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Circulation constrains the evolution of larval development modes and life histories in the coastal ocean

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Abstract. The evolutionary pressures that drive long larval planktonic durations in some coastal marine organisms, while allowing direct development in others, have been vigorously debated. We introduce into the argument the asymmetric dispersal of larvae by coastal currents and find that the strength of the currents helps determine which dispersal strategies are evolutionarily stable. In a spatially and temporally uniform coastal ocean of finite extent, direct development is always evolutionarily stable. For passively drifting larvae, long planktonic durations are stable when the ratio of mean to fluctuating currents is small and the rate at which larvae increase in size in the plankton is greater than the mortality rate (both in units of per time). However, larval behavior that reduces downstream larval dispersal for a given time in plankton will be selected for, consistent with widespread observations of behaviors that reduce dispersal of marine larvae. Larvae with long planktonic durations are shown to be favored not for the additional dispersal they allow, but for the additional fecundity that larval feeding in the plankton enables.

We analyzed the spatial distribution of larval life histories in a large database of coastal marine benthic invertebrates and documented a link between ocean circulation and the frequency of planktotrophy in the coastal ocean. The spatial variation in the frequency of species with planktotrophic larvae is largely consistent with our theory; increases in mean currents lead to a decrease in the fraction of species with planktotrophic larvae over a broad range of temperatures.

Key words: coastal oceanography; larval dispersal; life history; ocean circulation.

Introduction

In many marine species with sedentary adults, offspring disperse greater distances than in equivalent terrestrial species, with great impact on regional- and local-scale population dynamics (see Kinlan and Gaines 2003). There is a great debate around the evolutionary pressures that encourage, in some coastal marine organisms, the development of the long planktonic durations that enable this dispersal (e.g., Vance 1973*a*, *b*, Christiansen and Fenchel 1979, Levitan 2000; see Plate 1). Even among closely related taxa in similar habitats, larval dispersal strategies can differ dramatically. Is a long planktonic duration favored primarily for the dispersal it allows or for some other advantage it confers (Strathmann 1985)? Tempering this debate have been the observations that dispersal is often less than one would expect for a given planktonic larval duration (T_{PLD}) if we assume passive dispersal (Strathmann et al. 2002, Levin 2006, Shanks 2009). Broadly, these efforts have discussed the putative advantages of the increased dispersal caused by a longer T_{PLD}, and found that the dispersal provided by observed T_{PLD}'s is far in excess of that needed to obtain benefits of dispersal such as genetic mixing, finding new habitat, and escaping temporal fluctuations in habitat quality (Pechenik 1999). From this, it has been surmised that long T_{PLD} is favored for reasons other than dispersal, even as long-distance dispersal significantly alters the population and genetic dynamics of a species (e.g., Strathmann et al. 2002, Riginos et al. 2011).

The analyses cited in the previous paragraph have largely neglected the role of coastal currents in asymmetrically dispersing larvae downstream of their parents. Coastal regions are influenced by strong (>5 cm/s) average nearshore currents (Robinson and Brink 2006). A brief consideration of an extremely idealized model of a coastal organism with downstream dispersal further suggests that any novel trait that increases the time a larva spends in the plankton, and thus increases the distance mean currents transport the larva downstream, will reduce the fitness of an individual; begin by considering an organism that disperses in a coastal ocean in a population subdivided into demes, sensu Wilkins and Wakeley (2002) (Fig. 1). Each deme exports

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$(1-\alpha)$ of its larvae to the next deme downstream (to the right in Fig. 1) and retains α of its reproductive output. An increase in α is analogous to a decrease in T_{PLD} or to an increase in behaviors that encourage local retention. At the upstream edge of the species range (the left-most deme in the figure), there is no import of larvae from farther upstream. Assume these demes are occupied by a haploid population with two alleles, A and B, which modify the retention to be α^{A} and α^{B}, respectively. Adults carrying allele A produce R^{A} larvae that settle, and those carrying allele B produce R^{B} larvae. Generations are nonoverlapping. Focus on the farthest upstream deme, which receives no larval subsidy from upstream. The population N_1 of each allele will grow at a rate set by R and the fraction α that are retained, so the ratio of allele A to allele B in the population in the next generation will be the ratio of $N_1^{\mathrm{A}}(t+1)=\alpha^{\mathrm{A}}R^{\mathrm{A}}N_1^{\mathrm{A}}(t)$ to $N_1^{\mathrm{B}}(t+1)=\alpha^{\mathrm{B}}R^{\mathrm{B}}N_1^{\mathrm{B}}(t)$

$$N_1^{\mathrm{A}}(t+1)/N_1^{\mathrm{B}}(t+1)=[(\alpha^{\mathrm{A}}R^{\mathrm{A}})/(\alpha^{\mathrm{B}}R^{\mathrm{B}})]\Big(N_1^{\mathrm{A}}(t)/N_1^{\mathrm{B}}(t)\Big).$$

Thus, the ratio of allele A to B will increase in the upstream-most habitat if $[\alpha^{\mathrm{A}}R^{\mathrm{A}}]/[\alpha^{\mathrm{B}}R^{\mathrm{B}}] > 1$. This result shows that if allele A increases the downstream transport of larvae by decreasing α^{A}, its abundance will decrease unless there is corresponding increase in R^{A}. If the frequency of allele A falls in the upstream-most deme, it will decline in all the downstream demes as long as it does not have a fitness advantage in those downstream populations (Kawecki and Holt 2002). This simplest model hints that an allele that causes increased dispersal is only favored if it also is linked to an increase in fecundity (cf. Holt 2003), suggesting that the persistence of long-distance dispersal in coastal marine organisms may be a side effect of traits that that increase fecundity or confer some other advantage.

To quantify these results in terms of realistic oceanographic and life-history parameters, we must consider a more realistic model that captures the trade-offs between T_{PLD}, fecundity, and dispersal as a function of observable ocean currents in a spatially explicit domain that is not artificially separated into discrete demes. The biophysical conditions that allow a long T_{PLD} to be evolutionarily stable will be directly quantified, making it clear when and why a long T_{PLD} can be evolutionarily stable. The model is then extended to study the change in fitness driven by larval behaviors that modify dispersal distance to explain a potential origin for observed larval behaviors that reduce dispersal. Finally, we demonstrate that size-dependent mortality and growth are required for realistic predictions of larval size and T_{PLD}, linking these results with the prior literature. After analyzing the model, its predictions will be compared to a global data set of the frequency of larval planktotrophy and other larval life histories in order to understand how the model relates to observed distributions of larval strategies.

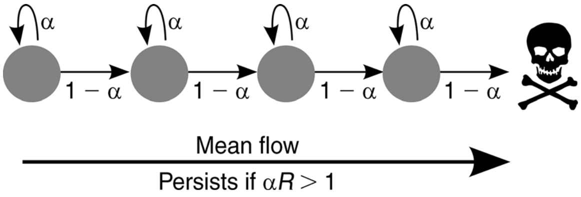

FIG. 1. A simple model of a marine coastal population depicted as a series of linked demes, with each deme exporting a fraction $(1-\alpha)$ of its larvae to the next deme downstream (to the right), and retaining a fraction α of the larvae within the deme. The death's head marks the end of the habitable domain.

METHODS

A more realistic model of dispersal and fitness

It is unrealistic to model the distribution of most coastal organisms as a series of discrete demes exchanging a relatively small number of migrants. Instead, there is a continuous distribution of individuals along the coast with some probability of dispersal upstream against the mean currents, even as most larvae move downstream (Siegel et al. 2003, 2008, Mitarai et al. 2008, Pringle et al. 2011). To capture these dynamics, we modeled a population along a finite extent of coastal ocean with spatially and temporally uniform habitat quality. The finite extent of the coastal ocean can be thought to represent that region of coast where the environmental conditions are within the physiological tolerance of the organism of interest. The size of the domain was always large enough that our results were not due to the loss of larvae off the downstream edge of the domain; a larger finite domain would not change the results.

The continuous distribution of the population was modeled as a series of discrete contiguous locations whose size was always much less than the potential dispersal distance, approximating a continuously distributed population. At each location, the population density and the frequency of alleles was kept as a continuous quantity, and the population density was limited by the spatially uniform carrying capacity of the habitat.

The generations were nonoverlapping. Each adult was assumed to release R larvae that would return to the coast and recruit, if population density did not limit recruitment. Thus, R is net of larval mortality and the loss of larvae that do not return to the coast (e.g., Jackson and Strathmann 1981), but does not include density-dependent reductions in fecundity. The larvae were moved, on average, a distance L_{adv} downstream of the parents, but with a standard deviation of L_{diff} around this distance due to variations in coastal flow (Byers and Pringle 2006). The dispersal kernel was Gaussian. Results for other kernels are presented in Appendix A.

To test how changes in dispersal affect fitness, we introduced two alleles, A and B, into the population, and for simplicity, we assumed the organisms are haploid, with no mutations. The allele frequency at a location after settlement was equal to the allele frequency in the larvae that recruit to that location. The frequency of A and B were inversely correlated due to zero-sum competition for space among the individuals carrying these alleles, a function of the density dependence in the model as in Wares and Pringle (2008). In each run of the model, A and B differed only slightly in dispersal and other characteristics. The model was repeatedly run to determine the relative fitness of the two alleles, sensu the "invasion fitness" of Metz et al. (1992). Details of model numerics and implementation are given in appendix B

Fitness and T_{PLD}*; understanding trade-offs*

To understand the effect on fitness of a change in T_{PLD}, it is necessary to understand the trade-offs between T_{PLD}, the mean and standard deviation of dispersal distance, and the realized fecundity of an organism (sensu Caswell 1981). There are three reasons to include these trade-offs in our study: First, the simple model presented in the *Introduction* hints that there are significant interactions between these parameters. Second, there is empirical evidence and theoretical support linking T_{PLD} and dispersal distance (Siegel et al. 2003 for a physical perspective, and Shanks 2009 for a biological perspective). Third, there is evidence linking T_{PLD} to fecundity through the interactions of T_{PLD} and the initial size of larvae, and, for related species, the initial size of larvae and fecundity (Strathmann 1985).

We first considered a sessile organism whose planktonic larvae drift passively with the currents. The larvae are obligate planktotrophs, and must reach a specific size to settle. If the larvae are large enough upon release, they will be able to settle directly; this represents direct development.

If larvae are released into a coastal ocean whose flow statistics are statistically stationary over the time larvae are in plankton, and over the path they travel, then L_{adv} and L_{diff} can be estimated from observable oceanic properties (Siegel et al. 2003) as follows:

$$L_{\mathrm{adv}} = UT_{\mathrm{PLD}} \tag{1}$$

with a random spread around this mean distance specified by

$$L_{\mathrm{diff}} = (\sigma^2 \tau_{\mathrm{L}} T_{\mathrm{PLD}})^{0.5}. \tag{2}$$

U is the mean alongshore current, σ is the standard deviation of the alongshore currents around that mean, and τ_{L} is the timescale of the fluctuations of the alongshore currents around the mean. More details on these parameters can be found in Siegel et al. (2003). All physical parameters are measured along the path of larvae, and can be affected by any larval behavior that alters that path, such as vertical migration, or by changes in the season that the larvae are released (Byers and Pringle 2006).

Following Vance (1973*a*) and Levitan (2000), we linked both the time the larvae spend in the plankton and the realized fecundity to the initial size of the larvae; support for these assumptions and descriptions of their weaknesses can be found in Strathmann (1985) and Christiansen and Fenchel (1979). Their parameterizations for time spent in plankton will be modified to a form that is both easier to relate to the observations in the literature and is more realistic. In appendix C, we show how our parameterization relates to theirs, and as a consequence, we make explicit the origin of the apparent disagreement between the results of Vance (1973*a*, *b*) and Levitan (2000). The first assumption is that there is a finite amount of maternal mass that can be allocated to reproduction, such that if the larvae halve their mass, then there will be twice as many larvae released:

$$N_{\mathrm{rel}} = M_{\mathrm{mat}}/S_{\mathrm{larv}} \tag{3}$$

where N_{rel} is the number of larvae released, M_{mat} is the mass the mother can allocate to reproduction, and S_{larv} is the mass of the larvae released. The larvae are assumed to have a mortality m per time in the plankton, and they gain mass at a rate of g per time. The variables m and g are assumed not to vary with larval size; this is relaxed in the third section of the *Results*. The mortality m includes all non-density-dependent mechanisms that prevent a larva from successfully recruiting; thus, it includes drifting offshore away from suitable habitat (Jackson and Strathmann 1981), as well as predation and other sources of direct mortality. At a time t after release, the number and size of larvae are

$$N(t) = N_{\mathrm{rel}} \exp(-mt) \qquad \text{and} \qquad S(t) = S_{\mathrm{larv}} \exp(gt).$$

If the larvae must reach a critical mass, S_{crit}, to settle so $S(T_{\mathrm{PLD}}) = S_{\mathrm{crit}}$, the T_{PLD} is

$$T_{\mathrm{PLD}} = g^{-1} \ln(S_{\mathrm{crit}}/S_{\mathrm{larv}}) \tag{4}$$

and since $N(T_{\mathrm{PLD}}) = R$, the number of larvae that reach this mass and thus are competent to settle will be

$$R = (M_{\mathrm{mat}}/S_{\mathrm{crit}}) \times \exp[(g-m)T_{\mathrm{PLD}}]. \tag{5}$$

(Post-settlement mortality can reduce R; if spatially uniform, it would have the same effect as reducing $M_{\mathrm{mat}}/S_{\mathrm{crit}}$. As we will see in Eqs. 6–8 below, this did not affect our results and we will neglect this mortality for now). There are two important corollaries to the above assumptions: First, from Eq. 5, the realized fecundity R increases with T_{PLD} if $(g-m) > 0$. Second, from Eqs. 1 and 2, both the mean and stochastic components of larval transport increase as T_{PLD} increases.

The dispersal and fecundity trade-offs described in Eqs. 1–5 are for nonoverlapping generations; in Byers and Pringle (2006), these results are extended to species with overlapping generations; the main differences are an increase in effective fecundity caused by reproduction over multiple years, and a potential increase in the stochastic component of larval transport due to interannual variability in the mean larval transport in each year.

Understanding the impact on fitness of changes in T_{PLD} in this model can seem daunting, for there are nine parameters to consider: U, σ, τ_L, T_{PLD}, g, m, M_{mat}, S_{crit}, and S_{larv}. This can be simplified greatly with dimensional analysis (Price 2003). The numerical model only depends on the three parameters (L_{adv}, L_{diff}, and R), and these are functions of only five parameters or combination of parameters (U, $\sigma^2\tau_L$, T_{PLD}, $g - m$, and $M_{\mathrm{mat}}/S_{\mathrm{crit}}$) in two fundamental units (time and length). The Buckingham-Π theorem says all possible solutions of this model can then be defined by three nondimensional parameters (Price 2003). The choice of nondimensional parameters is not prescribed, and we find the most useful choices are:

$$\Pi_1 = T_{\mathrm{PLD}}(g - m) \qquad (6)$$

$$\Pi_2 = U^2/\Big((g - m)\sigma^2\tau_L\Big) \qquad (7)$$

$$\Pi_3 = M_{\mathrm{mat}}/S_{\mathrm{crit}}. \qquad (8)$$

In the numerical modeling, we found that Π_3 influences whether a species can persist by controlling R (Byers and Pringle 2006). It does not control the relative fitness of changes in T_{PLD}. We did not consider it further except to note that the modeling confirms that, all other things being equal, an increase in Π_3 increases fitness; i.e., that if an allele can increase the resources applied to reproduction or decreases the size a larva must reach to settle successfully at no other fitness cost, it will improve fitness.

Π_1 is a "scaled larval duration"; the T_{PLD} scaled by larval growth rate less mortality $g - m$. From Eq. 5, if $g - m$ is negative, an increase in T_{PLD} will decrease realized fecundity, and if it is positive, an increase in T_{PLD} will increase realized fecundity. Π_2 is a "scaled advection"; it is the ratio of the fundamental biological time scale of the system $(g - m)^{-1}$ to $\sigma^2\tau_L/U^2$, the advective/diffusive timescale of the system. If the T_{PLD} is greater than $\sigma^2\tau_L/U^2$, the mean coastal current ("advection") dominates the transport of the larvae, and if it is less than $\sigma^2\tau_L/U^2$, the transport by stochastic eddies and other flow variations dominate the transport of larvae. Where the scaled advection Π_2 is large, the mean downstream transport of the larvae will dominate the dynamics of larval dispersal.

The model was run iteratively to determine the fitness change caused by an allele that leads to a slightly changed T_{PLD} (numerical details in Appendix B). All behavior of this model can be explained by the two parameters Π_1 and Π_2; it does not matter which combination of U, $\sigma^2\tau_L$, T_{PLD}, $g - m$ leads to a particular set of values for Π_1 and Π_2. Doubling $(g - m)$ and halving $\sigma^2\tau_L$ and T_{PLD} would produce a model with the same behavior as leaving those parameters unmolested because this change leaves Π_1 and Π_2 unchanged. The model was run for $\Pi_1 = -1.5$ to 1.5 and $\Pi_2 = -2.5$ to 2.5, and the dimensional parameters are recovered by holding U and $\sigma^2\tau_L$ constant and varying T_{PLD} and $g - m$ (this parameter range encompasses the range typically encountered by coastal larvae; an expanded range is shown in Appendix A).

Do life-histories patterns in the sea match predictions?

It has long been noticed that there are large-scale patterns in the distribution of different life-history modes in the sea (Thorson 1950), but there has been relatively little explanatory work linking them to the physical dynamics of the ocean aside from temperature (Clarke 1992, Pearse and Lockhart 2004, Fernández et al. 2009, and recently reviewed in Marshall et al. 2012 [hereafter DM]). To examine how currents modify the frequency of larval planktotrophy, we used life-history data from DM. They gathered life-history data from a large number of marine invertebrates distributed globally to understand the environmental variables that constrain life-history strategies in these organisms; we constrained our analysis to their records that are adjacent to continental coastlines. Details on the data selection and geographical distribution can be found in DM and in Appendix D. Circulation and sea-surface data from surface drifters compiled by Lumpkin and Garraffo (2005) were used to calculate the circulation components of Π_2. Following DM, annual averages of the monthly mean currents and monthly current variability were used; further details are found in Appendix D.

Π_2 is a composite of physical parameters controlling the mean and stochastic components of transport (U an $\sigma^2\tau$, respectively) and the biological parameter growth less mortality $(g - m)$. This latter term is poorly constrained. We assumed that its spatial variation is dominated by temperature; this is plausible (Houde 1989, Rumrill 1990, Pepin 1991, Hoegh-Guldberg and Pearse 1995), but there are surely other environmental constraints on growth, and the functional form of the relationship between $(g - m)$ and temperature is unclear. To cope with this uncertainty we made multiple logistic regressions, each within a narrow temperature range, for the presence of a planktotrophic larval stage against the log of U^2, $\sigma^2\tau$, and Π_2 (Table 1; the log-transformation enhances normality and makes Π_2 an additive function of the log of its components). By focusing on data from within narrow temperature ranges, we could focus on the effects of the physical variables U and $\sigma^2\tau$ independently of temperature and its effects on growth and mortality. Even within these temperature bands, the variability of $(g - m)$ must still be estimated to estimate Π_2. The increase in growth with temperature among a broad range of species is assumed to vary as described for within-species variation by O'Connor et al. (2007). Data on the variability of larval mortality with

TABLE 1. Summary table of the relationship between the fraction of marine invertebrate species with planktotrophic larvae (from Marshall et al. 2012) and the log-transformations of various physical variables that make up Π_2, along with log-transformed Π_2.

Temperature range (°C)	U^2	$\sigma^2\tau_L$	Π_2	N
7.5–11	√ (−)	√ (−)	√ (−)	34
11–15	√ (−)	×	√ (−)	107
15–20	√ (−)	×	√ (−)	63
20–27	√ (+)	×	√ (+)	154

Notes: Temperature ranges are chosen so that the fractional change in growth rate expected from the relationship of O'Connor et al. (2007) is the same over each temperature range. N is the number of data points in each analysis. Ticks (√) indicate a significant relationship ($P < 0.05$), and ×'s show no significant relationship; negative (–) and plus (+) symbols indicate a negative or positive relationship, respectively, between the predictor variable and larval planktotrophy. U is the mean currents experienced by the larvae in a Lagrangian sense, σ is the standard deviation of those currents (both in units of m/s), and τ_L is the Lagrangian decorrelation timescale of the currents in seconds. Further details of data analysis are given in Appendix D.

temperature is scarce. We assumed that mortality is dominated by predation, and the metabolism of predators, and thus, the rate of predation, scales as growth does (e.g., Houde 1989, Pepin 1991, both for fish larvae). These assumptions are hard to formally justify, but no better choice is apparent (see Rumrill 1990). From this, we could estimate how $(g - m)$ varied with temperature, but not its absolute value. Further details are given in Appendix D.

RESULTS

The relative fitness of a longer T_{PLD}

The results of the modeling are presented in Fig. 2A as a scaled selection coefficient s'. An s' of 1 indicates that a 10% increase in T_{PLD} leads to an $s = 0.1$ for the allele, and likewise, an s' of -1 leads to an $s = -0.1$. Thus, s' can be thought of as approximately the slope of a fitness surface, where an s' greater than zero indicates a longer T_{PLD} is favored, and less than zero indicates a shorter duration is favored. The solid curved line in Fig. 2A marks the boundary between positive and negative s' and marks a valley in the fitness surface (as indicated by the arrows). Organisms that start above the line will tend to increase their time in plankton, and thus the magnitude of the scaled time in plankton Π_1, while those that are below it will tend to decrease their time in plankton and the magnitude of Π_1.

An organism with a small T_{PLD}, so the scaled larval duration $\Pi_1 \approx 0$, is in an evolutionary stable state because s' is negative everywhere around this line. Any allele that causes a small increase in T_{PLD} will be selected against. Thus, the absence of a planktonic stage is always evolutionarily stable, and we would expect that in this model any organism that has a very short T_{PLD} to evolve toward a direct-development strategy, or some other strategy with no planktonic development.

The scaled advection Π_2 approaches zero where the mean current U is zero: This is essentially the limit of no ocean currents studied by Vance (1973*a*) and Levitan (2000). As they found, in this limit, a longer T_{PLD} is favored ($s' > 0$) when the growth rate of the larvae g exceeds the mortality rate of the larvae in the plankton m so $\Pi_1 > 0$. (Their debate over the uni- or bi-modal distribution of larval sizes is resolved in Appendix C.)

When is a longer T_{PLD} evolutionarily stable in the presence of mean currents? Nowhere that $\Pi_1 < 0$, thus, nowhere that $(g - m) < 0$ and a longer T_{PLD} reduces realized fecundity. However, where $\Pi_1 > 0$ and the scaled advection $\Pi_2 < \approx 1.9$ (either mean current U is small or the effective diffusivity caused by stochastic flows $\sigma^2\tau_L$ is large), there is a portion of Fig. 2A where s' is positive. (The limiting threshold of Π_2 for large Π_1 is shown in Appendix A: Fig. A1. The precise threshold of Π_2 depends on the dispersal kernel; other kernels are also shown in that appendix). In this region, there is an evolutionary pressure for an even longer T_{PLD}. This suggests an evolutionary instability leading to infinitely many infinitely small larvae (Eq. 3), leading to an infinite fecundity (Eq. 5).

These results suggest that, where mean currents are small or the flow is variable and where larval growth can exceed mortality, long planktonic durations can endure. Direct development is always an evolutionarily stable strategy. However, this model has several troubling aspects. It assumes larvae that are purely passive, despite much evidence that mean dispersal is less than would be expected for passive larvae. It also predicts larvae with either no planktonic dispersal, or an infinitely long planktonic duration and infinitely small larvae, which neglects the finite size of actual planktonic larvae and the presence of many lecithotrophic larvae with larval durations of several days (e.g., Grantham et al. 2003). We address the origin of larval behavior in the next section, and in doing so, explain the origin of the results presented in this section. In the following section, we also address the limits of the theory at long and short planktonic duration to clarify the origin of larvae of finite size and/or short planktonic duration.

The relative fitness of changes in T_{PLD}, reproduction, and dispersal

To understand why a long T_{PLD} is evolutionarily stable in some limits, and not others, we systematically altered the model by changing one parameter independently of the trade-offs linking it to the other parameters, and saw how this affected fitness. This served a dual purpose: If, for example, we altered the mean distance the larvae travel downstream L_{adv} by increasing it several percent while leaving other parameters unchanged, we can both judge if L_{adv} drives the results given in the previous section, and we can judge the evolutionary stability of behaviors that alter L_{adv} alone.

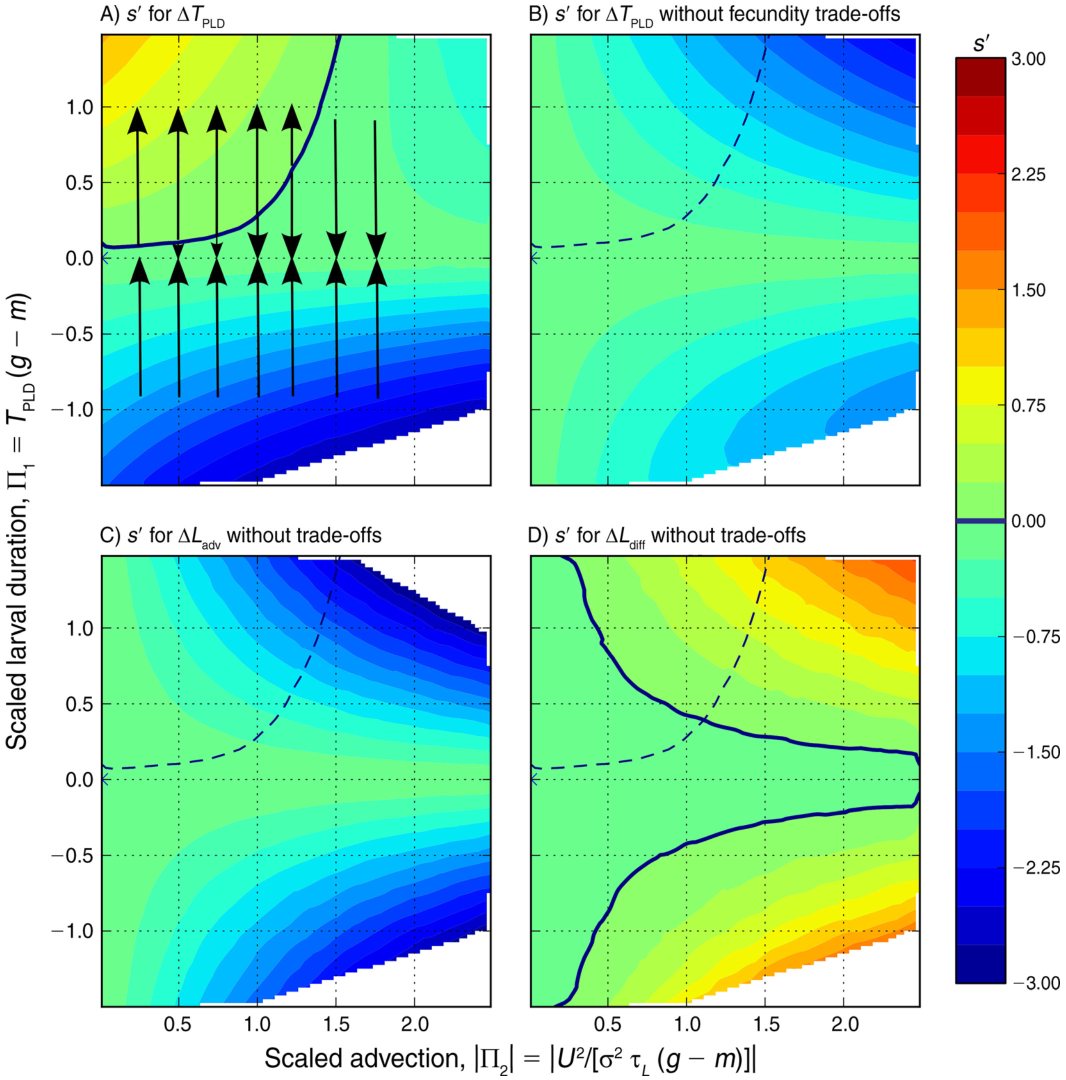

FIG. 2. (A) The scaled fitness s' caused by a change in the larval duration T_{PLD} for allele B. Where $s' = 1$, an allele that causes 10% increase in T_{PLD} is selected for with $s = 0.1$. Where negative, an increase in T_{PLD} decreases fitness. The solid line is the $s' = 0$ contour. The arrows indicate the direction T_{PLD} will evolve over time. (B) As in panel (A), but for a change in T_{PLD} that alters dispersal, but not fecundity. (C) As in panel (A), but for a change in mean downstream distance the larvae disperse, L_{adv}. (D) As in panel (A), but for a change in the standard deviation of the larval dispersal distance, L_{diff}. The dashed line in panels (B) through (D) is the same as the solid line in (A), and indicates the boundary where a longer T_{PLD} begins to confer increased fitness in a model that includes all trade-offs. The horizontal axis displays the magnitude of Π_2 because if $\Pi_1 < 0$, then $\Pi_2 < 0$. U is the mean currents experienced by the larvae in a Lagrangian sense, σ is the standard deviation of those currents (both in units of length/time), and τ_L is the Lagrangian decorrelation timescale of the currents. The parameters g and m are the growth and mortality of larvae respectively, both in units of time^{-1}.

Increasing the mean distance the larvae travel L_{adv} for a given T_{PLD} and leaving all other parameters as one would expect from Eqs. 2–5 decreases fitness for all possible parameters (Fig. 2C). This decrease in fitness is greater as time in plankton increases ($|\Pi_1|$ increases) and as the mean currents U increase or the variance in currents σ decreases ($|\Pi_2|$ increases). Thus, an increase in mean downstream transport of larvae, within the assumptions of this model, always decreases fitness, and any larval behavior that decreases the mean transport is, all other things equal, favored.

Increasing the time in plankton *without* changing fecundity, but with changes to both mean and stochastic dispersal as specified in Eqs. 1 and 2, always decreases fitness (Fig. 2B). The pattern of the decrease of fitness is strikingly similar to that caused by an increase of L_{adv} (compare Fig. 2B to C). This suggests that the main deleterious effect of increasing T_{PLD} with no fecundity trade-off is the increase in downstream larval transport. Conversely, the main benefit of increasing T_{PLD} with the fecundity trade-off is that, if $(g - m) > 0$, it increases fecundity (Fig. 2A). Thus, any behavior that decreases time in plankton, but leaves fecundity unchanged, will increase fitness.

Increasing the stochastic component of larval transport L_{diff}, but leaving all other parameters as one would expect from Eqs. 1–5 leads to a more complex pattern of fitness (Fig. 2D). Increasing L_{diff} increases the spread of larvae released from a single point, and so increases both downstream and upstream transport equally. Increasing L_{diff} increases fitness when time in plankton is larger ($|\Pi_1|$) and where the mean current U is large or the current variability σ is small (Π_2). These are parameter ranges where the downstream transport of larvae by the mean currents is important, suggesting that the main importance of L_{diff} is to counteract the mean downstream transport of larvae L_{adv}. Where an increased L_{diff} is favored, it would tend to push a species toward overlapping generations and iteroparity, for, as discussed in Byers and Pringle (2006), these will interact with interannual variability in the currents to increase $L_{\mathrm{diff.}}$

These results strongly suggest that long planktonic durations do not persist for the great downstream dispersal they allow; instead, this downstream dispersal is largely disadvantageous and will be selected against. This evolutionary pressure to reduce mean dispersal and, for some parameter ranges, increase the variability of dispersal, suggests selection for a rich set of dispersal behaviors that should be observable in many marine organisms, largely in the form of behaviors that reduce the alongshore transport of larvae and traits such as brooding structures, egg capsules, and gels that increase retention and reduce dispersal.

Impacts of neglected larval dynamics

In common with Vance (1973*a*, *b*), the theory developed in the prior two sections suggests that the evolutionary stable states are either an infinite number of infinitely small offspring or offspring that spend no time in the plankton. Neither result entirely matches observed life histories. Even for planktotrophic larvae with long $T_{\mathrm{PLD,}}$ most larvae are much larger than the smallest possible size for a multi-cellular organism (Bell and Mooers 1997). And many non-feeding larvae have some planktonic duration, albeit for a time shorter than planktotrophic larvae. For example, in Grantham et al.'s (2003) compilation of species along the California, Oregon, and Washington coasts in the United States, the median time in plankton of planktotrophes was 35 days, and the median for lecithotrophes was 5 days (cf. Mortensen 1921, Todd and Doyle 1981, Emlet et al. 1987, Hoegh-Guldberg and Pearse 1995).

These deviations from our predictions result from biological dynamics we neglected. We had neglected the changes in growth, g, and mortality, m, as larval size changes. While this is appropriate to understanding how circulation alters the fitness of planktonic dispersal stages, it discards a mechanism that limits the minimum size of larvae. As discussed in Peterson and Wroblewski (1984), mortality of marine larvae increases as size decreases. Kiflawi (2006) and Taylor and Williams (1984) convincingly argue that that the optimal initial size of larvae S_{larv} will occur where $g = m$ (see their Fig. 1). When in our simulations we included the power-law growth and mortality curves chosen so that there is an optimal larval size in the absence of a mean current ($U = 0$; e.g., see Taylor and Williams 1984, Kiflawi 2006), the results shown in Fig. 2 are qualitatively unchanged except for the presence of an evolutionary stable larval size with finite planktonic duration in the parameter space where we had predicted an evolutionary pressure causing a runaway to ever smaller larvae. Where there is a mean current, this optimal initial larval size S_{larv} occurs where $g > m$, i.e., at a larger larval size than would be expected without currents. Essentially, the downstream advection acts analogously to increased mortality. As Π_2 increases, the evolutionarily stable larval size increases, and the stable larval duration decreases, until the optimum crosses the threshold where shorter larval durations are favored. At that point, no planktonic larvae are favored, only direct development.

We also did not include in the model described in the *Methods* some dynamics that tend to promote moderate larval dispersal. A temporally uniform environment was assumed, with no stochastic disturbances to habitat, and we assumed that there is no penalty in settling near parents beyond that of the density dependence in the model. The environment is also assumed to be spatially uniform, with no small-scale patchiness in habitat quality. These neglected phenomena can provide some fitness advantage to moderate planktonic dispersal (e.g., Pechenik 1999, Burgess et al. 2013): But, as forcefully argued by Strathmann et al. (2002), observed planktonic durations in species with long planktonic durations are far in excess of those needed to provide the advantage (cf. Strathmann 1980, 1985). However, as they discussed, these phenomena may explain why some species with short (less than several days) planktonic durations have not always evolved toward having no planktonic duration.

Lecithotrophic larvae with long planktonic durations and without facultative feeding are never evolutionarily stable in our theory, because such larvae must be fully provisioned to reach critical settlement size at birth, and increasing their T_{PLD} does not cause an increase in fecundity (Marshall and Bolton 2007; Levitan 2000 discusses facultative feeding, cf. McEdward 1997). This is the case discussed in the last section and shown in Fig. 2C, where L_{adv} is increased without a fecundity trade-off. Their presence suggests either evolutionary constraints preventing the loss of a planktonic stage and development of direct development (Jablonski and Lutz 1983, Pechenik 1999), or phenomena which favor very long dispersal distances that we have not identified. We suspect that selection for increased offspring sizes post-metamorphosis drives the evolution of lecithotrophy in many species (Marshall and Morgan 2011). Because our model focuses on pre-metamorphic events alone, it is perhaps unsurprising that our model does not predict the evolutionary stability of lecithotrophy in these cases.

Model predictions and life-history patterns

The frequency of planktotrophic larvae shows a significant and expected decrease with increasing mean currents and Π_2 for all but the warmest temperature bin (Table 1 and Fig. 3, which shows the frequency of planktotrophy for the three cooler temperature ranges from the logistic regression; further details, including data distribution and goodness of fit, in Appendix D). The variation in frequency is large over oceanographically plausible current ranges. As might be expected, the regression suggests that, for a given ocean current there is more planktotrophy at warmer temperatures (the vertical differences between lines in Fig. 3); however, this interaction between temperature and the relationship of currents to planktotrophy is not statistically significant for the temperature ranges shown in Fig. 3, and its confirmation must await more data. As shown in DM, there is an increase in the frequency of planktotrophic larvae with temperature (their Table 1), suggesting the expected increase in planktotrophy with increasing ($g - m$). The relationship between the strength of the variable currents $\sigma^2\tau$ and the frequency of planktotrophy is not significant in three of the temperature ranges, and runs counter to the theory in the coldest temperature range.

DISCUSSION

The predictions of our model matched the spatial distributions of life history in the global coastal ocean. As predicted, the frequency of benthic species with planktotrophic larvae, relative to other life histories, decreased as the scaled advection Π_2 increased. We also detected relationships with the components of Π_2: increasing frequency of species with planktotrophic larvae associated with decreasing mean currents U and increasing growth less mortality ($g - m$), to the extent the latter can be assumed to be controlled by temperature.

That the effects of mean currents on the incidence of planktotrophy are less strong in warmer waters is perhaps unsurprising. Species with planktonic development are most prevalent in warmer waters (DM: Figs. 2 and 3), suggesting that these conditions favor this developmental mode. Warmer temperatures allow more rapid development, and so the negative effects of mean currents on dispersal and persistence are likely to be minimized under these circumstances. To illustrate, consider that in cooler climes, planktotrophic larvae must spend much longer in the plankton because of the strong temperature dependent development rates that larvae show. As such, even slight increases in mean currents will result in large decreases in persistence. In contrast, planktrophic larvae in warmer waters spend so little time in the plankton (relatively speaking) that even large increases in mean currents are unlikely to affect persistence strongly, reducing the importance of dispersal as a mechanism linking T_{PLD} to fitness (O'Connor et al. 2007).

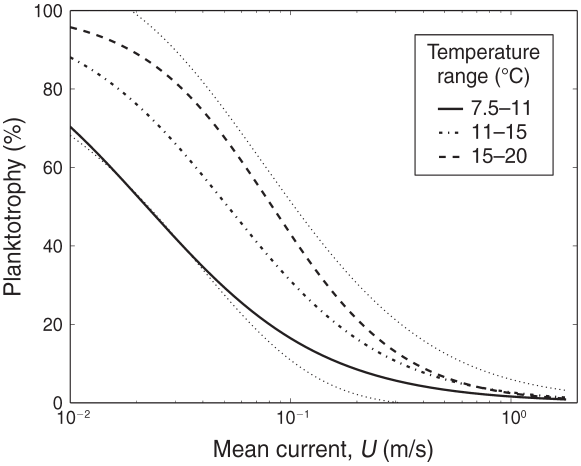

FIG. 3. The proportion of larval planktotrophy as a function of the mean ocean currents for the three temperature ranges showing a significant negative relationship between mean currents and life history, using percent planktotrophy from Marshall et al. (2012). The dotted lines are the ± standard error limits for the central temperature range; the other error lines are omitted for clarity, but are similar in magnitude. The differences between the three lines are not significant to $P < 0.05$. Further details of analysis are given in the *Methods* and Appendix D.

More speculatively, one might expect that larval behavior can more effectively decouple dispersal from the strength of mean circulation in warmer waters. Within developmental modes, egg sizes are smallest at high temperatures and largest at cool temperatures (DM). As such, the pre-feeding, non-swimming phase lasts much longer in cooler climes (larger eggs take longer to develop in their non-feeding stage, cooler eggs take longer to develop [Marshall and Bolton 2007, Marshall and Keough 2007]). Consequently, the potential for swimming behaviors to mitigate the effects of currents is greater in warmer climes than cooler. Validating this speculation will require quantitative observations of the relative effectiveness of behavior at reducing dispersal under different conditions.

The lack of the expected correlation between the variability of currents ($\sigma^2\tau$) and the frequency of planktotrophic larvae may be driven by the collinearity of the mean and variable currents. The log-transformed variability in the currents is strongly correlated with the mean current ($R = 0.88$ over all temperatures) and is less important to the scaled advection Π_2 than the mean currents (as can be seen by the similarity of the relationship to larval planktotrophy of both U^2 and Π_2). This suggests that any relationship between current variability and larval planktotrophy is masked by the stronger effect of the mean currents on Π_2.

In summary, we found that the observed distribution of the frequency of larval planktotrophy is broadly

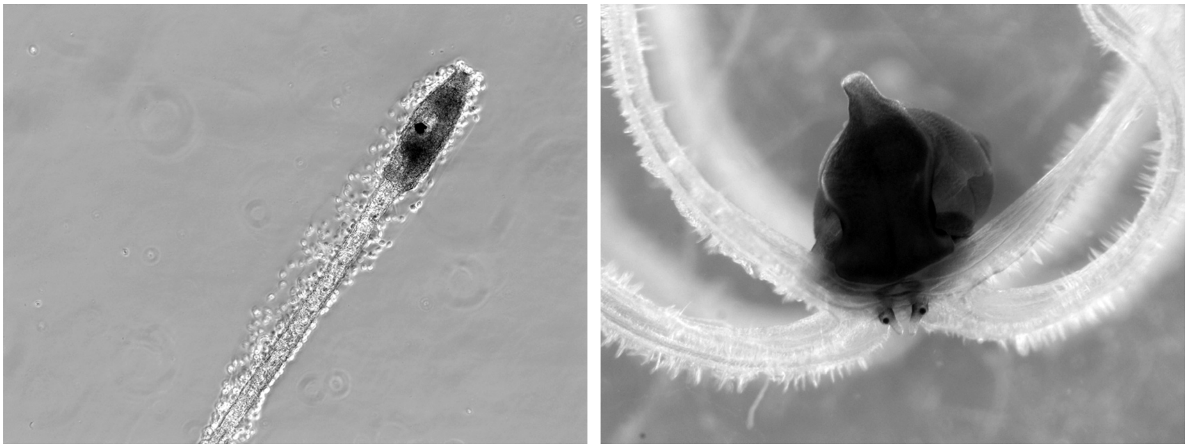

PLATE 1. (Left) Tadpole larvae of *Ciona intestinalis*, which has a typical dispersal time in the plankton of hours to minutes (Svane and Havenhand 1993). (Right) Late-stage larvae of *Concholepas concholepas*, with a planktonic stage of 3–12 months that can enable long distance larval dispersal. However, *C. concholepas* also exhibits diel migration and other vertical positioning behavior that will tend both to reduce dispersal, to enhance its ability to find prey to feed on, and to retain it in nearshore environments (Manríquez and Castilla 2011). Both larvae are about 1 mm in size. Photo credits: left, Amy Hooper; right, Patricio Manríquez.

consistent with our theory, documenting a link between temperature, ocean circulation, and life history for benthic species in the coastal ocean. Further examination of these relations must progress on two fronts: first, the inclusion of more species from more coastlines with a broader range of environmental conditions than Marshall et al. (2012), and secondly, the more detailed examination of larval behaviors in order to determine the true mean and variable currents *experienced by* larvae, instead of merely assuming the surface current is the relevant dispersal mechanism (cf. Byers and Pringle 2006).

CONCLUSIONS

Extending the work of Vance (1973*a*, *b*) and Levitan (2000) to include the effects of ocean circulation, we found that mean alongshore currents diminish the fitness of planktotrophic larvae. For benthic species on an open coast with limited spatiotemporal variation, direct development is always an evolutionarily stable strategy. Planktotrophy and long T_{PLD} is evolutionarily stable only when the larval growth rate is larger than larval mortality $(g - m) > 0$, and that the scaled advection experienced by the larvae (Π_2) is small.

Marine organisms with planktonic larvae, due to the long time they drift with the ocean currents, have the potential for much greater dispersal than similar terrestrial species with passive dispersal of propagules (Kinlan and Gaines 2003, Kinlan et al. 2005). We argue that great dispersal potential is favored in marine species not for dispersal per se, but for the larval feeding and additional fecundity allowed by long planktonic durations. When $(g - m) > 0$, larval feeding in the plankton can increase the effective fecundity of the adults without a corresponding increase in maternal investment (cf. Vance 1973*a*, Taylor and Williams 1984, Kiflawi 2006). While there are other explanations for planktonic dispersal that either invoke temporal and/or spatial stochasticity in habitat or the need to escape negative effects of settling too near parents, they do not seem to explain the very large dispersal potential of organisms with typical planktonic durations of tens of days or more (Strathmann et al. 2002; as discussed when we considered neglected larval dynamics, these other explanations for larval dispersal may explain the persistence of short larval durations within species with lecithotrophic larvae).

However, the observed dispersal of larvae is most often less than would be expected for particles drifting passively with the currents (Levin 2006, Cowen and Sponaugle 2009, Shanks 2009). Many larval strategies have been found that decrease the mean distance larvae are dispersed, either by decreasing exposure of larvae to advective currents, decreasing the time larvae spend in the plankton, and/or increasing the stochastic spread of larvae. Byers and Pringle (2006) found that a disproportionate fraction of the species in coastal Oregon release larvae in months where the mean currents are a minimum or across months where the mean currents reverse, serving to both decrease mean larval transport and increase the variability of this transport. Also striking are observations of nearshore crustacean larvae along the West Coast of North America: Many are found to use vertical positioning behavior to stay within the nearshore region with its much slower alongshore currents despite strong offshore transport near the surface (Morgan et al. 2009, Miller and Morgan 2013).

This reduction in alongshore dispersal is consistent with the predictions of our model, where increased downstream transport of larvae by mean currents reduces fitness and any strategies that tends to reduce the mean transport of larvae while leaving mortality and time in plankton unchanged will be favored.

Observed patterns of life-history distribution in the global coastal ocean are found to be broadly consistent with our prediction, with increased temperature and decreased mean alongshore currents associated with an increase in the fraction of species with planktotrophic larvae.

As with most simplified theories of complex systems, much of what can be learned from this theory comes from observations that appear to be inconsistent with its predictions; this disagreement identifies situations where, in often interesting ways, our assumptions are not valid. A theory is a mechanism to test assumptions. When a species with a long larval dispersal stage is identified where the scaled advection Π_2 is large, several questions are foremost: Does the larva have behavior that can minimize its exposure to the strong currents (or increase exposure to variable currents) sufficiently to reduce the Π_2 it experiences? Is the species present at that location because it is maintained by larval input from a more congenial upstream location? Or can it persist because of some inter-species competition effect not included in this model of intra-species competition (e.g., is it a "weedy" species that can only survive where other species have been eliminated by spatially and temporally ephemeral disturbances)? Even where the scaled advection is small, it is illuminating to consider the persistence of larval dispersal stages that do not obviously increase fecundity, as in the case of many lecithotrophes.

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Supplemental Material

Appendix A

Sensitivity to dispersal kernel shape (*Ecological Archives* E095-086-A1).

Appendix B

Numerical solution method (*Ecological Archives* E095-086-A2).

Appendix C

Reconciling Vance (1973*a*, *b*) and Levitan (2000) (*Ecological Archives* E095-086-A3).

Appendix D

Details of comparison of theory to observed life-history distribution (*Ecological Archives* E095-086-A4).

Appendix E

Variation of larval growth *g* with temperature (*Ecological Archives* E095-086-A5).