

Research

Larvae of coastal marine invertebrates enhance their settling success or benefits of planktonic development – but not both – through vertical swimming

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Oikos

130: 2260–2278, 2021

doi: 10.1111/oik.08585

Subject Editor: Scott Burgess

Editor-in-Chief: Dries Bonte

Accepted 23 September 2021

The planktonic larvae of many coastal marine invertebrates swim vertically during dispersal to exploit variation in current strength and direction, food abundance and mortality rate throughout the water column and offshore. Prior studies have estimated the effects of vertical swimming upon larval dispersal using mathematical models. However, most such studies consider just a small number of predefined swimming behaviors despite evidence that even seemingly insignificant changes to these behaviors can dramatically alter predictions of larval delivery. Additionally, the concurrent effects of vertical swimming upon predation risk, feeding opportunities and energy budgeting are not well characterized. We used a simple mathematical model of larval dispersal in upwelling-favorable conditions to investigate how a continuum of swimming behaviors affect these quantities simultaneously. Within this continuum, we identified two categories of successful behaviors. ‘Mean-onshore’ behaviors deliver most larvae to coastal habitats, but offer limited opportunities for feeding and alongshore movement during dispersal. By contrast, ‘mean-offshore’ behaviors deliver fewer larvae to shore, but permit more feeding, alongshore movement, and, potentially, safety from near-shore hazards. No behaviors considered achieved the benefits of both categories. We hypothesize that mean-onshore behaviors are advantageous for species with non-feeding larvae or sparse adult populations, while mean-offshore behaviors are advantageous for species with feeding larvae or crowded adult populations. Our results underscore the importance of considering how behavior interacts with environmental structure and individual biology while studying dispersal in marine and other ecosystems.

Keywords: advection–diffusion, coastal marine larvae, dispersal, mathematical model, stochastic process, vertical migration

Introduction

Many coastal marine invertebrates and benthic fish begin life as planktonic larvae (Levin and Bridges 1995, Pechenik 1999, Gerber et al. 2014) that can be transported

dozens or hundreds of kilometers from their parents' habitats by coastal currents (Largier 2003, Shanks et al. 2003, Shanks 2009). During this common life history stage, several processes must occur simultaneously. Larvae must develop until competent to metamorphose into their next life stage, at which point they typically must locate nearshore habitats or perish in the plankton ('offshore loss'; Rumrill 1990, Morgan 1995, Shanks 1995). Because metamorphosis is energetically expensive, larvae of many species feed during development, or are instead supplied with maternally derived energy sources (Levin and Bridges 1995, Shanks et al. 2003). Regardless of their nutritional modes, larvae must settle and begin metamorphosis with sufficient energy; those that fail to do so may experience reduced fitness later in life (Pechenik and Cerulli 1991, Pechenik 2006, Elkin and Marshall 2007) or may not complete metamorphosis at all (Lucas et al. 1979, Boidron-Metairon 1988). Finally, larvae must evade predation and other hazards as they develop and feed (Rumrill 1990, Morgan 1995, Young 1995, White et al. 2014). In summary, planktonic development is a delicate balancing act during which individuals must meet often-conflicting needs.

Larvae of several species regulate their depth within the water column to improve their chances of successfully settling into nearshore habitats and metamorphosing. Depth control is often achieved through vertical swimming, but may also result from changes in body structure and buoyancy throughout development (Chia et al. 1984, Levin and Bridges 1995, Young 1995). These adaptations are particularly important because while most larvae are slow swimmers ($0.1\text{--}2\text{ cm s}^{-1}$; Chia et al. 1984), conditions vary over smaller distances within the water column than in the cross- or alongshore directions (1–100 m compared with several km (Morgan 1995, Shanks 1995, Young 1995, Cowen et al. 2000, Sherr et al. 2005)). Therefore, swimming vertically to exploit depth-varying cross-shore currents with speeds of $1\text{--}30\text{ cm s}^{-1}$ is a more efficient means of regulating cross-shore movement than swimming horizontally (Shanks 1995) and can substantially alter both larval delivery to coastal habitats and alongshore dispersal (Rothlisberg et al. 1983, Cowen et al. 2000, 2006, Marta-Almeida et al. 2006, James et al. 2019). Food and predator abundance also vary with depth and cross-shore distance. The interaction of vertical swimming with horizontal currents allows larvae to exploit this spatial structure while moving toward or away from shore at the appropriate times (Shanks 1995).

The vertical swimming behaviors of invertebrate larvae are often matched to the environments in which they develop. In tidal estuaries, for instance, larvae may achieve offshore transport by residing in the offshore-moving upper layer of the water column during ebb tides and sinking to the slow-moving bottom layer during flood tides. The opposite behavior, in which larvae reside in the upper layer of the water column during flood tides, achieves onshore transport (Cronin and Forward 1986). These behaviors are called tidal vertical migrations (TVM), and have been documented in several estuarine invertebrates (Table 1). In non-tidal settings, many larvae regulate their depth on a circadian, rather than

circatidal, cycle. Diel vertical migrations (DVM), in which larvae reside near the surface at night and deeper during the day, allow individuals to take advantage of abundant food near the surface of the water while avoiding visually guided diurnal predators.

Swimming behaviors also reflect the changing needs of individuals throughout development and dispersal. Consider, for instance, larvae dispersing in the stratified flow typical of upwelling circulation, which features an offshore current at water's surface and an onshore current below (Fig. 1). Newly spawned larvae may reside near the surface to achieve offshore transport, removing them from nearshore predators and sibling competition. Older larvae of the same species could achieve transport toward nearshore habitats by residing in the onshore current below the surface (Shanks 1995). This behavior, known as an ontogenetic vertical migration (OVM), has been observed in larvae of many species, including the barnacle *Balanus nubilus* off southern California (Tapia et al. 2010) and the sponge *Rhopaloeides odorabile* in laboratory experiments (Whalan et al. 2008). Ontogenetic changes in depth or swimming behavior can also coincide with changes in nutritional mode (Tapia et al. 2010, Butler et al. 2011) and movement between open-coast and estuarine environments during dispersal (Queiroga et al. 2007, Morgan et al. 2014).

Vertical swimming is energetically costly (Sprung 1984) and the structure of the environment often makes it impossible to enjoy all benefits of swimming simultaneously. For instance, larvae exhibiting diel vertical migrations in the upwelling regime described above forgo feeding opportunities during daylight, and expose themselves to strong offshore currents in the surface while feeding during darkness. These currents transport larvae away from shore, potentially preventing them from locating coastal habitats later in development. Diel vertical migrations and other behaviors therefore have dramatic (and not necessarily advantageous) effects on larval transport, as well as feeding and predator avoidance. It is far from obvious which behaviors are advantageous or how they might affect the chances of an individual surviving to reproduction.

Several studies have investigated the benefits of vertical swimming behaviors for larval supply to and dispersal between coastal populations using computational models (reviewed by Metaxas and Saunders 2009; for examples, see Rothlisberg et al. 1983, Owens and Rothlisberg 1991, Cowen et al. 2000, 2006, Marta-Almeida et al. 2006, Sundelöf and Jonsson 2012, James et al. 2019). These studies generally argue that vertical migration results in greater nearshore retention and less alongshore movement of larvae than would be achieved by passive transport. However, to our knowledge, little has been done to contextualize this result by considering other aspects of larval biology affected by vertical swimming, such as predator avoidance and food access. Additionally, most such studies are based on computationally demanding hydrodynamic models (e.g. the regional ocean modeling system framework, ROMS) that limit the number of swimming behaviors one can reasonably consider. This is

Table 1. Examples of vertical swimming behavior reported in the literature, along with larval durations (LD) and nutritional modes (NM) of study organisms. Nutritional modes are feeding (F) and non-feeding (NF); for species with both feeding and non-feeding stages, modes are listed in chronological order. Behaviors are OVM, a single ontogenetic vertical migration from the surface to the bottom during development; diel vertical migrations (DVM) with periods of light (darkness) spent near the bottom (surface); reverse diel vertical migrations (RDVM) with periods of darkness (light) spent near the bottom (surface). Where no reference is provided for larval duration or nutritional mode, the information is provided by the referenced study of larval movement. Italicized locations denote laboratory and mesocosm, rather than field, observations.

Species	LD (days)	NM	Study	Location and description	Behavior
Crustaceans					
<i>Atelecyclus rotundatus</i>	45–90 ^a	F ^a	dos Santos et al. 2008	open coast with upwelling – Portugal	DVM
<i>Balanus glandula</i>	21–28 ^b	F/NF ^b	Morgan and Fisher 2010	upwelling shadow – northern California, US	reverse OVM (deep then shallow)
<i>Balanus nubilus</i>	14–28 ^c	F/NF ^b	Tapia et al. 2010	southern California, US	OVM
<i>Cancer</i> spp.	60–150 ^d	F ^e	Shanks 1986	southern California, US	DVM, then RDVM
<i>Carcinus maenas</i>	50 ^f –80 ^g	F ^e	Queiroga et al. 2007 ^h	open coast with upwelling – Portugal	DVM
			Queiroga et al. 2007 ⁱ	tidal estuary – Portugal	TVM (megalopae)
			Queiroga et al. 2002	microtidal system – Gullmarsfjord, Sweden	DVM
<i>Chthamalus</i> spp.	30–50 ^j	F/NF ⁱ	Queiroga et al. 2007	open coast with upwelling – Portugal	DVM (cyprids only)
<i>Hemigrapsus oregonensis</i>	≤ 58 ^k	F ^e	Tapia et al. 2010 Miller and Morgan 2013	southern California, US <i>experimental column – northern California, US</i>	passive (nauplii only) TVM
<i>Hemigrapsus</i> spp.	15–55 ^{g,o}	F ^{g,o}	Morgan and Fisher 2010	upwelling shadow – northern California, US	DVM
<i>Jehlius cirratus</i>	22–41 ^l	F ^m	Bonicelli et al. 2016	open coast with upwelling – El Quisco Bay, Chile	shallow DVM, then deep DVM
<i>Nihonotrypaea harmandi</i>	20–30	F	Tamaki et al. 2010	tidal estuary – Ariake Sound, Kyushu, Japan	mixed TVM and DVM
<i>Notobalanus flosculus</i>	39 ^l	F/NF ^m	Bonicelli et al. 2016	open coast with upwelling – El Quisco Bay, Chile	DVM, then reside in surface
<i>Notochthamalus scabrosus</i>	22–41 ^l	F/NF ^m	Bonicelli et al. 2016	open coast with upwelling – El Quisco Bay, Chile	shallow DVM, then deep DVM
<i>Pachygrapsus crassipes</i>	< 100 ⁿ	F ⁿ	Morgan and Fisher 2010	northern California, US	DVM
<i>Pagurus</i> spp.	13–100 ^o	F ^o	Morgan and Fisher 2010	upwelling shadow – northern California, US	OVM and DVM
<i>Panulirus argus</i>	180	NF/F/NF	Butler et al. 2011	<i>experimental column – Florida Keys, Florida, US</i>	shallow DVM, then deep DVM
<i>Petrolisthes cinctipes</i>	45 ^p	F ^p	Miller and Morgan 2013	<i>experimental column – Northern California, US</i>	DVM
Echinoderms					
<i>Amphiura filiformis</i>	21–42	F	Guillam et al. 2020	stratified bay – Bay of Douarnenez, Brittany, France	Deep
<i>Dendraster excentricus</i>	2–9 ^o	F	Pennington and Emlet 1986 Pennington and Emlet 1986	<i>lab/mesocosm – East Sound, Washington, US</i> weak-current embayment – East Sound, Washington, US	DVM near surface
<i>Ophiocomina nigra</i>	21–42	F	Guillam et al. 2020	stratified bay – Bay of Douarnenez, Brittany, France	hybrid: DVM then deep
<i>Ophiothrix fragilis</i>	21–42	F	Guillam et al. 2020	stratified bay – Bay of Douarnenez, Brittany, France	DVM near-surface
Mollusks					
<i>Brachidontes granula</i>	≥ 55 ^q	F ^q	Bonicelli et al. 2016	open coast with upwelling – El Quisco Bay, Chile	late stages near surface
<i>Concholepas concholepas</i>	90 ^r	F	Poulin et al. 2002b	open coast with upwelling – El Quisco Bay, Chile	RDVM during competence
<i>Kelletia kelletii</i>	≥ 35	F	Romero et al. 2012	southern California, US	DVM then deeper, less pronounced DVM
<i>Mytilus edulis</i>	32 ^d	F	Dobretsov and Miron 2001	Kandalakshsky Gulf, White Sea, Russia	reverse OVM (deep, then shallow)

(Continued)

Table 1. Continued

Species	LD (days)	NM	Study	Location and description	Behavior
<i>Perumytilus purpuratus</i>	14–18 ^s	NF ⁱ	Bonicelli et al. 2016	open coast with upwelling – El Quisco Bay, Chile	late stages near surface
<i>Semimytilus algosus</i>	27 ^u	F ⁱ	Bonicelli et al. 2016	open coast with upwelling – El Quisco Bay, Chile	late stages near surface
<i>Strombus gigas</i>	35 ^v	F	Barile et al. 1994	lab/mesocosm – Caribbean	possibly DVM
Other invertebrates					
<i>Limulus polyphemus</i>	20–50 ^w	F ^x	Ehlinger and Tankersley 2006	experimental column – New Jersey, US	endogenously cued TVM
<i>Owenia fusiformis</i>	30	F ^y	Thiébaud et al. 1992	partially mixed estuary – Bay of Siene, English Channel, France	OVM
<i>Rhopaloeides odorabile</i>	≤ 5	NF	Whalan et al. 2008	experimental column – Great Barrier Reef, Australia	OVM

^a Hong and Ingle 1987. ^b Hiebert et al. 2015. ^c Morgan and Fisher 2010. ^d Grantham et al. 2003. ^e Sulkin et al. 1998. ^f Dawirs 1985. ^g Shanks et al. 2003. ^h See also dos Santos et al. 2008. ⁱ See also Queiroga et al. 1997. ^j Burrows et al. 1999. ^k Hart 1931. ^l Tapia et al. 2010. ^m Lagos et al. 2007. ⁿ Schlotterbeck 1976. ^o O'Connor et al. 2007. ^p Ceballos-Osuna et al. 2013. ^q Campos and Ramorino 1980. ^r Poulin et al. 2002a. ^s Šmietanka et al. 2018. ^t Lagos et al. 2007 report feeding, but Campos and Ramorino 1980 and Šmietanka et al. 2018 report non-feeding. ^u Bigatti et al. 2014. ^v Mitton et al. 1989. ^w Ehlinger and Tankersley 2004. ^x Ehlinger and Tankersley 2006 report feeding, but O'Connor et al. 2007 report non-feeding. ^y Wilson 1932.

problematic because, as emphasized by Sundelöf and Jonsson (2012), even seemingly trivial details of how researchers model swimming can dramatically alter the fates of simulated larvae.

In this paper, we addressed some of these shortcomings by modeling how a broad class of vertical swimming behaviors affect several aspects of larval biology. These behaviors included passive transport, diel vertical migrations, a single ontogenetic migration from the surface to the bottom, and an ontogenetic shift from diel vertical migrations to residing

in the bottom only. Outputs of interest included the fraction of larvae exhibiting such behaviors that ultimately settle into coastal habitats, the energetic costs of those behaviors and the resulting opportunities for feeding and movement between coastal populations. We accommodated this large set of behaviors by relying on a simple approximation to coastal oceanography. Specifically, we limited the scope of our study to larval dispersal in the upwelling circulation described above, which we approximated as an advection–diffusion process with two layers. Upwelling circulation is common, at

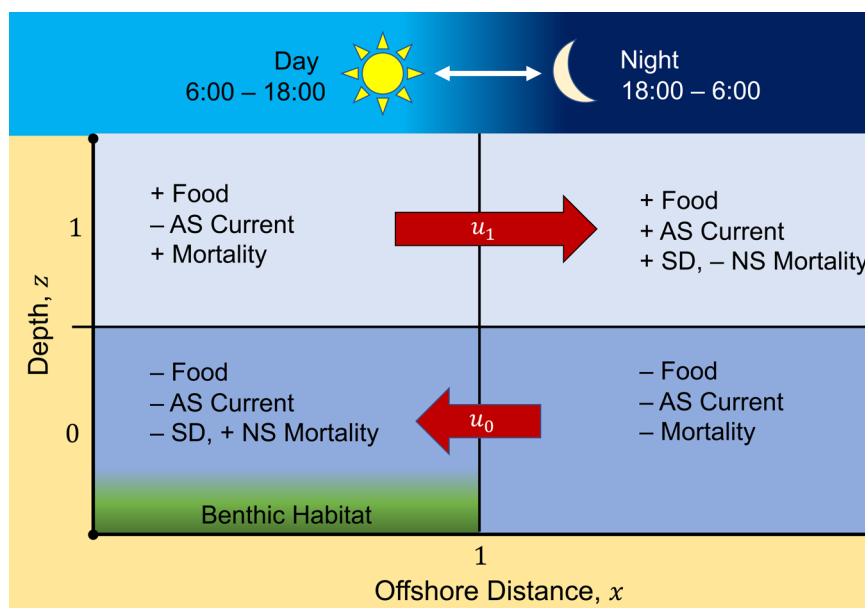


Figure 1. Diagram of the two-layer model of upwelling circulation. AS = alongshore; SD = surface/diurnal; NS = nearshore. The red arrows show the directions and relative magnitudes of advection in the two layers, u_0 and u_1 . The elevated mortality in the surface layer with SD mortality applies during daytime only.

least seasonally, on the eastern boundaries of oceans, including off the west coasts of the United States, Peru, Chile, Portugal, Morocco, Namibia and South Africa (Chavez and Messié 2009). Although upwelling is not persistent in many coastal environment around the world, it is representative of the types of depth-stratified currents that marine larvae exploit during dispersal.

We identified two classes of viable vertical swimming behaviors: one in which larvae risk offshore loss but enhance their feeding and alongshore dispersal opportunities, and one in which larvae forgo feeding and alongshore transport to remain close to their natal habitats. Below, we quantified how and why these classes of behaviors differ, specifically in upwelling systems, and discussed the biological, ecological and environmental features that may favor one class over another. This work underscores the importance of considering several behaviors and biological needs in parallel with the surrounding physics when modeling the dispersal of coastal marine larvae, as well as propagules in other ecosystems.

Methods

We explored how a continuous class of vertical swimming behaviors affect dispersal success, energy use, access to food and movement between coastal habitats using an idealized 2D model of a larva's movement in upwelling-favorable conditions. The modeled environment, illustrated in Fig. 1, represented a cross-section of the water perpendicular to a long, homogeneous coastline. It consisted of two layers: a surface layer, $z=1$, and a bottom layer, $z=0$.

Suppose that benthic adults are uniformly distributed over a nearshore habitat of width H (km). The model tracks the movement of a single larva spawned from this habitat at midnight, time $t=0$ (days). Let $X_t \geq 0$ (km) be the larva's distance from shore t days after spawning, and let z_t denote the layer the larva occupies t days after spawning, such that $z_t=1$ ($z_t=0$) when the larva is in the surface (bottom) layer. Vertical swimming behaviors were captured by z_t , which was either specified ahead of time (for active behaviors) or allowed to vary randomly (for passive transport), as described in Swimming behaviors. Meanwhile, the larva's cross-shore position changed according to the stochastic differential equation

$$\begin{cases} dX_t = U(X_t, z_t)dt + \sqrt{2K(X_t, z_t)}dW_t, \\ X_0 \sim \text{uniform}([0, H]), \\ X = 0 \text{ is a reflecting boundary.} \end{cases} \quad (2.1)$$

In this model, $U(X, z)$ (km day⁻¹) represents the expected offshore velocity of the larva at location (X, z) due to a residual cross-shore current (i.e. advection) and $K(X, z)$ (km² day⁻¹) represents variance in the larva's velocity due to movements on length- and timescales shorter than those of larval dispersal (i.e. diffusion). These finer movements are approximated by a mean-zero stochastic term featuring the differential of a standard Brownian motion, dW_t (day^{1/2}). The relative magnitudes

of U and K are highly dependent upon the length- and time-scales under consideration, with spatial and temporal variability in the strength of advection decreasing the absolute value of U and increasing K (Okubo and Levin 2001, Largier 2003). In this study, we chose estimates of U and K appropriate for the dispersal of the larvae produced by a single adult in one reproductive season. However, we also varied these parameters in the course of our analysis.

Nondimensionalization

Our model was not intended to capture the behavior of larvae of any particular species or the physics of any specific upwelling system. Therefore, it was convenient to simplify the model and group together equivalent biophysical scenarios through nondimensionalization, or the rescaling of variables by units relevant to the dispersal of a single larva. We trivially rescaled time by units of days, $t' = t \text{ day}^{-1}$, so that we could easily model periodic swimming behaviors such as diel vertical migrations. Because this rescaling made no numerical difference in our model, we shall suppress the apostrophe on t' throughout this paper, continuing to refer to time as t .

Many rescalings of the larva's offshore distance, X_t (km), were possible. We rescaled by the width of the nearshore habitat, $x_t = H^{-1} X_t$, because it allowed us to focus on the strengths of advection and diffusion while holding habitat size constant at 1. Finally, the two-layer formulation of depth, z_t , was already unitless and could not be further simplified through rescaling.

The rescalings above produced the dimensionless model

$$\begin{cases} dx_t = u(x_t, z_t)dt + \sqrt{2k(x_t, z_t)}dw_t, \\ x_0 \sim \text{uniform}([0, 1]), \\ x = 0 \text{ is a reflecting boundary} \end{cases} \quad (2.2)$$

with dimensionless advection and diffusion rates

$$u(x, z) = H^{-1}U(Hx, z)\text{day} \text{ and } k(x, z) = H^{-2}K(Hx, z)\text{day} \quad (2.3)$$

Here, $w_t = W_t \text{ day}^{-1/2}$ is a unitless Brownian motion. The parameters of the original model, these rescalings, and the resulting parameters of the dimensionless model are summarized in Table 2.

Upwelling circulation

We approximated upwelling circulation within our two-layer model by assuming that advection was offshore in the surface layer and onshore in the bottom layer,

$$u(x, 1) > 0 \text{ and } u(x, 0) < 0 \quad (2.4)$$

We assumed further that the advection and diffusion rates varied with depth, but not offshore distance; that is, $u(x, z) = u_z$

Table 2. Summary of symbols used in the dimensional (upper) and dimensionless (lower) models, along with appropriate ranges and default values (where applicable). The values provided represent typical values for benthic invertebrates in upwelling systems, but organisms and environments outside of these ranges certainly exist in nature.

Variable	Units	Meaning	Range	Default ^a
T	day	time	–	–
X_t	km	offshore distance of modeled larva	–	–
z_t	–	layer occupied by modeled larva	0 or 1	–
H	km	width of nearshore benthic habitat	0.01–10 ^b	5
U	km day ^{−1}	cross-shore advection velocity	−25 to +25 ^c	−2.5 or 10 ^d
K	km ² day ^{−1}	cross-shore diffusivity	1–100 ^e	50 or 100 ^d
Variable	Expression	Meaning	Range	Default
t' (t)	t day ^{−1}	time (dimensionless)	–	–
x_t	$H^{-1} X_t$	offshore distance of modeled larva	–	–
z_t	z_t	layer occupied by modeled larva	0 or 1	–
u_0	$U(X,0) \times H^{-1}$ day	cross-shore advection velocity of bottom layer	−2500 to 0	−0.5
u_1	$U(X,1) \times H^{-1}$ day	cross-shore advection velocity of surface layer	0–2500	2
k_0	$K(X,0) \times H^{-2}$ day	cross-shore diffusivity of bottom layer	0.1–10 ⁶	2
k_1	$K(X,1) \times H^{-2}$ day	cross-shore diffusivity of surface layer	0.1–10 ⁶	4
T	–	larval duration (in days)	<1 to 180 ^f	30
T_C	–	pre-competence duration (in days)	0.17–0.97 ^g	18
μ_0	–	mortality rate offshore (NS) or in bottom (SD)	0.001–0.14 ^h	0.0125
μ_1	–	mortality rate nearshore (NS) or in surface during day (SD)	0.001–0.14 ^h	0.05
a	–	fraction of day in surface during first phase of dispersal	0–1	–
b	–	fraction of dispersal occupied by the first phase	0–1	–
λ_0	–	mean residence time of passive larva in bottom	–	13/24 ⁱ
λ_1	–	mean residence time of passive larva in bottom	–	1/24 ⁱ

^a Default values for the dimensional parameters were used only to choose defaults for the nondimensional parameters. ^b Rasmuson 2013, Nickols et al. 2015. ^c Shanks 1995. ^d The first value is for the lower layer and the second is for the upper layer. ^e Largier 2003. ^f Shanks et al. 2003, Shanks 2009. ^g Wang and Widdows 1991. ^h Rumrill 1990, White et al. 2014. ⁱ Supporting information.

and $k(x,z)=k_z$ for $z=0, 1$. In general, we fixed $u_1=-4u_0$ and $k_1=2k_0$; however, further simulations demonstrated that exact ratios chosen did not qualitatively effect the results of our study.

The effects on larval dispersal of cross-shore variability in current strength, such as due to coastal boundary layers and other oceanographic features, are discussed and modeled extensively in the literature (Largier 2004, Shanks 2009, Nickols et al. 2012, 2013, Meyer et al. 2021a). In preliminary simulations, the effects of a coastal boundary layer were frequently overshadowed by those of vertical swimming. A description of the interactions of these features with vertical swimming is beyond the scope of this paper.

Settling, death and offshore loss

Suppose that larvae of the modeled species are viable for T days after spawning (that is, the larval duration is T). The dispersal of a modeled larva terminated in one of three ways: successful settling into the nearshore habitat, premature death (e.g. due to predation), or the failure to locate a suitable habitat before time $t=T$ ('offshore loss'). Let

$$T_* = \text{Time at which settling, death or offshore loss occurs} \quad (2.5)$$

so that an individual larva disperses for a total of $T_* \leq T$ days.

We assumed that larvae were competent to initiate metamorphosis from ages $t=T_C$ to $t=T$, and that a competent larva would settle immediately into the nearshore habitat, $[0, 1]$, if it reached it at any time $T_* \in [T_C, T]$. We also subjected dispersing larvae to a location- and time-dependent instantaneous mortality rate, $\mu(t,x,z)$, such that

$$\Pr\{\text{Larva dies during } [t, t + \Delta t] \mid x_t = x, z_t = z\} \approx \mu(t,x,z)\Delta t \quad (2.6)$$

for a small time increment Δt . If the larva died, T_* denoted its time of death. Any larva that neither settled nor died before $t=T$ was considered lost and assigned $T_*=T$.

We considered two different mortality schemes. In surface-diurnal (SD) mortality, larvae experienced an elevated mortality rate in the surface layer during daylight, which we assumed lasted from 6:00 to 18:00:

$$\mu_{SD}(t,x,z) = \begin{cases} \mu_1 & \text{if } z=1 \text{ and } t(\text{mod } 1) \in [0.25, 0.75], \\ \mu_0 & \text{otherwise} \end{cases} \quad (2.7)$$

where $\mu_0 < \mu_1$. In nearshore (NS) mortality, larvae instead experienced an elevated mortality rate over a nearshore region that we assumed to be approximately equal in size to the nearshore habitat:

$$\mu_{NS}(t,x,z) = \begin{cases} \mu_1 & \text{if } x \in [0, 1], \\ \mu_0 & \text{otherwise} \end{cases} \quad (2.8)$$

where $\mu_0 < \mu_1$. This assumption was justified because the nearshore region of elevated mortality may simply be the habitat of a different coastal species.

Swimming behaviors and classification

We modeled the cross-shore transport of both passive and active larvae. Passively transported larvae switched randomly between the bottom and surface layers. The amount of time spent in layer z was an exponentially distributed random variable with mean λ_z days, such that the larva's depth z_i was a Markov (memoryless) process. Active larvae exhibited two-phase swimming patterns. The first phase occupied a fraction $b \in [0, 1]$ of the entire larval duration. During the first phase, larvae visited the surface each night for $a \in [0, 1]$ days, starting $a/2$ days before midnight and ending $a/2$ days after midnight.

During the second phase, larvae switched to continually residing in the bottom layer. This generic behavior captures diel vertical migrations (if $0 < a < 1$ and $b = 1$), a single ontogenetic vertical migration (if $a = 1$ and $0 < b < 1$), and combinations thereof (see Fig. 2a and the examples in Fig. 3a, c, e, g).

We omitted vertical advection for both passive and active larvae. While upward currents near the coast are typical in upwelling regimes, such currents are slow enough compared with larval swimming and sinking to be considered negligible in most cases ($\ll 0.1 \text{ cm s}^{-1}$, (Liang et al. 2017), compared with $0.1\text{--}2 \text{ cm s}^{-1}$ (Chia et al. 1984)). For active larvae, we also omitted vertical diffusion under the assumption that the effects of random movements were small compared with those of active swimming.

Our analysis explored the full trait-space of behaviors parameterized by $(a, b) \in [0, 1]^2$. We facilitated this analysis

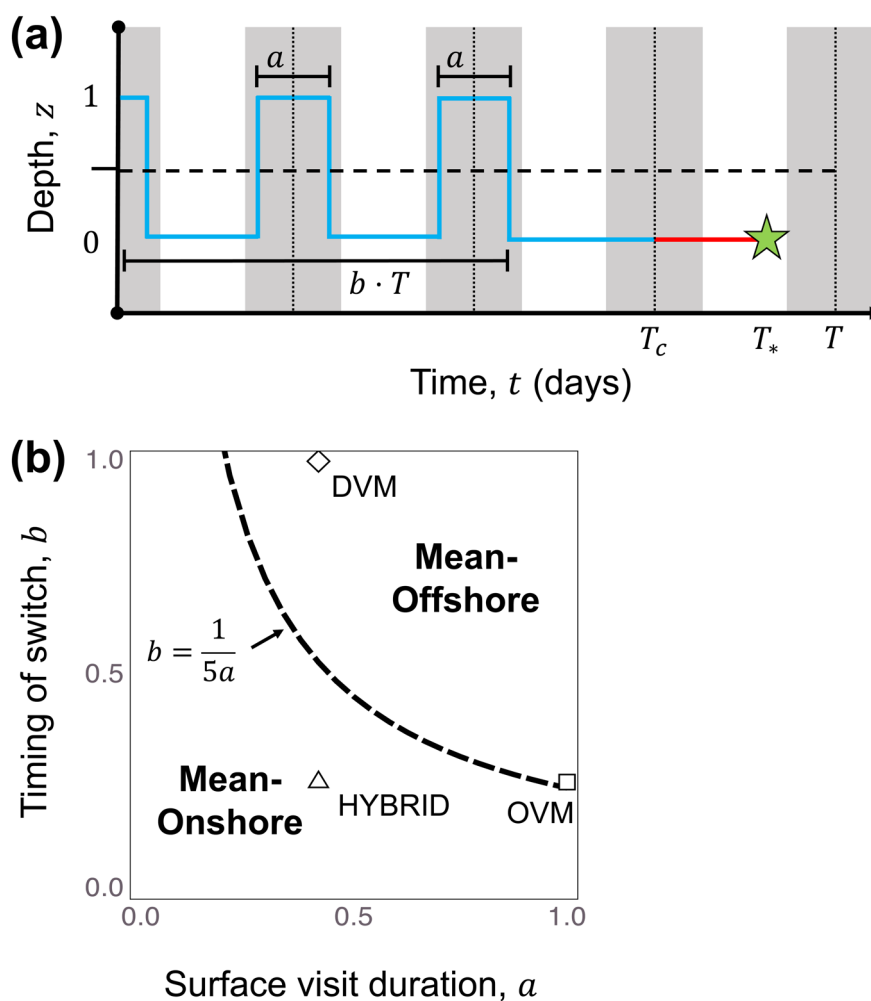


Figure 2. The active swimming behaviors we modeled are described using two parameters: $a \in [0, 1]$, the fraction of each day larvae spend in the surface during the first phase of dispersal, and $b \in [0, 1]$, the fraction of the larval duration elapsed at the end of that first phase, after which the larva resides continually in the bottom layer. (a) Depth, z , over time of a larva exhibiting such a behavior. The line is blue when the larva is pre-competent and red when the larva is competent to settle. The green star denotes the time T at which dispersal ends due to either settling or death. (b) The continuous trait-space of all active behaviors we considered. The dashed curve $b = 1/5a$ separates behaviors (a, b) resulting in mean-onshore versus mean-offshore advection. The plotted points show the locations of the three active examples OVM (borderline), DVM (mean-offshore) and HYBRID (mean-onshore) shown in Fig. 3.

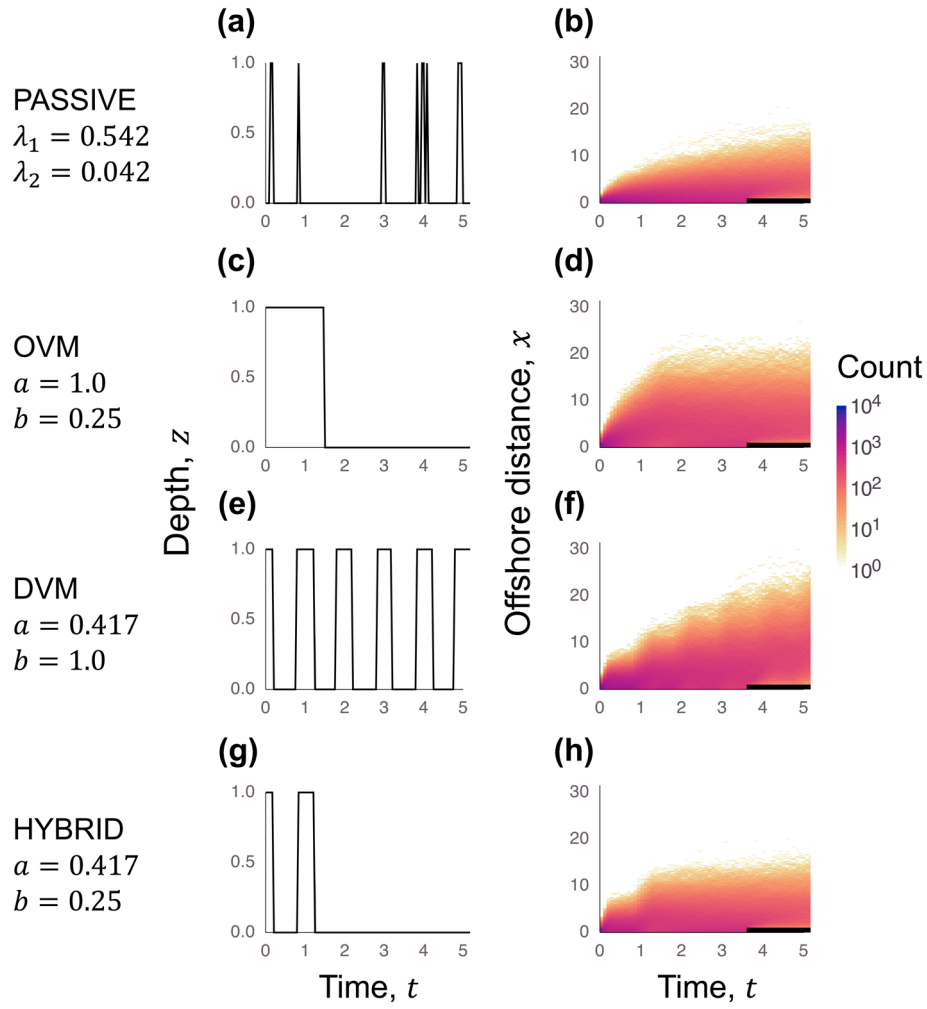


Figure 3. Our analysis highlights the performance of passively transported larvae (PASSIVE) and larvae exhibiting three active behaviors from the trait-space in Fig. 2 (ontogenetic vertical migration, OVM; diel vertical migrations, DVM; and HYBRID, a combination thereof). Parameters for each behavior are listed in the left column of this figure. (a, c, e, g) show the depths over time, z , of individual larvae exhibiting the PASSIVE, OVM, DVM and HYBRID example behaviors, respectively. (b, d, f, h) are 2D histograms showing the offshore distances over time, x , of 10^4 simulated larvae exhibiting the PASSIVE, OVM, DVM and HYBRID example behaviors. The black rectangles in the lower-right corners of these histograms represent the times, t , and locations, x , for which settling is possible.

by introducing a binary classification that categorized swimming behaviors (including passive transport) by whether they resulted in mean movement toward or away from shore over the entire dispersal duration, T . We referred to behaviors in these classes as mean-onshore and mean-offshore behaviors. Active behaviors parameterized using a and b were categorized analytically: if a behavior (a, b) lay above/below the curve

$$b = -\frac{u_0}{(u_1 - u_0)a} = \frac{1}{5a} \quad (2.9)$$

in the ab -plane, it was mean-offshore/-onshore (Fig. 2b; see Supporting information for details). This classification was useful because in the modeled upwelling regime, the mean movement of larvae resulted primarily from how much time larvae spent in the surface layer compared with the bottom layer. In turn, this determined how much time larvae spent

nearshore compared with offshore. Thus, we anticipated greater variation in the probability of settling and other important quantities across these behavioral classes than within them.

Simulations

We quantified how the active behaviors described above affect larval dispersal by simulating $N = 10^4$ larvae (that is, numerically solving (2.2)) using the default parameters in Table 2 for each behavior (a, b) in a 25×25 uniform mesh on $[0, 1]^2$. For each behavior, we estimated the probability that an individual larva settles, S , as

$$S \approx \frac{\text{number of settled larvae}}{N} \quad (2.10)$$

This probability should be interpreted as a proxy for total larval supply to coastal populations, neglecting possible differences in the number of larvae spawned across behaviors (discussed later).

We performed the same analysis with $T = 5$ instead of 30 to visualize how behaviors affect S over a shorter larval duration. We also determined the sensitivity of S to the strengths of advection and diffusion by performing the same analysis two additional times, first with $u_1 = 4$ instead of 2 and then with $k_1 = 8$ instead of 4. These simulations allowed us to estimate the partial derivatives

$$\left. \frac{\partial S}{\partial p} \right|_{p=\hat{p}} \approx \frac{S(2\hat{p}) - S(\hat{p})}{\hat{p}} \quad (2.11)$$

where p represents u_1 or k_1 and $\hat{p}$ represents the corresponding default value. As we varied T , u_1 and k_1 , we preserved the relationships $T_c = 0.6T$, $u_1 = -4u_0$ and $k_1 = 2k_0$.

We highlighted how behaviors in different parts of the (a, b) trait-space compared with passive transport and each other by focusing on four specific example behaviors: PASSIVE (passive transport), OVM (a single ontogenetic vertical migration partway through dispersal), DVM (diel vertical migrations throughout dispersal) and HYBRID (diel vertical migrations until partway through dispersal). The parameter values for each example, presented in Fig. 3, were selected to illustrate key differences within the trait-space; they are not derived from data and are not intended to capture the behaviors of any particular organisms.

We simulated the dispersal of $N = 10^4$ larvae exhibiting each example behavior using the default parameter values in Table 2. We also repeated this analysis while varying u_1 from 0 to 10 and k_1 from 1 to 100, again preserving the relationships $u_1 = -4u_0$ and $k_1 = 2k_0$.

Proxies for larval performance

We recorded each simulated larva's total dispersal time, T_* , its total time spent in the surface layer, T_{surface} and its total time spent 5 habitat widths or more (that is, $x_i \geq 5$) from shore, T_{offshore} . We also recorded the number of vertical migrations performed during dispersal by each larva, VM . These quantities serve as proxies for the conditions to which larvae were exposed during dispersal (e.g. surface versus bottom, nearshore versus offshore) and the energetic demands of the behaviors larvae performed. The choice of five habitat widths for computing T_{offshore} was arbitrary; other reference distances of the same magnitude did not produce qualitatively different results. Averaging these quantities over settled larvae only (that is, estimating each quantity's expected value conditioned upon settling) resulted in four proxy measurements that correlate with biological quantities of interest:

1. Mean total dispersal time,

$$MT_* = \mathbf{E}[T_* \mid \text{settling}] \quad (2.12)$$

correlates positively with mortality risk (Rumrill 1990), alongshore dispersal distance (Shanks et al. 2003) and energy consumption for maintenance. Alternatively, MT_{surface} correlates negatively with the retention of larvae near their natal habitats.

2. Mean surface time,

$$MT_{\text{surface}} = \mathbf{E}[T_{\text{surface}} \mid \text{settling}] \quad (2.13)$$

correlates positively with access to food and alongshore dispersal distance and negatively with nearshore retention. In the surface-diurnal mortality scheme, MT_{surface} also correlates positively with mortality risk.

3. Mean offshore time,

$$MT_{\text{offshore}} = \mathbf{E}[T_{\text{offshore}} \mid \text{settling}] \quad (2.14)$$

correlates positively with alongshore dispersal distance (Largier 2003) and negatively with nearshore retention. In the nearshore mortality scheme, MT_{offshore} also correlates positively with mortality risk.

4. Mean vertical migrations,

$$MVM = \mathbf{E}[VM \mid \text{settling}] \quad (2.15)$$

correlates positively with energy consumption for locomotion.

It is critical that these averages are conditioned upon settling, since the experiences of non-settling larvae are not relevant for the reproductive fitness resulting from a swimming behavior.

The proxy measurements above and their correlates are summarized in Table 3. These correlations are based on the environmental structure assumed in Fig. 1, and do not necessarily apply to other conditions. Additionally, the proxies should not be interpreted as perfect predictors of these correlates. Notwithstanding these limitations, these proxies are useful because they do not introduce further parameters or sub-models that could obfuscate the mechanisms underlying our results.

Results

Throughout the forthcoming analysis, we observed no significant difference in results across mortality schemes (surface-diurnal, SD versus nearshore, NS). Here we present the results using surface-diurnal mortality as illustrative of both cases.

Mean-onshore and mean-offshore behaviors

Visualizing the final positions, x_{T_*} , of larvae performing the example behaviors PASSIVE, OVM, DVM and HYBRID illustrated a key distinction between mean-onshore and

Table 3. Summary and descriptions of the five quantities used to measure the effects of vertical swimming behaviors on larval dispersal in an upwelling regime.

Quantity	Symbol	Correlates
Settling probability	S	Larval supply to coastal habitats
Mean dispersal time	MT_*	+ Alongshore dispersal, predation risk, energy consumption (maintenance) – Retention near natal habitat
Mean surface time	MT_{surface}	+ Alongshore dispersal, offshore movement, food access, SD predation risk – Retention near natal habitat, NS predation risk
Mean offshore time	MT_{offshore}	+ Alongshore dispersal – Retention near natal habitat, NS predation risk
Mean vertical migrations	MVM	+ Energy consumption (locomotion)

mean-offshore behaviors (Fig. 4). PASSIVE appeared to be a mean-onshore behavior. Most PASSIVE larvae, regardless of fate, finished dispersal within 10 habitat widths of shore (Fig. 4a), although some outliers died or were lost further offshore. By contrast, DVM appeared to be mean-offshore. Excluding settled larvae, most individuals performing DVM finished dispersal 10–40 habitat widths from shore. For this behavior, larvae finishing dispersal closer than 10 (or more than 40) habitat widths from shore – including settling larvae – were, in a sense, outliers.

The classification of DVM as mean-offshore agreed with the prediction made by the analytical criterion in Eq. 2.9 (Fig. 2b). The criterion also predicted HYBRID as mean-onshore and OVM as on the boundary between the two classes. These predictions are confirmed in Fig. 4b, d, respectively: most HYBRID larvae finish dispersal within 10 habitat

widths of shore, while roughly equal fractions of OVM larvae finish within or beyond 15 habitat widths. Thus, although the classes mean-onshore and -offshore are better viewed as extremes on a continuum than as mutually exclusive categories, our analytical formulation of these categories is validated by Fig. 4.

Probability of settling

We computed the probability of a larva successfully settling within the nearshore habitat, S , over larval durations of $T=5$ and 30 (Fig. 5a–b) for all active behaviors in the (a,b) trait-space and the PASSIVE archetype. For both larval durations, S varied from just above 0 to approximately 0.75 across active behaviors. PASSIVE resulted in a comparatively high probability of settling in both cases: 0.62 for $T=5$, and 0.55 for $T=30$. This was unsurprising given the observation above that

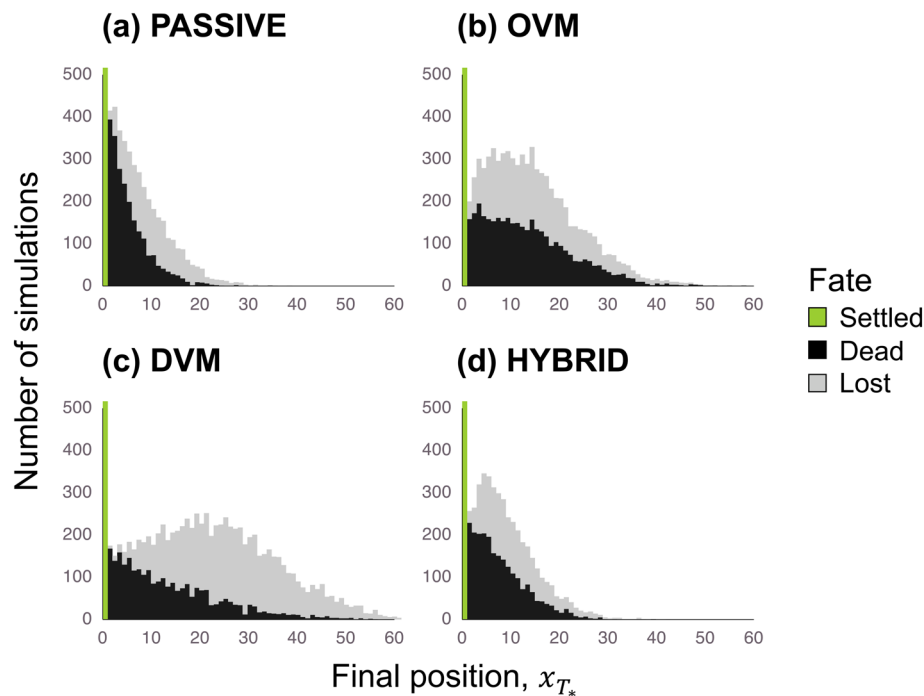


Figure 4. Stacked histograms of the final positions, x_{T_*} , of 10^4 simulated larvae for each of the example behaviors shown in Fig. 3, color-coded by the fates larvae encounter: settling in green, death in black and offshore loss in gray. (a) PASSIVE; (b) OVM; (c) DVM; (d) HYBRID. Settled larvae necessarily finish dispersal in the nearshore habitat $[0,1]$, resulting in histogram bars far taller than 500. The histogram bars showing settled larvae in $[0,1]$ are truncated to allow visualization of larvae finishing in other locations on the same axes.

PASSIVE is a mean-onshore behavior that leads most larvae to finish dispersal close to shore.

Other mean-onshore behaviors (e.g. those below the dashed curves in Fig. 5a–b) generally resulted in greater probabilities of settling than mean-offshore behaviors. This difference was more pronounced over the long larval duration $T = 30$ than over the short one, $T = 5$. In particular, S decreased gradually as daily visits to the surface were lengthed (a was increased) or ceased later (b was increased) over larval duration $T = 5$ (Fig. 5a). On the other hand, S decreased rapidly with increasing a and b over the curve separating mean-onshore and mean-offshore behaviors for larval duration $T = 30$ (Fig. 5b).

Mean-onshore and mean-offshore behaviors were affected differently by changes in advection or diffusion strength. For mean-onshore behaviors, the probability of settling, S , increased with respect to advection strength and decreased with respect to diffusion strength (that is, $\partial S/\partial u_1 > 0$ and $\partial S/\partial k_1 < 0$) while mean-offshore behaviors showed the opposite trend (Fig. 5c–d). This is also shown in Fig. 6a–b, where S is plotted as a function of u_1 and k_1 , respectively, for the mean-offshore behaviors PASSIVE and HYBRID, the mean-offshore behavior DVM and the borderline behavior OVM. Importantly,

strong advection expanded the differences in S across behaviors, while strong diffusion compressed those differences. Very strong diffusion (e.g. $k_1 > 50$), however, decreased the probability of settling for all four example behaviors.

Proxy measurements and correlates

We computed the four proxy measurements from in Table 3 for settled larvae performing the PASSIVE example behavior and each active behavior in the (a, b) trait-space. Mean-onshore behaviors (including PASSIVE) resulted in smaller values of MT , than mean-offshore behaviors simply because they limited the movement of larvae away from shore during pre-competence (Fig. 7a). Consequently, we expect mean-onshore behaviors to result in lower energy usage for maintenance, reduced risk of mortality during dispersal, and greater nearshore retention compared with most mean-offshore behaviors.

The mean-onshore versus mean-offshore classification does not capture all trends in mean dispersal time, MT , with respect to swimming behavior (a, b) . Although most mean-offshore behaviors resulted in longer mean dispersal times than mean-onshore behaviors, the mean-offshore behaviors

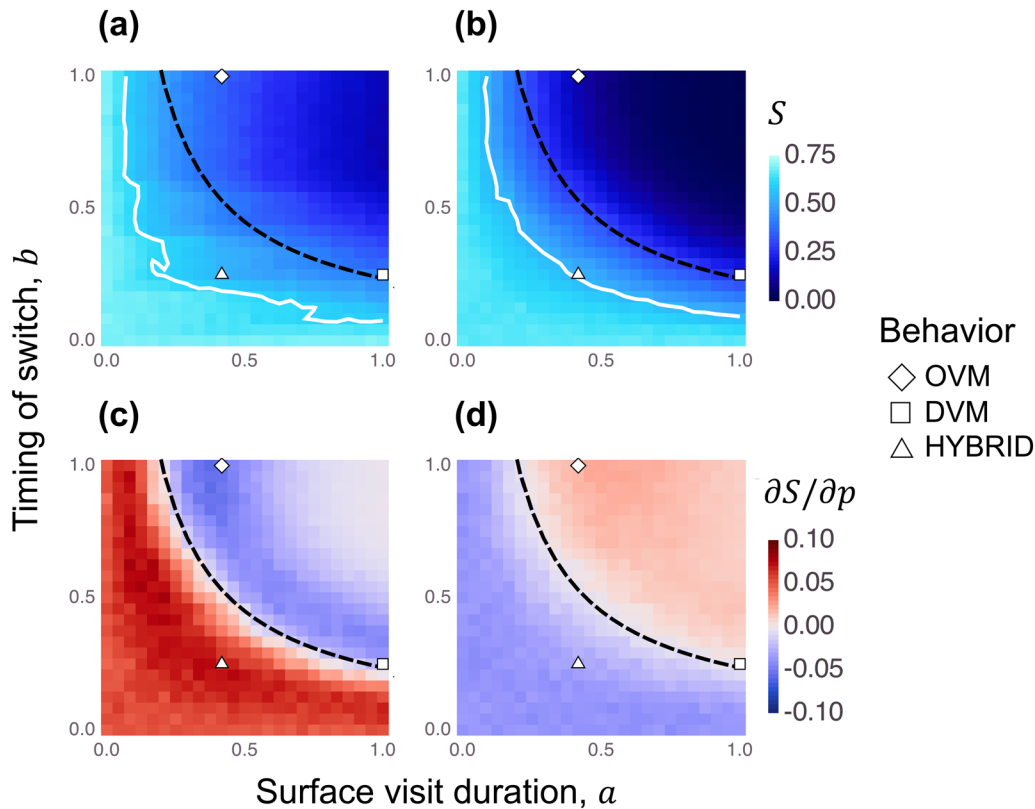


Figure 5. The fraction of $N = 10^4$ simulated larvae settling while performing a given behavior approximates S , the probability that a single larva exhibiting that behavior will settle. (a) and (b) show S for larvae with larval durations of $T = 5$ and 30 , respectively, for each active behavior (a, b) in the trait-space shown in Fig. 2. The white contour lines show the values of S attained by the PASSIVE example behavior. (c) and (d) show the derivative of S with respect to the strengths of advection, u_1 and diffusion, k_1 , respectively. In all four panels, the black dashed curve is $b = 1/5a$, which separates mean-onshore (below) and mean-offshore (above) behaviors. The white plotted points show the locations of the example behaviors OVM (square), DVM (diamond) and HYBRID (triangle) in the trait-space.

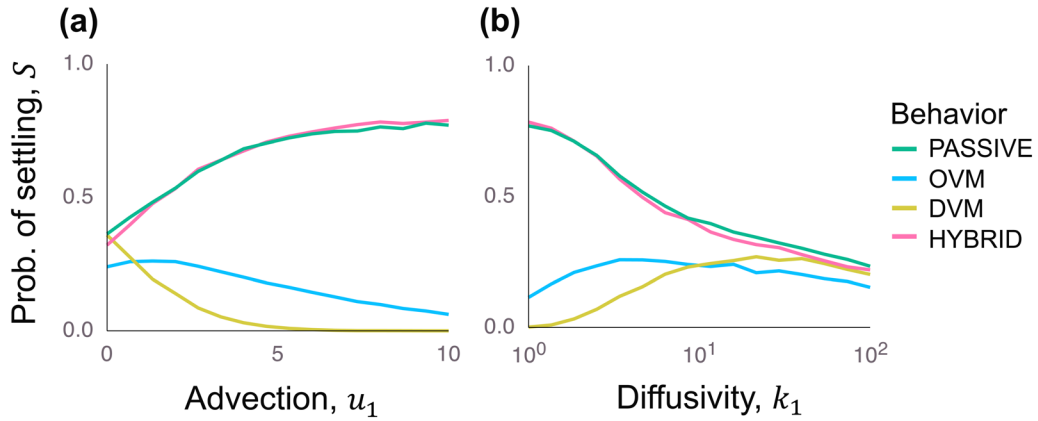


Figure 6. The probability of a larva settling, S , as a function of (a) surface advection strength, u_1 , and (b) surface diffusivity, k_1 , while using the four example behaviors in Fig. 3: PASSIVE in green, OVM in blue, DVM in yellow and HYBRID in pink. Observe that while increasing u_1 expands the differences across behaviors, increasing k_1 shrinks those differences.

that visited the surface late in dispersal (with $b > 0.75$ and $a > 0.25$) resulted in similar mean dispersal times to many mean-onshore behaviors. This is potentially counterintuitive, since later visits to the offshore-moving surface should delay, rather than advance, settling into nearshore habitats. Because

we averaged over settled larvae only (rather than all larvae), this result indicates that behaviors requiring late visits to the surface precluded late settling. That is, larvae that successfully settled while performing these behaviors did so early instead of continuing to visit the surface. Those that failed to settle

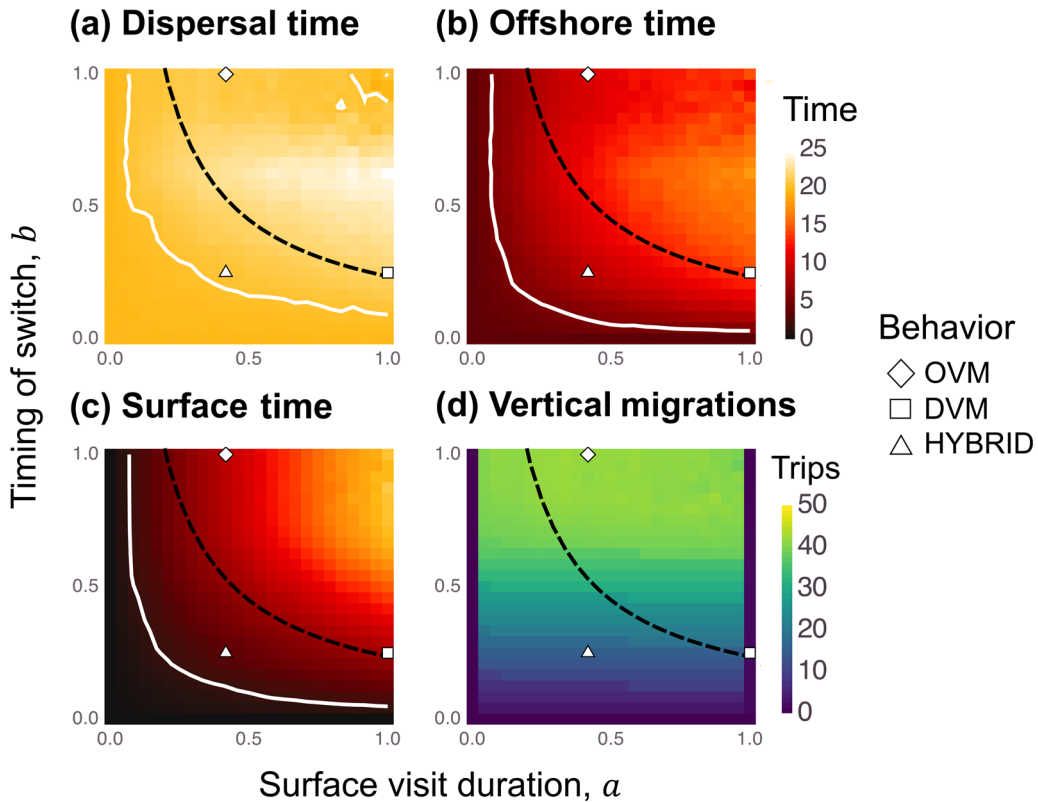


Figure 7. The proxy measurements (a) mean total dispersal time, MT , (b) mean offshore time, MT_{offshore} , (c) mean surface time, MT_{surface} and (d) mean vertical migrations, MVM , for each swimming behavior (a, b) in the trait-space in Fig. 2. As in Fig. 5, the black dashed line shows the curve $b = 1/5a$ separating mean-onshore and mean-offshore behaviors, the white contours show the values of each proxy measurement attained by the PASSIVE behavior, and the white points show the positions of the behaviors OVM (square), DVM (diamond) and HYBRID (triangle) in the trait-space. (a, b, c) all share the color bar to the right of (b). No contour for the PASSIVE behavior is shown in (d) because passively transported larvae do not exhibit any active vertical migrations.

early were transported offshore during surface visits and did not settle at all. Comparison of Fig. 5a–b with Fig. 7 reveals that while few larvae settle while performing such behaviors, successful settlers achieve greater alongshore dispersal and less exposure to nearshore hazards than larvae performing mean-onshore behaviors with a similar energy cost.

The relationship between swimming behavior (a, b) and mean offshore time, MT_{offshore} , mirrored that of swimming behavior and mean dispersal time (Fig. 7b), with the mean-offshore behaviors that switch to the lower layer near the middle of dispersal ($b \approx 0.6$) spending the most time offshore. In fact, these behaviors' long mean dispersal times appeared to be precisely the result of their spending time far from shore, rather than settling early. According to the correlations in Table 3, larvae performing these behaviors would likely experience greater alongshore transport (as suggested by MT , as well) and safety from nearshore predators. In contrast, larvae performing mean-onshore behaviors or mean-offshore behaviors that require late visits to the surface ($b \geq 0.75$) have shorter mean offshore times and would likely experience greater nearshore retention prior to settling.

The relationship between mean surface time, MT_{surface} , and swimming behavior is nearly opposite that of the probability of settling, S , and swimming behavior (compare Fig. 7c and Fig. 5b). MT_{surface} is better predicted by the mean-onshore/mean-offshore classes than MT , or MT_{offshore} . Settled larvae exhibiting mean-offshore behaviors generally spent more time in the surface before settling than those exhibiting mean-onshore behaviors. As a result, such larvae may experience greater access to food, greater alongshore dispersal, less retention near their parents' habitats and lower exposure to nearshore predators. By contrast, mean surface time predicts that larvae exhibiting mean-onshore behaviors would experience limited food access and dispersal from their parents' habitats.

Mean vertical migrations, MVM, are predicted well by a and b (Fig. 7d). Ontogenetic vertical migration-like behaviors that visit the surface only once ($a = 1$) and behaviors that avoid the surface altogether ($a = 0$) perform just 1 or 0 vertical migrations, regardless of b . For all values of a in between, larvae reliably perform two vertical migrations per day, one before midnight and one after, for the entire first phase of dispersal, resulting in approximately $2Tb$ vertical migrations total. However, this linear trend between mean vertical migrations and b is slightly influenced by the nonlinear relationship between b and mean dispersal time discussed above: later surface visits require that larvae settle earlier, resulting in slightly fewer vertical migrations for values of b close to 1 than intermediate values of b . We observed no significant difference in MVM between mean-onshore and mean-offshore behaviors, except that the behaviors with the lowest MVM were all mean-onshore (Fig. 7d). These results indicate that how late in dispersal larvae cease their vertical migrations is a good predictor of energy spent on locomotion, but whether a behavior results in mean-onshore or mean-offshore transport is not.

Discussion

We modeled larval dispersal in an upwelling system to assess how larval vertical swimming behaviors affected the fraction of larvae that successfully settle, as well as a set of proxy measurements that covary with predation risk, potential dispersal between coastal habitats, and energy budgeting. The simplicity of our model compared with state-of-the-art hydrodynamic simulations facilitated our exploration of a continuum of behaviors, rather than the handful of user-defined ones to which more complex studies are often limited. This continuum included behaviors commonly reported in upwelling systems, such as diel vertical migrations, a single ontogenetic vertical migration from the surface to the bottom, and combinations thereof.

Our results support the conclusion of prior modeling studies that vertical swimming in a stratified current can significantly alter larval supply to and dispersal between coastal habitats, and, therefore, that accurate predictions of coastal population dynamics require that behavior be included alongside oceanographic factors (Rothlisberg et al. 1983, Owens and Rothlisberg 1991, Cowen et al. 2000, 2006, Marta-Almeida et al. 2006, Metaxas and Saunders 2009, Sundelöf and Jonsson 2012, James et al. 2019). The longer the larval duration or the greater the strength of cross-shore advection relative to diffusion, the greater the effect of swimming upon dispersal. On the other hand, when diffusion is much stronger than advection (i.e. variable currents dominate persistent ones), the influence of behavior upon dispersal outcomes is diminished. That the strengths of advection and diffusion have opposite effects on the influence of swimming underscores how locomotion helps larvae exploit predictable structure in the environment, provided such structure exists.

We identified two classes of successful swimming behaviors within the trait-space considered. Mean-onshore behaviors moved larvae, on average, toward shore, resulting in a greater probability of settling but limited opportunities for feeding, alongshore movement and other benefits of planktonic development. Mean-offshore behaviors moved larvae away from shore and generally placed them in the surface layer for more time, resulting in greater feeding opportunities and alongshore movement despite a lower probability of settling. These behavioral classes illustrate that the conflicting needs of dispersing larvae create a tradeoff between settling success and other advantages of planktonic development. Vertical swimming allows larvae to reap either of these sets of benefits, but only at the expense of the other.

Mean-onshore and -offshore behaviors: physical differences

Larvae that successfully settled while performing mean-onshore behaviors typically did so because of the mean current (advection) they experienced. By contrast, larvae performing these behaviors failed to settle either due to stochastic variations in their velocities (that is, diffusion) that moved them against this mean current, or else due to

Table 4. A summary of the key differences between mean-onshore and mean-offshore larval swimming behaviors. We provide examples of behaviors in each class; specify how the probability of settling, S , and the proxy measurements in Fig. 7 vary across classes; interpret those proxy measurements in terms of their assumed covariates; and speculate regarding the organismal, ecological and environmental attributes that may favor each class. Where appropriate, we list figures to support each claim. VM=vertical migration, SD=surface/diurnal mortality, NS=nearshore mortality, Pop.=population.

	Mean-onshore	Mean-offshore	Figure
Behaviors	PASSIVE	DVM	4a, c
	HYBRID	OVM	4b, d
	early ontogenetic VM	later ontogenetic VM	2c
	diel VMs, short surface visits	diel VMs, longer surface visits	2c
	hybrid with less surface time	hybrid with more surface time	2c
Settling probability, S	high	low	5a–b, 6
Sensitivity to advection, $\partial S/\partial u_1$	positive	negative	5c, 6a
Sensitivity to diffusivity, $\partial S/\partial k_1$	negative	positive ^a	5d, 6b
Mean dispersal time	short	long ^b	7a
Mean offshore time	short	long ^b	7b
Mean surface time	short	long	7c
Mean vertical migrations	varies	varies	7d
Nearshore retention	more	less	7a–b
Alongshore dispersal	less	more	7a–c
SD predation	less	more	7d
NS predation	more	less	7c
Maintenance energy	less	more	7a
Locomotion energy	varies	varies	7d
Food access	less	more	7c
Favorable species attributes	non-feeding	feeding	
	fewer expensive larvae	many cheap larvae	
	expensive maintenance	cheap maintenance	
	cheap metamorphosis	expensive metamorphosis	
	pop. limited by larval supply	pop. limited by adult interactions	
Favorable environmental attributes	advection stronger than diffusion	advection weaker than diffusion	
	high mortality rate	low mortality rate	
	scarce food	abundant food	

^a S increased over smaller values of k_1 for mean-offshore behaviors, but decreased with larger values of k_1 for all behaviors considered. ^b Some mean-offshore behaviors with late visits to the surface (that is, greater b) have low mean dispersal and offshore times among settling larvae – larvae exhibiting such behaviors are unable to settle late in dispersal.

predation. Larvae performing mean-offshore behaviors experienced an opposite effect, with many individuals failing to settle due to net-offshore advection, and a few successful settlers delivered to the nearshore habitat through diffusion in the opposite direction.

Classical diffusion theory provides an intuitive visual that illustrates an important difference between settling due to advection and settling due to diffusion. According to the theory, the positions of a set of particles (i.e. larvae) diffusing for a fixed amount of time (in this case, the larval duration, T) should be approximately normally distributed with mean equal to the particles' net advection and variance equal to their net diffusion (Okubo and Levin 2001). For mean-onshore behaviors like PASSIVE, the mode of this distribution was at the coast and included all settled larvae, while the tail of the distribution extended offshore and included only wasted larvae. However, for mean-offshore behaviors such as DVM, the mode of this distribution was offshore and contained only failed larvae. All successful settlers were located in the distribution's left tail, and were essentially outliers among all larvae. The trajectories of these successful outliers, at times, defied our expectations – for instance, when we observed earlier settling among larvae performing behaviors

that should have resulted in offshore movement late in dispersal, and consequently, delayed settling. Researchers studying dispersal in heterogeneous environments – marine and otherwise – should be aware that the experiences of successful dispersers may differ from those of 'typical' (and unsuccessful) ones.

Although our analysis focused on dispersal in an upwelling system, mean-onshore and mean-offshore behaviors should exist in other settings where larvae rely on directed and variable currents for delivery to coastal habitats. Larvae could exploit tides, internal waves, wind-driven currents and other phenomena known to affect the cross-shelf transport of larvae using behaviors besides those considered here (Shanks 1995). More generally, the notion that organisms can successfully disperse by behaving in ways that alter their mean transport or its variance is relevant in any setting where movement is well-approximated by an advection–diffusion process.

Mean-onshore and -offshore behaviors: biological differences

As mentioned in the Methods section, the time- and length-scales of a diffusion problem determine the appropriate

advection and diffusion parameter values (Largier 2003). We chose values appropriate for dispersal within a single reproductive season. Thus, the following discussion of ecological and evolutionary differences between mean-onshore and -offshore behaviors applies mainly in relatively stable, uniform settings. Environmental variability on a multi-generational time-scale would produce greater diffusivity and weaker advection than what we modeled; as observed earlier in this Discussion (and Fig. 6), these changes would shrink the dramatic differences we noted between swimming behaviors.

Mean-onshore and mean-offshore behaviors exposed settling larvae to different conditions during dispersal. In the upwelling system we modeled, larvae performing mean-onshore behaviors were subjected mainly to the nearshore conditions within the lower layer of the water column. These larvae would have experienced few of the benefits most often associated with planktonic development, having limited access to food, little reprieve from nearshore predation and little exposure to the alongshore currents that facilitate dispersal between coastal populations. Weighing these disadvantages against a high probability of settling, one may regard mean-onshore behaviors as 'low risk, low reward.' These behaviors could benefit species with non-feeding larvae that are unaffected by limited food access. Non-feeding larvae would also benefit from the earlier settling we observed in mean-onshore behaviors, since they have no way to replenish their energy prior to metamorphosis. Most observations of late settling negatively impacting the fitness of invertebrates beyond metamorphosis ('carry-over effects') are in non-feeding larvae (Pechenik 2006), and non-feeding larvae of some species avoid late settling through other adaptations like decreased habitat selectivity (Elkin and Marshall 2007). Finally, organisms with non-feeding larvae generally produce fewer larvae than those with feeding larvae, since non-feeding larvae are more costly to produce (Vance 1973, Christiansen and Fenchel 1979, Perron and Carrier 1981, Rumrill 1990, Levin and Bridges 1995, Levitan 2000). Consequently, mean-onshore behaviors could limit the number of these expensive larvae wasted during dispersal and ensure that sufficiently many larvae return to shore despite fewer being spawned.

Mean-offshore behaviors, on the other hand, should be considered 'high risk, high reward.' Larvae performing such behaviors spend more time in the surface and far offshore than larvae performing mean-onshore behaviors, and could receive greater access to food, opportunities for alongshore travel, and safety from nearshore hazards. This would be advantageous for organisms with feeding larvae that are cheaply produced (Vance 1973, Christiansen and Fenchel 1979, Perron and Carrier 1981, Levitan 2000), able to delay settling without a significant decrease in fitness (Pechenik and Cerulli 1991, Pechenik 2006, Elkin and Marshall 2007), and are usually spawned in such large numbers that only a small fraction must successfully settle to sustain a population (Rumrill 1990). While each individual larva has a small chance of settling, those that succeed would also arrive onshore with more energy for metamorphosis than larvae performing mean-onshore behaviors. Such larvae may also

receive the benefits of dispersal between coastal populations, including an escape from competition with siblings and parents (Strathmann 1974).

Given this speculative correlation between nutritional mode and behavioral type, we can also narrow the set of behaviors considered that are likely to appear in nature based on their energetic costs. For instance, if mean-onshore behaviors are particularly favorable for non-feeding larvae, then we should expect the most common mean-onshore behaviors in nature to be those which conserve the most energy for metamorphosis – that is, those resulting in short dispersal times and requiring few vertical migrations. Examples include completely passive drifting or a single ontogenetic migration from the surface to deeper in the water column early in development. While a rigorous test of this hypothesis is beyond the scope of this article, laboratory and field studies have indeed reported this latter behavior in the non-feeding larvae of the ascidian *Ecteinascidia turbinata* (Young 1986), the sponge *Rhopaloeides odorabile* (Whalan et al. 2008), the coral *Pocillopora verrucosa* (Mulla et al. 2020) and the bryozoans *Celleporella hyalina* (Ryland 1960) and certain *Bugula* spp. (Wendt and Woollacott 1999). On the other hand, energetically costly mean-offshore behaviors like diel vertical migrations that avoid nearshore and diurnal predators and promote dispersal between habitats (at least, in the scenario modeled here) could be viable for feeding larvae, provided that these behaviors also provide adequate feeding opportunities (see Table 1 for examples).

The ecology of benthic post-larval individuals may also affect the favorability of different larval swimming behaviors. Roughgarden et al. (1988) observed that while some coastal populations maintain a relatively stable size over time, others may fluctuate dramatically. The authors argued that those stable populations receive a sufficiently large larval supply to saturate the carrying capacity of coastal adult habitats. By contrast, fluctuating populations are limited by larval supply to the coast, which varies with offshore conditions. A population limited by larval supply to the coast could benefit more from mean-onshore behaviors that boost dispersal success (Fig. 5a–b). On the other hand, a population close to its carrying capacity might benefit from mean-offshore behaviors for two reasons. First, the increased larval supply to the coast resulting from mean-onshore behaviors would be unnecessary if a smaller larval supply is sufficient to saturate the carrying capacity of the coastal adult population. Second, mean-offshore behaviors generally provide greater feeding opportunities that can improve the chances of those few settling larvae surviving metamorphosis and post-larval growth (Holland and Spencer 1973, Pechenik and Cerulli 1991, Videla et al. 1998, Pechenik 2006).

Metapopulations of coastal marine invertebrates depend upon the dispersal of larvae between coastal sites for connectivity. Strathmann (1974) argued that within environments with unpredictable spatial variability over time, the dispersal of an adult's larvae over a broad area reduces variation in reproductive success, since some larvae will typically land in a suitable habitat. Accordingly, Strathmann initially suggested

that greater larval dispersal distances would be advantageous in such settings. However, Palmer and Strathmann (1981) later demonstrated that this is only partially true: when spatial variability is predictable over time, large-scale dispersal prevents organisms from exploiting reliably favorable habitats. Thus, while it is tempting to list greater dispersal between habitats as an advantage of mean-offshore behaviors over mean-onshore ones, doing so may be misguided. Except in settings where habitat quality has a high variance and low autocorrelation (which is not typical), greater dispersal potential is not strictly beneficial.

Although we described movement as deterministic and pre-programmed, real larvae do not move in lockstep (Young 1986). Variation in the timing of vertical migrations results in a spreading out of larvae that seem to exhibit the 'same' behavior, some of which is captured in our model and others by diffusivity (Largier 2003). We further explored the effects of this variation by considering a continuum of behaviors alongside specific examples, since the behaviors of a given species are more likely to comprise a region, rather than a point, in the (a,b) trait-space. We described behaviors as being either mean-onshore or mean-offshore, but it is possible for larvae to exhibit a set of behaviors straddling the boundary between these classes. This may help spread risk among an individual's offspring, with some experiencing the risks and rewards of mean-offshore behaviors and others enjoying the nearshore retention of mean-onshore behaviors.

Importance of mortality rate structure

Our analysis considered two larval mortality scenarios that may have played a role in the evolution of dispersive larvae and their swimming behaviors. Elevated nearshore mortality due to coastal benthic predators and competition between larvae and their siblings or parents is often argued to have selected for planktonic (rather than benthic) development, with dispersal occurring incidentally (Pechenik 1999, Levin 2006, Burgess et al. 2016). Diurnal predation in the surface due to visually guided predators, when combined with an incentive for larvae to visit the surface at night (e.g. feeding or different currents), is frequently used to justify behaviors such as diel vertical migrations (Mangel and Clark 1988, Shanks 1995).

We observed few important differences across these mortality schemes in the effects of swimming behaviors upon the probability and timing of larval settling. This was surprising because intuition suggests that nearshore and diurnal surface mortality would reward different behaviors. Nearshore mortality rewards mean-offshore behaviors that allow larvae to quickly escape the hazardous coastline, such as an ontogenetic migration from the surface to the bottom partway through development. Diurnal surface mortality penalizes this behavior, but rewards others that avoid the surface during daylight regardless of the offshore movement they effect. While the choice of mortality rate structure influenced the absolute probability of settling associated with each behavior, it did not qualitatively change how this probability varied over the trait-space considered.

The independence of these trends from the mortality scheme is undoubtedly due to the mortality parameters we used: if we had chosen the rates μ_i to be larger and to differ more across high- and low-mortality regions (or, if we had simulated a larval duration longer than $T = 30$ days), we would have seen a stronger effect of the mortality rate structure. Our mortality rates were based on recent estimates by White et al. (2014), who argued that instantaneous larval mortality rates have historically been overestimated due to the large fraction of larvae lost offshore. Using these values, offshore loss proved a greater source of larval wastage than mortality, such that the spatial structure of the mortality rate had little impact on the relationship between behavior and larval supply. Thus, we expect that our analysis would have produced similar results if other mortality schemes were considered, such as elevated mortality in the lower layer due to benthic predators.

Connolly and Baird (2010) and Moneghetti et al. (2019) illustrated that variable mortality throughout the larval duration (particularly in tandem with individual-level variability in the timing of competence and senescence) qualitatively alters dispersal kernels in ways that can impact population dynamical predictions. Similarly, Meyer et al. (2021a) suggested that spatially variable mortality rates could influence dispersal kernels by determining how far offshore successful larvae reside prior to settling and the alongshore currents they experience. In general, spatial and temporal variability in the mortality rate should have similar effects on dispersal kernels because larval age and position co-vary; that is, larvae are more likely to be in certain locations at certain points in the larval duration. Our analysis only considered alongshore movement through proxy measurements (dispersal time and time spent far offshore), and only over a single larval duration. In this setting, our results did not support a strong effect of mortality rate variability upon alongshore movement. However, it is plausible that we might have seen an effect if we had modeled alongshore movement explicitly, as was done by Connolly and Baird (2010) and Moneghetti et al. (2019). Furthermore, even a weak effect of the mortality rate on the dispersal kernel can alter population dynamics when propagated through several generations.

Conclusion

We conclude by offering some recommendations to theoretical and experimental ecologists concerned with the impact of vertical swimming upon larval and coastal ecology. Our analysis highlighted the importance of including aspects of larval dispersal besides movement, such as energetics and predation risk, while modeling vertical swimming. Although the relationship between feeding, energy use, and swimming is difficult to quantify holistically (rather than in separate pieces, as we have done) due to the diversity of larval types and modes of nutrition and locomotion, energetics may, in fact, be a key determinant of the behaviors exhibited by a given species in a particular environment. Predation risk is more readily incorporated into modeling studies. Larval mortality rates are notoriously difficult to

measure in the field (Rumrill 1990, Morgan 1995, White et al. 2014), but even uniform mortality rates interact with vertical swimming due to the effect of behavior on dispersal time. Furthermore, although the effects of mortality rate structure highlighted by Connolly and Baird (2010), Moneghetti et al. (2019) and Meyer et al. (2021a) were not evident in this study, we emphasize that mortality rate structure can have unexpected consequences and deserves greater attention in future modeling studies, especially when considering population dynamics.

We hypothesized that in an environment with stratified currents (for example, upwelling circulation), feeding and non-feeding larvae are likely to exhibit different types of behaviors – the former prioritizing alongshore dispersal, predator avoidance, and feeding opportunities, and the latter prioritizing nearshore retention and early settling. A systematic analysis of published studies on vertical swimming in the field could test this hypothesis and generalize it to settings other than upwelling. One potential obstacle is the variety of ways in which swimming behaviors are quantified, which is largely due to the persistent challenges of observing microscopic larvae in the field. For instance, Young (1986) collected detailed observations on how *Ecteinascidia turbinata* tadpole larvae (which are macroscopic) change their activity levels and directions over time, but it is not clear how these observations should be compared against the larval depth profiles presented in studies such as that of Shanks (1986). Therefore, testing the relationship between swimming behavior and nutritional mode (or other predictors) will require new analytical methods for comparing these data or further empirical observations collected in a standardized way.

Acknowledgements – The authors thank Steven G. Morgan and Scott Burgess for providing invaluable feedback on earlier drafts of this article.

Funding – ADM was funded by a teaching stipend and departmental fellowship from the UC Davis Department of Mathematics. AH and JLL did not receive funding for this research.

Author contributions

Alexander D. Meyer: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (lead); Software (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Alan Hastings:** Conceptualization (equal); Methodology (supporting); Supervision (equal); Writing – review and editing (supporting). **John L. Largier:** Conceptualization (equal); Methodology (supporting); Supervision (equal); Writing – review and editing (supporting).

Data availability statement

Codes for performing the simulations and analyses presented in this paper are available from GitHub at <<https://github.com/alexdmeyer/larva-vertical-swimming-oikos>> (Meyer et al. 2021b).

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