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Variation in Oceanographic Resistance of the World's Coastlines to Invasion by Species With Planktonic Dispersal

James E. Byers¹  | James M. Pringle²¹Odum School of Ecology, University of Georgia, Athens, Georgia, USA | ²Institute for the Study of Earth, Oceans, and Space, University of New Hampshire, Durham, New Hampshire, USA**Correspondence:** James E. Byers (jebyers@uga.edu)**Received:** 3 June 2024 | **Revised:** 22 August 2024 | **Accepted:** 27 August 2024**Editor:** Dustin John Marshall**Funding:** This study was supported by NSF funding from OCE-1947954 to J.M.P. and 1947884 to J.E.B.**Keywords:** larval dispersal | physical-biological coupling | recruitment | settlement

ABSTRACT

For marine species with planktonic dispersal, invasion of open ocean coastlines is impaired by the physical adversity of ocean currents moving larvae downstream and offshore. The extent species are affected by physical adversity depends on interactions of the currents with larval life history traits such as planktonic duration, depth and seasonality. Ecologists have struggled to understand how these traits expose species to adverse ocean currents and affect their ability to persist when introduced to novel habitat. We use a high-resolution global ocean model to isolate the role of ocean currents on the persistence of a larval-producing species introduced to every open coastline of the world. We find physical adversity to invasion varies globally by several orders of magnitude. Larval duration is the most influential life history trait because increased duration prolongs species' exposure to ocean currents. Furthermore, variation of physical adversity with life history elucidates how trade-offs between dispersal traits vary globally.

1 | Introduction

For decades, ecologists have sought to understand how changes in the duration, phenology and behaviour of the planktonic dispersal stages of organisms interact with the circulation of the ocean to modify their ability to invade, that is, persist where introduced to a novel location (Pineda, Hare, and Sponaugle 2007; Pappalardo et al. 2015; Edmunds et al. 2018; Swearer, Trembl, and Shima 2019; White et al. 2019; Krumhansl et al. 2023). These planktonic stages are the main dispersal stage for many meroplanktonic organisms, including benthic invertebrates, seagrasses and seaweeds (Strathmann 1985; Schilling et al. 2024). A principal barrier to predicting net invasion outcomes is the multiple combinations of planktonic life history traits that interact to determine how likely an introduced species is to persist. For example, how can one compare whether a 4-day shorter larval

duration or a 20% reduced planktonic mortality would be more likely to allow an introduced species to persist? Furthermore, are trade-offs between these traits the same everywhere on the globe, or do they vary predictably with geography and the associated ocean currents at each site?

Biological invasion has two important initial steps—arrival and persistence of a species. Here we focus on persistence, and thus the invasion criterion, that is, the ability of a species to increase when rare once introduced in small numbers (MacArthur and Levins 1967; Byers 2000; Grainger, Levine, and Gilbert 2019). In the ocean, the invasion criterion is heavily influenced by larval life history traits interacting with the ocean currents that disperse propagules. The resulting physical-biological coupling can be a strong force dominating life in the ocean, including invasion success (e.g.,

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Brickman 2014; Ryan et al. 2014; Jaspers et al. 2018; Haak, Cowles, and Danylchuk 2019). If an area does not have currents carrying larvae away, such as in an enclosed embayment, populations there are considered closed. In such areas, to persist after initial introduction, a newly introduced species must simply compete sufficiently strongly such that, while its population is small, its realised population growth rate is greater than one, that is, each adult on average must leave more than one offspring that is able to reproduce. But in an open population, such as along an open coastline, there usually must be an even greater realised population growth, to offset emigration from the region of introduction caused by ocean currents (Byers and Pringle 2006). We call this additional required realised population growth the ‘physical adversity’ caused by the ocean currents.

Here we quantify the physical adversity along an open coast as a function of the regional ocean currents and a species’ dispersal traits and life history, and discuss where this estimate is valid. Quantifying the current-caused physical adversity to invasion, while important in its own right, is also key to providing a common currency with which we can compare changes in different aspects of dispersal and biotic factors interacting with ocean currents. Specifically, we evaluate whether the introduction into a location on the open coast of a small number of individuals with a given set of larval life history traits will persist (i.e., invade) or go locally extinct. In our framework, all biotic factors (e.g., larval mortality, fecundity, competitive exclusion, predation) are represented as a realised population growth rate, and all changes in dispersal parameters are measured by how they alter the critical realised population growth rate a species must have to persist. This allows us to isolate and compare the biological and physical controls on the ability of an introduced species to persist. The critical realised population growth rate (defined in more detail below) becomes a common currency that can be used to understand the differences between larval dispersal behaviours and how they are impacted by regional oceanography, allowing us to compare disparate factors that affect competitiveness and invasibility.

This framing allows us to isolate the effect of ocean currents on invasion, evaluating the viability of every parcel of open coastline based on the adversity of its physical current regime. As the critical realised population growth needed for an organism to persist increases, the ease of invasion of the coastline—its ‘invasibility’—decreases. High resolution global ocean models now make it possible to estimate globally this critical realised population growth and the invasibility of each coastline, in each season, for different larval depths and durations. Thus, we can identify coastlines with high physical adversity to invasion, and what, if any, larval strategies might make them less adverse.

1.1 | Invasibility and Dispersal

The focus of this work is on the critical realised population growth rate and invasibility along open coastlines where the dispersal distance of larvae varies slowly in space. We build on the work of Byers and Pringle (2006) who analysed when a species could persist along a finite habitat with spatially

uniform dispersal (i.e., where the dispersal distance of larvae at the location of their parents is similar to the dispersal distance of larvae where they recruit). We do not consider the effects of small embayments that retain larvae, and locations where the alongshore currents vary rapidly along shore. The criterion for when alongshore variation matters, and the effects of alongshore variation, are discussed further in Data S1. Byers and Pringle (2006) argue that it is easier for species to persist in these regions, but these regions will be considered in separate papers because their analyses must include very different methods. So while we present our results along the entire global coastal ocean, our criteria can be too stringent in embayments and other places where dispersal varies over length-scales smaller than the dispersal distance in a single generation.

To understand the trade-offs of different dispersal parameters and to quantify the relative invasibility of the world’s open coastlines, we quantify when an introduction is able to lead to a population that persists at the location of introduction (Byers and Pringle 2006). If a species is introduced into an isolated and well-mixed habitat, it can only persist if its abundance increases when rare, that is, if its realised population growth rate at low density is sufficiently positive ($R > 1$) (Tilman 1982). R is the number of larvae per adult over a lifetime that would successfully recruit to any site and grow to reproductive competency when the species is at low density. This growth rate is net of any negative biotic interactions (e.g., competition with native species) or environmental filters (e.g., temperature, salinity).

For population persistence, there is a consideration that is unique to advective environments like the ocean. Most coastal habitats are not closed; they have a large alongshore extent, and usually a dominant direction (‘downstream’) of alongshore transport. The average larva is more likely to move in one direction along the coast than another (Robinson and Brink 2006). Byers and Pringle (2006) show analytically that this mean transport will work to cause an introduced species to go locally extinct at the location of introduction as the average larva is swept downstream and the centre of gravity of the introduced population is moved downstream. They find the R for the introduced species necessary to compensate for the transport of many larvae downstream and allow persistence where it was introduced is:

$$\ln R > \frac{L_{\text{adv}}^2}{2L_{\text{diff}}^2} \quad (1)$$

where L_{adv} is the mean distance of the larvae that return to a location where they can recruit have moved downstream from their parents and L_{diff} is the standard deviation of that distance (Table 1). Both are defined for all larvae released during an individual’s lifetime. As L_{adv} increases, more larvae are moved downstream and a larger R is needed to allow persistence at the point of introduction. When L_{adv} is finite, increasing L_{diff} increases the stochastic transport of larvae, returns more larvae back to the point of introduction, and decreases the R needed to allow persistence at the point of introduction. Thus, the ratio of $L_{\text{adv}}/L_{\text{diff}}$ determines the population growth R required to allow persistence at the point of introduction.

TABLE 1 | Terminology used in this study.

L_{adv}	The vector-mean distance that larvae in a cohort that return to suitable (i.e., nearshore) habitat are moved downstream from their parents
L_{diff}	The standard deviation of the distance that larvae that return to suitable habitat are moved downstream from their parents
F_R	The fraction of mature, surviving larvae that are returned to habitat anywhere along the coast
R_A	Number of larvae produced per adult that survive their planktonic larval duration and recruit and mature successfully, or would have done so if they had been returned to nearshore habitat. This means R_A would be the population growth rate based on all biological attributes (e.g., larval mortality, fecundity, competitive exclusion, predation) if we neglected loss of larvae due to transport of ocean currents
R_C	Minimum (critical) R_A needed to overcome the transport of larvae away from the introduction site by ocean currents
Physical adversity	Synonymous with R_C , representing how hard the advective physical currents make persistence for a population at a location based on the organism's life history traits

We can better understand how circulation controls invasibility by breaking R into two parts, $F_R R_A$ so that $R = F_R R_A$:

$$\ln(R) = \ln(F_R R_A) = \ln(F_R) + \ln(R_A) \quad (2)$$

where R_A is the number of larvae produced per adult that survive their planktonic larval duration (PLD) and would recruit and reach reproductive maturity provided they reach suitable habitat. Thus, R_A differs from R by including not only successful recruits, but also larvae that survive to competency but do not return to suitable habitat. F_R is the fraction of those larvae that are delivered (returned) to the habitat anywhere along the coast, and is bound by 0 and 1. Only larvae that return to habitat can contribute to the realised fecundity (R), so $R = F_R R_A$. Substituting $F_R R_A$ for R into Equation (1) and using Equation (2) shows that for a population to establish, there is a critical value of R_A , R_C :

$$\ln(R_C) = \frac{(L_{adv}^2)}{(2L_{diff}^2)} - \ln(F_R) \quad (3)$$

such that the invasion will only succeed if $R_A > R_C$. This definition of R_C isolates the influence of physical delivery of larvae on invasibility. R_A contains the biological aspects that affect production and mortality of larvae, their ability to recruit, and their ability to reach reproductive maturity (including all interspecific competition). R_C represents the minimum level of R_A needed to combat the adverse effects of ocean currents for both downstream drift ($L_{adv}^2/2L_{diff}^2$) and offshore loss ($1-F_R$) that are made explicit. Because $F_R \leq 1$, $\ln(F_R) \leq 0$, and thus as F_R decreases (i.e., the offshore loss increases) R_C will increase. Because a larger R_C means a species needs a larger R_A (e.g., higher fecundity, lower mortality, increased ability to compete for habitat) to persist in the face of larval transport by ocean currents, we refer to R_C as the 'physical adversity'. R_C represents the amount that R_A must exceed what it would need to be in a closed environment for an introduced species to persist at the point of introduction.

Equation (3) quantifies the larval production needed to return enough larvae to the introduction point to allow the species to

persist there in the face of downstream and offshore transport that reduce larval return to the introduction point. Changes in PLD, larval depth, phenology, or other larval parameters affect the larvae's interaction with the currents that disperse them, and thus will change R_C . The change in R_C is a measure of how those life-history parameter changes affect the ability of the introduced species to persist, and R_C is a common currency with which we can compare the effects of changes in dispersal parameters as well as biotic factors that contribute to R_A . For example, if a change in the season of dispersal would increase R_C by 10% for a particular species at a particular location, but at the same time would reduce larval mortality by 10% and thus increase R_A by 10%, we could conclude that the combined effect of these changes would have counteracting effects, and thus no net effect on the ability of an introduction to persist.

2 | Why and When Can an Increase of R_C Be Interpreted as a Decrease in Competitiveness Between Two Species?

The competitiveness of a species is affected by many factors, including especially the relative abundance over other competitors. Typically, the relative competitiveness of a species is density-dependent; thus, at low abundance (i.e., after a new introduction) its competitiveness can be very different than when abundant (Hasegawa 2016; Lamb, Satgé, and Jodice 2017). Here we focus on competitiveness when a species is at low abundance. In this limit, a greater R_C means more reproductive output must be used to offset immigration away from the habitat, and thus less reproductive output is retained to allow local growth. Given two newly introduced species, for a given reproductive output, we would expect the one with a smaller R_C to increase its population at a site of introduction more quickly, all other things being equal. Under such conditions, a species with lower R_C has fewer of its larvae being lost to currents, and thus more going towards local population growth. This does not mean all other things are equal, because changes in dispersal life history can also change R_A by, for example, changing larval mortality. But changes in the

physical adversity (R_C) capture the effects of the interaction between dispersal life history and ocean currents on relative competitiveness.

3 | Methods

Precalculated trajectories from the Mercator Global Ocean Model (GLORYS12V1) were used to calculate all larval dispersal paths from 2007 to 2022 that leave and return to a near coast habitat using the publicly available EZfate package developed by J. Pringle (<https://github.com/JamiePringle/EZfate>). The model is forced with surface fluxes from numerical atmospheric models and assimilates multiple sources of in situ and remotely sensed ocean data to get an optimal estimate of ocean currents (Cummings and Smedstad 2013; Lellouche et al. 2013). The Mercator Global Ocean Model, despite its global scope, has been shown to have good skill in predicting coastal currents and is superior to other global models at all time scales (e.g., Wilkin and Hunter 2013; Amaya et al. 2023). It includes wind- and river-driven current variability, and resolves inter-annual variability in currents such as El Niño (Amaya et al. 2023).

The model has a $1/12^\circ$ resolution; $1/12^\circ$ of longitude is 9 km at the equator, and 5 km at 60° N. Lagrangian particle tracks representing larval pathways were calculated with the Ocean Parcels version 2.2 (Delandmeter and van Sebille 2019), and particles were released every half day. Because a larva only contributes to dispersal if it returns to suitable habitat, the spatial structure of habitat is an important control on dispersal and the invasibility of a region. We defined habitat as the two closest model grid cells (or about $1/6^\circ$) to land or water shallower than the larval depth (Pringle 2023). Defining the 'habitat' as two model grid-cells wide increases the number of larvae that return to the habitat and thus the statistical robustness of the larval dispersal statistics. The habitat grid cells and release points of simulated larvae can be viewed in the figures for F_R in the Interactive Supplement.

Particle releases were grouped into 3-month seasons: January–March; April–June; July–September; and October–December. Larvae were fixed at 1, 20 and 40 m depth, and it was assumed that larval behaviour or buoyancy will keep the larvae fixed at those depths even in the presence of vertical currents. These depths were chosen to be either above or below the surface Ekman layer in most locations. To explore the role that depth variation might play, we also simulated larvae released at 1 m whose depth could change when transported by vertical ocean currents, but neglecting vertical diffusion (hereafter, 1 m variable depth); we compared these against the results where larvae were fixed at 1 m fixed depth. We explored three PLDs for the main analysis (4, 14 and 30 days), but used more PLDs for the case studies discussed below. Statistics were computed for all paths calculated from 2007 to 2022, and so represent the average dispersal over this period.

For each grid-cell in the habitat, L_{adv} , L_{diff} and F_R are estimated for each vertical depth and PLD combination for each season. F_R is the fraction of larvae that are produced and delivered to habitat anywhere along the coast. L_{adv} is the distance from the release point to the mean location of particles that return to the habitat after a set time, the PLD. The mean location is defined as the point that has the minimum sum of the squared great-circle distances to each of the returning points, and L_{diff} is the square-root of the mean sum of squared distance from each particle that returned to habitat to the mean location. Because calculations over this time period include the inter-annual variability of the annual mean currents in the estimate of L_{diff} , L_{diff} will be somewhat overestimated for semelparous species whose larval releases will not capture this variability (Byers and Pringle 2006; Peniston and Burgess 2024). With estimates of L_{adv} , L_{diff} and F_R , the physical adversity (R_C) for a species with a coastal habitat is calculated for each larval release point with Equation (3). To explore the relatedness between all component variables (L_{adv} , L_{diff} , F_R and L_{adv}^2/L_{diff}^2) and the computed variable $[\ln(R_C)]$ at every coastal grid cell for every planktonic larval duration (PLD)—depth—season combination, we used nonparametric

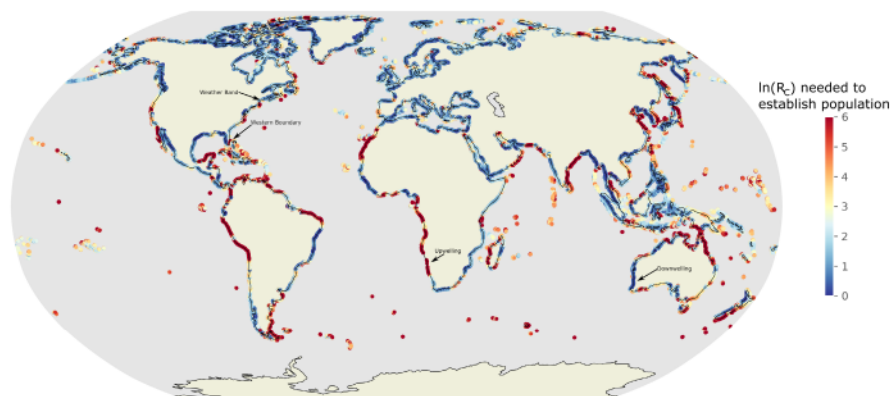


FIGURE 1 | The physical adversity of open coastlines of the world to invasion. The colours indicate the natural log of the physical adversity $\ln(R_C)$ for a meroplankton species. This sets the minimum R_A necessary for an introduced species to overcome the dispersal by ocean currents and persist along the world's coastlines for species with larvae that spawn from April–June, have PLD = 30, and are fixed at 1 m depth. Dark blue indicates lower, and red greater, population growth rates needed to establish after introduction. One way to increase R_A would be to increase fecundity, all other things being equal. Relative to dark blue, dark red values would signify ≈ 400 times (e^6) more required fecundity necessary for persistence, that is, to overcome the physical forces working against establishment. Interactive figures which allow closer examination of regions for all combinations of seasons, larval depths and PLDs are in the Interactive Supplement: https://jamiepringle.github.io/ByersPringle_InteractiveVisualization/.

correlations (Spearman's ρ). Nonparametric tests were desirable because they are robust to non-normal distributions that are common with ratios.

Although we calculate exact values of $\ln(R_C)$, we emphasise our focus is the relative changes in R_C between different areas of coast and between different dispersal parameters, because these will be more robust to changes in F_R with variation in the cross-shelf extent of a species' habitat. When we compute the difference between $\ln(R_C)$'s, any constant fractional change to R_C caused by a smaller cross-shelf extent of the habitat will be cancelled out. This occurs because if the two R_C 's are altered by the same factor α , then $\ln(\alpha R_{C1}) - \ln(\alpha R_{C2}) = \ln(\alpha R_{C1}/(\alpha R_{C2})) = \ln(R_{C1}) - \ln(R_{C2})$.

Finally, to illustrate how different oceanographic regimes interact with different larval dispersal parameters to alter the invasibility of a coast to larvae with different life histories, we analysed four case studies that represent four distinct contrasts in larval transport: upwelling circulation, downwelling circulation, large alongshore mean transport and large alongshore variability in transport.

4 | Results

For species spawning in April–June, with larvae that remain at 1 m depth and a PLD of 30 days, there is substantial heterogeneity around the globe in the physical adversity to invasion (Figure 1). Physical adversity is quantified in the figure by $\ln(R_C)$, the log of the critical growth rate R_C , the minimum population growth rate that allows persistence given the physical oceanography at each location, with larger values indicating increased adversity. The coastal grid cells with the most physical adversity (greatest R_C , dark red) require that a species have an $\ln(R_A) > 6$, or $R_A > 400$, to persist if introduced. Even blue represents $\ln(R_A) > 1$, or $R_A > 2.7$ for persistence, which would be equivalent to more than a doubling of the population per generation if the larvae did not disperse away from their parents. Values of R_C are placed into context of typical fecundity and mortality rates in Box 1 (Grounding the relative values of R_C), but values above 2 would be considered large for most organisms.

4.1 | Relative Influence on $\ln(R_C)$

The parameters of Equation (3) (L_{adv} , L_{diff} and F_R), and their correlations, reveal that globally the variability in the return of larvae to habitat (F_R) usually has a greater effect on $\ln(R_C)$ than variability in the loss downstream L_{adv}^2/L_{diff}^2 (Table S1, Figure S1). At 1 m depth for April to June release and PLD = 30, the non-parametric correlation (Spearman's ρ) between $\ln(R_C)$ and $\ln(F_R)$ is -0.81 , for $\ln(R_C)$ and $L_{adv}^2/(2L_{diff}^2)$ it is 0.54 . These correlations have similar magnitude for all depths and seasons, but the correlations between $\ln(R_C)$ and $L_{adv}^2/(2L_{diff}^2)$ increase slightly with decreasing PLD (Table S1). One reason for the often stronger influence of F_R is that at all larval depths, seasons, and durations, L_{adv} and L_{diff} are largely correlated (median Spearman $\rho = 0.72$; all correlations significant at $p < 0.05$, Figure S1). Thus, a portion of the variability in each term cancels when one computes L_{adv}^2/L_{diff}^2 , leaving more scope for the variation in $\ln(F_R)$.

BOX 1 | Grounding the relative values of R_C .

To place the values of R_C estimated above in context, consider a simplified example. An individual that produces 2,000,000 larvae with an 80% daily survival probability over a 30 days PLD with 100% of the surviving larvae successfully settling, would have 2476 recruiting larvae. Low daily survival rates often continue for post-metamorphic larvae and juveniles even if settled in proper refugia habitat (e.g., Moksnes et al. 1998). Given another 60 days for the organism to reach reproductive competency with a 90% daily survival rate, this results in 4.4 recruits that reach reproductive competency, so an R_A of 4.4. Extending the time to competency or decreasing the survival rate will both reduce R_A . Thus, $R_C = 400$ [$\ln(R_C) = 6$] is a seemingly high population growth rate to be met, and thus likely represents areas of very low invasion probability due to the high physical adversity. Even blue areas in Figure 1 have physical conditions that make them not necessarily easy to invade, as the light blue areas represent $\ln(R_C) = 2.5$, or $R_C \approx 12$. Any colour but the darkest blue represents R_C values that could strongly constrain the ability of introduced species to persist and invade.

Note that some species may have initial propagule production far larger than 2,000,000 larvae used in our example. But those that do, do not necessarily have higher R_A values. Rather, such species often have their high production drastically diminished by offsetting factors such as high rates of mortality caused by more time needed in the plankton to reach competency, or more time to reach reproductive competency post-settlement (Vance 1973; Strathmann 1985). Our numerical example is meant only for illustrative purposes because there is a large amount of uncertainty due to estimates of planktonic mortality rates that are highly unconstrained.

to influence $\ln(R_C)$. Results for 1 m variable depth were similar to 1 m fixed depth, except that 1 m fixed depth larvae almost always had a greater F_R and thus a lower $\ln(R_C)$ (Figures S2, S3). This was true across PLD's and seasons.

4.2 | Global Sensitivity to Changes in Larval Characteristics (Depth, Duration, Seasonality)

At the global scale (i.e., averaged across all sites), season has little influence on $\ln(R_C)$ (Table 2). Opposing seasons in the two hemispheres may cancel out some of the seasonal effect at the global scale. The influence of depth is subtle, with 1 m having higher median $\ln(R_C)$ values than 20 and 40 m for PLD of 4, all depths having similar medians at PLD of 14, and both 1 m and 20 m having sizably lower medians than 40 m for PLD = 30 (Table 2, Figures S4, S5). PLD has the largest effect on $\ln(R_C)$, with increases in PLD from 4 to 30 days increasing the median threshold $\ln(R_C)$ by roughly 0.6–1.0, equivalent to multiplying R_C by 1.8–2.7 (Table 2). Thus, other than for PLD, there is little global averaged impact on the physical adversity to invasion and the relative competitiveness of a species due to changes in larval dispersal parameters.

TABLE 2 | Median amount of physical adversity [$\ln(R_C)$] that must be overcome to enable successful invasion calculated across all coastal grid cells for all combinations of PLD (4, 14 and 30 days), season, and fixed depth (1, 20 and 40 m). Lower $\ln(R_C)$ values indicate higher potential for invasion.

Season	PLD (days)		
	4	14	30
Depth = 1 m			
Jan–Mar	0.66	1.10	1.27
Apr–June	0.60	1.04	1.22
July–Sept	0.74	1.15	1.31
Oct–Dec	0.67	1.11	1.30
Depth = 20 m			
Jan–Mar	0.53	1.03	1.38
Apr–June	0.46	0.94	1.32
July–Sept	0.50	0.99	1.33
Oct–Dec	0.51	1.01	1.37
Depth = 40 m			
Jan–Mar	0.56	1.12	1.62
Apr–June	0.51	1.05	1.57
July–Sept	0.54	1.08	1.58
Oct–Dec	0.55	1.12	1.64

4.3 | Spatially Explicit Sensitivity Analyses

However, the global averaged sensitivity analyses mask important regional differences. A spatial analysis of sensitivity demonstrates which specific areas of the global coastline are sensitive to depth and season, and thus where these factors can influence $\ln(R_C)$ (Figure 2). In Figure 2, differences in $\ln(R_C)$ for each habitat cell are shown for different depths (panel A) and seasons (panel B) (in the Interactive Supplement, this is shown for other depths and seasons). A difference in $\ln(R_C)$ of 2 is equivalent to a ratio between the two R_C 's of $e^2 = 7.4$, so that a change in larval depth or spawning season causing a change of this magnitude has the same effect on the ability of an introduced species to persist as a factor of 7.4 change in fecundity would. Very large variation between regions is evident in these figures (Figure 2). A large proportion of the spatial difference in the sensitivity to depth is driven by spatial variation in F_R (Interactive Suppl.; Figure S6).

4.4 | Case Studies

Much of the underlying regional variation in invasion sensitivity (Figure 2) can be explained in the context of four representative physical oceanographic regimes that contrast strongly with one another: upwelling regions, downwelling regions, western boundary current regions and temperate weather band-dominated regions. As representative regions we chose 20-km stretches of the coast of Namibia as an upwelling

system, Perth, Australia as a downwelling region, West Beach Florida on the east coast of Florida as a Western Boundary system, and the Gulf of Maine as a temperate weather band system.

Upwelling regions occur where the alongshore wind drives an offshore surface Ekman transport in the top 10–20 m, balanced by a return flow at a depth determined by the topography and stratification (Lentz and Chapman 2004). Consistent with expectations from the physics, we found that upwelling led to the offshore loss of surface larvae and to the retention of larvae that maintain their depths below the surface Ekman layer (Morgan et al. 2018; Figure 3). Larval loss offshore increases R_C , so upwelling regions will show much greater R_C at 1 m depth than 20 m depth (Figure 2A, teal in Figure 3). Overall, at 1 m, invasion in the upwelling system will have a greater R_C , and thus require a much higher R_A to satisfy Equation (3) and allow persistence relative to the other three oceanographic regimes, which have similar R_C (Figure 3). Thus, in upwelling regions, a species with surface larvae would need much greater fecundity or much less larval mortality relative to species with larvae below the surface Ekman layer in order to persist.

Downwelling systems occur where the winds blow in the opposite alongshore direction as upwelling systems (e.g., Perth, Australia), and show the reverse pattern of increased larval fraction retained for surface larvae, decreased retention for those below the surface Ekman layer, and decreased surface R_C relative to depth (Figure 2A, red in Figure 3). Both upwelling and downwelling systems show great sensitivity to the vertical position of the larvae and strong dependence of cross-shelf circulation with depth. Being fixed at 1 m depth, as opposed to 1 m variable depth, mostly increased the fraction returned to habitat, especially where there is downwelling (Figures S2, S3). In monsoonal systems (e.g., the Horn of Africa, India), there is strong seasonal reversal of winds, seasonal switching from upwelling to downwelling, and correspondingly strong seasonal variation in which depth strategy requires the least R_C (Figure 2B, Figure 3, Interactive Supplement). In downwelling regions, species with surface larvae, especially larvae fixed to the surface, will have increased competitiveness relative to species with larvae below the surface Ekman layer.

Where strong western boundary currents exist along narrow continental shelves (e.g. the East Coast of Florida, USA, or portions of the Brazilian and South-Eastern Japanese coasts), the strong alongshore currents will rapidly move larvae downstream. Accordingly, L_{adv} increases rapidly with PLD (grey in Figure 3). Although there is large alongshore transport (L_{adv}), it does not heavily influence $\ln(R_C)$ in this western boundary system because the advection is moderately offset by high variation (L_{diff}) (Figure 3, middle row). These systems do not have a consistent relation between R_C and seasonality or depth of larval release.

In many mid-latitude temperate systems, like the Gulf of Maine, the winds are dominated by passing storms and the seasonal mean winds are weak relative to the 2- to 4-day weather band variability. With weak mean winds and strong variable winds, any mean upwelling or downwelling is weak relative to the weather-system driven variability, which itself tends to

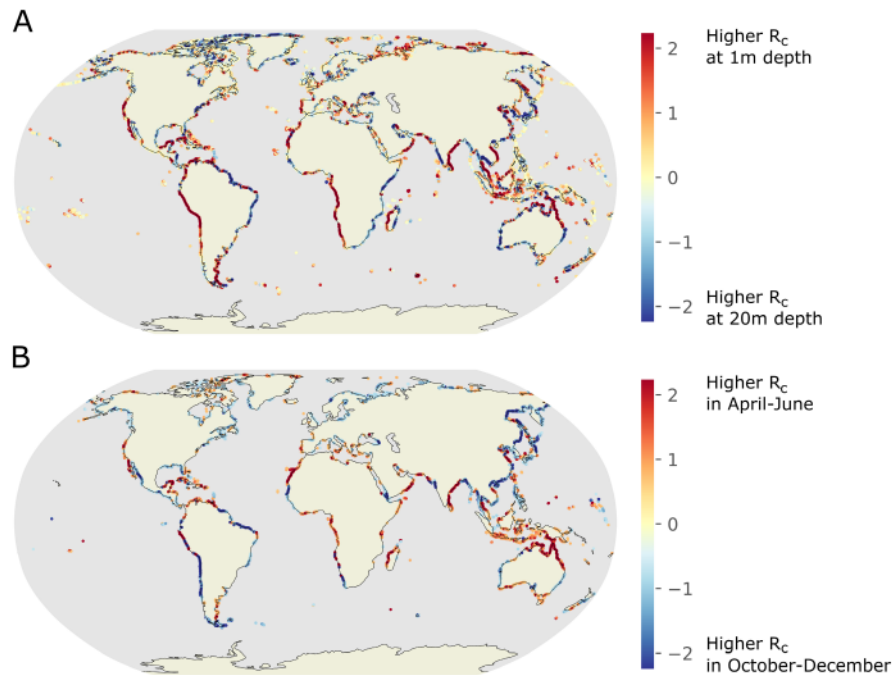


FIGURE 2 | The site-specific sensitivity of the physical adversity to invasion to the effects of larval depth and season of larval release. The sensitivity of the natural log of the physical adversity $\ln(R_C)$ to (A) vertical depth of larvae and B) larval seasonality with PLD 30. (A) $\ln(R_C)$ at 1 m depth minus $\ln(R_C)$ at 20 m depth during April to June. Red indicates greater physical adversity R_C at the surface; blue indicates greater R_C at depth. Thus, red indicates a species would need a greater R_A (e.g., greater fecundity, less mortality) at the surface to persist after introduction. (B) $\ln(R_C)$ during April to June minus $\ln(R_C)$ during October to December for 1 m depth. Red indicates greater physical adversity, and thus, for example, greater fecundity needed during April–June; blue indicates greater physical adversity during October to December. Changes in $|\ln(R_C)| < 1.0$ are not plotted; thus, areas that are blank are where season or depth are less important. Data for $\ln(R_C)$ for all seasons and multiple depths are available in the Interactive Supplement.

average out over a long PLD. Thus, L_{diff} is large relative to L_{adv} , R_C is relatively small, and the physical adversity does not vary with the depth of larvae nearly as strongly as in systems with mean Upwelling/Downwelling flows (Figure 2A, lavender in Figure 3).

These four descriptions of the representative flow regimes are simplified. But they provide a framework for thinking about how larval seasonality, depth and duration interact with location to determine relative competitiveness and invasibility.

5 | Discussion

Globally, physical adversity to invasion by introduced coastal meroplanktonic species (R_C) varies spatially by over two orders of magnitude (Figure 1). In areas of high adversity far more larvae must be produced or survive to compensate for larval loss to currents and to allow invasion, so that $R_A > R_C$ (Equation 3). Because the currents influence these species by transporting their larvae, the greatest spatial heterogeneity and the highest median critical growth rate to allow invasion, R_C , occur with large PLDs that allow the greatest amount of time for currents to act upon the larvae (Table 2, Figure 3). With larger PLDs, the larval production necessary for a species to establish increases because more larvae are needed to compensate for the larvae swept offshore and downstream by currents and lost from the system.

Changes in R_C can be used to assess the difference in relative competitiveness caused by changes in larval behaviour or timing. In virtually all cases, increased PLD would lower the competitiveness of a species, all other things being equal. In Pringle et al. (2014), a similar logic is used to argue that a longer PLD is only evolutionarily stable if it is associated with greater realized fecundity. The constraint against long PLDs is particularly strong where the fraction of larvae returned to the coast (F_R) is small or the strength of downstream loss (L_{adv}^2/L_{diff}^2) is high. In these locations, species with crawl-away larvae would often be relatively more competitive and more able to invade, helping to explain the correlation between stronger currents and planktonic development (Pringle et al. 2014).

The criterion for persistence, $R_A > R_C$, separates the criterion for invasion into two parts: R_A which includes all biotic factors such as fecundity, mortality before and after recruitment, and interspecific competition for habitat and R_C which captures the interaction of dispersal life history with ocean currents on the ability of an introduced species to persist at a location. This separation becomes useful when, for example, we seek to understand how range boundaries might shift as climate changes (Pringle et al. 2017). A range shift requires an invasion into a new region. Changes in climate can change both the local circulation by, for example, altering the intensity of upwelling, and also local larval production, mortality, and interspecific competition (Kendall et al. 2016; Bashevkin et al. 2020). By explicitly separating these different effects, we can judge how

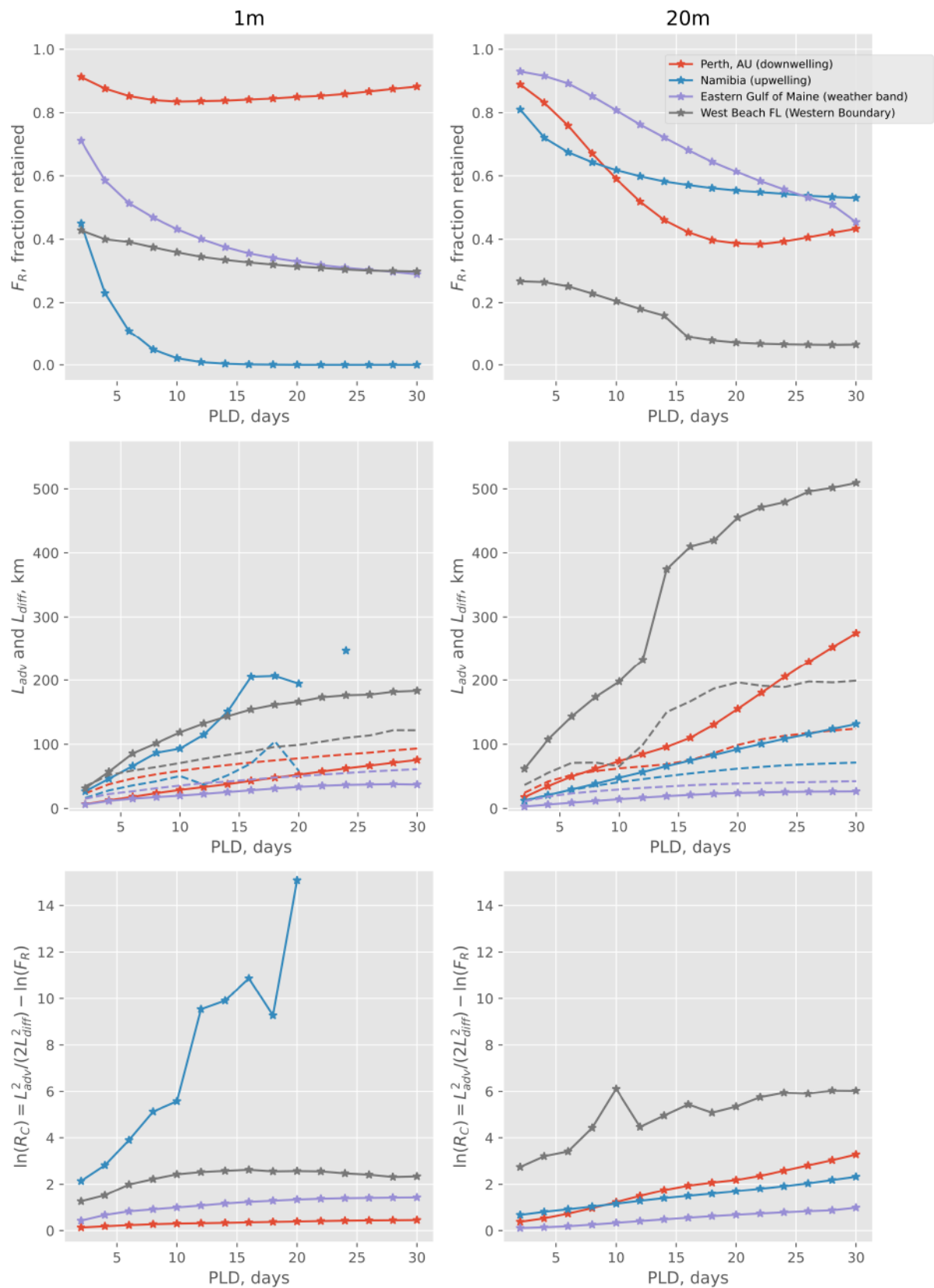


FIGURE 3 | Sensitivity of the physical adversity to invasion $\ln(R_C)$ and its components to local physical oceanographic effects within four distinct oceanographic regimes at two depths. For all panels, the left column depicts larvae at 1 m depth; the right column depicts larvae at 20 m depth. Top: Fraction retained (F_R) for the four oceanographic regions as a function of planktonic duration (PLD). Middle: Mean larval transport distance L_{adv} (solid lines) and standard deviation L_{diff} (dashed) as a function of larval planktonic duration (PLD) for the four regions. Because so few larvae are retained at 1 m depth in Namibia with $PLD > 20$, L_{adv} and L_{diff} and $\ln(R_C)$ are not computable for these PLD. Bottom: Natural log of physical adversity $\ln(R_C)$ as a function of larval planktonic duration (PLD) for the four regions. The centre of each region of release is indicated on Figure 1 with black arrows.

the physical and biological aspects interact, and the relative importance of each. For example, reduced upwelling could both increase surface temperatures and decrease offshore transport. Warmer water could allow larvae to mature faster, reducing their planktonic mortality, and decreased offshore transport should reduce larval loss offshore (i.e., increase F_R). Both of these influences would tend to make it easier for non-upwelling adapted species (i.e., species lacking life history characteristics specifically adapted to maximise retention amid the traditional physical conditions of upwelling regions) to invade upwelling regions. Furthermore, our framework allows one to judge which effect—reduced mortality or increased F_R —most strongly influences invasion potential.

Likewise, separating the effects of ocean transport from biotic parameters can help explain observed biogeographic patterns. For example, many coastal locations in polar regions have low physical adversity R_C (Figure 1), but they should not necessarily be interpreted as easy places to invade. Cold water also reduces the rate at which larvae develop, increasing PLD (Epifanio et al. 1998; O'Connor et al. 2007), and Pringle et al. (2014) show that this interacts with larval mortality to reduce the number of larvae which can recruit, reducing R_A in these regions. This reduction makes it less likely that $R_A > R_C$, and is consistent with the observed scarcity of long planktonic larval life histories in native species at high latitudes where water is cold (Thorson 1950; Alvarez-Noriega et al. 2020). Similarly, it has been seen that planktonic dispersal is less common among native species where mean currents are swift and we would expect a large L_{adv} and, consequently, a large R_C (Marshall et al. 2012; Pringle et al. 2014).

The physical adversity R_C that affects the persistence of introduced species is sensitive to the depth and season of release of larvae, but only where the current is season- or depth-dependent. In upwelling regions, larvae fixed to a depth below the surface Ekman layer are strongly favoured. In downwelling regions, larvae fixed to a depth within the surface Ekman layer are strongly favoured. In places where upwelling and downwelling vary with season (e.g., monsoonal regions), seasonality will be important. Surface-released larvae that passively vary their depth, that is, with currents, are almost universally retained less than larvae that are fixed to 1 m (Figure S3); this is especially true in downwelling regions (Figure S2) where surface-starting larvae are typically downwelled at the coast and then moved offshore at depth. In locations with strong upwelling or downwelling, changes in larval depth will profoundly affect the physical adversity experienced by a species.

The advantage that a particular larval behaviour or phenology gives a species in its relative competitiveness or its ability to invade varies with location. In the case of invasion, if we assume most species are evolutionarily optimised for their native habitat, this suggests that an invader will be more likely to succeed in a new location if the native range of an invading species has similar current patterns to the place it has been introduced to. In such cases, the species may already be adapted to spawning at appropriate depths and seasons to minimise $\ln(R_C)$. For example, larvae being at a depth below the surface Ekman layer will aid retention within the world's upwelling locations (Figure 2). Thus, a successful invasion may not only require matches

between source and destination environmental characteristics that are traditionally considered like temperature, salinity and habitat (Stohlgren et al. 2010; Crall et al. 2013), but also matches of current regimes.

As we have emphasised throughout, these results are most applicable to open coasts. The effect of embayments is poorly represented in this work both because Equation (1) was developed assuming a long relatively straight coastline and because for many smaller embayments the Mercator Ocean Model resolution of $1/12^\circ$ is relatively coarse. Once a species has established in an embayment, larvae that leave the embayment could colonise the coast downstream from the embayment (Pringle et al. 2011). The role of embayments (or other regions where L_{adv} , L_{diff} and F_R vary over short alongshore distance) in altering the relative competitiveness of a species and in enabling invasion by increasing retention and subsidizing invasions downstream is a promising area of future work. This present work cannot usefully comment on the observed pattern of increased invasibility of embayments (e.g., Cohen and Carlton 1998; Ruiz et al. 2000; Wasson, Fenn, and Pearse 2005).

In conclusion, oceanographic currents are a first-order control on the relative competitiveness of coastal meroplankton and their ability to persist and invade where introduced. Both offshore and downstream loss of larvae in currents are important (Equation 3, Figure 1). Larvae with long PLD are more subject to transport and loss in such currents (Figure 3). Different depth and seasonality of larvae can expose them to different, more favourable, current regimes and enable easier invasibility. However, only certain coastal areas of the world are places where depth and season affect the currents enough to substantially alter the relative competitiveness of species manifesting different depth and seasonal release traits (Figure 2; Figure S2). Such areas where currents are depth- and season-sensitive will also be places where in practice it will be more challenging for newly introduced species to persist, because there are only a narrow set of larval traits which, if they are locally appropriate, greatly increase the competitiveness of a species. In these regions, we hypothesise introduced species originating from locations with similar circulation patterns will be more likely to succeed.

Author Contributions

Conceptualization: J.E.B., J.M.P.; Methodology: J.E.B., J.M.P.; Investigation: J.E.B., J.M.P.; Visualization: J.M.P.; Funding acquisition: J.E.B., J.M.P.; Supervision: J.E.B., J.M.P.; Writing – original draft: J.E.B.; Writing – review and editing: J.E.B., J.M.P.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The code to retrieve dispersal data and generate the statistics shown in the paper are available at: <https://github.com/JamiePringle/Byers>

Pringle_InteractiveVisualization (DOI 10.5281/zenodo.13362806). The Lagrangian paths and software to analyse them can be found at the EZfate GitHub site: <https://github.com/JamiePringle/EZfate> (DOI 10.5281/zenodo.10214924). The interactive figures can be found at https://jamiepringle.github.io/ByersPringle_InteractiveVisualization/ (also DOI 10.5281/zenodo.13362806).

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14520>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.