Ocean currents and competitive strength interact to cluster benthic species range boundaries in the coastal ocean

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ABSTRACT: Dispersal of many coastal marine species is mediated by flows with strong directionality; bathymetric and topographic effects lead to strong alongshore variability in this transport. Using a simple model of the population dynamics of competing benthic species in a coastal ocean, we found that alongshore variability in dispersal can lead to clustering of species range boundaries for species whose dispersal is dominated by coastal currents. Furthermore, species can be absent from areas where they would have a relative competitive advantage because the presence or absence of a species is determined not only by local conditions but also by propagule supply, which is often affected by larval transport from far upstream. Our model demonstrates the quantitative linkages between alongshore variation in coastal currents, spatial gradients in competitive strength, and the geographic extent of a species. We show that the predictions of the model are consistent with observed species distributions in the Gulf of Maine and Mid-Atlantic Bight, USA. A mechanism for extensive coexistence of competing species where range boundaries cluster is described. The implication of the clustering highlighted by our model suggests that for species whose dispersal is dominated by long-distance planktonic periods, climate change induced changes in the relative competitiveness of species will lead to abrupt changes in species range boundaries and not gradual range extension.

KEY WORDS: Range limits · Drift paradox · Biogeography · Dispersal · Advection · Larvae

INTRODUCTION

Multiple factors contribute to setting the geographic range of a species. Principal among these are the interaction between the physiological tolerances of the species, the distribution of environmental conditions, and, for some systems, interspecific interactions, especially competition (Hutchins 1947, Case & Taper 2000; a summary of the terrestrial literature is in the introduction of Eckhart et al. 2011). Dispersal can modify how these interactions set the geographic range of a species; in systems where dispersal is not spatially biased (isotropic), it is primarily assumed to expand range boundaries by providing subsidy from regions of abundance, allowing the persistence of a species where it is less competitive (Gotelli 1991).

However, in many systems, dispersal is spatially biased (anisotropic). Spatially biased dispersal occurs in marine and similar systems (e.g. rivers, streams, terrestrial systems with wind dispersal) when dispersal is strongly influenced by currents or winds with a preferred directionality (Siegel et al. 2003). Gaylord & Gaines (2000) found that spatial variation in currents could keep competitively neutral species sepa-

rate. Byers & Pringle (2006) found that in the absence of inter-species competition, anisotropic dispersal can reduce a species range, shifting it downstream and increasing the fecundity necessary for a species to persist at any location. They emphasized that within marine systems, there are fluctuations in the flow driven by eddies or temporal variation in the winds that allow larvae to move 'upstream' against the mean currents, and emphasized the importance of these 'upstream' transports to population persistence. Here we build on the work of Byers & Pringle (2006) to include effects of interspecies competition.

We examined how environmentally driven gradients in relative competitiveness or fecundity of a species interact with alongshore variation in larval transport and retention to establish the upstream-most extent of its range. The result is a criterion for the maintenance of the upstream edge of a geographic range as a function of local circulation and the relative competeiveness of 2 competing species. This work extends previous studies by explicitly modeling the interaction between environmentally driven gradients in relative competitiveness or absolute fecundity and realistic downstream-biased dispersal (Gaylord & Gaines 2000 did not include competition; Case et al. 2005 only considered isotropic diffusion). The results will help us to understand what fixes species ranges in marine and other systems with downstream-biased dispersal, where competing species with biased dispersal can coexist, and how their distributions will respond to changes in climate.

In coastal oceans, clusters of species boundaries are often found to occur in regions where there are strong spatial gradients in water temperature. These clusters have been attributed to temperature tolerances and to the dependence of relative competiveness on temperature, and to the increased likelihood that the environmental limit of a species will be reached in a location where those environmental conditions are changing rapidly in space (Hutchins 1947). In explicit tests of the relative importance of environmental gradients (like temperature) and dispersal in fixing species ranges, neither alone receives overwhelming support (summarized by Gaines et al. 2009). We examined how alongshore variation in alongshore dispersal can create clusters of range boundaries on their own, and how the same circulation patterns that cause this variation will also lead to regions of enhanced temperature gradients. This will clarify how alongshore variability in currents can contribute to range boundaries directly, by altering dispersal, and indirectly, by altering the alongshore distribution of temperature.

As a test case, we used circulation data derived from surface drifters for the Gulf of Maine and the adjacent part of the Mid-Atlantic Bight, USA (Manning et al. 2009), to predict the location of clusters of upstream species boundaries. These predictions were compared to observed biogeographic patterns in benthic marine invertebrates. Benthic marine invertebrates, a group that dominates marine macroscopic biodiversity, provide an ideal test group in which to examine the interactions of environmental gradients and circulation. The adults are often sessile or have limited dispersal, and their dispersal is dominated by a larval stage. Available data encompass many phyla (e.g. Arthropoda, Mollusca, Echinodermata, Annelida) that contain many species with a planktonic larval stage in their life cycle for which dispersal is mediated by ocean currents (Strathmann 1987). Both the circulation and species distributions in this region are well studied, and the area contains several well-established biogeographic boundaries (e.g. Bay of Fundy, Cape Cod).

METHODS

Criterion for existence of upstream boundaries

Given complete knowledge of the population connectivity, habitat suitability, and relative competitiveness of 2 benthic species with planktonic dispersal, it would be straightforward to describe how they would interact to set each other's ranges. However, this knowledge is rarely straightforward to obtain (Connolly & Roughgarden 1999). Instead, we examined the statistics of larval delivery to a location to discover if that point could be the upstream-most range boundary for a given species in an advective environment. We focused on the upstream edge because once a species can persist at a point, its persistence farther downstream can be partly (and sometimes largely) driven by larval subsidies from upstream. Thus criteria are found for a local condition that allows the species to persist on a regional scale. We assumed that while environmental tolerances are ultimately defined by the limited adaptability of species, sensu Eckhart et al. (2011) and Sexton et al. (2009), the locations of their range boundaries within the region they can tolerate can be modified by dispersal and competition.

Two cases are considered: (1) two interacting species that have the same dispersal and produce the same number of larvae that eventually reach habitat, but which compete for habitat and have spatially

varying and different abilities to compete for the habitat. This case examines differences in relative fitness caused by post-dispersal processes including relative abilities in recruitment and growth compared to another species with which it shares resources (especially space and food); (2) two interacting species that compete equally for habitat once larvae reach suitable habitat but have different numbers of larvae which reach the habitat. This case examines differences in relative fitness caused by pre-settlement processes, including spatially differing production of larvae and spatial differences in larval mortality while in the plankton.

Thus, our 2 cases cover dynamics either pre-settlement or during and after settlement in systems with competition. The 2 cases are equivalent when dispersal is spatially unbiased (Sexton et al. 2009 and citations therein). However it is not clear that this should be so when currents spatially bias dispersal (e.g. anisotropic dispersal), because the effect of interspecies differences pre-dispersal might be shifted downstream by the spatially biased dispersal. For each case, a criterion will be developed for the persistence of the downstream species at and downstream of its upstream limit.

Case 1: Two species that differ during and after settlement

We assume a competitive interaction between 2 species such that the total population of the 2 species is set by the carrying capacity of the habitat, but the relative ability of each species to compete for the habitat is a function of location. The 'upstream' species is favored upstream of a location, and the 'downstream' species is favored downstream of that location. We also assume that individuals of both species produce the same number of larvae that survive dispersal and that could recruit and reproduce in the absence of density dependence and competition. A criterion is found for the minimum inter-species difference in competiveness at the upstream range boundary ('the boundary') of the downstream species to allow the downstream species to persist at that location. The downstream species does not exist upstream of the boundary.

The criterion is based on a single robust assumption about conditions at the boundary of the downstream species: for the downstream species to persist at the boundary, the fraction of its larvae that recruit to that location and survive to reproduce there (relative to all competing species' larvae that reach that location)

must be equal to the fraction of adults of the downstream species relative to competing adults of the other species at the boundary. This criterion exists because the relative frequency of the 2 species in the next generation at a location is set by the fraction of larvae that settle and survive to reproduce there. If the fraction recruiting and surviving to reproduce is less, the species fails to replace itself and the fraction of the downstream species at that point will continually decrease over generations until the point of local extinction. In the development below, generations are non-overlapping; the results are robust to deviations from this assumption. Overlapping generations were examined by Pringle et al. (2009), who found that persistence of the downstream species depends on the number of larvae that recruit and survive to reproduction over the adult lifetime. Thus the statements above apply when averaged over an adult's lifetime, weighted by recruitment in each reproductive event.

We parameterize larval delivery to the upstream boundary with 2 parameters: f_{ret}, the fraction of all competing larvae (of either species) returning to the boundary that originate at and downstream of the boundary, and f_{up}, the fraction that come from upstream of the boundary (and must, by definition, only include larvae of the upstream species). $f_{ret} + f_{up} = 1$, and these parameters can be estimated as below from knowledge of circulation (see the Supplement at www.int-res.com/articles/suppl/m567p029_supp.pdf [Section SI-1]), or could potentially be estimated from observations of larval settlement at the boundary (e.g. DiBacco & Levin 2000). We make a further limiting assumption that the dispersal parameters are the same for each species; this assumption is relaxed in the Discussion and in the Supplement (see Section SI-5) (cf. Lutscher et al. 2007, Salomon et al. 2010, Bode et al. 2011, Aiken & Navarrete 2014).

The larval delivery parameters f_{ret} and f_{up} are then used to understand the relation between the relative fraction of adults of different species at the boundary to the relative frequencies of the larvae of the different species arriving at the boundary (Fig. 1). At the boundary, the fraction of adults of the upstream and downstream species are P_{up} and P_{down}, so $P_{up} + P_{down} = 1$. The fraction of larvae reaching the boundary location (though not necessarily recruiting and surviving to reproduction) is L_{up} for the larvae of the upstream species, and L_{down} for those of the downstream species ($L_{up} + L_{down} = 1$). As assumed above, each species produces the same number of larvae per adult which survive dispersal. L_{up} is then $P_{up}f_{ret} + f_{up}$. $P_{up}f_{ret}$ is the product of the fraction of the upstream species in the downstream region, P_{up}, with the frac-
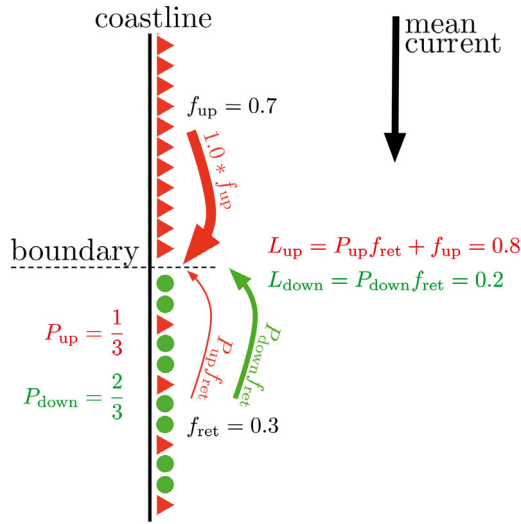
Fig. 1. Model and hypothetical numerical example of the maintenance of the upstream boundary (dashed line) of a species (green circles) against the effects of a mean current (black arrow) that transports most larvae downstream. The downstream species does not exist any farther upstream than this upstream boundary. The upstream species is represented by the red triangles. f_{up}: fraction of all larvae arriving to the boundary that were produced upstream of it, f_{ret}: fraction of all larvae arriving to the boundary that were produced at the boundary region as well as locations farther downstream. P_{up}: fraction of adults at and immediately downstream of the boundary composed of the upstream species, P_{down}: fraction of adults immediately downstream of the boundary that are of the downstream type. From these parameters, we can compute the fraction of larvae arriving at the boundary which consist of the upstream species (L_{up}) and the downstream species (L_{down}). The relative size of these larval deliveries is indicated by the thickness of the arrows, and the arrows are labeled with the term of the equations for L_{up} and L_{down} that each arrow represents (red: upstream species, green: downstream species)

tion of the larvae from that region, f_{ret}, and f_{up} is the product of the fraction of the upstream species in the upstream region (1.0) and the fraction of the larvae that arrive to the boundary from upstream, f_{up}. Likewise, the relative fraction of larvae of the downstream species at the boundary is $L_{down} = P_{down}f_{ret}$.

In a case where there is no difference in competitiveness between the upstream and downstream species, so each larvae has an equal chance to successfully recruit, the fraction of the downstream species in the next generation (P_{down}^{next}) will be proportional to the fraction of the downstream type in the larvae returning to the boundary (using $P_{up} + P_{down} = 1$):

$$P_{down}^{next} = \frac{L_{down}}{L_{down} + L_{up}} = \frac{P_{down}f_{ret}}{P_{down}f_{ret} + P_{up}f_{ret} + f_{up}} = P_{down}f_{ret} \quad (1)$$

Since f_{ret} must be <1 if there is any larval input from upstream, P_{down} must decrease each generation.

Thus without competitive differences, there can be no stable boundary between the 2 species if there is any larval input from upstream. As an example, in Fig. 1 we see that the fraction of the downstream species downstream of the boundary is 2/3, but only 20% of all larvae arriving at the boundary are of the downstream type (L_{down}). This is because many of the larvae arriving at the boundary are from upstream ($f_{up} > 0$) and of the upstream species and because some of the larvae arriving to the boundary from downstream are of the upstream type ($P_{up} > 0$). In the absence of any competitive advantage for the downstream type, this low return of downstream larvae would reduce the frequency of the downstream species to 20% over an adult lifetime; this frequency would continue to decline with time until local extinction of the downstream species.

However, if ΔC is the fractional increase in relative competitiveness, and a single larva of the downstream species is $(1 + \Delta C)$ more likely to successfully recruit and reach reproductive competency downstream of the boundary than a larva of the upstream species, we can re-write Eq. (1) as

$$P_{down}^{next} = \frac{(1+\Delta C)L_{down}}{(1+\Delta C)L_{down} + L_{up}}$$
$$= \frac{(1+\Delta C)P_{down}f_{ret}}{(1+\Delta C)P_{down}f_{ret} + P_{up}f_{ret} + f_{up}} \quad (2)$$

In this case, there can be a stable boundary. To find it, we set P_{down}^{next} to P_{down} in Eq. (2) to find a ΔC for which P_{down} does not change in time. Then by solving for ΔC in the limit that P_{down} approaches 0, we can find the minimum ΔC required for a boundary to persist:

$$\Delta C_{min} = \frac{f_{up}}{f_{ret}} = \frac{1 - f_{ret}}{f_{ret}} \quad (3)$$

Case 2: Two species that differ pre-settlement

Under this scenario, the species differ in the number of larvae that reach a habitat, but each larva is equally competitive for that habitat. The relative difference in the number of larvae produced per adult that can reach a given site is ΔR, such that the downstream species has $(1 + \Delta R)$ greater larval delivery per adult than the upstream species at the boundary. ΔR is chosen as the notation because one source of the difference in larval number could be spatially varying fecundity, but the difference could also be driven by differing mortality during dispersal. We can then write

$$L_{\mathrm{down}} = \frac{(1 + \Delta R) P_{\mathrm{down}} f_{\mathrm{ret}}}{(1 + \Delta R) P_{\mathrm{down}} + P_{\mathrm{up}}}$$

and   (4)

$$L_{\mathrm{up}} = \frac{P_{\mathrm{up}} f_{\mathrm{ret}}}{(1 + \Delta R) P_{\mathrm{down}} + P_{\mathrm{up}}} + f_{\mathrm{up}}$$

where L_{down} and L_{up} are normalized so that $L_{\mathrm{down}} + L_{\mathrm{up}} = f_{\mathrm{ret}} + f_{\mathrm{up}} = 1$, as above. Inter- and intraspecific competition leading to density dependence is assumed to be of the same intensity (sensu Case et al. 2005). The role of ΔR in aiding retention of the downstream species in the next generation can be expressed as:

$$P_{\mathrm{down}}^{\mathrm{next}} = \frac{L_{\mathrm{down}}}{L_{\mathrm{down}} + L_{\mathrm{up}}} = \frac{(1 + \Delta R) P_{\mathrm{down}} f_{\mathrm{ret}}}{(1 + \Delta R) P_{\mathrm{down}} + P_{\mathrm{up}}} \qquad (5)$$

which can be solved as above for the minimum ΔR required for a boundary to persist:

$$\Delta R_{\mathrm{min}} = \frac{f_{\mathrm{up}}}{f_{\mathrm{ret}}} = \frac{1 - f_{\mathrm{ret}}}{f_{\mathrm{ret}}} \qquad (6)$$

This result is identical to the previous case (Eq. 3), illustrating that, as in systems with isotropic dispersal, a change in either relative pre-settlement larval production and survival or relative post-settlement competitiveness have the same effect on persistence of an upstream species boundary (cf. Sexton et al. (2009) for similar results with isotropic dispersal). Hereafter, we shall treat these 2 cases as equivalent, and thus when we discuss the effects of spatial variation in competitiveness, it should be read to also apply to spatial changes in the relative fecundity/mortality of 2 species.

Population structure downstream of the range boundary

The criterion for the persistence of a downstream species at the boundary does not mean that a competitively inferior upstream species must have a downstream boundary at the same point. The upstream species, because it is supported by a larval subsidy from upstream, will exist for some distance downstream of the boundary before being vanquished by the competitively superior downstream species. This can be illustrated by re-writing Eq. (2) to be applicable downstream of the boundary (so P_{down} can be non-zero at farther upstream points) and in steady state (so P_{down} is the same from generation to generation). In these limits, where P_{down}^{n} is the population of the downstream species at location n

and n increases downstream, $L_{\mathrm{up}}^{n} = P_{\mathrm{up}}^{n} f_{\mathrm{ret}} + P_{\mathrm{up}}^{n-1} f_{\mathrm{up}}$ and $L_{\mathrm{down}}^{n} = P_{\mathrm{down}}^{n} f_{\mathrm{ret}} + P_{\mathrm{down}}^{n-1} f_{\mathrm{up}}$ and P_{down} can be solved iteratively from the upstream boundary with

$$P_{\mathrm{down}}^{n} = \frac{(1 + \Delta C) L_{\mathrm{down}}}{(1 + \Delta C) L_{\mathrm{down}} + L_{\mathrm{up}}} =$$

$$\frac{(1 + \Delta C) \cdot (f_{\mathrm{up}} P_{\mathrm{down}}^{n-1} + f_{\mathrm{ret}} P_{\mathrm{down}}^{n})}{f_{\mathrm{up}} P_{\mathrm{up}}^{n-1} + f_{\mathrm{ret}} P_{\mathrm{up}}^{n} + (1 + \Delta C) \cdot (f_{\mathrm{up}} P_{\mathrm{down}}^{n-1} + f_{\mathrm{ret}} P_{\mathrm{down}}^{n})} \qquad (7)$$

using $P_{\mathrm{down}} + P_{\mathrm{up}} = 1$ to solve for P_{up}. These solutions will be described further in the discussion.

Interpretation of criteria

If a species can persist at a point, the species will also persist downstream of the point where it has a relative competitive or fecundity advantage because loss of larvae downstream can be balanced by larval immigration from upstream. This can easily be seen from Eq. (7), where if the population of the downstream species exists at a point $(n-1)$ where it is favored, it must also exist at the next downstream point (n) as long as there is some larval input from upstream (i.e. f_{up} is not 0). Thus, the local condition in Eq. (3) for the persistence of an upstream-most species boundary is a regional condition for the persistence of a species where the time-averaged currents continue in the same direction (i.e. 'downstream' does not change direction).

Eq. (3) shows that as the fraction of larvae retained in a region f_{ret} increases (as one would expect for short larval duration), the relative competitiveness advantage needed for a species to have an upstream boundary at a location limits to 0. In this limit, the location of a species range boundary becomes controlled by where the relative fitness of competing organisms changes from favoring one to the other (ΔC changes from positive to negative, passing through 0). Thus, in the limit of very short larval duration and thus small dispersal, persistence is governed by local differences in relative competitiveness and the nature of dispersal becomes less important. This is similar to the results with isotropic dispersal (for example, for many terrestrial species), where the transition between ranges of competing species is, in the absence of other mechanisms to bias range boundaries, centered on where the relative competitiveness of the competing species changes from favoring one to the other species (Sexton et al. 2009).

There are subtleties that are concealed in the derivation of the criteria for Eq. (3). It is likely that the relative competitiveness between 2 species is a continu-

ous function of environmental conditions and thus a continuous function of location. However, in Eq. (3), we represent these parameters at the upstream boundary of a species range with a single competitive value. We should think of this single value as the average for those adults whose larvae are returned to the boundary. Thus ΔC is an average of the competitiveness difference over a spatial extent defined by the dispersal of larvae to the upstream boundary. In the Supplement (Sections SI-2 and SI-3), we show how this spatial extent can be quantified as a function of the observed larval dispersal for coastlines with simple geometries.

Nonetheless, from the point of view of the downstream species, an increase in larval retention (f_{ret}) decreases the competitiveness advantage or fecundity needed for its upstream range boundary to persist, while an increase in larval input from the upstream species (f_{up}) increases the competitive advantage needed for the boundary to persist. More generally than Gaylord & Gaines (2000), who used idealized coastal circulations and neutral species interactions, we find that even subtle alongshore variations in alongshore transport that increase the local retention of larvae or reduce larval input from upstream will increase the likelihood of a species boundary persisting.

Oceanographic data

To qualitatively test these criteria against observed species distributions, we must estimate larval dispersal and retention. This was done for the Scotian Shelf/Gulf of Maine region. The mean currents (Fig. 2) from the Scotian Shelf to Cape Hatteras are to the southwest, largely parallel to the coast (Lentz 2008). At Cape Cod, the coastal current diverges offshore, leading to a region of sluggish circulation in the Nantucket Shoals region (Manning et al. 2009). The Bay of Fundy is a well-known region of enhanced retention (Aretxabaleta et al. 2008, 2009).

Connectivity was defined by 911 NOAA drifters released from 1998 through 2013 from the Gulf of Maine to the Mid-Atlantic Bight (Manning et al.
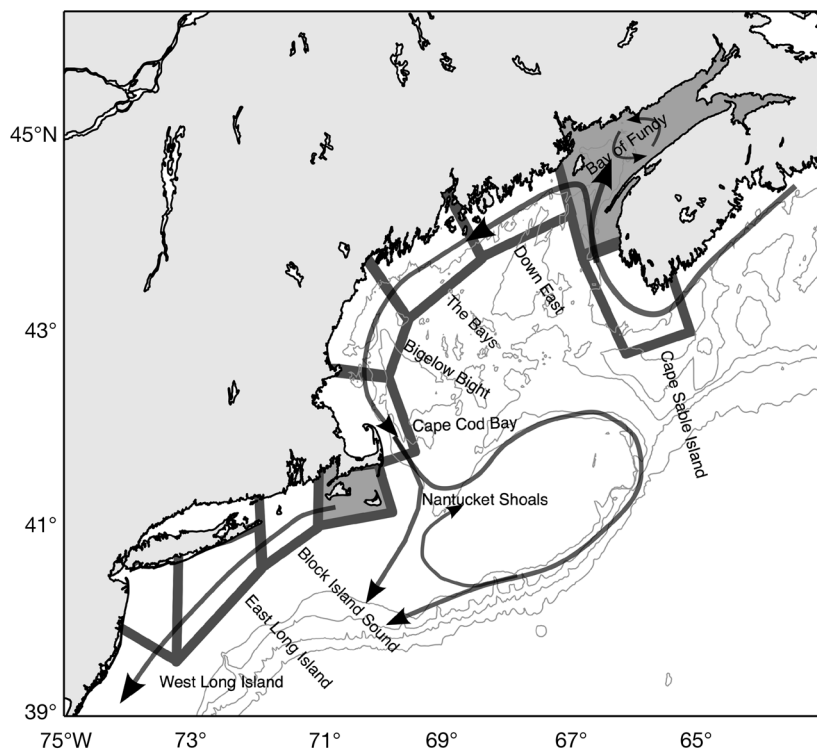

Fig. 2. Surface coastal currents (thinner lines + arrows) of the Gulf of Maine, bathymetry, and modeling regions (thick lines). The shaded regions are marine eco-regions where there is an enhanced number of northern range boundaries for species with long larval duration (Spalding et al. 2007, Pappalardo et al. 2015). The 100, 200, 1000, and 2000 m isobaths are shown

2009). Most drifters were drogued to 1 m depth and released in the spring or summer. The drifter tracks are shown as a function of region in Fig. S1 in the Supplement. A drifter is counted if it enters a region and is still functioning a time T later; if at that time it is in one of the regions, the 2 regions are connected. T is a proxy for the larval duration; because the drifters are at the surface where the currents are greatest and are without behavior, this is an upper limit of dispersal (Lentz 2008). A single drifter may define connectivity between multiple regions. Not all drifters that survive a time T connect regions; some drift out of any region, either downstream or offshore. These data are used to define a connectivity matrix **E** such that each element

$$\mathbf{E}_{ij} = n_{ij}/N_i \qquad (8)$$

where n_{ij} is the number of drifters that leave region i and a time T later are in region j and N_i is the number of drifters that leave region i and are still functioning a time T later. The resulting connectivity matrix is used to calculate f_{ret} (Fig. 3) for the regions shown in Fig. 2 and for a time in plankton T of 3 and 15 d. These planktonic durations are typical for short- and
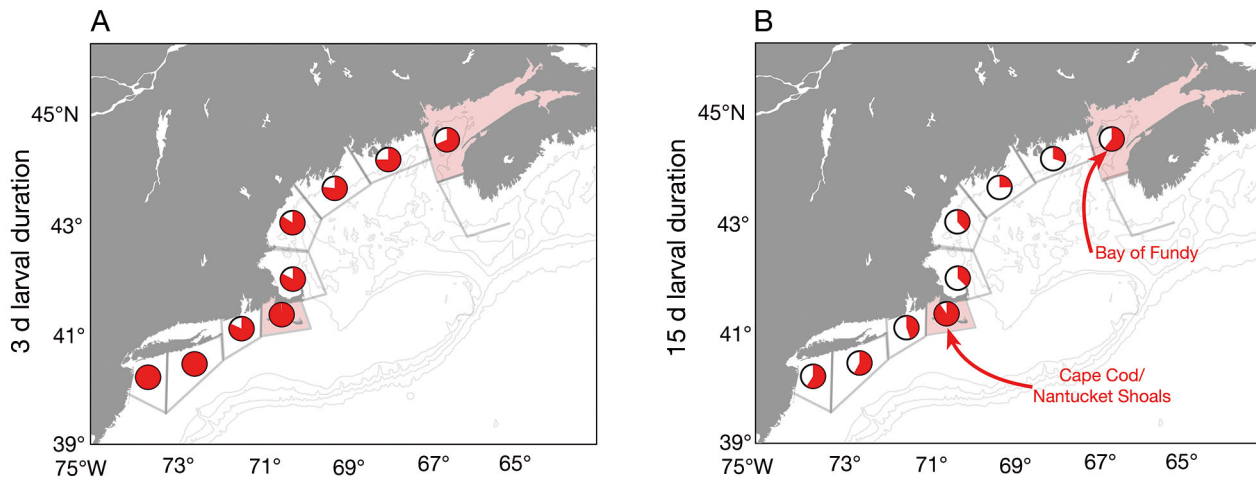
Fig. 3. f_{ret}, the fraction of larvae recruiting that originated locally and downstream relative to total recruitment, for a larval duration of (A) 3 d and (B) 15 d. A high proportion of red indicates a retentive location. The gray lines separate the marine ecoregions as shown in Fig. 2. No value for f_{ret} is shown for the Cape Sable Island region because f_{ret} cannot be calculated for the upstream-most region, since the data do not allow us to estimate the fraction of larvae settling there from even farther upstream. All fractions are estimated from surface drifter data

long-distance planktonic dispersers in the Gulf of Maine (Pappalardo et al. 2015). In the Supplement (Section SI-4), **E** is used to parameterize an inter-active population model illustrating the interaction of 2 competing species for a wider range of dispersal times (Fig. S4).

The alongshore temperature is used to compare alternative theories of range boundary maintenance below. The seasonal mean temperature from the World Ocean Atlas 2013 is extracted from points along the coast in the study region for the oceanographic summer (July, August, and September) and winter (January, February, and March) (Locarnini et al. 2013).

RESULTS AND DISCUSSION

The criteria developed above predict that in competing species, the downstream species can maintain its upstream boundary with a reduced competitive-ness differential (ΔC) where f_{ret}, the fraction of larvae recruiting that originated locally, is larger. Thus, all other things being equal, we would expect upstream species boundaries to cluster in regions of high larval retention (where f_{ret} is a local maximum). This prediction can be compared to the observations of Pappalardo et al. (2015) of enhanced numbers of upstream range boundaries in the Bay of Fundy and at Cape Cod for benthic marine organisms whose mean depth of occurrence is less than 20 m. These observed boundary clusters are asymmetric; they include many upstream limits for species, and fewer downstream limits.

In the analyses of longer larval duration (T = 15 d, Fig. 3B, longer durations in Fig. S4), there are clear local maxima in f_{ret} at the Cape Cod/Nantucket Shoals region, and in the Bay of Fundy. At Cape Cod, the coastal current diverges offshore, leading to a region of sluggish circulation and enhanced tidal mixing in the Nantucket Shoals region and reduced connectivity with upstream regions (Manning et al. 2009 and Fig. S1), and the Bay of Fundy is a well-known region of enhanced retention (Aretxabaleta et al. 2008, 2009). This is consistent with the observations of clusters of range boundaries for species with long larval duration (and thus presumably potential for long larval dispersal distances) in Pappalardo et al. (2015). These dynamics can be seen in the interactive population model presented in Fig. S4 at www.int-res.com/articles/suppl/m567p029_supp.html, where 3 variables can be manipulated: (1) the location and (2) magnitude of the change in competitive strength, and (3) the larval duration of the competing species. As predicted above, the location of an upstream boundary for competing species with long larval durations does not directly follow the location of the change in relative competitiveness. Instead, the boundary moves to the next downstream region of relatively high retention (the enhanced f_{ret} at Cape Cod and the Bay of Fundy) that is most nearly downstream of the point in space where a species starts to be competitively dominant again.

In the analyses of short larval duration (T = 3 d, Fig. 3A), there are no clear isolated maxima in larval retention f_{ret} at either Cape Cod or the Bay of Fundy, or elsewhere along the coast. This suggests that the

previously observed peaks in upstream boundaries for species with short larval duration in both regions (Pappalardo et al. 2015) is not driven by alongshore variation in retention. However, it is worth noting that at Cape Cod, the fraction of upstream boundaries is larger for species with longer larval durations than shorter, suggesting that the long-distance dispersers are more sensitive to this oceanographic feature (Pappalardo et al. 2015).

Clusters of range boundaries have also been explained by regions of increased gradients in water properties such as temperature. Essentially, the boundaries of a critical tolerance window for a given environmental variable is more likely to exist within

a region if the water properties change greatly within that region (Hutchins 1947). However, in the Gulf of Maine, temperature gradients can offer at best a partial explanation. In Fig. 4, the coastal temperature in winter and summer is presented. At Cape Cod, there is a localized dip in temperature at the cape that briefly interrupts a regional poleward cooling trend in both winter and summer, but it is limited to a 25 km stretch of shoreline and is associated with enhanced mixing in Nantucket Shoals (Limeburner & Beardsley 1982). It seems unlikely that a regional feature of such limited extent would set range boundaries for species with long larval durations, as it is smaller than the dispersal distance of these larvae (e.g. see dispersal estimates from Siegel et al. 2003, Pringle et al. 2011, and Fig. S1). We would expect larvae with long planktonic durations to be able to pass across it in both directions in each generation. Thus it is unlikely that the cluster of range boundaries at Cape Cod is explained by this localized anomaly in surface water temperature. The situation is somewhat different near the Bay of Fundy. Immediately poleward of the bay, near the southern-most extent of Nova Scotia, there is a sharp poleward drop in temperature in the winter, and a sharp poleward increase in temperature in the summer. These temperature transitions are associated with enhanced mixing in the bay and divergence of a portion of the alongshore flow where the Scotian Shelf enters the Gulf of Maine, and extend over the entire Scotian Shelf (Hannah et al. 2001, Aretxabaleta et al. 2008). While the seasonal reversal of the temperature change is unusual, one can create plausible scenarios for how it would anchor the upstream species boundaries (e.g. interacting sets of species whose relative fitness is more sensitive to winter than summer temperatures).

Nonetheless, the work above does not suggest that the regional alongshore gradients in temperature (or other water properties) are unimportant. The criterion given above in Eq. (3) requires a difference in competitiveness for an upstream species boundary to persist, and there must be some spatial variation in the difference in competitiveness for one species not to be more competitive everywhere (and thus to exist everywhere). Competi-
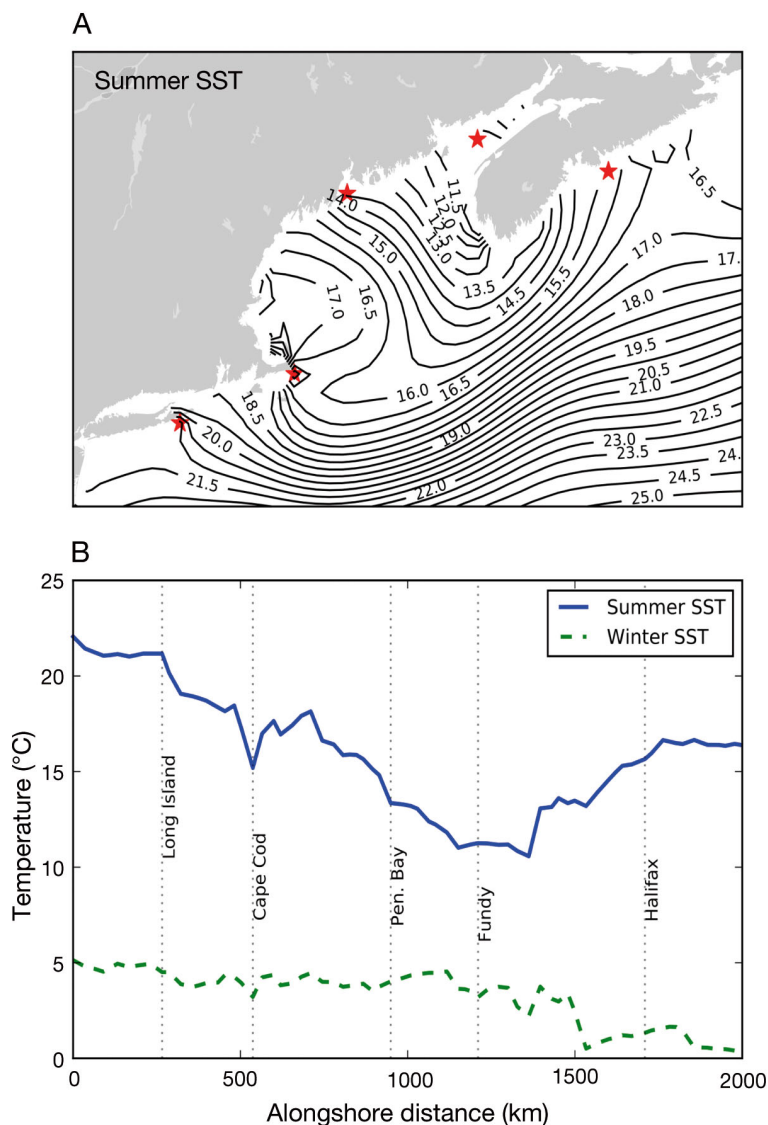

Fig. 4. (A) Summer surface temperatures (°C) from the World Ocean Atlas 0.25° dataset. Red stars mark locations labeled in panel B. (B) Seasonal average coastal surface temperatures along the coast for both winter and summer

tion is highly context dependent, and the spatial gradient in competitiveness could well be due to gradients in temperature, salinity, or other water properties that affect competitiveness.

Further, in most coastal oceans, there would be a strong correlation between enhanced larval retention and enhanced regional gradients in temperature. The Gulf of Maine is unusual in that much of its temperature structure is caused by regional variation in intense tidal mixing (Robinson & Brink 2006). In more typical coastal oceans, the alongshore variation in temperature is controlled in part by alongshore currents. This correlation is illustrated by a simple model of alongshore temperature variation which has proven successful in the Mid-Atlantic Bight, and which should be informative along many coasts in the absence of intense upwelling or tidal mixing (Lentz 2010). The model assumes that the temperature evolution of a parcel of water at the surface is simply the surface heat flux into the parcel, and the alongshore variation of temperature is given by the integral of the surface heat flux along the path of surface water. A necessary result of this model is that the alongshore gradient in temperature is proportional to (alongshore velocity)$^{-1}$, all other things being equal. This relationship occurs because the temperature of the parcel is changing at a fixed rate per time due to

surface heating or cooling — thus, the more slowly the parcel moves, the greater the spatial gradient in temperature. Therefore, anything that interrupts or reduces the alongshore transport of water parcels (simultaneously reducing the alongshore velocity of that parcel and thus increasing f_{ret}) will increase the alongshore temperature gradient. This suggests we would often expect the alongshore variations in retention and temperature to interact to concentrate the upstream range limits of many species at the same locations.

The species range dynamics described above also suggest a mechanism for the coexistence of species with different relative competitiveness. The population of the upstream species can remain substantial even well downstream of the point where a competitively superior downstream species can persist. This is illustrated in Fig. 5, where solutions to Eq. (7) are shown for an f_{ret} everywhere equal to 0.5 and a relative competiveness (ΔC) of 5, 50, and 100% greater than needed for the downstream species to persist; the upstream species remains present even where the downstream species exists. Thus, downstream-biased dispersal shifts the boundary of an upstream species downstream of where it ceases to be competitively superior; its abundance slowly decreases with increasing distance downstream of the transition.
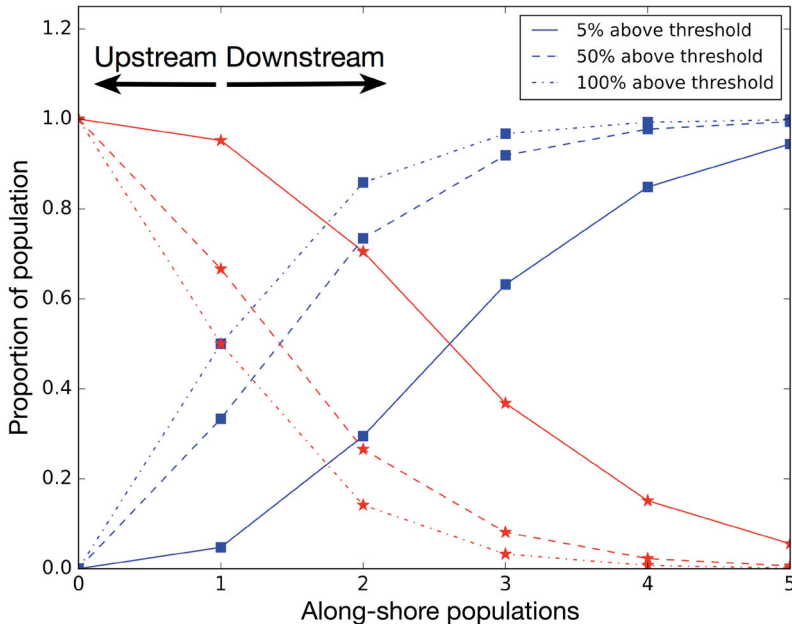
These results are consistent with the species boundaries documented by Pappalardo et al. (2015), where upstream species boundaries are more clustered than downstream boundaries. The ability of dispersal to maintain a species where it is competitively inferior has been described in the ecological literature (e.g. Gotelli 1991 and citations therein); what our work illustrates is that these dynamics will be ubiquitous in the coastal ocean due to the asymmetric dispersal of larvae by ocean currents (see Nagylaki 1978), Pringle et al. 2011, and Pringle & Wares 2007 for similar ideas in a population-genetics context).

Several other dispersal-driven mechanisms for coexistence of species with differing competiveness have been described. Those of Lutscher et al. (2007), Salomon et al. (2010), and Bode et al. (2011) differ from our work because they depend on the difference in the dispersal distance of the 2

Fig. 5. Spatial evolution of the species favored upstream (red stars) and downstream (blue squares) of location 1, where f_{ret}, the fraction of larvae recruiting that originated locally and downstream relative to total recruitment, is 0.5 everywhere, and ΔC, the change in relative competitiveness, is 5, 50, and 100% greater than the minimum ΔC, which allows the downstream species to persist

competing species. Our mechanism differs from those described by Aiken & Navarrete (2014) and Berkley et al. (2010) because their mechanisms explicitly neglect source/sink dynamics and are driven by stochastic circulation and population dynamics.

Efforts to estimate environmental tolerances of a species from its distribution will be confounded by larval dispersal. As described above, a species whose dispersal is long and determined by local currents can be absent where it is competitively superior and present where it is competitively inferior; in both cases, its range is shifted downstream. Thus efforts to estimate its environmental tolerances will be biased towards conditions prevalent downstream of where the species is truly best adapted wherever the mean circulation biases larval transport downstream. This can potentially confound efforts to use ecological niche models to estimate climate-induced shifts in species ranges (Phillips et al. 2006). These ideas have also been presaged by similar analyses in the population-genetics context (Hare et al. 2005). Likewise, the interactions of 2 species at a spot on the coastline cannot be fully understood without knowledge of the overall distributions of their ranges and their dispersal. Coexistence (or the lack thereof) may have nothing to do with a site-specific measure of competitive strength, but may be due to immigration from elsewhere.

The pinning of upstream range boundaries to regions of anomalous alongshore larval transport will alter how benthic species with long planktonic dispersal stages will respond to climate change. It has been assumed that species with short-distance dispersal will respond more slowly to changes in climate (Harley et al. 2006); it is assumed, often tacitly, that changes in range boundaries are only limited by their ability to disperse to newly congenial habitat. However, in coastal environments with mean currents, the short larval duration species can track changes in the environment more closely than species with long-distance larval dispersal, as long as their upstream invasion speed is greater than the local climate velocity (sensu Pinsky et al. 2013). Species with longer larval dispersal may remain pinned to regional oceanographic features that modify connectivity, and thus f_{ret}, until they are favored in a similar oceanographic feature farther upstream. Because the retentive circulation features in the Bay of Fundy, Nantucket Shoals/Cape Cod, and elsewhere (e.g. Mace & Morgan 2006, Vander Woude et al. 2006) are often bathymetrically driven, their location should not change much in a changing climate. Thus, we

expect to see range expansion in species with long larval durations as a mixture of periods of stasis punctuated by abrupt upstream movement of range boundaries to the next retention region, while species with short larval durations may change their ranges more continuously along the coast. These results are an interesting complement to results suggesting that species with the ability to disperse by swimming against the mean currents (e.g. fish) can closely track changing environmental conditions (Pinsky et al. 2013, Sunday et al. 2015).

It is worth noting that the models of competing species developed above can also be applied to alleles with different fitness within a single species — e.g. see the similarity between the species level model and results of Byers & Pringle (2006) and the evaluation of intraspecific diversity of Pringle & Wares (2007). This concordance could go a long way to explaining the overlap of regions of many biogeographic transitions and regions of many allelic clines (Wares 2002, Pelc et al. 2009, Altman et al. 2013, Ewers-Saucedo et al. 2016). The coexistence mechanism described above may also suggest an explanation for why marine protected regions set aside to protect high species diversity also often serendipitously protect regions of enhanced genetic diversity (Small & Wares 2010).

While it qualitatively fits the distribution of boundaries in the study region, the model of species boundaries in competing species developed above is far from a complete description of how ocean transport interacts with spatially varying inter-species interactions to set species boundaries. To gain a deeper understanding of how dispersal structures range boundaries in the ocean, one could begin by trying to understand how species with different dispersal strategies interact (e.g. building on Lutscher et al. 2007, Salomon et al. 2010, Bode et al. 2011, and Aiken & Navarrete 2014; see discussion in the Supplement, Section SI-5). Furthermore, our model only includes simple competitive interactions between 2 species. The focus on competition is certainly justifiable since it is a major process governing community assembly rules. Many theories and models have been built on the colonization–competition tradeoff that is manifested in species life histories (e.g. lottery model, supply-side ecology, etc.), especially for habitats like the rocky intertidal and shallow subtidal zones where space is often a limiting resource. However, other interactions, for example mutualistic interactions and predation, may have a role in setting community structure, but their interactions with dispersal in marine systems has not been well studied.

While we are confident that the dynamics described here will be important in many coastal oceans, we think much more remains to be understood.

CONCLUSION

Prior efforts to quantify the role of coastal ocean circulation in structuring biogeographic or phylogeographic boundaries in the ocean have either assumed highly idealized coastal circulation (Gaylord & Gaines 2000) or highly idealized descriptions of larval dispersal (Byers & Pringle 2006, Pringle & Wares 2007), or they have analyzed an entire connectivity matrix (e.g. Cowen et al. 2006). The former approaches are so idealized they can be hard to apply in typical coastal settings; the latter requires a daunting amount of larval collection or numerical modeling, and the resulting matrix can be hard to interpret. By focusing on the dynamics of upstream boundaries, our model helps to isolate the local aspects of connectivity that are most important to defining the spatial extent of a species on a regional scale. The summary statistic used in Eq. (3) to discover the relative competiveness needed to maintain a boundary, the local larval retention f_{ret}, can be used to analyze connectivity matrices or local larval settlement data to understand their implication for range boundaries. The patterns of species range boundaries we would predict from estimates of larval retention f_{ret} in the Gulf of Maine/Mid-Atlantic Bight are consistent with observed biogeographic transition zones for species with long planktonic durations.

For coastal benthic species whose dispersal is dominated by ocean currents, we find that the locations of upstream boundaries are determined by the interaction of larval retention and environmentally mediated gradients in relative competitiveness. The upstream extent of a species range is most likely to occur where either or both are maximized. No similar constraint exists for the downstream extent of a range. Because the oceanographic features associated with regions of enhanced retention (increased f_{ret}) are also associated with enhanced environmental gradients (Savidge et al. 2013), we expect the upstream extent of species ranges to cluster at these locations. We expect that as climate changes, ranges of species with long-distance dispersing planktonic larvae will remain fixed at one such location until they rapidly shift to the next; thus regions with an enhanced frequency of upstream species range boundaries should be monitored for signs of shifting ranges.

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