



Are Coastal Marine Larvae Dispersed Less Than Would Be Expected by Ocean Currents?

James M. Pringle*

Ocean Process Analysis Laboratory, University of New Hampshire, 139 Morse Hall, Durham, New Hampshire 03824

Abstract

The distance that offspring disperse from their parents affects how a species responds to habitat disturbance, climate change, and interspecific interactions. For many benthic species, this dispersal is via planktonic larvae, but the distance these larvae disperse is difficult to observe directly. Dispersal distance has usually been estimated indirectly by combining an observed quantity (e.g., the rate of spread of an invasive organism or genetic similarity between locations) with a model that links that quantity to the dispersal of larvae. The estimates of dispersal distance based on the speed of spread of invasive organisms have led many researchers to conclude that the larvae of most of these organisms disperse much less than would be expected if they were being passively transported by the expected ocean currents (Shanks et al.; Shanks). I argue that the discrepancy is instead caused by the choice of model linking dispersal distance to invasion speed. Their model neglected the impact of life history, population growth, and oceanographic parameters on invasion speed. When dispersal distance is estimated from a more complete model of invasion speed, it is found that larval dispersal distance is not much less than would be expected for larvae drifting in the observed ocean currents.

Introduction

The dispersal of offspring away from their parents controls the connectivity between adjacent regions of habitat. This distance that larvae disperse drives many important ecological processes, including the ability to maintain genetic diversity and adapt to local conditions (van Dijk *et al.*, 2009; Sanford and Kelly, 2011; Griffiths *et al.*, 2021), inter- and intraspecific competition dynamics (Lutscher *et al.*, 2007), and response to local habitat disturbance (Lundquist *et al.*, 2010; Fraser *et al.*, 2018). In many benthic species, the dispersal is dominated by a planktonic dispersal stage (Marshall *et al.*, 2012; Álvarez-Noriega *et al.*, 2020), but because of the small size of the larvae, it is extremely difficult to directly estimate their dispersal by tracking individual larvae (Pineda *et al.*, 2007). Because of the importance of dispersal, there has been considerable effort to estimate the distance that larvae that recruit successfully have moved away from their parents.

The dispersal of larvae has been estimated by assuming that they are passively transported by ocean currents (perhaps with some control of their depth) and by using ocean currents to predict their dispersal distance (Siegel *et al.*, 2003; e.g., Mitarai *et al.*, 2008). Given the difficulty of directly observing larval dispersal (Pineda *et al.*, 2007), it has been difficult to test these predictions directly. Instead, researchers have found an observable quantity, assumed a model of the observed quantity in which it is a function of dispersal, and inverted that model to predict dispersal distance from the observed quantity. Necessarily, the quality of the estimate of dispersal is a function of the skill of the model linking the observed quantity to dispersal distance.

Attempts to test the estimates of larval dispersal distance derived from ocean currents have often failed, and the results of the tests have been interpreted to suggest that larval dispersal is either very much less than would be expected from passive transport by ocean currents (Swearer

Received 3 October 2023; Accepted 20 June 2024; Published online 26 August 2024.

* Email: jpringle@unh.edu.

Abbreviations: ALS, Shanks *et al.* (2003) and Shanks (2009); PLD, larval planktonic duration.

Online enhancement: appendix.

et al., 2002, p. 200; Shanks *et al.*, 2003; Levin, 2006; Shanks, 2009) or not simply correlated to predictions of dispersal distance from ocean currents and larval life history (Weersing and Toonen, 2009; Esser *et al.*, 2023).

Two observables have often been used: the rate of spread of an invasive species (Shanks *et al.*, 2003; Shanks, 2009) and the change in genetic distance between individuals as a function of the physical distance between them (isolation by distance) (Kinlan and Gaines, 2003; Weersing and Toonen, 2009; Selkoe *et al.*, 2010; Selkoe and Toonen, 2011; Carrier *et al.*, 2017; Esser *et al.*, 2023). The focus of this work is on estimates of dispersal based on observations of invasion speed; estimates based on genetic distance are addressed elsewhere (Teller, 2022; Teller and Pringle, 2023; JMP, unpubl. manuscript).

In a pair of influential papers, Shanks *et al.* (2003) and Shanks (2009) (hereafter, ALS) compare estimates of dispersal distance based on mean ocean currents to their estimates of larval dispersal. These articles are examined here because ALS have been widely cited and are included in reviews of larval dispersal in support of the idea that larval dispersal is usually much less than would be expected from ocean currents (Levin, 2006; *e.g.*, Emlet, 2022). The focus is on the species ALS describe with planktonic durations greater than 10 h and whose estimated dispersal is greater than 1 km. Of the estimates of dispersal for these species in ALS, 21 of 24 (88%) are derived from observations of the rate of spread of an invasion. Species with relatively long planktonic durations and <1-km dispersal distances are not included because, as described in Shanks *et al.* (2003), they consist of species whose larvae rapidly move to very

near, or in, the bottom, where current is weak. Shanks (2009) states that even for the subset of species with larger dispersal (his criterion is dispersal >20 km), planktonic duration is a poor descriptor of dispersal distance and the dispersal distance is less than would be expected for passive particles.

It is argued below that these conclusions are greatly overstated. The ALS use of a model that neglects species life history, an oversimplified description of the statistics of larval dispersal, in addition to inappropriate estimates of mean ocean currents, leads to systematic errors in estimations of larval dispersal distance and their relation to ocean currents and larval duration. More accurate estimates of mean ocean currents and more realistic models of invasion speed that incorporate a species' life history eliminate much of the discrepancy between observations of invasion speed and oceanographically derived estimates of larval dispersal distance. The sensitivity of these results to the details of the life histories of individual species highlights the importance of careful model specification when using a model to estimate one quantity (here, dispersal) from an observed quantity (*i.e.*, invasion speed).

Summary of ALS Methods and Results

For most species in their dataset with a dispersal distance greater than a kilometer, ALS estimate larval dispersal distance from the invasion speed of introduced species (the blue points in Fig. 1; the data are taken directly from ALS). They assumed a model of range expansion in which the yearly extension of the invasion front for newly introduced species is the same as the mean downstream dispersal

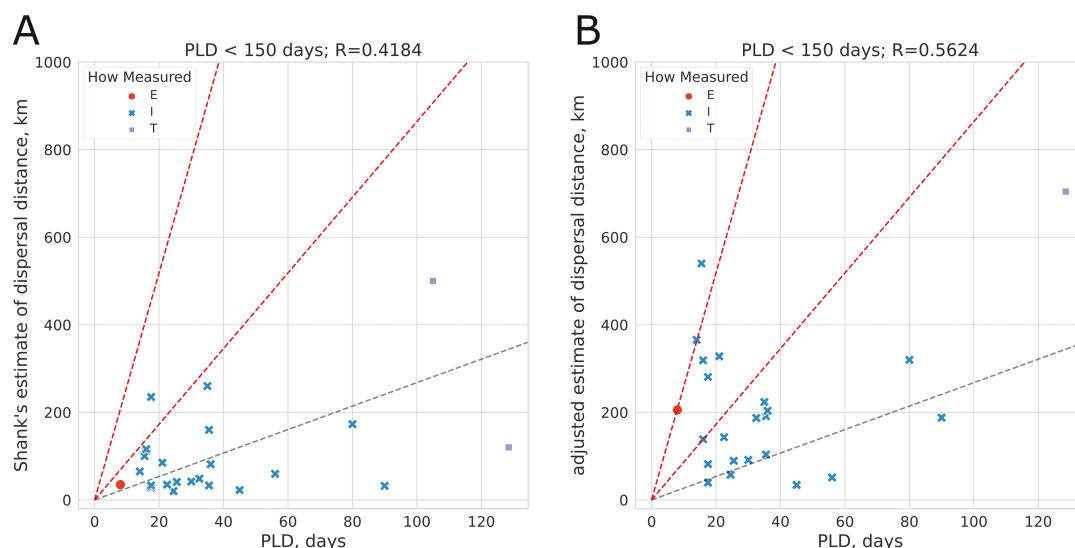


Figure 1. Two estimates of larval dispersal distance as a function of larval planktonic duration (PLD). (A) Estimated larval dispersal distance from Shanks *et al.* (2003) and Shanks (2009) as a function of PLD for all species whose dispersal distance is greater than 1 km and planktonic duration is less than 150 days. The color of the points indicates how the dispersal distance was estimated, where “E” is from experimental data, “T” is from tagged larvae, and “I” is from invasion speed data. Most of the data come from invasion speed estimates. The dashed lines indicate the expected relationship between distance and PLD for Shanks's velocity estimates of 30 cm s⁻¹, 10 cm s⁻¹ (red dashed lines), and a Lagrangian model-derived estimate of 3.1 cm s⁻¹ (gray dashed line) for mean alongshore flows. (B) Same as (A) but with the estimated dispersal distance corrected for lifespan and assuming a per-generation population growth rate R' of 2.0.

distance of individuals. These estimates were then compared by ALS to the dispersal that would be expected for ALS's literature-derived estimates of larval planktonic duration (PLD) and their assumed typical values of mean coastal alongshore currents of 10 and 30 cm s⁻¹ (Fig. 1A). Nearly all points are found to disperse less than ALS's estimate for transport by coastal currents. Both the assumed mean coastal currents and the model of range expansion are examined below.

Methods

How is dispersal distance defined in ALS and in this work?

Before discussing how to estimate dispersal distance from invasion speed, it is important to precisely define dispersal distance. Shanks *et al.* (2003, p. S160) define the “mean realized dispersal distance” as “the distance that the mean propagule disperses from an adult source population.” It is unclear whether this distance is defined in a vector or scalar sense. They go on to state that “we then assume that at this distance, settlement rates are sufficient to sustain a substantive recipient adult population.” It is not made clear what “the mean propagule” is, nor is it made clear why it should be assumed that the settlement rates at the mean dispersal distance are sufficient to sustain a “substantive recipient adult population” (or, indeed, what this “substantive recipient adult population” level is). This definition juxtaposes two ideas, one a measure of dispersal distance, the other a measure of population sustainability. This juxtaposition will be seen below to be unhelpful.

More typically, dispersal distance is defined solely as a function of how far larvae move before recruitment. Two different dispersal distances are commonly defined, following studies of dispersal of larvae by ocean currents (Siegel *et al.*, 2003). The mean larval dispersal distance, L_{adv} , is defined as the distance between the parent and the spatial average location of all the larvae that recruit (Fig. 2). A second length scale of dispersal is L_{diff} , the standard deviation of the distance of all recruits around the average recruitment

location (Fig. 2); L_{adv} will be most influenced by the time-mean vector-average current velocity computed along the larval pathway, while L_{diff} will be mostly influenced by deviations of the current from that mean (Siegel *et al.*, 2003). Since most of the species analyzed in ALS are coastal organisms whose ranges have one dimension that is significantly longer than the other, these length scales will be defined here along a single alongshore direction. All dispersal distances are defined for the larvae that survive to recruit to suitable habitat and do not include larvae that die before recruiting or do not reach suitable habitat. It will be assumed in the analysis below that the dispersal kernel is Gaussian, but none of the conclusions of this work will be qualitatively altered for other kernels. The effects of other kernel shapes on dispersal can be straightforwardly quantified (Kot *et al.*, 1996; Pachepsky *et al.*, 2005; Pringle *et al.*, 2009).

It is unclear which definition of dispersal distance, L_{adv} or L_{diff} , is implicitly being used by ALS. Because both are important components of dispersal (Siegel *et al.*, 2003), population dynamics (Fisher, 1937; Pachepsky *et al.*, 2005; Byers and Pringle, 2006; Lutscher *et al.*, 2010), and phylogeography (Pringle and Wares, 2007; Altman *et al.*, 2013; Wares *et al.*, 2021), both are analyzed.

How does invasion speed relate to larval dispersal?

Because ALS observe invasion speed and use it to estimate dispersal distance, it is necessary to have a quantitative understanding of the dispersal and life history parameters that control invasion speed. Invasion speed is customarily defined as the distance the invasion front of an introduced species moves away from the point of introduction each generation. The invasion front is the location where the population exceeds some arbitrary population density that is much less than the carrying capacity of the environment for the invader (Fisher, 1937).

For now, the mean larval dispersal L_{adv} is neglected, and it is assumed that larvae are dispersed evenly around their parents, so only L_{diff} is nonzero. It has long been known (Fisher, 1937) that in this limit, the invasion speed depends on the population growth rate of the invader at densities much less than the carrying capacity (the potential growth rate) but not on the choice of population threshold or intraspecific density dependent growth. Invasion speed is sensitive to Allee effects; here it is assumed there are none. The invasion speed is also sensitive to interspecific density-dependent effects.

To illustrate the dependence of invasion speed on the potential growth rate, a simple multispecies model is described that assumes that any invading species will interact simply with the existing populations so that the number of adults in the next generation at a location depends on the habitat available at that location (*i.e.*, the difference between the population after adult mortality and the carrying capacity including all species) and that the fraction of the

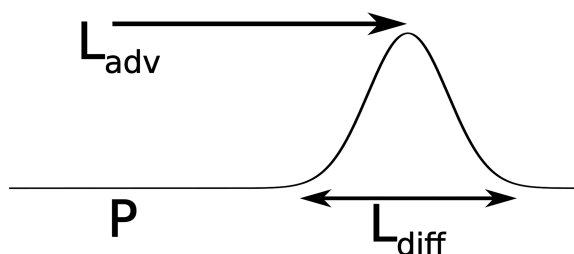


Figure 2. Dispersal of larvae from the location of a parent P along a coast defined by three parameters: the mean downstream distance the larvae settle from their parents (L_{adv}), the standard deviation of the larval settlement location around the mean location of settlement (L_{diff}), and the shape of the probability distribution function of the larval settlement distribution (the “dispersal kernel”).

invaders in the next generation will be the same as the fraction of the invading larvae in the recruits. In the discrete generation semelparous limit, and assuming the species competing with the invader have the same dispersal characteristics as the invader, the invader's invasion speed will be (following Byers and Pringle, 2006)

$$C_{\text{invasion}} = L_{\text{diff}} \sqrt{2 \ln(R')}, \quad (1)$$

where R' is the ratio of larval production between the invader and the native competitors; this production is net of mortality in the plankton and loss offshore; R' must be greater than 1 for invasion to happen (*i.e.*, the invader must outcompete natives to persist). The source of the code that implements this population model and all others presented in this paper is given in the “Data Accessibility” section.

The speed C_{invasion} is the model's estimate of the invasion speed; ALS assume this speed is the same as the dispersal distance. But C_{invasion} is not the same as the dispersal distance L_{diff} , even in this simplest of models, it is also a function of the relative population growth rate of the invader R' . In Figure 3A, the spread of a semelparous invader

(blue lines) into a habitat of semelparous natives (red lines) is shown three generations after introduction for three different values of R' . As R' increases, the invasion front spreads further, because it takes a smaller fraction of the invader's larvae to found a population that exceeds the invasion threshold. In Figure 3B, the spread of an invader (blue lines) is shown three generations after introduction for three different values of dispersal distance L_{diff} . As expected, the invasion front moves further and faster when L_{diff} is greater. Both increased dispersal and increased relative growth of the invader increase the invasion speed.

Equivalently, if it is assumed, as ALS do, that L_{diff} is equal to C_{invasion} , a change in relative growth R' will lead to an error in our estimate of L_{diff} . For these semelparous cases with no mean currents, C_{invasion} will be less than the true L_{diff} , and ALS's estimate of the dispersal distance will be less than the actual dispersal distance L_{diff} when $2 \ln(R')$ is less than 1 and R' is less than 1.65 (Fig. 4A, which shows the ratio C_{invasion} to L_{diff}). An R' of 1.65 occurs when the invader's potential growth rate is 65% greater than that of the native species, or, equivalently, over 10 generations the population of the invader will grow by a factor of 150.

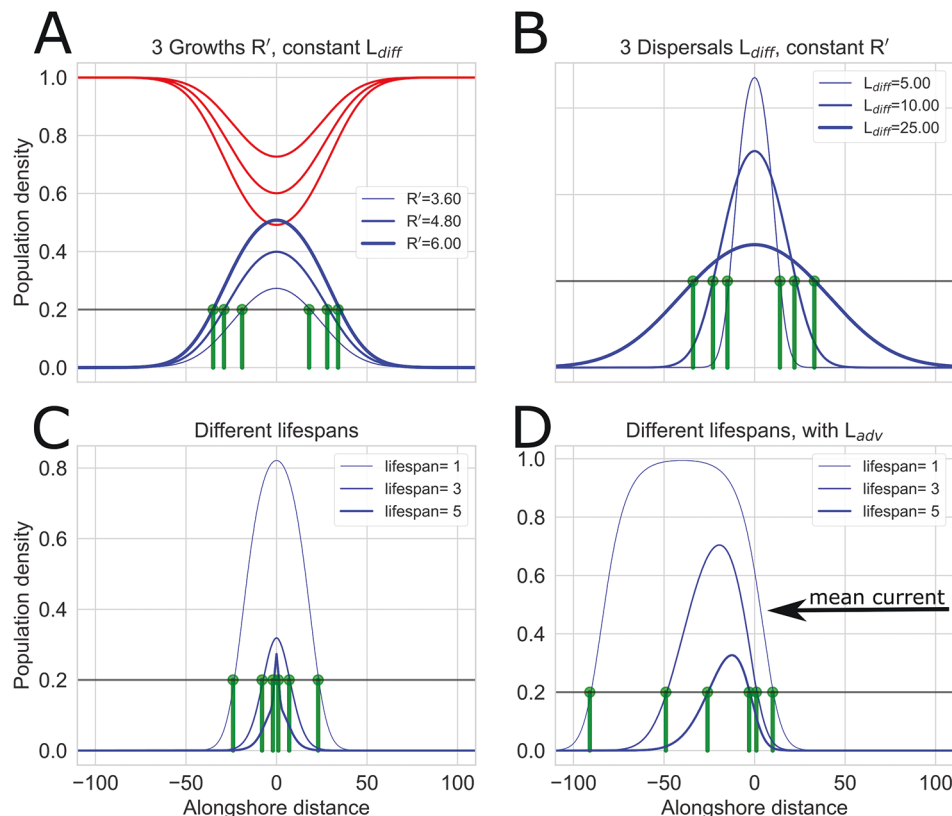


Figure 3. Dispersal of an invader (blue lines) into the native organisms (red lines) with time. The location of the invasion front is defined as the location where the total population of the invader exceeds 0.2, and it is marked with green vertical lines and circles. (A) Spread of an invasion in three generations for three values of the relative growth rate of the invader (R') for semelparous species. Standard deviation of larval dispersal (L_{diff}) = 15 km and mean downstream dispersal (L_{adv}) = 0 for all cases. (B) Same as (A) but with a fixed R' of 3.6 and three values of L_{diff} . The native population is not shown for clarity in this panel or the following panels. (C) Progress of an invasion after four generations when both the native and invading species have lifespans of 1, 3, and 5 generations. The total population for all ages of the invader is shown. $R' = 3.0$; $L_{\text{diff}} = 5$; $L_{\text{adv}} = 0$. (D) Same as (C) except with a current that moves larvae to the left (as indicated by the arrow), with $L_{\text{adv}} = 5$ for eight generations.

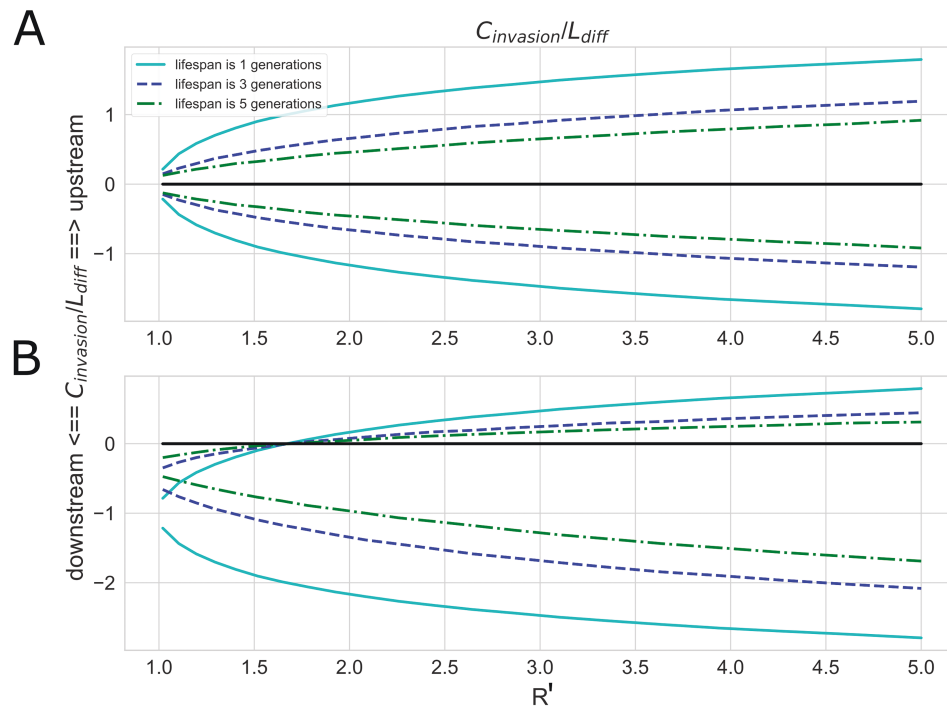


Figure 4. Ratio of the invasion speed $C_{invasion}$ to the standard deviation of larval dispersal L_{diff} for organisms that live 1, 3, and 5 generations. Since there is dispersal in both directions along the coast, there is a negative and positive ratio. Shanks *et al.* (2003) and Shanks (2009) assume that the magnitude of this ratio is always 1. (A) $C_{invasion}$ when there is no mean downstream dispersal ($L_{adv} = 0$). (B) $C_{invasion}$ when L_{adv} is equal to the standard deviation of larval dispersal L_{diff} . The downstream direction is the negative direction on the y-axis. The black line indicates an invasion speed of zero.

The relation between invasion speed and dispersal is also a function of the lifespan of the competing organisms. In Figure 3C, the invasion is shown for invaders and competing native species that live multiple generations and reproduce equally each generation. The lifespan of the species is varied, and the invader spreads more rapidly when the invader and native species have shorter lifespans.

The primary reason the invasion speed is reduced when lifespan is increased is that under this model of limited habitat, the native species cannot be replaced by the invader before an individual of the native species dies and makes habitat available (Fig. 5). If it takes 5 years for an adult of the native species to die, it will be 5 years until that habitat can be invaded. The invasion speed is thus, for this model of competition, most sensitive to the lifespan of the native species. This is clearly dependent on the exact nature of competition between the species. The mathematical details underlying this reduction have long been known and are described in Pringle *et al.* (2009) and the citations therein. Figure 4 shows the ratio $C_{invasion}$ to L_{diff} , which ALS assume is always 1. It can be seen that if this ratio is less than 1, $C_{invasion}$ will be less than L_{diff} and ALS will underestimate L_{diff} when R' is less than 3.5 for organisms that live for three generations and less than 5 for species that live for five generations. These instances of R' are equivalent to an increase in the invading population by a factor of 280,000 and 10,000,000, respectively, over 10 generations.

The assumption that larvae will be as likely to settle upstream of their parents as downstream is, for species with significant planktonic dispersal, oceanographically naive. Most coastal systems have currents with a preferred directionality and a nonzero mean flow with a significant variability around that flow. For the global coastal ocean, this is very well documented and is true regardless of the depth of the larvae (summarized in Robinson and Brink, 2006). The simplest oceanographically realistic model of larval dispersal will include not only the standard deviation of larval dispersal (the L_{diff} above) but also the mean transport in a specific direction (L_{adv} , Fig. 2) (Siegel *et al.*, 2003). This asymmetry in the dispersal will cause an asymmetry in the invasion speed/generation, with faster invasion in the downstream direction and a slower invasion speed upstream (Pringle *et al.*, 2011). If the relative fecundity of the invader is not large enough, the invader will be flushed downstream and (at least locally) lost from the system (for semelparous species see Byers and Pringle, 2006; for iteroparous species and non-Gaussian dispersal see Pringle *et al.*, 2009). This can be clearly seen in Figure 4B, where even for $R' > 1$ the “upstream” invasion speed can be negative, resulting in the invading organism’s distribution being moved downstream and driven to local extinction. Even for larger relative growth rates R' the upstream invasion speed per generation is much less than L_{adv} and L_{diff} , so that $C_{invasion}$ will be a very significant underestimate of

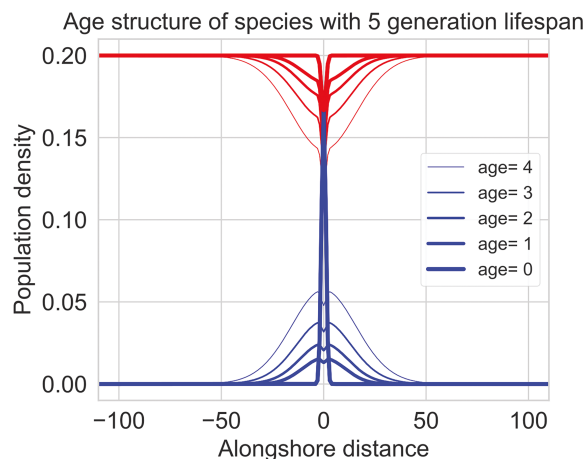


Figure 5. Dispersal of an invader (blue lines) into the native organisms (red lines) five generations after an initial introduction of the invaders. Both invading and native species live for five generations. The line width indicates age, with age 0 being the most recently recruited populations. Relative growth rate of the invader $R' = 4.8$; standard deviation of larval dispersal $L_{diff} = 10$ km; mean downstream dispersal $L_{adv} = 0$ km.

dispersal distances. In the downstream distance and for large enough R' , $C_{invasion}$ can be larger than the dispersal distances, leading it to be an overestimate of dispersal distance. In either case, $C_{invasion}$ is not a good estimator of either dispersal distance; ALS do not specify whether their invasion data were gathered from upstream or downstream of the location of introduction, so no correction for the preferential downstream transport of larvae can be made.

Results

How does the dependence of $C_{invasion}$ on life history effect estimates of dispersal?

The goal of ALS and this work is to estimate dispersal (either or both L_{adv} and L_{diff}) from observations of the invasion speed $C_{invasion}$. This is difficult because of the dependence of $C_{invasion}$ on life history parameters that are often poorly understood for an invading species, such as its lifespan, the age structure of reproduction, and relative growth rates R' . The nature of the competitive interactions of invaders with native species that set relative growth rates R' is particularly opaque. But to give an idea of the magnitude of change in estimated L_{diff} as a function of a single life history parameter, the effect of lifespan on the estimate of L_{diff} can be estimated. Literature estimates of the lifespan of the species whose dispersal was estimated from invasion speed in ALS are given in Table S1. It is assumed that the lifespan of the assemblage of native species that compete with the invader is the same as the invader's lifespan and that they have similar dispersal characteristics; R' is assumed to be 2 for all species, and L_{adv} is assumed to be 0. These are clearly rough and ready assumptions, whose only purpose is to illustrate the magnitude of the effect of a more

complete model of the relationship between L_{diff} and $C_{invasion}$.

The model used to calculate Figure 3 is used to convert the invasion speed of ALS to an estimate of L_{diff} ; this estimate is shown in Figure 1B. This simple model improves the correlation between estimates of invasion speed and PLD (Pearson's correlation R from 0.41 to 0.56) and makes them more consistent with observed coastal currents (the dashed lines of Fig. 1).

This comparison will not bear much weight; too many unconstrained assumptions about life history and species interactions are needed. The life histories and competitive interactions described above certainly do not cover the range of life histories of invading species, native species, or their interactions. But they illustrate that the invasion speed per generation observed for a species is unlikely to be the same as either dispersal length scale (L_{adv} or L_{diff}) and will often underestimate the dispersal distance by a large factor. Illustrating the uncertainty in invasion speed estimates caused by uncertainty in our knowledge of the life history parameters is the fundamental point of this work: a model that implicitly assumes that the dispersal distance of larvae is the invasion distance per generation is an inaccurate model, for the invasion speed depends on much more than just a single measure of dispersal distance.

The “typical” magnitude of alongshore currents in the coastal ocean

The ALS estimate of larval dispersal distance was compared to expectations from currents of $10\text{--}30\text{ cm s}^{-1}$. It was assumed that these were “typical” coastal currents and that the distance the larvae would be transported would scale as the product of these velocities and the PLD. This estimate was labeled “Passive Dispersal” in Shanks's (2009) figure 1. Nearly all of the estimated dispersal distances for individual species in ALS were less than this “Passive Dispersal” distance, and this discrepancy was used as evidence that dispersal was less than would be expected for purely planktonic larvae.

This raises a question: are $10\text{--}30\text{ cm s}^{-1}$ currents typical of the currents experienced by larvae of coastal organisms that enter the plankton from near the coast and return to settle near the coast? Mean currents on the shelf are often weaker, especially near the coast (Largier, 2003), and usually less than these values. In the Mid-Atlantic Bight, annual mean depth-averaged currents are about 4 cm s^{-1} across the shelf until the 50-m isobath, then increase linearly to 9 cm s^{-1} at the shelf break (Lentz, 2008). Along the Californian coast, there is considerable variation in alongshore currents, some associated with alongshore changes in shelf width and seasonal forcing (Lentz and Chapman, 1989; Lentz, 1994; Pringle, 2002; Pringle and Dever, 2009). Glider data over the Californian Shelf (Rudnick *et al.*, 2017) from south of Pt. Conception to Monterey Bay suggest that depth-averaged currents are 5 cm s^{-1} or less inshore

of the 500-m isobath, while north of Pt. Reyes depth and time mean springtime currents are roughly $1\text{--}3\text{ cm s}^{-1}$ inshore of 90 m (Lentz and Chapman, 1989; Pringle and Dever, 2009). All of these values are much less than $10\text{--}30\text{ cm s}^{-1}$.

These observations are geographically and temporally limited. They are also hard to interpret in the context of larvae whose motion is relevant to a species' dispersal only when they leave and return to suitable habitat. For larvae, the relevant mean speed is the speed averaged over the Lagrangian path of larvae that return to suitable habitat (Siegel *et al.*, 2003 has an excellent model of this). Most species in ALS are coastal or near coastal, and so the currents they experienced will be biased toward nearshore current speeds.

To integrate over a broader range of locations and years, and to explicitly include only the currents that are relevant to successful larvae, dispersal is estimated with a Lagrangian model of larvae in a numerical model. The currents come from the Mercator global 1/12 degree ocean model, which has shown skill in estimating coastal currents (e.g., Wilkin and Hunter, 2013). Over the East and West Coasts of the United States, Lagrangian particles are released at every model grid point between the coast and the 25-m isobath (the “habitat”). Lagrangian particles fixed to 1-m depth are released twice a day at every habitat point from April to June (the oceanographic spring) for 2007–2022, using the OceanParcels particle tracking package (Delandmeter and Van Sebille, 2019) and the EZfate package (Pringle, 2023). This period encompasses multiple El Niño and La Niña years. These particles are included in the calculation of statistics if they start and end in a habitat grid cell after 16 days; this is the “PLD” of the modeled particles. This choice of PLD is arbitrary but is typical of many larvae with longer planktonic durations. The results are not very sensitive to this choice (for a more detailed discussion see Siegel *et al.*, 2003). The “mean speed” is defined by computing the average location of settlement of particles from a release point, where the average location is the point with the minimum sum-of-square distance to all successfully settling particles. The mean dispersal distance L_{adv} is the distance from the release point to the average settlement location, and the average speed is this distance divided by the PLD of 16 days.

The mean speed in this model for the East Coast for larvae that successfully return to habitat is 3.68 cm s^{-1} , with a standard deviation of $\pm 3.0\text{ cm s}^{-1}$, and $2.48 \pm 1.61\text{ cm s}^{-1}$ on the West Coast. The probability distribution of average speed from all release point velocities on the East and West Coasts of the United States is right skewed, extending from 0 to about 10 cm s^{-1} (Fig. 6). These results are consistent with the observational data cited above. Thus, the “typical” currents described by ALS are three to 10 times greater than observed and modeled coastal currents at the surface (deeper currents will often be less). A more representative value of 3.1 cm s^{-1} (the average of the East and West Coast currents given above) is shown as a gray line in Figure 1

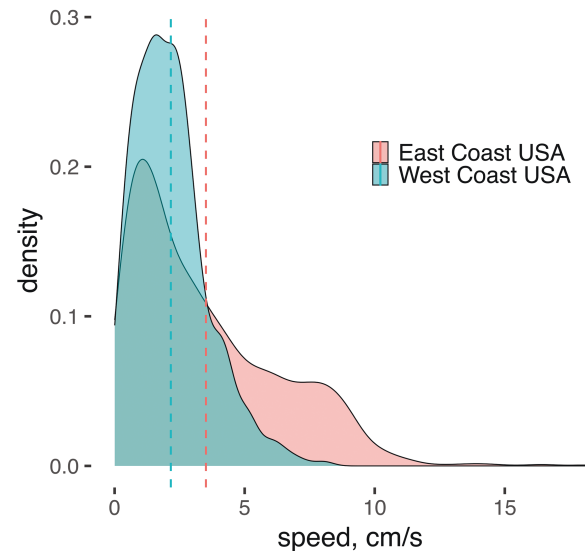


Figure 6. Probability distribution function of mean advection speed calculated over 16 days for Lagrangian particles fixed to 1-m depth and released from, and returning to, points inshore of the 25-m isobath for April, May, and June 2007–2022 in the Mercator global 1/12 degree ocean model. The vertical lines indicate the mean velocities of 3.68 cm s^{-1} on the East Coast and 2.48 cm s^{-1} on the West Coast of the United States.

and can be seen to more closely fit the estimates of dispersal. This speed is broadly consistent with Siegel *et al.*'s (2003) estimate of Lagrangian speed of 5 cm s^{-1} , which is based on the observed currents in central California during the upwelling season.

Discussion

An estimate of dispersal distance obtained by observing a quantity other than dispersal distance and using an implicit or explicit model to link the observation to dispersal distance is only as good as the model linking the observations to dispersal distance, in addition to the knowledge of other life history traits important to the model. Estimates of larval dispersal based on the invasion speed of introduced species will usually underestimate dispersal distance if it is assumed that the only life history parameter that affects invasion speed is the dispersal distance. Any comparison to expected dispersal will be suspect. Further, the expected dispersal distance should be compared to accurate estimates of the ocean's currents. The conclusion in ALS that “observed” dispersal distance is much less than would be expected for particles advected by coastal currents is not supported when the estimate of dispersal distance from invasion speed is computed with a more realistic model of invasion speed based on Fisher (1937) and when these estimates are compared to more oceanographically realistic estimates of Lagrangian dispersal by ocean currents.

This is not to claim that larval behavior does not affect larval transport; there is much evidence that it can. Larvae are observed to regulate depth in upwelling regions (Morgan and Fisher, 2010; Morgan, 2014); ALS observe that

larvae that seek the bottom experience greatly reduced invasion speeds. Analysis of evolutionarily stable states for the development of dispersal behavior suggests that strong evolutionary pressure exists to reduce mean larval dispersal L_{adv} (Pringle *et al.*, 2014). There is considerable evidence that larvae can modulate their transport (DiBacco and Chadwick, 2001; Shanks and Shearman, 2009; *etc.*). Nothing above addresses cross-shelf transport. I simply suggest that this behavior may not affect their mean along-shore transport as strongly and as universally as has often been assumed.

Invasion speed is not the only quantity used to estimate dispersal distance. Genetic isolation by distance has often been used to estimate dispersal, compare to estimates of dispersal, or correlate with quantities expected to be related to dispersal, like PLD (Siegel *et al.*, 2003; Bradbury *et al.*, 2008; Weersing and Toonen, 2009; Selkoe and Toonen, 2011; Esser *et al.*, 2023). These works have often shown a weak link between expectations of dispersal from ocean currents and estimates from isolation by distance. But all of these results depend on knowledge of the population density and an assumption that dispersal is as likely to move a larva upstream of its parents as downstream (Wright, 1943; Rousset, 1997). The former can vary greatly between species, and the latter is a poor representation of coastal transport. Work that includes mean downstream transport of larvae finds that it can have very large effects on the distribution of genetic diversity (Pringle and Wares, 2007; Wares and Pringle, 2008; Teller and Pringle, 2023), and spatially resolved empirical studies of landscape genetics have found that genetic difference often does not increase smoothly with separation but is focused in geographically limited regions (Altman *et al.*, 2013; Wares *et al.*, 2021). This suggests that an accurate quantitative linkage between dispersal and genetic distance also requires an oceanographically and biologically realistic model of the link between the two.

The conclusions that we make when we interpret observations are only as strong as the model that links our observations to what we wish to know. If we cannot observe directly what we wish to know, we must be sure that we understand the models that link observations to conclusions.

Data Availability

The software for the population models used in Figures 1B, 2, 3, 4, and 5 can be found at <https://github.com/JamiePringle/SimpleInvasionModel>. The code to generate Figure 6 can also be found there, and it uses EZfate from <https://github.com/JamiePringle/EZfate> to retrieve precomputed Lagrangian particle trackways and analyze them.

Acknowledgments

This work has benefited strongly by comments and discussions with Jeb Byers, Paula Pappalardo, and John

Wares. The work was funded by National Science Foundation Division of Ocean Sciences award 1947954.

Literature Cited

- Altman, S., J. D. Robinson, J. M. Pringle, J. E. Byers, and J. P. Wares. 2013. Edges and overlaps in Northwest Atlantic phylogeography. *Diversity* 5: 263–275.
- Álvarez-Noriega, M., S. C. Burgess, J. E. Byers, J. M. Pringle, J. P. Wares, and D. J. Marshall. 2020. Global biogeography of marine dispersal potential. *Nat. Ecol. Evol.* 4: 1196–1203.
- Bradbury, I. R., B. Laurel, P. V. R. Snelgrove, P. Bentzen, and S. E. Campana. 2008. Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proc. R. Soc. B* 275: 1803–1809.
- Byers, J. E., and J. M. Pringle. 2006. Going against the flow: retention, range limits and invasions in advective environments. *Mar. Ecol. Prog. Ser.* 313: 27–41.
- Carrier, T., A. Reitzel, and A. Heyland, eds. 2017. Genetic analysis of larval dispersal, gene flow, and connectivity. Pp. 164–189 in *Evolutionary Ecology of Marine Invertebrate Larvae*. Oxford University Press, Oxford.
- Delandmeter, P., and E. Van Sebille. 2019. The Parcels v2.0 Lagrangian framework: new field interpolation schemes. *Geosci. Model Dev.* 12: 3571–3584.
- DiBacco, C., and D. B. Chadwick. 2001. Assessing the dispersal and exchange of brachyuran larvae between regions of San Diego Bay, California and near-shore coastal habitats using elemental fingerprinting. *J. Mar. Res.* 59: 53–78.
- Emlet, R. B. 2022. Where do larvae go? Some go really far, but others maybe not that far. *Biol. Bull.* 243: 9–11.
- Esser, E., J. Pringle, and J. Byers. 2023. Neither larval duration nor dispersal distance predict spatial genetic diversity in planktonic dispersing species. *Mar. Ecol. Prog. Ser.* 721: 161–167.
- Fisher, R. A. 1937. The wave of advance of advantageous genes. *Ann. Eugen.* 7: 269.
- Fraser, C. I., I. D. Davies, D. Bryant, and J. M. Waters. 2018. How disturbance and dispersal influence intraspecific structure. *J. Ecol.* 106: 1298–1306.
- Griffiths, S. M., M. J. Butler, D. C. Behringer, T. Pérez, and R. F. Preziosi. 2021. Oceanographic features and limited dispersal shape the population genetic structure of the vase sponge *Ircinia campana* in the Greater Caribbean. *Heredity* 126: 63–76.
- Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84: 2007–2020.

- Kot, M., M. A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. *Ecology* 77: 2027–2042.
- Largier, J. L. 2003. Considerations in estimating larval dispersal distances from oceanographic data. *Ecol. Appl.* 13: 71–89.
- Lentz, S. J. 1994. Current dynamics over the northern California inner-shelf. *J. Phys. Oceanogr.* 24: 2461–2478.
- Lentz, S. J. 2008. Observations of the mean circulation over the Middle Atlantic Bight continental shelf. *J. Phys. Oceanogr.* 38: 1203–1221.
- Lentz, S. J., and D. C. Chapman. 1989. Seasonal differences in the current and temperature variability over the northern California Shelf during the Coastal Ocean Dynamics Experiment. *J. Geophys. Res. Oceans* 94: 12571–12592.
- Levin, L. A. 2006. Recent progress in understanding larval dispersal: new directions and digressions. *Integr. Comp. Biol.* 46: 282–297.
- Lundquist, C. J., S. F. Thrush, G. Coco, and J. E. Hewitt. 2010. Interactions between disturbance and dispersal reduce persistence thresholds in a benthic community. *Mar. Ecol. Prog. Ser.* 413: 217–228.
- Lutscher, F., E. McCauley, and M. A. Lewis. 2007. Spatial patterns and coexistence mechanisms in systems with unidirectional flow. *Theor. Popul. Biol.* 71: 267–277.
- Lutscher, F., R. Nisbet, and E. Pachepsky. 2010. Population persistence in the face of advection. *Theor. Ecol.* 3: 271–284.
- Marshall, D. J., P. J. Krug, E. K. Kupriyanova, M. Byrne, and R. B. Emlet. 2012. The biogeography of marine invertebrate life histories. *Annu. Rev. Ecol. Evol. Syst.* 43: 97–114.
- Mitarai, S., D. A. Siegel, and K. B. Winters. 2008. A numerical study of stochastic larval settlement in the California Current system. *J. Mar. Syst.* 69: 295–309.
- Morgan, S. G. 2014. Behaviorally mediated larval transport in upwelling systems. *Adv. Oceanogr.* 2014: 364214.
- Morgan, S. G., and J. L. Fisher. 2010. Larval behavior regulates nearshore retention and offshore migration in an upwelling shadow and along the open coast. *Mar. Ecol. Prog. Ser.* 404: 109–126.
- Pachepsky, E., F. Lutscher, R. M. Nisbet, and M. A. Lewis. 2005. Persistence, spread and the drift paradox. *Theor. Popul. Biol.* 67: 61–73.
- Pineda, J., J. A. Hare, and S. Sponaugle. 2007. Larval transport and dispersal in the coastal ocean and consequences for population connectivity. *Oceanography* 20: 22–39.
- Pringle, J., and J. Wares. 2007. Going against the flow: maintenance of alongshore variation in allele frequency in a coastal ocean. *Mar. Ecol. Prog. Ser.* 335: 69–84.
- Pringle, J., F. Lutscher, and E. Glick. 2009. Going against the flow: effects of non-Gaussian dispersal kernels and reproduction over multiple generations. *Mar. Ecol. Prog. Ser.* 377: 13–17.
- Pringle, J. M. 2002. Enhancement of wind-driven upwelling and downwelling by alongshore bathymetric variability. *J. Phys. Oceanogr.* 32: 3101–3112.
- Pringle, J. M. 2023. EZfate, a tool for estimating larval connectivity in the global coastal ocean. [Online]. Available: <https://zenodo.org/doi/10.5281/zenodo.10214924> [2024, April 23].
- Pringle, J. M., and E. P. Dever. 2009. Dynamics of wind-driven upwelling and relaxation between Monterey Bay and Point Arena: local-, regional-, and gyre-scale controls. *J. Geophys. Res. Oceans* 114: C07003.
- Pringle, J. M., A. M. H. Blakeslee, J. E. Byers, and J. Roman. 2011. Asymmetric dispersal allows an upstream region to control population structure throughout a species' range. *Proc. Natl. Acad. Sci. USA* 108: 15288–15293.
- Pringle, J. M., J. E. Byers, P. Pappalardo, J. P. Wares, and D. J. Marshall. 2014. Circulation constrains the evolution of larval development modes and life histories in the coastal ocean. *Ecology* 95: 1022–1032.
- Robinson, A., and K. H. Brink. 2006. *The Sea*, Vol. 14A, B, *The Global Coastal Ocean: Interdisciplinary Regional Studies and Synthesis*. Harvard University Press, Cambridge, MA.
- Rousset, F. 1997. Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics* 145: 1219–1228.
- Rudnick, D. L., K. D. Zaba, R. E. Todd, and R. E. Davis. 2017. A climatology of the California Current System from a network of underwater gliders. *Prog. Oceanogr.* 154: 64–106.
- Sanford, E., and M. W. Kelly. 2011. Local adaptation in marine invertebrates. *Annu. Rev. Mar. Sci.* 3: 509–535.
- Selkoe, K. A., and R. J. Toonen. 2011. Marine connectivity: a new look at pelagic larval duration and genetic metrics of dispersal. *Mar. Ecol. Prog. Ser.* 436: 291–305.
- Selkoe, K. A., J. R. Watson, T. B. Horin, M. Iacchei, S. Mitarai, D. A. Siegel, S. D. Gaines, and R. J. Toonen. 2010. Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. *Mol. Ecol.* 19: 3708–3726.
- Shanks, A. L. 2009. Pelagic larval duration and dispersal distance revisited. *Biol. Bull.* 216: 373–385.
- Shanks, A. L., and R. K. Shearman. 2009. Paradigm lost? Cross-shelf distributions of intertidal invertebrate larvae are unaffected by upwelling or downwelling. *Mar. Ecol. Prog. Ser.* 385: 189–204.
- Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.* 13: 159–169.

- Siegel, D. A., B. P. Kinlan, B. Gaylord, and S. D. Gaines. 2003. Lagrangian descriptions of marine larval dispersion. *Mar. Ecol. Prog. Ser.* **260**: 83–96.
- Swearer, S. E., J. S. Shima, M. E. Hellberg, S. R. Thorrold, G. P. Jones, D. R. Robertson, S. G. Morgan, K. A. Selkoe, G. M. Ruiz, and R. R. Warner. 2002. Evidence of self-recruitment in demersal marine populations. *Bull. Mar. Sci.* **70**: 251–271.
- Teller, K. G. 2022. Estimation and consequences of asymmetric dispersal on the genetics of coastal marine organisms in 1-d habitats. PhD dissertation, University of New Hampshire.
- Teller, K. G., and J. M. Pringle. 2023. Determining the most recent common ancestor in a finite linear habitat with asymmetric dispersal. *Theor. Popul. Biol.* **153**: 91–101.
- van Dijk, J. K., B. I. van Tussenbroek, K. Jiménez-Durán, G. J. Márquez-Guzmán, and J. Ouborg. 2009. High levels of gene flow and low population genetic structure related to high dispersal potential of a tropical marine angiosperm. *Mar. Ecol. Prog. Ser.* **390**: 67–77.
- Wares, J. P., and J. M. Pringle. 2008. Drift by drift: effective population size is limited by advection. *BMC Evol. Biol.* **8**: 235.
- Wares, J. P., A. E. Strand, and E. E. Sotka. 2021. Diversity, divergence and density: how habitat and hybrid zone dynamics maintain a genomic cline in an intertidal barnacle. *J. Biogeogr.* **48**: 2174–2185.
- Weersing, K., and R. J. Toonen. 2009. Population genetics, larval dispersal, and connectivity in marine systems. *Mar. Ecol. Prog. Ser.* **393**: 1–12.
- Wilkin, J. L., and E. J. Hunter. 2013. An assessment of the skill of real-time models of Mid-Atlantic Bight continental shelf circulation. *J. Geophys. Res. Oceans* **118**: 2919–2933.
- Wright, S. 1943. Isolation by distance. *Genetics* **28**: 114.