaries is driven by sea water temperature, we would expect higher proportions of boundaries in regions with abrupt changes in temperature, with poleward limits most likely to be affected by the lowest temperature an organism can tolerate and equatorward limits by the highest temperature it can tolerate (Sunday et al. 2012). If northern range limits in the study area were imposed by the distribution of winter temperatures alone, we would expect peaks in northern boundaries at Cape Hatteras and Cape Cod where we observed a noticeable decrease in sea water temperature, but not at the Bay of Fundy where there is only a local minimum (black line in Fig. 4A).

To quantitatively explore the role of temperature we constructed a null model defined by published data on thermal tolerance (Peck and Conway 2000, Compton et al. 2007, Sunday et al. 2011) for marine invertebrates in the northern hemisphere (Supplementary material Appendix 1, Table A3). We used the minimum temperature tolerated to define the poleward boundaries, and maximum temperatures tolerated to define the equatorward boundaries. The poleward boundary of each species was defined as the northern-most location (within the limits of our study area) where the minimum climatological temperature calculated from historical water-temperature observations is greater than the minimum temperature the species can tolerate, and similarly for the equatorward boundary. Temperature data was obtained from hydrographic casts from the World Ocean Database (WODs) up to 2012. Because the available data on thermal

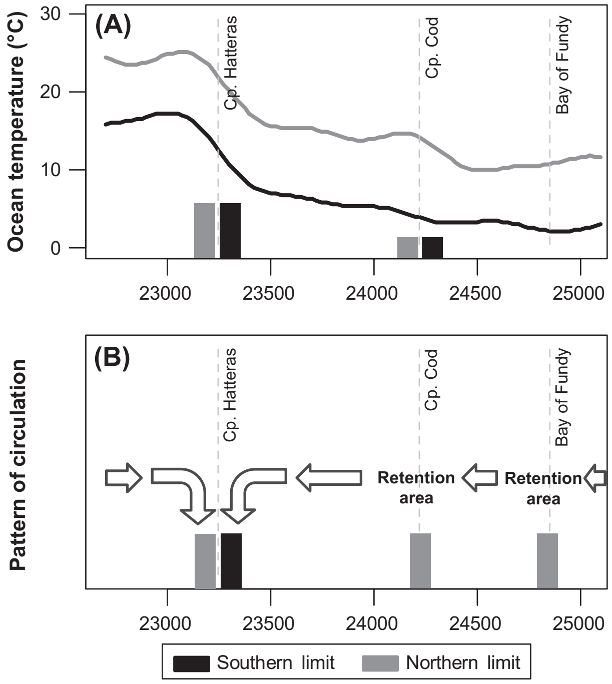

Figure 4. Hypothesized mechanisms that could drive the distribution of range boundaries. (A) Ocean temperature distribution along the coast. Average winter (black line) and summer (gray line) sea water temperature. (B) The arrows schematize the current directions along the coast. The rectangles represent locations of the expected boundaries.

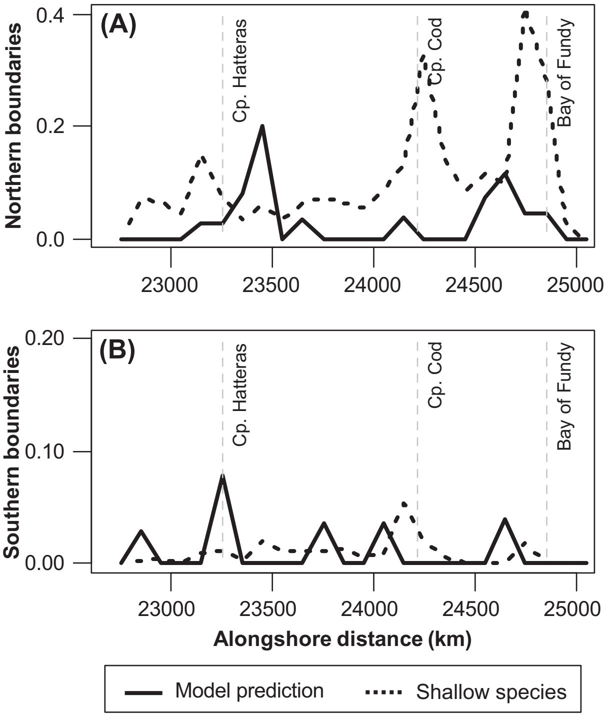

Figure 5. Distribution of the frequency of northern (A) and southern (B) range boundaries predicted by the null model of thermal tolerance. Solid lines are the distributions predicted by the null model, dashed lines show the distributions of boundaries found for shallow species. Alongshore distance increases in a poleward direction.

tolerance could be geographically biased, we focused on the expected location of boundaries and not the magnitude of the peaks. Predictions were limited to shallow species because of the availability of temperature tolerance data. We observed that the peaks in the frequency of northern and southern boundaries predicted from the temperature model do not match well with the observed peaks (Fig. 5); the temperature-predicted peaks in northern boundaries are shifted to the north of the observed peak by 300 km at Cape Hatteras. The major temperature-predicted peak in the Gulf of Maine is shifted to be between the observed peaks at Cape Cod and the Bay of Fundy, with a smaller peak near Cape Cod. Similar mismatches are observed with the southern boundaries. We are not claiming that temperature is unimportant to species ranges, as it likely sets the large scale fitness landscape, but other phenomena can shift species boundaries by hundreds of kilometers and concentrate them at particular locations (Endler 1977).

Pattern of circulation

If temperature alone was affecting species boundaries, we should find similar patterns between species that have short or long larval dispersal. But the higher proportion of northern range boundaries found for species with long pelagic larva (Fig. 3G, D) suggest that the pattern of circulation and directionality of currents are playing an important role to explain location of boundaries. Reductions in connectivity driven by ocean currents or retention zones could shift species boundaries from the maximum species range defined by environmental tolerances (Gaylord and Gaines 2000, Byers and Pringle 2006, Gaines et al. 2009) and create an excess of northern or southern boundaries, depending on the direction of the main currents. These regions will tend to attract species boundaries because the reduction in the larval transport of competing species from upstream will facilitate the establishment of a downstream species (Pringle and Wares 2007).

There are four locations within our study area that meet these criteria: Cape Hatteras, Cape Cod, Georges Bank and Bay of Fundy (Fig. 1). Cape Hatteras is an area of converging currents; the main flow offshore at Cape Hatteras where both currents converge reduces the larval transport around the cape because most water and larvae are transported offshore (Savidge and Bane 2001). There is a reduction in connectivity around Cape Cod (in Nantucket shoals) as most of the southward flow from the Gulf of Maine diverges from the coast at Cape Cod and flows either around Georges Bank or to the outer shelf (Pettigrew et al. 2005, Manning et al. 2009). In addition, there is enhanced retention around Georges Bank, but because the boundaries in our study were placed at the closest shore, any species boundaries on Georges Bank would be placed at Cape Cod. Finally, the Bay of Fundy is also a region of enhanced retention caused by persistent gyres at the mouth of and in the Bay (Aretxabaleta et al. 2008). Thus, to the extent that currents fix the exact positions of the range boundaries, we would expect an increased frequency of ranges boundaries at the Bay of Fundy, Cape Cod, and Cape Hatteras (Fig. 4B). This is consistent with what is observed (Fig. 2 and 3).

Nevertheless, we would expect to see currents more prominently affect species with long larval durations, whose larvae can be transported great distances by the currents, and less of an effect for species whose larvae spend only a short time or no time in the plankton (Wares et al. 2001, Byers and Pringle 2006). But because species with short larval durations also showed significant peaks at Cape Hatteras, Cape Cod and Bay of Fundy, other mechanisms are also likely to be involved. For example, using simulation models that explore the dynamics in riverine systems it has been shown that directional dispersal in the downstream direction could favor an inferior competitor in the upstream portion (Levine 2003). In the context of our study it is possible that in regions of reduced larval transport from upstream (such as just downstream from a cape), there are fewer propagules from upstream species competing for niche space, which would allow species to persist even though they might be competitively excluded just on the other (upstream) side of the cape. At this point this discrepancy remains a significant caveat to our conclusions, and suggests further areas of work.

Habitat

Another mechanism that can create biogeographic boundaries in some fraction of species is alongshore variation in habitat. At Cape Cod and along the shelf until Cape Hatteras, there is a higher fraction of southern boundaries than northern boundaries in the deep species (Fig. 3A–H). This excess of southern over northern boundaries is unique in our dataset, but perhaps reflects the change in the habitat available to deep species south of Cape Cod. To the extent that habitat area affects the number of species, this pattern could be explained by the fraction of the shelf between 50 and 300 m (dark blue in Fig. 1) that decreases markedly south of the Gulf of Maine, and then disappears towards Cape Hatteras. The impact of other potentially important changes in habitat type on species boundaries, such as from mud sandy bottoms and salt marshes in the Middle Atlantic Bight to high proportion of rocky shore in the Gulf of Maine (Wilkinson et al. 2009), must wait for further analyses.

Conclusions

Since 2000 there has been a reawakening in the need to delimit biogeographic units that allow for better conservation strategies, both in the terrestrial and marine realm (Olson et al. 2001, Lourie and Vincent 2004, Blanchette et al. 2008, Wilkinson et al. 2009). A better biogeographic resolution can help to define representative areas to focus conservation efforts or to design representative systems of protected areas (Olson et al. 2001, Spalding et al. 2007). Our analysis of 1770 species from five major invertebrate phyla both quantifies better the nature of species boundaries in the coastal ocean and illuminates the interacting biological and physical dynamics which maintain them at their current location. Comparing the expected distribution of species boundaries if they were determined solely by alongshore variation in temperature to the observed species boundaries did not produce a good match. Instead, we found that peaks in species boundaries were more likely to occur where there were oceanographic features that reduced alongshore larval transport or retained larvae. Species limits must be fundamentally set by their environmental tolerances (Pörtner 2002, Sunday et al. 2012), but these results suggest that the exact location of the species range boundaries are heavily influenced by oceanographic features, in particular, retention zones. This might explain why species boundaries are concentrated in narrow geographical ranges even while the physiological tolerances likely vary between species.

The observed asymmetry in species boundaries has important implications for the evolution of species communities as climate changes and species tend to shift their ranges towards the pole. Because many of the species that exist poleward of the boundaries persist toward the tropics, the poleward movement of tropical or temperate species is likely to involve fewer interactions between novel species than we might expect. Moreover, the responses to a warming ocean may be different than what is usually expected. Instead of species distributions shifting gradually towards the pole following the increases in ocean temperature as has been shown for some marine ectotherms (Parmesan and Yohe 2003, Sunday et al. 2012), our results suggest that in species that are strongly structured by the currents, we could see abrupt jumps spanning across one retention zone to the other. This is because the structure of currents is determined as much by bathymetry and large scale ocean structure as anything else and the locations where the temperature gradients are sharpest may remain fixed. Because we find that species boundaries tend to be pinned to oceanographic features, it suggests that monitoring for the shift of species ranges with a changing climate should focus on these locations.

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Supplementary material (Appendix ECOG-01135 at < www.ecography.org/readers/appendix >). Appendix 1.