Larval and adult traits coevolve in response to coastal oceanography to shape marine dispersal kernels

James H. Peniston and Scott C. Burgess

Department of Biological Science, Florida State University, 319 Stadium Drive, Tallahassee,
8 FL, 32306-4296, USA.

Scott Burgess ORCID: 0000-0002-0348-3453
James H. Peniston ORCID: 0000-0003-3577-1035

Keywords: *dispersal evolution, life history, directional dispersal, marine larvae, integral projection model, adaptive dynamics*

Abstract (currently 200 words, which is the max)

Dispersal emerges as an outcome of organismal traits and external forcings. However, it remains unclear how the emergent dispersal kernel evolves as a by-product of selection on the underlying traits. This question is particularly compelling in coastal marine systems where dispersal is tied to development and reproduction, and where directional currents bias larval dispersal downstream causing selection for retention. We modelled the dynamics of a metapopulation along a finite coastline using an integral projection model and adaptive dynamics to understand how asymmetric coastal currents influence the evolution of larval (pelagic larval duration) and adult (spawning frequency) life history traits, which indirectly shape the evolution of dispersal kernels. Selection induced by unidirectional currents favors the release of larvae over multiple time periods, allowing long pelagic larval durations and long-distance dispersal to be maintained in marine life cycles in situations where they were previously predicted to be selected against. Two evolutionary stable strategies emerged: one with a long pelagic larval duration and many spawning events resulting in a dispersal kernel with a larger mean and variance, and another with a short pelagic larval duration and few spawning events resulting in a dispersal kernel with a smaller mean and variance. Our theory shows how the statistics of coastal ocean flows are important agents of selection that can generate multiple, often co-occurring, evolutionary outcomes for marine life history traits that affect dispersal.

Introduction

Dispersal has fundamentally important consequences for the demographic and genetic structure of populations, and how species respond and adapt to changing conditions (Clobert et al. 2012; Travis et al. 2013). As a result, it is important to understand how dispersal evolves. Decades of work by theoreticians has focused on dispersal propensity or dispersal distance as the evolving trait and shown how kin competition, inbreeding, and spatio-temporal variation can select for dispersal (Starrfelt and Kokko 2012). However, dispersal in nature arises as an outcome of the biological traits of organisms and external forcings (e.g., wind and water currents) that both affect movement, fitness, and the final distribution of dispersal distances (Burgess et al. 2016). Therefore, challenges remain in explaining how dispersal actually evolves in nature, rather than how it can evolve. That is, there is a need to identify which traits cause dispersal outcomes, and what factors cause selection on those traits to influence the pattern of dispersal that emerges and changes through evolutionary processes (Burgess et al. 2016). This challenge is particularly prevalent in marine systems, where dispersal is tied to early development in complex life cycles, and traits that influence dispersal outcomes are also traits that influence development and reproduction.

In many marine invertebrates and fishes, adults are sessile or demersal, but their microscopic larval offspring are capable of dispersing great distances in ocean currents (kilometers to 100's of kilometers in some species), mostly during obligate periods of development when larvae feed and are incapable of settling (Kinlan and Gaines 2003; Shanks 2009). However, the ease of larval dispersal in ocean currents creates problems. Along many coastlines, the average current is unidirectional over the timescales that dispersal occurs (Davis 1985). As a result, passive larvae drift downstream, which results in larvae being constantly washed away from settlement habitat (Gaylord and Gaines 2000; Largier 2003; Siegel et al. 2003). If there is not enough upstream retention, downstream dispersal ultimately leads to population extinction (Byers and Pringle 2006). This results in a 'drift-paradox', where adult populations persist despite the threat of a net downstream loss of larvae (Müller 1982; Speirs and Gurney 2001; Müller 1982; Speirs and Gurney 2001; Pachepsky et al. 2005; Shanks and Eckert 2005; Byers and Pringle 2006). Therefore, the ubiquity of alongshore currents in coastal habitats should select for dispersal traits that increase upstream retention, but may also result in downstream dispersal as a consequence.

One trait that can influence dispersal and upstream retention is pelagic larval duration (Grantham et al. 2003; Shanks 2009; Treml et al. 2015; Cecino and Treml 2021). Shorter pelagic larval durations decrease the risk that passively dispersing larvae are transported and lost downstream on average (Siegel et al. 2003; Byers and Pringle 2006). Recent analyses considering the role of ubiquitous alongshore currents in coastal habitats have shown that stronger currents should lead to the loss of pelagic larvae from marine life cycles all together (Pringle et al. 2014), suggesting that species with feeding larvae (planktotrophy) should only be found where currents are relatively weak. When mean currents are weak relative to the stochastic variation in currents, there are potential advantages to longer larval durations that relate to greater growth and survival in pelagic versus benthic habitats, but not necessarily for the dispersal they facilitate (Burgess et al. 2016; Meyer et al. 2021*a*; Iwasa et al. 2022). There is a large literature on the evolution of marine reproductive strategies based on egg size-number trade-offs where egg size affects larval development times depending on whether larvae feed or not (Vance 1973; Strathmann 1985; Emlet et al. 1987; Levitan 2000; Marshall and Keough 2007). This theory predicts that longer larval durations evolve when selection favors the production of many small offspring that feed for themselves away from adult habitat, but require longer to feed and develop independently to a size and stage required for settlement back into adult habitats (Vance 1973; Strathmann 1985; Emlet et al. 1987; Levitan 2000). Therefore, because egg size affects development time, which in turn affects the potential for upstream retention, ocean currents should strongly modify how marine egg size-number trade-offs evolve (Reitzel et al. 2004; Shanks and Eckert 2005; Pringle et al. 2014).

Despite most analyses on the causes of marine dispersal focusing on the traits of larvae, especially larval behaviors (Leis 2006; Morgan 2014), traits that affect dispersal and upstream retention may also include those of the less mobile adult stages. Parents not only control larval duration via the effects of egg size, but also the timing, frequency, and, in some cases, location in which offspring are released into coastal flow fields (Strathmann 1982; Morgan and Christy 1995; Reitzel et al. 2004). In particular, unidirectional alongshore currents often reverse direction on many coastlines due to wind or seasons. Releasing offspring on multiple occasions can increase retention by increasing the variability in advection that batches of larvae encounter among different releases. Accessing greater variability in currents over multiple releases increases the chance that enough of a parent’s lifetime reproductive output occasionally moves upstream against the average downstream flow compared to releasing only one batch of larvae (Byers and Pringle 2006). So while larval behaviors can also increase retention (Paris and Cowen 2004; Metaxas and Saunders 2009; Bottesch et al. 2016; Burgess et al. 2022), adult traits also control dispersal by when and how often larvae are released into the current. Small dispersing larval stages and marine life histories are therefore not at the whim of strong physical forcing. Instead, the physical forcing itself causes selection on life history traits, and the pattern of dispersal that emerges can evolve (Burgess et al. 2016).

Our goal here was to develop theory that helps us understand how coastal oceanographic processes affect the evolutionary outcome of traits that affect dispersal. Most previous theory has considered reproductive strategies in the absence of oceanography (Vance 1973; Levitan 2000), considered dispersal itself as the evolving trait rather than the underlying traits of the individuals that interact with currents to give rise to dispersal patterns (Shaw et al. 2019), or only focused on larval traits (Pringle et al. 2014). We use an adaptive dynamics framework to present new theory showing how asymmetric coastal currents influence the coevolution of pelagic larval duration and adult spawning frequency in coastal ecosystems. We consider lifetime dispersal kernels as the dispersal kernel of all larvae released over an individual's lifespan. Our model shows how the evolutionary stable combination of pelagic larval duration and spawning frequency changes with oceanographic conditions and indirectly affects the expectation for marine dispersal kernels. We show that for many realistic coastal oceanographic conditions, there are two evolutionarily stable life history strategies: one with a longer pelagic larval duration and higher spawning frequency and another with a shorter pelagic larval duration and lower spawning frequency, leading to different expected dispersal kernels under the same flow regime.

Model Description:

We model the dynamics of a metapopulation along a finite coastline using an integral projection model structured by space and age. The integral projection model framework is quite general, however, and can be adapted for different assumptions by replacing any of the functions below with another suitable function.

We study the phenotypic evolution of pelagic larval duration (T_{PLD}) and number of spawning events per individual parent (N_{spawn}) by analyzing this model with an adaptive dynamics methodology, which allows for both frequency- and density-dependent dynamics (McGill and Brown 2007; Rees and Ellner 2016). Adaptive dynamics works by introducing a mutant with a small change in either T_{PLD} or N_{spawn} into a stabilized population of residents and calculating the invasion growth rate of its lineage. We determine the evolutionary stable phenotypes by iterating this process and finding the phenotypes that cannot be invaded by mutants with small changes. Trait values that cannot be invaded are referred to as evolutionary stable strategies (ESSs), and can be thought of as the endpoint, or outcome, of evolution.

In our results, we first discuss the evolution of T_{PLD} and N_{spawn} separately, that is, assuming one trait evolves while the other trait does not evolve. These analyses provide a useful understanding of how each trait independently affects each other's evolution given the currents. We then consider a model where both traits coevolve (*i.e.*, affect each other simultaneously and reciprocally) and determine the evolutionary stable combinations of trait values.

The ratio of mean alongshore flow (U) to short timescale fluctuations in currents (σ, that is, current fluctuations over the timescales captured by U) is a key descriptor of how oceanographic conditions affect dispersal evolution (Pringle et al. 2014). We will refer to this ratio as "scaled alongshore flow" and present results of life history evolution for $0 \leq U / \sigma \leq 2$, which captures a realistic range of oceanographic conditions (Robinson and Brink 2006).

Relationship between pelagic larval duration and fecundity

Individuals either produce many small eggs or fewer larger eggs. We model this size-number trade-off by defining the number of eggs released f as the total amount of material contributed to egg production C divided by the egg volume s_{egg}, that is $f = \dfrac{C}{s_{\mathrm{egg}}}$.

There is empirical evidence that egg size affects pelagic larval duration depending on whether larvae feed or not. For feeding (planktotrophic) larvae, pelagic larval duration decreases with egg size, especially in echinoderms (Vance 1973; Emlet et al. 1987; Levitan 2000; Marshall and Keough 2007; Marshall et al. 2018). Here, we focus on feeding larvae because we are initially interested in explaining how long-distance dispersal is maintained in marine invertebrate and fish life histories, and to also compare our results to previous models of pelagic larval duration in coastal oceans (e.g., Pringle et al. 2014). However, future studies should consider non-feeding larvae or other traits that affect larval duration.

We model the negative relationship between the pelagic larval duration and egg size following Pringle et al. (2014) such that

$$T_{\mathrm{PLD}} = \frac{1}{g}\ln\left(\frac{s_{\mathrm{crit}}}{s_{\mathrm{egg}}}\right) \qquad \text{(eq. 1)},$$

which can be rearranged as

$$s_{\mathrm{egg}} = \frac{s_{\mathrm{crit}}}{\exp\left(gT_{\mathrm{PLD}}\right)} \qquad \text{(eq. 2)},$$

where T_{PLD} is pelagic larval duration, g is the rate at which larvae gain mass during feeding, and s_{crit} is critical size that the egg must reach to settle. A given increase in egg size for smaller eggs reduces T_{PLD} more than the same increase in egg size for larger eggs.

Larval mortality

We assume that the probability of larvae surviving through the pelagic stage decreases with pelagic larval duration and increases with egg size such that is given by

$$\exp\left[-\frac{mT_{\mathrm{PLD}}}{s_{\mathrm{egg}}}\right], \qquad \text{(eq. 3)}$$

where m is the baseline daily larval mortality rate. The survival benefits of larger larvae can arise from larger larvae acquiring more energy, using proportionally less energy, or being less susceptible to predation (Marshall et al. 2018). More generally, equation (3) can be treated as a heuristic assumption that leads to a hump-shaped relationship between egg size and number of larvae that survive the pelagic phase. Such a relationship is an important concept in the marine life history literature because it allows for an optimal intermediate egg size, depending on the parameter values (Smith and Fretwell 1974; Levitan 2000).

Given equation 3 and the egg size-number tradeoff above, the number of larvae that survive the pelagic phase is

$$f = \frac{C}{s_{\text{egg}}} exp\left[- \frac{mT_{\text{PLD}}}{s_{\text{egg}}} \right] \qquad \text{(eq. 4).}$$

We only consider scenarios where larval growth rate is greater than the larval mortality rate (g-m > 0), because otherwise there is always selection for no pelagic larval stage and this has been explored previously (Pringle et al. 2014; Iwasa et al. 2022).

Relationship between pelagic larval duration and the dispersal kernel

Dispersal is dependent on mean alongshore flow (U), the standard deviation in alongshore flow (σ), the Lagrangian decorrelation timescale (τ), and pelagic larval duration (T_{PLD}). Siegel et al. (2003) show the mean dispersal distance (advection) is

$$L_{\text{adv}} = UT_{\text{PLD}},$$

and the standard deviation in dispersal distance (diffusion) is

$$L_{\text{diff}} = \left(\sigma^2 \tau T_{\text{PLD}} \right)^{0.5}.$$

Based on basic oceanographic principles, a Gaussian dispersal kernel is used for passively dispersed larvae (Largier 2003). Thus, the probability of dispersing from location x to y is given by

$$k(x,y) = \left(\frac{1}{L_{\text{diff}}\sqrt{2\pi}}\right)\exp\left(\frac{\left(y-\left(x+L_{\text{adv}}\right)\right)^{2}}{L_{\text{diff}}^{2}}\right). \qquad \text{(eq. 5)}$$

For a discussion of the sensitivity of upstream retention and selection on long pelagic larval durations to non-Gaussian dispersal kernels see (Pringle et al. 2009, 2014).

Recruitment competition

We assume that larvae can only settle at a site if there is an available microsite (e.g., space on a rock) and that there are only K microsites available at each site. Larvae have lottery competition for microsites (Chesson and Warner 1981; Warner and Chesson 1985). That is, the number of lineage i (mutant or resident) larvae that successfully settle is proportional to the relative frequency of that lineage among larvae arriving at the site. Therefore, the expected number of lineage i individuals that establish themselves at site x is given by

$$r\left(n_{ix}\right) = \mu\frac{n_{ix}}{n_{ix}+n_{jx}}, \qquad \text{(eq. 6)}$$

where n_{ix} is number of lineage i larvae arriving at site x and μ is the number of unoccupied microsites, which is given by K minus the total number of adults that died the previous time step.

Post-settlement dynamics

After settlement, individuals live for up to N_{spawn} time steps and release larvae each time step. The probability of post-settlement individuals surviving to the next time step is given by the function $s(a)$, where a is age. $s(a)$ can be any age-dependent mortality function, but we will assume that all post-settlement individuals have the same mortality rate A_m until reaching age N_{spawn}, at which point they all die. For all presented results we divide the annual amount of material contributed to egg production C by N_{spawn} such that lifetime investment in egg production is fixed if there is no adult mortality (e.g., individuals could either produce 100 eggs ten separate times or produce 1000 eggs all during one spawning event). We make this assumption because we are interested in the specific effects of spawning frequency *per se* and this assumption controls for the increased lifetime fecundity that might accrue with increased spawning frequency, or the amount of material contributed to egg production C that might increase as adults grow (Marshall et al. 2022). Future studies could consider additional complexities that emerge from specific relationships between spawning frequency and fecundity.

Temporal fluctuations in alongshore flow

We investigate the effect of variation in alongshore flow rates that takes place on time scales equivalent to spawning frequency. For simplicity we will refer to these fluctuations as interannual variation in flow, which is accurate if time steps in our model are treated as years. However, the time steps can be treated as any unit of time longer than the Lagrangian decorrelation timescale (which we set to 4 days, Davis 1985), and "interannual" fluctuations can be interpreted as among time step fluctuations.

We incorporate such interannual variation in flow rates into our model by replacing diffusion (L_{diff}) with an estimate for the standard deviation of larval dispersal distance for all larvae released over the lifetime of an adult, $L_{\mathrm{diffeffect}}$, which was developed by Byers and Pringle (2006)

$$L_{\mathrm{diffeffect}}=\sqrt{\left(L_{\mathrm{diff}}^2+\left(1-\frac{1}{N_{\mathrm{spawn}}}\right)\sigma_{L_{\mathrm{adv}}}^2\right)}, \qquad \text{(equation 7)}$$

where $\sigma_{L_{\text{adv}}}$ is the interannual standard deviation in L_{adv}. Given our equation for L_{adv} above, $\sigma_{L_{\text{adv}}}$ is $\sigma_{\text{IA}} T_{\text{PLD}}$, where σ^2_{IA} is the interannual variation in mean flow rates U. Note that, if $\sigma_{\text{IA}} > 0$ and $N_{spawn} > 1$, then $L_{\text{diffeffect}} > L_{\text{diff}}$. We checked the robustness of using this estimation of $L_{\text{diffeffect}}$ using the direct simulation methods described in the Appendix.

Integral projection model

Metapopulation dynamics are given by the set of coupled equations

$$N_0(y, t+1) = r\left(\sum_{a=0}^{N_{\text{spawn}}} \int_0^L f\, k(y,x)\, N_a(x,t)\, \mathrm{d}x\right) \qquad \text{(eq. 8)}$$

$$N_a(y, t+1) = s(a)\, N_{a-1}(x,t)\,. \qquad \text{(eq. 9)}$$

$N_0(y, t+1)$ is the number of larvae (age 0) individuals that settle at site y in timestep $t + 1$. $N_a(y, t)$ is the number of age a individuals at site y at timestep t. f is the number of larvae that survive the pelagic phase (eq [4]), $k(y,x)$ is the probability of dispersing from site x to site y (eq [5]). $s(a)$ gives the probability of age a individuals surviving to age a+1. L is the length of the coastline. If necessary for the study system, equations [8–9] can be adapted such that mortality rate, fecundity, and larvae size can vary with age.

Calculating invasion fitness

Invasion fitness λ is calculated as the initial growth rate of a mutant lineage introduced into, and competing with, a stabilized resident metapopulation. As long as the resident population's local retention is positive, the resident population will fill all microsites along the coast. Therefore, the long-term stable resident distribution is K at all sites. The stable age distribution of residents is then given by (Dewi and Chesson 2003)

$$N_{ar} = \frac{l_{ar}}{\sum_{a=1}^{N_{spawn}} l_{ar}}$$

where l_{ar} is the probability of surviving to age a. We can the rewrite the recruitment function (eq. 6) as

$$r(n_{mx}) = \frac{\left(\sum_{a=1}^{a_{max}} s(a)\, N_{ar} K\right) n_{mx}}{\sum_{a=1}^{a_{max}} \int_{0}^{L} f(a)\, k(y,x,a)\, N_{ar} K \,\mathrm{d}x}. \qquad \text{(eq. 10)}$$

Note that the number of unoccupied sites μ is now given by the sum of age-specific adult mortality rates $s(a)$ multiplied by the stabilized number of resident adults in that age class $N_{ar}K$. Also, the denominator no longer includes mutants because invader density is by definition very low and can therefore be assumed to not affect density dependence. In essence, this is now a density-independent model where the resident metapopulation distribution is treated like an environmental factor affecting recruitment and growth of the mutant population.

Following Ellner and Rees (2006), we calculate invasion growth rates by numerically evaluating our model using the midpoint rule. Details of this protocol are included in the Appendix. We checked the robustness of our assumption that the resident population is stationary and our estimate of $L_{\mathrm{diffeffect}}$ by comparing our results to stochastic simulations which tracked the population dynamics of residents and stochastically varied flow rates. These simulations confirmed the key patterns seen in our deterministic model the Appendix. We focus our analysis on the deterministic model, however, because results of the stochastic model are dependent on specific assumptions about how stochasticity and density dependence are implemented, and while important process could emerge from the stochasticity, the goal of this paper is to make general conclusions about the evolution of T_{PLD} and N_{spawn} in coastal systems.

Results

Evolution of pelagic larval duration (T_{PLD})

No mean alongshore flow

Without ocean currents (*i.e.*, U=0 and σ=0), there is only one pelagic larval duration (T_{PLD}) that is an evolutionarily stable strategy (ESS) and it occurs at the T_{PLD} which maximizes the total number of larvae that survive the pelagic phase (Figure 1). This result recovers classic results from previous models without oceanography (Smith and Fretwell 1974; Levitan 2000).

If there are short timescale fluctuations in flow, but still no mean alongshore flow (*i.e.* U=0 and σ>0), the ESS T_{PLD} will slightly decrease from the optimum of 38.35 days shown in figure 1 (Figure 2 when scaled alongshore flow is 0). The slight decrease occurs because our model assumes there is a limited range of habitable coastline and a higher T_{PLD} leads to more individuals dispersing away from the source location and thus being lost off the upstream or downstream edge of the habitable range. However, this effect is small. Given our baseline parameter values, the ESS T_{PLD} never decreased more than 3 days even given the highest values of σ we would expect to see in nature.

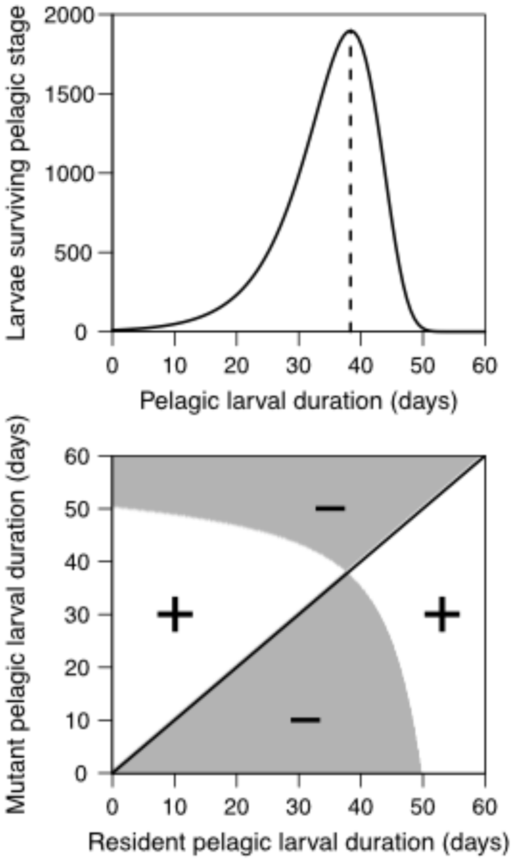

Figure 1. Evolution of pelagic larval duration (T_{PLD}) without considering oceanography. Top panel: total number of larvae that survive the pelagic phase (*f*) as a function of pelagic larval duration given by equation 4. Dashed vertical line denotes the optimal pelagic larval duration that gives the maximum number of surviving larvae. Bottom panel: Pairwise invasion plot. Invasion fitness of the mutant is greater than 1 in the white areas and less than 1 in the grey areas. The black line denotes the 1:1 line where the invasion fitness of the mutant is 1. Note that the evolutionary stable pelagic larval duration in the bottom panel occurs at the value that maximizes the number of surviving larvae. Parameters: τ=4, C=0.1, s_{crit}=0.0103, g = 0.16, m =5×10^{-7}, A_m=0.1.

Effects of scaled alongshore flow on the evolution of pelagic larval duration

As the mean alongshore flow (U) current increases, relative to short timescale fluctuations in currents (σ), which we refer to as “scaled alongshore flow”, there is selection for decreased T_{PLD} (Figure 2). For small to moderate values of scaled alongshore flow ($<\approx 1$), there is only one evolutionary stable T_{PLD}, the value of which is relatively high but decreases as scaled alongshore flow increases for a given number of spawning events. For high values of scaled alongshore flow ($>\approx 1$), there are two evolutionary stable T_{PLD} values, one of which is at the minimum possible T_{PLD} (we set this minimum $T_{\mathrm{PLD}} = \tau$). The two ESSs are separated by an unstable equilibrium (indicated by the dashed lines in Figure 2 for each N_{spawn}). If the population with a given N_{spawn} begins with a T_{PLD} below this unstable equilibrium, evolution by a series of small mutations will lead the population to the lower evolutionary stable T_{PLD}. Alternatively, if the population begins with a T_{PLD} above this unstable equilibrium, evolution by a series of small mutations will lead the population to the higher evolutionary stable T_{PLD}. Figure 3 shows pairwise invasion plots for examples when there is one ESS or two ESSs for T_{PLD}.

These general results presented as evolutionary stable strategies for semelparous organisms are qualitatively similar to what Pringle et al (2014) showed in terms of selection coefficients in non-overlapping generations. There is selection for the pelagic larval durations that lead to the most larvae at or upstream of the source location (Pringle et al. 2014). With low scaled alongshore flow, enough local retention occurs with both short and long T_{PLD}, but a longer T_{PLD} maximizes fecundity because it is associated with the production of smaller, more numerous eggs. In contrast, with high scaled alongshore, a long T_{PLD} results in not enough local retention to offset the losses of larvae downstream. As a result, upstream retention is greatest with a short T_{PLD} because it minimizes downstream dispersal. However, unlike Pringle et al. (2014) we show a continuous decline in ESS T_{PLD} as scaled alongshore flow increases up until the ESS T_{PLD} reaches the minimum value. In other words, for any given scaled alongshore flow below a certain strength (~1.0 in with our parameters), there is a unique ESS T_{PLD} (Figure 2). This differs from the results of Pringle et al. (2014) which only predicted two possible evolutionary stable pelagic larval durations: the maximum possible value and the minimum possible value.

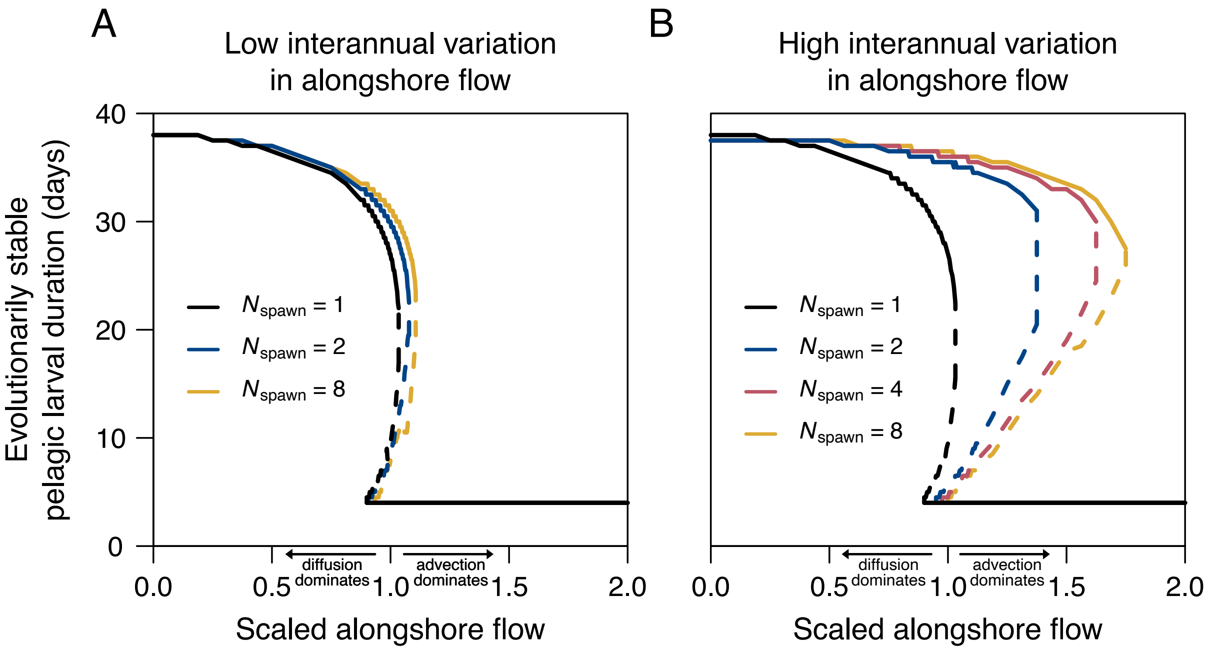

Figure 2. Effect of scaled alongshore flow and the number of spawning events (N_{spawn}) on the evolutionary stable pelagic larval duration (T_{PLD}). Panel A shows results when the standard deviation of interannual mean flow rates is σ_{IA}=0.012 (meters/second) and panel B shows results for when σ_{IA}=0.035 (meters/second). Solid lines denote evolutionary stable values of T_{PLD} while

dashed lines denote unstable equilibrium values of T_{PLD}. Different colors denote different numbers of spawning events (N_{spawn}) as indicated in the figure legend. Parameters: σ=8000 (meters/day), τ=4, C=0.1, s_{crit}=0.0103, g = 0.16, m =5×10^{-7}, A_m=0.1, K=200, length of coastline = 100 kilometers, minimum value of T_{PLD} was set to τ.

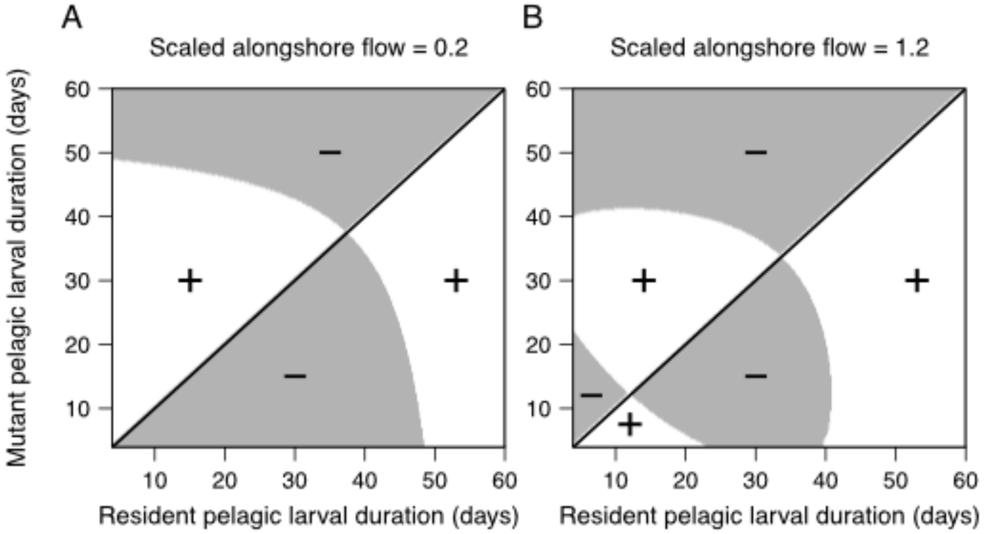

Figure 3. Example pairwise invasion plots for when there is one ESS (left panel) or two ESSs (right panel). Invasion fitness of the mutant is greater than 1 in the white areas and less than 1 in the grey areas. The black line denotes the 1:1 line where the invasion fitness of the mutant is 1.0. In both plots, N_{spawn} = 2 and all parameters are the same as in figure 2B.

Effects of the number of spawning events on the evolution of pelagic larval duration

The number of spawning events (N_{spawn}) changes the pelagic larval duration that is evolutionarily stable under a given flow regime. Spawning more often longer pelagic larval durations to both remain evolutionarily stable for higher mean scaled alongshore flow rates (Figure 2). For instance, consider a mean scaled alongshore flow of 1.5 in Figure 2B. If

N_{spawn}=1, the only ESS T_{PLD} is at 4 days (the minimum T_{PLD}), but if N_{spawn}=8, T_{PLD}=35.5 is evolutionarily stable as well as T_{PLD} of 4 days. As interannual variation in mean flow rates increases ($\sigma_{\mathrm{IA}} > 0$), increasing N_{spawn} allows for higher ESS values of T_{PLD}. Increasing N_{spawn} increases the range of scaled alongshore flow rates where there are two ESS T_{PLD} values because spawning on multiple occasions has a smaller effect on the lower evolutionarily stable pelagic larval duration than then upper one (Figure 2).

The reasons why longer pelagic larval durations become evolutionarily stable when spawning is more frequent can be understood in terms of what Byers and Pringle (2006) showed for population persistence. Larvae released in different years are exposed to different mean alongshore current speeds and directions. Parents that release larvae in multiple years have greater dispersion in their lifetime dispersal kernel (the dispersal kernel of all larvae released over an individual's lifespan). Increased dispersion allows parents to retain more larvae at or upstream of their spawning location without necessarily increasing fecundity. However, longer pelagic larval durations both increase dispersion and increase fecundity. Therefore, in our adaptive dynamics framework, spawning more frequently (increasing dispersion and upstream retention), together with the effect of longer pelagic larval durations (increasing dispersion and fecundity), allows longer T_{PLD} to become evolutionarily stable in addition to short pelagic larval durations. In contrast, short pelagic larval durations are the only evolutionarily stable strategy in non-overlapping generations with high scaled alongshore flow.

Evolution of the number of spawning events (N_{spawn})

Larger interannual fluctuations typically lead to greater evolutionarily stable numbers of spawning events (Figure 4, but see Figure A1 for a counter example). In addition, longer pelagic larval durations and greater scaled alongshore flow speeds also lead to greater evolutionarily stable number of spawning events (Figure 4). At low scaled alongshore flow, the evolutionarily stable number of spawning events is always 1 because increasing N_{spawn} increases the diffusion experienced over the lifetime on an individual (increasing $L_{diffeffect}$ when $\sigma_{\mathrm{IA}}>0$), and increases the number of offspring dispersing away from the source location which reduces local growth rates. As scaled alongshore flow increases however, the evolutionarily stable number of spawning events increases to offset the increased loss of larvae downstream, and it increases quicker with longer pelagic larval durations (Figure 4). Longer pelagic larval durations lead to greater downstream losses, more so as scaled alongshore flow increases. Therefore, more frequent spawning evolves to increase retention and offset the downstream losses from increasingly longer pelagic larval durations.

Adult mortality has the effect of decreasing the rate at which the evolutionarily stable number of spawning events increases with scaled alongshore flow (Figure 4 vs Figure A2). With adult mortality, individuals with higher N_{spawn} values have lower expected lifetime fecundity than when there is no adult mortality (Figure 4). For a given pelagic larval duration, the evolutionarily stable number of spawning events is not affected by any increase in fecundity that might arise from repeated spawning because we deliberately held potential lifetime fecundity constant for all N_{spawn} values.

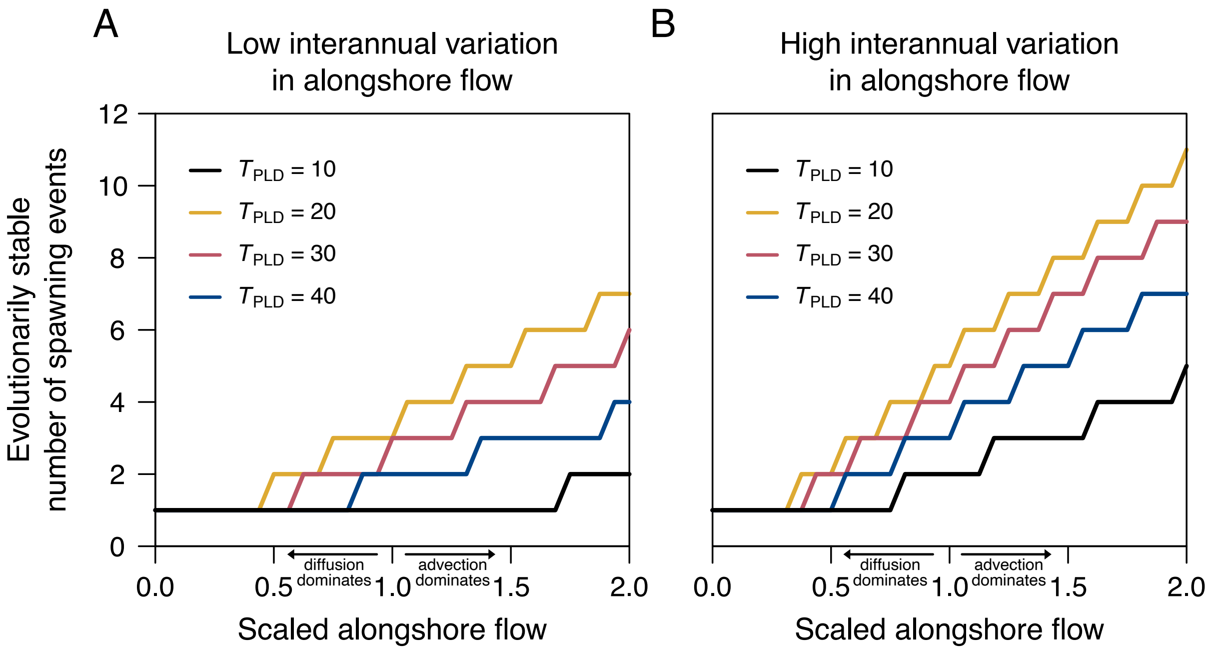

Figure 4. Effect of scaled alongshore flow and pelagic larval duration (T_{PLD}) on the evolutionarily stable number of spawning events (N_{spawn}) when there is adult mortality A_m=0.1. Panel A shows results when the standard deviation of interannual mean flow rates σ_{IA}=0.012 meters/second and panel B shows results for when σ_{IA}=0.035 meters/second. Different colors denote different pelagic larval durations as indicated in the figure legend. All other parameters are the same as in figure 2.

Coevolution of pelagic larval duration and the number of spawning events

When pelagic larval duration and the number of spawning events coevolve, three insights emerge (Figure 5). First, when scaled alongshore flow is low, a single long pelagic larval duration and a single small number of spawning events are evolutionarily stable, and similar to when they evolve independently. Second, when scaled alongshore flow is high, a single short pelagic larval duration and a single large number of spawning events are evolutionarily stable, also similar to when they evolve independently. Third, and in contrast to outcomes when each trait evolves independently, at intermediate scaled alongshore flows, two combinations of pelagic larval duration and number of spawning events are evolutionarily stable: one with a long pelagic larval duration and many spawning events, and another with a short pelagic larval duration and few spawning events (Figure 5). In particular, two evolutionarily stable numbers of spawning events at higher scaled alongshore flow was not predicted when considering the evolution of the number of spawning events in isolation (Figure 4). With greater degrees of interannual variation, there is a greater range of scaled alongshore flow values that lead to two evolutionarily stable combinations of pelagic larval duration and number of spawning events. The initial trait values determine whether the traits evolve to the upper of lower ESSs (Figure A3)

An outcome of coevolution at low scaled alongshore flow values is that the evolutionarily stable pelagic larval duration does not always decrease monotonically with increased scaled alongshore flow as it does when pelagic larval duration evolves independently (compare Figure 2 to Figure 5). The ESS T_{PLD} can increase with an increased scaled alongshore flow (e.g., scaled advection ~0.5–0.7 in Figure 5A) when selection favors in increase in spawning frequency, which then allows a higher pelagic larval duration to be stable in that current (Figure 4).

At intermediate values of scaled alongshore flow where two combinations of pelagic larval duration and number of spawning events are evolutionarily stable, the evolution of spawning events effects the maximum value of scaled alongshore flow where the upper ESS combination is stable. As seen in Figure 2, if only T_{PLD} evolves, the upper ESS remains stable with higher scaled alongshore flow if there is a higher value of N_{spawn}. Therefore, if there is a higher ESS N_{spawn} for a given scaled alongshore flow in the coevolutionary model, the upper ESS

N_{spawn} values remain stable with more scaled alongshore flow. In contrast, the evolution of spawning frequency has little effect on pelagic larval duration in the lower ESS combination. The lower ESS T_{PLD} is always the minimum possible value and thus the lower ESS N_{spawn} evolves how as it does when it evolved independently with a fixed T_{PLD} (Figure 4). At the highest values of scaled alongshore flow, the upper ESS combination is no longer stable and only the lower combination of traits remains.

Effects of coevolution of pelagic larval duration and the number of spawning events on lifetime dispersal kernels

The theory presented here shows how three key aspects of coastal oceanographic regimes (mean alongshore currents U, short-term stochasticity in currents σ, and interannual variation in mean alongshore currents inter σ_{IA}) select on both larval and adult traits to increase upstream retention and alter the expected mean and spread of lifetime dispersal kernels.

When scaled alongshore flow is low, organisms evolve a long pelagic larval duration and a single spawning release, which results in a high fecundity and dispersal kernels with a mean shifted downstream and high variance (e.g., Figure 7C). When scaled alongshore flow is high, organisms evolve short pelagic larval durations and fewer spawning events, which results in a low fecundity and evolutionarily stable dispersal kernels with a low downstream mean and low variance (*e.g.*, orange distribution in Figure 7D). However, when interannual variation in mean alongshore currents is high, a second dispersal kernel with a mean distance shifted downstream and a much higher spread in dispersal distances is also evolutionarily stable (*e.g.*, red distribution in Figure 7D). This second dispersal kernel is the result of selection for a long pelagic larval duration (which leads to high fecundity) and high spawning frequency, which is just another way to counter the downstream losses of larvae, but results in much greater mean and variance in dispersal distances as a consequence.

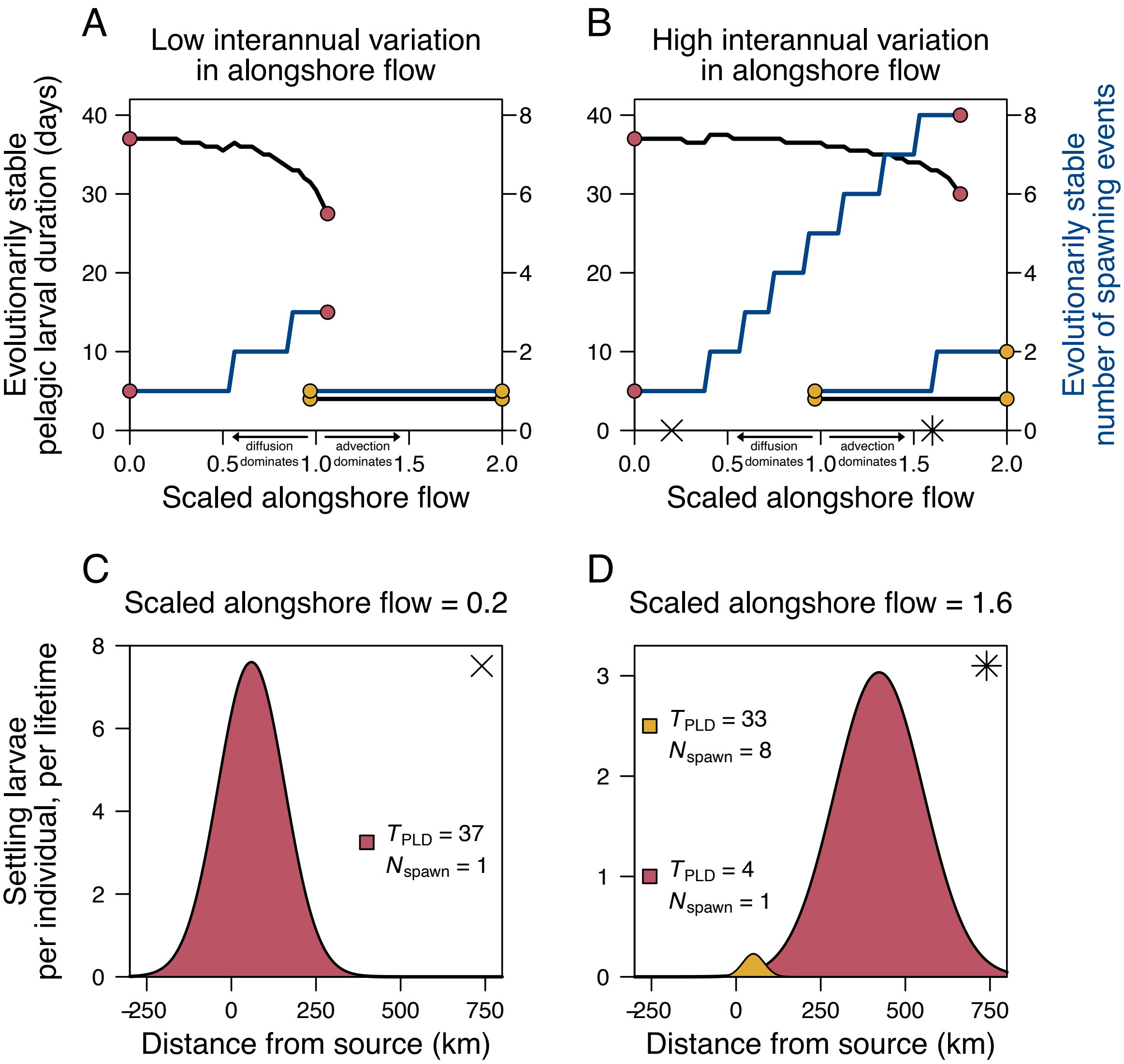

Figure 5. Coevolution of pelagic larval duration (T_{PLD}) and number of spawning events (N_{spawn}). Top panels show the evolutionarily stable values of T_{PLD} (black lines) and N_{spawn} (blue lines) for different degrees of scaled alongshore flow with a low standard deviation of interannual mean flow rates (A; σ_{IA}=0.012 meters/second) or high standard deviation of interannual mean flow

rates (B; σ_{IA}=0.035 meters/second). Lines denoted with the same color circles are evolutionarily stable together. Note that at intermediate values of scaled alongshore flow there are two combinations of T_{PLD} and N_{spawn} that are evolutionarily stable: one where both T_{PLD} and N_{spawn} are at high values and where they are both at low values. Bottom panels show the distribution of larvae released by one individual over its lifetime for different evolutionarily stable life history strategies that emerge with high interannual variation in alongshore flow. Panel C shows a case with low scaled alongshore flow when there is only one evolutionarily stable life history and panel D shows a case with intermediate scaled alongshore flow when there are two evolutionarily stable life history strategies. Note difference in scale bars between panels C and D. Parameters the same as in Figure 2.

Discussion

We sought to understand how coastal oceanographic processes affect the evolution of marine life history traits and how that could indirectly affect the expected distribution of dispersal distances. Along most coastlines, there is usually a dominant water flow direction that biases larval dispersal downstream, and stochastic events during dispersal (like eddies and weather), as well as seasonal and yearly changes in mean flow speed and direction, that slow or reverse currents allowing occasional upstream retention (Largier 2003; Lumpkin and Garraffo 2005; Shanks and Eckert 2005). These common features of coastal environments act as agents of selection on marine life history traits that affect dispersal, and could potentially explain the evolution of dispersal without invoking the traditional causes of inbreeding, kin competition, and environmental variability. The new and key results emerging from our theory are especially relevant on coastlines with relatively high mean flow rates and high interannual variation in flow rates (Largier 2003; Lumpkin and Garraffo 2005). First, selection induced by coastal oceanography favors the release of larvae over multiple time periods, rather than all at once. Releasing larvae on multiple occasions allows individuals to retain more larvae to avoid extinction from net downstream larval loss by increasing the variance in their lifetime dispersal kernel. Doing so reduces the costs of long pelagic larval durations predicted in Pringle et al (2013). Costs are reduced by offsetting downstream losses under strong currents, allowing long pelagic larval durations to be maintained in marine life cycles if it allows individuals to access greater fecundity through reduced parental investment per offspring. Second, while pelagic larval duration and the number of spawning events both affect dispersal, the evolution of the number of spawning events affects the evolution of pelagic larval duration, and vice versa. Such coevolution between larval and adult traits changes how currents affect the evolution of each trait separately and the expected dispersal distances that evolve in a given current regime. Third, the same current regime can give rise to populations with quite different evolutionarily stable pelagic larval durations and spawning frequencies. Finally, the evolution of quite different pelagic larval durations and spawning frequency gives rise to dispersal kernels with very different means and variances in dispersal distances. Our model is structured in such a way that it can be parameterized with data to explore specific situations. The main implication of our findings is that the statistics of coastal ocean flows are important agents of selection that can generate multiple, often co-occurring, evolutionary outcomes for marine life history traits that affect dispersal.

Our findings offer a new explanation for the disconnect between the diversity of pelagic larval durations and spawning frequencies found co-occurring in nature and the predictions from classic marine life history theory that species should produce either many small eggs or few large eggs (Vance 1973), or a single intermediate optimal egg sizes depending on larval growth and mortality rates (e.g., Levitan 2000). A given combination of larval growth and mortality rates can lead to a range of evolutionarily stable life history strategies depending on the oceanographic conditions during the time in which larvae are released. Our adaptive dynamics approach allows us to identify oceanographic conditions where two different life history strategies are evolutionarily stable, and which one evolves depends on a population's evolutionary starting point. For instance, closely related species might evolve very different pelagic larval durations and spawning frequencies if they live on coastlines with different currents, or spawn at different times of the year with different currents. Moreover, even on the same section of coast, similar species could evolve dramatically different pelagic larval durations and spawning frequencies simply because of their different evolutionary histories. Combining these effects with among-species differences in larval growth rates, larval mortality rates, adult mortality rates, and other parameters, all of which lead to different evolutionarily stable life histories, it becomes clearer how a diversity of life histories can be seen in nature on any given stretch of coastline.

By showing how dispersal kernels can be shaped by the coevolution of larval and adult traits, our results imply that considering either larval or adult traits in isolation might produce incorrect predictions about how life history traits and dispersal kernels evolve. Previous marine dispersal theory has either modeled the dispersal kernel inherently as an unconstrained trait responding to habitat heterogeneity (Shaw et al. 2019) or only modeled selection on larval traits (Pringle et al. 2014). Byers and Pringle (2006) showed that spawning over multiple time periods could increase population persistence and spread through upstream retention but did not consider the evolution of either pelagic larval duration or spawning frequency. Shanks and Eckert compiled data on nearshore and shelf/slope fishes and crustaceans and made the case that both adult traits (e.g., longevity, the number of broods per year) and larval traits (e.g., pelagic larval durations) have evolved to exploit eddies and counter-currents to aid in larval retention. Our theory provides a framework to understand how selection for larval retention influences the evolution of both larval and adult traits.

In the presented form, our model makes qualitive predictions about the evolution of marine life histories for a board range of realistic parameters, but its integral projection model structure makes it easily adaptable to match specific systems. When populations are structured in multiple dimensions (e.g., space and age), integral projection models typically require the estimation of many fewer parameters than an equivalent matrix population model (Ellner and Rees 2006). Empirical estimates of the parameters in our model could be used to give specific predictions about evolutionary outcomes in specific situations. Perhaps more usefully, however, any of the functions that give transition probabilities between stages could also be replaced with empirically estimated relationships. For instance, we assume a specific relationship between egg size and the probability of surviving the pelagic larval stage (eq. 1–3). Researchers interested in a specific species could instead estimate this relationship by collecting data and fitting a statistical model, such as (Graham et al. 2008; Connolly and Baird 2010; Moneghetti et al. 2019). This new estimated function could then replace equation 3 and thus f in equation 8. It is important to note though, when applying our model to real systems, researchers should take care to estimate oceanographic statistics on a spatiotemporal scale relevant to their study species. For instance, the annual mean alongshore flow rate might be an inappropriate measure for predicting life history evolution of a species that only spawns in April each year.

Many of the qualitative predictions from our models match empirical patterns. For instance, the prediction that there should be shorter pelagic larval durations with stronger scaled alongshore flow is supported by evidence that the proportion of marine invertebrate species with planktotrophic decreases with scaled alongshore flow rate (Marshall et al. 2012; Pringle et al. 2014). Data from the fishes and crustaceans off the coast of California also support our predictions that species will have longer pelagic larval durations with greater short-time scale fluctuations in alongshore flow and higher spawning frequencies with greater inter-spawning-event variation in alongshore flow (Shanks and Eckert 2005). Shanks and Eckert (2005) also found a positive correlation between maximum age and pelagic larval duration, which matches our coevolutionary predictions if living longer equates to more spawning events. Empirical studies also emphasize a factor not included in our model, the timing of spawning (e.g., Morgan and Christy 1995; Reitzel et al. 2004; Shanks and Eckert 2005), which affects the scaled alongshore flow and interannual variation experienced, finding that a disproportionate number of species have evolved to spawn during seasons with relatively low alongshore flow rates or across months when currents reverse directions (Shanks and Eckert 2005; Byers and Pringle 2006). Other factors not included in our model are cross-shore currents and larval swimming behavior which could interact to affect the realized scaled alongshore flow (Largier 2003; Meyer et al. 2021*a*). However, like all simplifications of complex phenomena, our model serves the purpose of re-orientating and focusing empirical research, and learning why observations match or do not match model predictions. In particular, it provides predictions of the parameter space where larval behaviors would have greater or less impact and how they could possibly substitute for the role of pelagic larval duration or spawning frequency.

In the future, our model could be extended to include other concepts from the marine dispersal literature such as non-Gaussian dispersal kernels (Pringle et al. 2009; Chiswell 2012; Stover et al. 2014), non-feeding larvae (Marshall and Bolton 2007; Marshall and Keough 2007), swimming behavior (Meyer et al. 2021*a*; Burgess et al. 2022), or spatial heterogeneity in habitat availability or quality (Baskett et al. 2007; Meyer et al. 2021*b*). Ultimately, a comprehensive theory of dispersal evolution, applicable to both terrestrial and marine organisms, will integrate the ideas discussed here that focus on the evolution of traits that give rise to dispersal outcomes with key factors in dispersal evolution theory that directly cause selection on dispersal outcomes (e.g., variation in local conditions, kin selection, and inbreeding depression; Clobert et al. 2012).

Literature cited

Baskett, M. L., J. S. Weitz, and S. A. Levin. 2007. The evolution of dispersal in reserve networks. The American Naturalist 170:59–78.

Bottesch, M., G. Gerlach, M. Halbach, A. Bally, M. J. Kingsford, and H. Mouritsen. 2016. A magnetic compass that might help coral reef fish larvae return to their natal reef. Current Biology 26:R1266–R1267.

Burgess, S. C., M. L. Baskett, R. K. Grosberg, S. G. Morgan, and R. R. Strathmann. 2016. When is dispersal for dispersal? Unifying marine and terrestrial perspectives. Biological Reviews 91:867–882.

Burgess, S. C., M. Bode, J. M. Leis, and L. B. Mason. 2022. Individual variation in marine larval-fish swimming speed and the emergence of dispersal kernels. Oikos 2022:e08896.

Byers, J., and J. Pringle. 2006. Going against the flow: retention, range limits and invasions in advective environments. Marine Ecology Progress Series 313:27–41.

Cecino, G., and E. A. Treml. 2021. Local connections and the larval competency strongly influence marine metapopulation persistence. Ecological Applications 31:e02302.

Chesson, P. L., and R. R. Warner. 1981. Environmental Variability Promotes Coexistence in Lottery Competitive Systems. The American Naturalist 117:923–943.

Chiswell, S. M. 2012. Non-Gaussian larval dispersal kernels in Gaussian ocean flows. Aquatic Biology 16:203–208.

Clobert, J., M. Baguette, T. G. Benton, and J. M. Bullock, eds. 2012. Dispersal Ecology and Evolution. Oxford University Press, Oxford, United Kingdom.

Connolly, S. R., and A. H. Baird. 2010. Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. Ecology 91:3572–3583.

Davis, R. E. 1985. Drifter observations of coastal surface currents during CODE: The statistical and dynamical views. Journal of Geophysical Research: Oceans 90:4756–4772.

Dewi, S., and P. Chesson. 2003. The age-structured lottery model. Theoretical Population Biology, Understanding the role of environmental vatiation in population and community dynamics 64:331–343.

Ellner, S. P., and M. Rees. 2006. Integral projection models for species with complex demography. The American Naturalist 167:410–428.

Emlet, R. B., L. R. McEdward, and R. R. Strathmann. 1987. Echinoderm larval ecology viewed from the egg. Pages 55–136 *in* M. Jangoux and J. M. Lawrence, eds. Echinoderm studies (Vol. 2). CRC Press, London, UK.

Gaylord, B., and S. D. Gaines. 2000. Temperature or Transport? Range Limits in Marine Species Mediated Solely by Flow. The American Naturalist 155:769–789.

Graham, E. M., A. H. Baird, and S. R. Connolly. 2008. Survival dynamics of scleractinian coral larvae and implications for dispersal. Coral Reefs 27:529–539.

Grantham, B. A., G. L. Eckert, and A. L. Shanks. 2003. Dispersal potential of marine invertebrates in diverse habitats. Ecological Applications 13:108–116.

Iwasa, Y., Y. Yusa, and S. Yamaguchi. 2022. Evolutionary game of life-cycle types in marine benthic invertebrates: Feeding larvae versus nonfeeding larvae versus direct development. Journal of Theoretical Biology 537:111019.

Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84:2007–2020.

Largier, J. L. 2003. Considerations in estimating larval dispersal distances from oceanographic data. Ecological Applications 13:71–89.

Leis, J. M. 2006. Are larvae of demersal fishes plankton or nekton? Pages 57–141 *in*Advances in Marine Biology (Vol. 51). Academic Press.

Levitan, D. R. 2000. Optimal egg size in marine invertebrates: theory and phylogenetic analysis of the critical relationship between egg size and development time in echinoids. The American Naturalist 156:175–192.

Lumpkin, R., and Z. Garraffo. 2005. Evaluating the decomposition of tropical atlantic drifter observations. Journal of Atmospheric and Oceanic Technology 22:1403–1415.

Marshall, D. J., D. R. Barneche, and C. R. White. 2022. How does spawning frequency scale with body size in marine fishes? Fish and Fisheries 23:316–323.

Marshall, D. J., and T. F. Bolton. 2007. Effects of egg size on the development time of non-feeding larvae. The Biological Bulletin 212:6–11.

Marshall, D. J., and M. J. Keough. 2007. The evolutionary ecology of offspring size in marine invertebrates. Advances in Marine Biology 53:1–60.

Marshall, D. J., P. J. Krug, E. K. Kupriyanova, M. Byrne, and R. B. Emlet. 2012. The biogeography of marine invertebrate life histories. Annual Review of Ecology, Evolution, and Systematics 43:97–114.

Marshall, D. J., A. K. Pettersen, and H. Cameron. 2018. A global synthesis of offspring size variation, its eco-evolutionary causes and consequences. Functional Ecology 32:1436–1446.

McGill, B. J., and J. S. Brown. 2007. Evolutionary game theory and adaptive dynamics of continuous traits. Annual Review of Ecology, Evolution, and Systematics 38:403–435.

Metaxas, A., and M. Saunders. 2009. Quantifying the “bio-” components in biophysical models of larval transport in marine benthic invertebrates: advances and pitfalls. The Biological Bulletin 216:257–272.

Meyer, A. D., A. Hastings, and J. L. Largier. 2021*a*. Larvae of coastal marine invertebrates enhance their settling success or benefits of planktonic development – but not both – through vertical swimming. Oikos 130:2260–2278.

———. 2021*b*. Spatial heterogeneity of mortality and diffusion rates determines larval delivery to adult habitats for coastal marine populations. Theoretical Ecology 14:525–541.

Moneghetti, J., J. Figueiredo, A. H. Baird, and S. R. Connolly. 2019. High-frequency sampling and piecewise models reshape dispersal kernels of a common reef coral. Ecology 100:e02730.

Morgan, S. G. 2014. Behaviorally mediated larval transport in upwelling systems. Advances in Oceanography 2014:e364214.

Morgan, S. G., and J. H. Christy. 1995. Adaptive significance of the timing of larval release by crabs. The American Naturalist 145:457–479.

Müller, K. 1982. The colonization cycle of freshwater insects. Oecologia 52:202–207.

Pachepsky, E., F. Lutscher, R. M. Nisbet, and M. A. Lewis. 2005. Persistence, spread and the drift paradox. Theoretical Population Biology 67:61–73.

Paris, C. B., and R. K. Cowen. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. Limnology and Oceanography 49:1964–1979.

Pringle, J., F. Lutscher, and E. Glick. 2009. Going against the flow: effects of non-Gaussian dispersal kernels and reproduction over multiple generations. Marine Ecology Progress Series 377:13–17.

Pringle, J. M., J. E. Byers, P. Pappalardo, J. P. Wares, and D. Marshall. 2014. Circulation constrains the evolution of larval development modes and life histories in the coastal ocean. Ecology 95:1022–1032.

Rees, M., and S. P. Ellner. 2016. Evolving integral projection models: evolutionary demography meets eco-evolutionary dynamics. Methods in Ecology and Evolution 7:157–170.

Reitzel, A. M., B. G. Miner, and L. R. McEdward. 2004. Relationships between spawning date and larval development time for benthic marine invertebrates: a modeling approach. Marine Ecology Progress Series 280:13–23.

Robinson, A. R., and K. H. Brink, eds. 2006. The Sea (Vol. Volume 14A, B. The global coastal ocean: interdisciplinary regional studies and synthesis). Harvard University Press, Cambridge, Massachusetts, USA.

Shanks, A. L. 2009. Pelagic larval duration and dispersal distance revisited. The Biological Bulletin 216:373–385.

Shanks, A. L., and G. L. Eckert. 2005. Population persistence of california current fishes and benthic crustaceans: a marine drift paradox. Ecological Monographs 75:505–524.

Shaw, A. K., C. C. D'Aloia, and P. M. Buston. 2019. The evolution of marine larval dispersal kernels in spatially structured habitats: analytical models, individual-based simulations, and comparisons with empirical estimates. The American Naturalist 193:424–435.

Siegel, D., B. Kinlan, B. Gaylord, and S. Gaines. 2003. Lagrangian descriptions of marine larval dispersion. Marine Ecology Progress Series 260:83–96.

Smith, C. C., and S. D. Fretwell. 1974. The optimal balance between size and number of offspring. The American Naturalist 108:499–506.

Speirs, D. C., and W. S. C. Gurney. 2001. Population persistence in rivers and estuaries. Ecology 82:1219–1237.

Starrfelt, J., and H. Kokko. 2012. The theory of dispersal under multiple influences. Pages 19–28 *in*Dispersal Ecology and Evolution. Oxford University Press.

Stover, J. P., B. E. Kendall, and R. M. Nisbet. 2014. Consequences of dispersal heterogeneity for population spread and persistence. Bulletin of Mathematical Biology 76:2681–2710.

Strathmann, R. 1982. Selection for retention or export of larvae in estuaries. Pages 521–536 *in* V. S. Kennedy, ed. Estuarine comparisons. Academic Press.

Strathmann, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. Annual Review of Ecology and Systematics 16:339–361.

Travis, J. M. J., M. Delgado, G. Bocedi, M. Baguette, K. Bartoń, D. Bonte, I. Boulangeat, et al. 2013. Dispersal and species' responses to climate change. Oikos 122:1532–1540.

Treml, E. A., J. R. Ford, K. P. Black, and S. E. Swearer. 2015. Identifying the key biophysical drivers, connectivity outcomes, and metapopulation consequences of larval dispersal in the sea. Movement Ecology 3:17.

Vance, R. R. 1973. On reproductive strategies in marine benthic invertebrates. The American Naturalist 107:339–352.

Warner, R. R., and P. L. Chesson. 1985. Coexistence Mediated by Recruitment Fluctuations: A Field Guide to the Storage Effect. The American Naturalist 125:769–787.