Title

Great Risk, Grave Uncertainty, and Making Your Own Luck: The Dispersal of Coastal Marine Invertebrate Larvae in Heterogeneous Environments

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Great Risk, Grave Uncertainty, and Making Your Own Luck: The Dispersal of Coastal Marine Invertebrate Larvae in Heterogeneous Environments

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To Mom, Joe, Daniel, and Aubrey,
my East Coast Support Team.

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Great Risk, Grave Uncertainty, and Making Your Own Luck:
Dispersal and Behavior of Coastal Marine Invertebrate Larvae in Heterogeneous Environments

Abstract

Many coastal marine invertebrates and fish begin life as planktonic larvae that can be transported several kilometers offshore by coastal currents. To have any hope of surviving to reproduction, larvae must avoid predators during dispersal and return to shore with enough energy for further development. Most larvae fail to do so, prompting Rumrill (1990) to begin his review of larval mortality by stating that coastal marine animal larvae "lead transitory lives of great risk and grave uncertainty." I examine, using stochastic modeling, how these risks and uncertainties are shaped—and in some cases, overcome—by the passive and active interactions of larvae with spatially varying features of their environments. Chapter 2 focuses on the consequences of increased larval mortality near the coast compared with offshore. The relative safety of offshore waters is often mentioned in discussions of the evolutionary origins of planktonic larvae, but is omitted by most modeling studies. I show that ignoring this feature may, in some cases, substantially alter predictions of coastal population dynamics and connectivity. Furthermore, oceanographic features that slow nearshore larval movement (such as coastal boundary layers) are double-edged swords, limiting the offshore loss of larvae but also preventing larvae from escaping nearshore hazards.

Chapters 3 and 4 illustrate how larvae improve their chances of success by slowly swimming vertically to exploit differences in current velocity, food abundance, and predation throughout the water column. In Chapter 3, I consider a broad, continuous set of behaviors for larvae dispersing in an idealized environment approximating the two-layer flow typical of upwelling circulation. I show that while some behaviors successfully increase feeding opportunities and alongshore movement or limit the fraction of larvae that are lost offshore, no behaviors I modeled achieve both at once. I speculate that the former class of behaviors is suitable for organisms that spawn many cheap, long-lived larvae that feed during dispersal, while the latter is preferable for organisms with fewer, more expensive larvae that cannot feed. I extend this analysis in Chapter 4 by using dynamic programming to construct behaviors that optimize a metric of success that balances delivery to coastal habitats, predation risk, and energy budgeting. I demonstrate that some behaviors observed

in nature are optimal in specific conditions, and that there exist realistic non-optimal behaviors that perform reliably well as conditions are varied. I hypothesize that many behaviors observed in nature result from selection for success in both typical or static conditions as well as extreme or variable ones. More broadly, I emphasize in Chapters 3 and 4 that predictable spatial structure in the environment creates an opportunity for larvae to change their destinies, and that these changes are most evident when mortality and energetics are considered alongside larval delivery to coastal habitats.

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CHAPTER 1

Introduction

1.1. Context

Understanding how organisms and populations disperse from one habitat to another is among the most enduring challenges in ecology (Hanski, 1998, Levin et al, 2003, Lewis et al, 2016, Okubo and Levin, 2001, Ronce, 2007, Skellam, 1951). Dispersal plays a critical role in determining where species can thrive (Fagan et al, 2009) and how much space they require (Okubo and Levin, 2001), as well as their ability to compete and coexist with other species (Okubo and Levin, 2001, Skellam, 1951). Dispersal also lies at the center of several ecological applications, including the management of invasive species (Lewis et al, 2016), the conservation of threatened and harvested ones (Levin, 2006, Lubchenco et al, 2003), and the assessment of how stressors associated with climate change might affect populations in the future (Gerber et al, 2014, Li et al, 2014). Finally, the ecology and evolution of dispersal is a complex, multifaceted topic that invites an interdisciplinary approach, drawing together people and ideas from biology, physics, chemistry, mathematics, and more (Okubo and Levin, 2001).

Researchers have characterized spectacular diversity in when, how, and why organisms disperse. Dispersive early life stages, such as the seeds of many plants (Levin et al, 2003) and the larvae or spores of many benthic fish, invertebrates, and kelps (Levin and Bridges, 1995, Shanks et al, 2003), are common among sedentary and sessile organisms. On the other hand, organisms with motile adults are capable of dispersal throughout their lifetimes, and there exist organisms that can only disperse at the very ends of their lives, such as periodical cicadas (Lehmann-Ziebarth et al, 2005). Mechanisms of dispersal range from the active (i.e., locomotion) to the completely passive (e.g., movement by winds), with many organisms relying on combinations of both (Okubo and Levin, 2001, Shanks, 1995).

The ultimate causes of dispersal and the pressures which select for it vary across systems and remain active research areas (Burgess et al, 2016, Hamilton and May, 1977, Palmer and Strathmann, 1981, Ronce, 2007, Shaw et al, 2019). Benefits of dispersal include the easing of competition with siblings and parents, the potential for organisms to reach better habitats than the ones into which they were born (Hamilton and May, 1977, Strathmann, 1974), and an escape from local parasites and pathogens (Ronce, 2007). However, dispersal also incurs several costs. Movement is expensive for some organisms, and there is no guarantee that dispersers will find habitats that are suitable, let alone better than those they left (Morgan, 1995a, Palmer and Strathmann, 1981). Dispersers are also vulnerable to consumption by other organisms (especially when they are small, such as seeds or larvae) (Morgan, 1995a, Skellam, 1951). Because of these costs, there exist cases where dispersal is merely an accidental byproduct of movement for other purposes. For example, Burgess et al (2016) argued that the larvae of many benthic marine invertebrates and fish are planktonic simply because the benthos is too dangerous a place for early development. For all its risks, planktonic development offers an escape from nearshore and benthic predators; dispersal between habitats occurs as a consequence of unpredictable currents during development. This hypothesis is supported by the abundance of mechanisms by which marine larvae limit, rather than enhance, their dispersal offshore and between habitats (Burgess et al, 2016, Levin, 2006, Pechenik, 1999).

Dispersal ecology invites a mathematical treatment for both practical and theoretical reasons. From a purely practical standpoint, tracking the movement of dispersing organisms can be challenging. This is particularly true of organisms' dispersive early life stages, which are often simultaneously minuscule and numerous, may be transported very long distances, and often move through media where sampling is challenging, such as far offshore or high above sea level (Gerber et al, 2014, Levin, 2006, Levin et al, 2003, Okubo and Levin, 2001, Shanks et al, 2003, Suter, 1999). These difficulties are compounded by the fact that in many cases, very few of these dispersing entities successfully locate habitats and survive until reproduction (Skellam, 1951): even if tracking individuals during were simple, the probability of observing individuals whose experiences represent those of the reproductive population is minute. From a theoretical perspective, dispersal welcomes the use of mathematics because although organisms rely on diverse dispersal mechanisms, the physics governing their movements (and its approximations) are universal. The analogy between dispersing populations and diffusing molecules is often accurate enough to further justify the use of principles from physics in dispersal ecology (Okubo and Levin, 2001). Finally, the population dynamics of organisms over space and time are amenable to mathematical approaches for the same reasons as dynamics over time *per se*: dynamics can occur on larger and longer scales than we can feasibly measure, and the governing principles that produce observed dynamics cannot always be discerned through observations alone.

The research I present in this dissertation uses mathematical models to study how the dispersal of coastal marine invertebrate larvae is shaped by passive and active interactions between larvae and the coastal environment. Modeling research on larval dispersal has now existed for at least 35 years (e.g., Roughgarden and Iwasa (1986), and see review by Gaines and Lafferty (1995)), and has steadily accelerated due to parallel increases in computing power and interest in protecting coastal populations and resources (Gerber et al, 2014, Levin, 2006, Lubchenco et al, 2003). Much of this research (Cowen et al, 2006, Donahue et al, 2015, Gaines et al, 2003, Largier, 2003, 2004, Marta-Almeida et al, 2006, Paris et al, 2007, Rothlisberg et al, 1983, Roughgarden et al, 1988, Siegel et al, 2008) focuses on how larval biology and behavior and coastal oceanography influence dispersal between coastal populations or marine reserves (or metapopulations and reserve networks). This emphasis on the movement of larvae is justified—as Gaines and Lafferty (1995) point out, it is generally impossible to explain or predict coastal population dynamics without modeling larvae. However, modelers often neglect other processes occurring during dispersal, even though these are central to many explanations of why larvae exhibit the behaviors seen in nature, or why larvae develop in the plankton at all.

Chapters 2-4 of my dissertation present three research projects, each of which deploys a mathematical model to understand larval dispersal and its concurrent processes. These chapters are intended to be published separately in academic journals: Chapter 2 was published in *Theoretical Ecology* in May, 2021 (Meyer et al, 2021); Chapter 3 was recently submitted for review; and Chapter 4 is being prepared for submission. Below, I summarize the background biology, methods, and main results of these projects.

1.2. Larval Ecology: A Brief Primer

Most coastal marine invertebrates and many reef fish begin life as dispersive planktonic larvae (Gerber et al, 2014, Levin, 2006, Pechenik, 1999). Subject to coastal currents and turbulence, these larvae can be transported dozens or hundreds of kilometers off- and alongshore of their parents' habitats (Shanks, 1995, 2009, Shanks et al, 2003). In contrast, adults of these species are generally slow-moving (e.g., crabs, urchins, sea snails) or completely sessile (e.g., barnacles, tunicates, anemones) (Levin and Bridges, 1995). Thus, movement during the larval stage comprises the majority of lifetime displacement for many such organisms, and is the main driver of connectivity between coastal populations (Gerber et al, 2014, Levin, 2006, Pechenik, 1999). It follows that the experiences and behaviors of these larvae during dispersal have important consequences for coastal population and metapopulation dynamics.

The successful dispersal of a larva typically begins with spawning from, and ends with settling into, a nearshore habitat (Shanks, 1995). The period between spawning and settling, called the larval duration, lasts for as little as a few minutes (as in the tunicate *Ecteinascidia turbinate*) up to nearly one year (as in the giant triton, *Cymatium pathenopeum*) (Shanks et al, 2003). During the larval duration, individuals undergo developmental changes in preparation for metamorphosing into post-larvae upon settling. Larvae of some species feed to acquire energy for development and other processes (feeding, or planktotrophic, larvae), while larvae of others are spawned with maternally supplied energy sources but are unable to eat (non-feeding, or lecithotrophic, larvae; see Levin and Bridges (1995)). Regardless of their nutritional modes, larvae must finish dispersal in suitable habitats and with sufficient energy to undergo metamorphosis (Elkin and Marshall, 2007, Pechenik, 1999, Shanks, 1995).

Dispersal is dangerous, and only a small fraction of larvae succeeds (Morgan, 1995a, Rumrill, 1990, White et al, 2014). Reproductive adult benthic invertebrates may produce millions of fertilized embryos (Christiansen and Fenchel, 1979, Levitan, 1995, Rumrill, 1990), of which perhaps 1% (and possibly far less) survives through metamorphosis (Rumrill, 1990). The remainder are consumed en route by predators, lost to the open ocean, or unable to locate suitable settling sites due to crowding (Morgan, 1995a, Roughgarden et al, 1988). Rumrill (1990) attempted to estimate instantaneous larval mortality rates by reviewing the literature on estimated survivorship. Although White et al

(2014) revised Rumrill's estimates of the mortality rate downward, the sentiment expressed in the first sentence of Rumrill's abstract endures: "[Planktonic larvae] lead transitory lives of great risk and grave uncertainty."

Cowen et al (2000) used a simple diffusion model to illustrate that if larvae merely dispersed passively from coastal habitats, the fraction of larvae lost asea would be unacceptably large. The authors concluded that there exist mechanisms by which the offshore movement of larvae is limited, and suggested that swimming to take advantage of depth-varying cross-shore currents is one such mechanism. In fact, it is well documented that larval transport, as well as exposure to predators, energy consumption, and feeding opportunities, are shaped by several incidental and deliberate interactions between individuals and the heterogeneous structure of the coastal environment. That is, some environmental features directly influence the fates of larvae (Largier, 2004), and others can be exploited through adaptations and behavior (Shanks, 1995, Young, 1995).

1.3. Spatial Heterogeneity of the Mortality and Diffusion Rates

It is seemingly paradoxical that planktonic larval development is so common in nature despite the tremendous risks that larvae face. The argument that planktonic development is an ontogenetic migration of vulnerable larvae away from nearshore predators and sibling competition, with dispersal occurring incidentally, seems to resolve this tension (Burgess et al, 2016, Levin, 2006, Pechenik, 1999, Strathmann, 1974). However, it is not clear how these nearshore dangers might affect larval dispersal on ecological, rather than evolutionary, timescales. When is it advantageous to substitute offshore risks (e.g., being lost offshore) for nearshore ones? How does a hazardous coastline alter predictions of dispersal between habitats? And is the balance of near- and offshore perils affected by a coastal boundary layer (CBL) that slows movement near that coast?

In Chapter 2, I address these questions by modeling the dispersal, mortality, and habitat selection of a single passively floating larva using a reaction-diffusion equation and its underlying stochastic process. Unlike previous modeling studies that use spatially uniform mortality rates or ignore mortality altogether (Cowen et al, 2000, 2006, Paris et al, 2007, Roughgarden et al, 1988, Siegel et al, 2008), my analysis assumes that the larval mortality rate is elevated over a region adjacent to shore and weaker offshore. I derive expressions for the probabilities of the modeled larva (or the fractions of a large population of larvae) dying prematurely, settling into a nearshore habitat, or being lost offshore that can be evaluated numerically. I show that the probability of a larva settling can vary by over an order of magnitude with the difference between the nearshore and offshore mortality rates. I also demonstrate that when larvae experience reduced predation offshore, their probability of settling is maximized by an intermediate diffusion rate. In this case, a low-diffusivity coastal boundary layer reduces this probability by preventing larvae from reaching safer offshore conditions. Finally, I show that low mortality offshore results in a greater fraction of successful larvae having spent a long time far offshore, exposed to strong alongshore currents, than would otherwise be predicted. Thus, the structure of the mortality rate also has consequences for the alongshore movement of larvae between habitats—a topic of particular interest in the fisheries, conservation, and metapopulation dynamics literatures.

1.4. Consequences of Vertical Swimming: Beyond Alongshore Movement

The modeling literature on larval vertical swimming is understandably biased toward predicting movement between populations (Cowen et al, 2006, Marta-Almeida et al, 2006, Owens and Rothlisberg, 1991, Paris et al, 2007, Rothlisberg et al, 1983, Sundelöf and Jonsson, 2012). These models generally predict that the vertical swimming behaviors seen in nature, such as diel vertical migrations (i.e., visiting the surface only at night), promote the nearshore retention of larvae, and therefore that populations are less “open” and offshore loss less extreme than intuition suggests. This important observation, however, does not explain how these behaviors manage the often conflicting needs of predator avoidance and feeding alongside delivery to coastal habitats. There could be several ways in which larvae achieve nearshore retention. Why are behaviors like DVM observed so often in the field and laboratory?

In Chapters 3 and 4, I use a stochastic model of larval dispersal in an idealized environment to explore how vertical swimming behaviors affect larval delivery to adult habitats, predation risk, energy use, access to food, and (in Chapter 3) potential for alongshore movement. The modeled environment approximates upwelling circulation, a common occurrence off western coasts worldwide, using just two layers: a surface layer that flows offshore, and a bottom layer that flows onshore. This heterogeneous flow is necessary to illustrate how behaviors allow larvae to exploit the structure of their environment.

In Chapter 3, I consider a broad, continuous "trait-space" of swimming behaviors that includes DVM, ontogenetic vertical migration (OVM) with a single depth change partway through development, and combinations thereof. This contrasts with previous modeling studies that examine just one or a handful of prescribed behaviors. I argue that the continuity of this trait-space is essential because noisy observations of larval swimming (e.g., Shanks (1986)) suggest that individuals do not perform precisely the same behaviors in lockstep. Additionally, Sundelöf and Jonsson (2012) found that small decisions regarding how these behaviors are modeled, such as whether DVM is described using a square wave or a sinusoid, can dramatically alter their effects on dispersal. I show that in the modeled environment (and presumably others where currents reliably point in opposite directions), there exist two general categories of behaviors. "Advection-driven" behaviors are low-risk and produce net-onshore transport, resulting in nearshore retention of larvae but little potential for alongshore dispersal, fewer feeding opportunities, and no safety from nearshore dangers. "Diffusion-compensated" behaviors produce net-offshore transport, such that larvae only return to shore through random movements against this mean. These behaviors are riskier because they do not effect nearshore retention, but in turn allow greater off- and alongshore movement. I theorize that these behavioral types may better suit species with short-lived non-feeding larvae or long-lived feeding larvae, respectively.

In Chapter 4, I use both bottom-up and top-down approaches to propose and assess the advantages of larval behaviors. First, I compute behaviors *de novo* that maximize a metric of larval success via dynamic programming, an optimization method often applied in behavioral ecology (Mangel and Clark, 1988). This metric balances the requirements that larvae avoid predators and return to shore at the end of dispersal with sufficient energy to metamorphose. I show that in several contexts, optimal behaviors resemble those seen in nature, such as OVM. Next, I compare these optima against a few prescribed "near-optima" based on the true optima, my findings in Chapter 3, and the literature. My results illustrate that while optimal behaviors are context-dependent and sensitive to many factors, the success of these near-optima is robust. I hypothesize, based on these results, that natural selection favors behaviors like OVM because they are successful (if not optimal) in a wide range of conditions that includes both the typical or stable and the extreme or volatile.

CHAPTER 2

Spatial heterogeneity of mortality and diffusion rates determines larval delivery to adult habitats for coastal marine populations

Abstract

Many benthic animals begin life with a planktonic larval stage during which coastal currents may move individuals far from shore. This trait is believed to allow individuals to develop away from nearshore predators and sibling competition, based on the assumption that mortality rates are weaker offshore. However, larvae developing offshore often fail to locate suitable coastal habitats. This results in a trade-off between nearshore mortality and offshore loss with consequences for larval delivery to adult habitats that have not been fully appreciated. We use a reaction-diffusion model to show that when the nearshore larval mortality rate is high, larval supply can vary more than 10-fold with the offshore mortality rate. If this offshore rate is weak, then larval supply is maximized by an intermediate diffusion rate or larval duration. While a low-diffusivity coastal boundary layer typically improves the larval supply by decreasing offshore loss, it can also reduce the larval supply by preventing individuals from exploiting low offshore mortality rates. Finally, the cross-shore structure of the mortality rate may influence the alongshore transport of larvae by determining how far offshore they reside prior to settling, and consequently the alongshore currents they experience. Our observations contrast with the prior argument that larval supply decreases with diffusivity and larval duration due to offshore loss, and challenge the widespread decision to omit cross-shore heterogeneity from studies of alongshore movement. Scenarios in which spatial variability in the mortality rate has a large effect on recruitment are important both for understanding the biological consequences of the larval stage and from a modeling perspective.

2.1. Introduction

Biphasic life cycles, featuring a planktonic larval stage and a sedentary adult stage separated by metamorphosis, are common among benthic invertebrates and reef fish (Gerber et al, 2014, Levin and Bridges, 1995, Pechenik, 1999). Although the exact details of the larval stage vary across species, a successful trajectory might progress as follows: spawning or hatching in the benthos or bottom waters; transport (by diffusion, advection, and in many cases, locomotion) away from the natal habitat; development in the water column until competent for metamorphosis; transport toward a suitable benthic habitat; and settling into this habitat for metamorphosis (Shanks, 1995). However, very few spawned larvae actually settle, while the vast majority either succumb to predation and other hazards ("mortality") or fail to find a suitable habitat before senescence ("offshore loss") (Morgan, 1995b, Rumrill, 1990, White et al, 2014).

It is often asserted that planktonic development did not arise as an adaptation for dispersal, but rather as an ontogenetic migration that removes vulnerable offspring from sibling competition and coastal predators (including the larvae's parents), with dispersal occurring as a consequence (Levin, 2006, Morgan, 1995b, Pechenik, 1999, Shanks, 1995, Strathmann, 1974). The claim rests on the belief that larvae experience greater mortality rates near the shore than elsewhere. However, this argument is confounded by the fact that larvae transported far from coastal habitats instead face an increased risk of offshore loss (Cowen et al, 2000, Morgan, 1995b, Rumrill, 1990). The spatial segregation of these two sources of larval loss results in a trade-off between mortality and loss with offshore travel, in which movement away from one hazard seemingly brings larvae closer to the other. In other words, dispersing larvae find themselves "between a rock and a hard place."

Assuming that the commonness of dispersive larvae in nature indicates that this life history strategy is in some way adaptive, one or more of the following statements about larval dispersal should be true:

(i) The risk of mortality near the shore is so great that the probability of returning from offshore to settle is greater than that of surviving near the coast.

(ii) There are mechanisms by which the trade-off of offshore movement can be managed, such that larvae can escape mortality near the shore without greatly increasing their risk of offshore loss, or vice versa.

(iii) Despite the risks, species with dispersive larva produce sufficiently many successful offspring to replenish the adult population. There are benefits to planktonic development and dispersal that are not adequately captured by the fraction of larvae that ultimately settles.

Theory and examples supporting statements (ii) and (iii) are common in the literature, while (i) is usually taken as axiomatic for the evolution of planktonic, rather than benthically reared, offspring.

Mechanisms for managing the trade-off between offshore loss and mortality can be biotic or abiotic. Biotic mechanisms include horizontal and vertical locomotion by larvae of some species to influence net changes to their advection and diffusion, but the ability to do so varies across taxa (Cowen et al, 2000, Largier, 2003, Paris et al, 2007, Shanks, 1986, Young, 1995). Abiotic mechanisms, on the other hand, are relevant to individuals of all species in a given environment. Retention zones and coastal boundary layers (CBLs) in which movement is slow have long been recognized as common oceanographic phenomena that reduce offshore loss by keeping larvae close to shore (Largier, 2003, 2004, Morgan, 1995b, Nickols et al, 2013, Shanks, 2009). These mechanisms may, in some cases, also act to mitigate trade-offs between offshore loss and mortality by allowing larvae to escape high nearshore mortality rates without being swept too far away. In other cases—particularly when the mortality rate is high over much of the CBL or the habitat into which larvae must settle—one would expect nearshore retention to exacerbate mortality. Further investigation is needed to determine how low-diffusivity coastal regions interact with the mortality-offshore loss trade-off.

Undoubtedly, there are benefits to planktonic development that extend beyond ensuring a sufficiently large reproductive yield. These include many of the the usual benefits to dispersal and range expansion seen in both aquatic and terrestrial ecosystems, such as escaping crowding, inbreeding, and pathogens or parasites; the ability to colonize new and potentially better habitats; and increased resilience against local disturbances (Burgess et al, 2016, Hamilton and May, 1977, Shaw et al, 2019, Strathmann, 1974). Larval dispersal may also allow larvae to access and benefit from different food sources in the offshore waters than would be accessible nearshore or in the benthos. Additionally, planktonic development may allow for multiple kinds of bet-hedging against environmental variability. By having larvae settle in several different habitats along the shore, individuals may reduce the probability of having all of their offspring wiped out by a localized stochastic disturbance (Strathmann, 1974). Organisms may also bet-hedge by exploiting the trade-off between offshore loss and mortality inherent in cross-shore dispersal. If nearshore mortality rates and offshore diffusivity vary annually, but independently, then exposing individual offspring to either (but not both) of these sources of loss reduces the probability that a bad year will extinguish all of an individual's progeny.

The present chapter investigates the conditions needed for the risk of nearshore mortality to outweigh that of offshore offshore loss (that is, statement (i)), and how these conditions are affected by a CBL (statement (ii)), a mechanism usually held to improve recruitment. Despite the evolutionary significance ascribed to cross-shore heterogeneity in the larval mortality rate, there have been surprisingly few attempts to measure mortality rates in nature (but see Rumrill (1990) and White et al (2014)). This is largely due to the many challenges researchers face tracking individual larvae *in situ*, as well as obstacles to direct measurement of the mortality rate itself. Yet, although mathematical models are commonly used to study larval dispersal and the connectivity of coastal metapopulations, even theoretical studies often assume the mortality rate to be uniform in space, or are agnostic about offshore mortality (or mortality in general) as an important source of wastage compared to nearshore mortality and offshore loss (Cowen and Sponaugle, 2008, Cowen et al, 2000, 2006, Nickols et al, 2015, Paris et al, 2007, Roughgarden et al, 1988, Siegel et al, 2008). Excluding cross-shore structure in the mortality rate allows researchers to focus on other aspects of dispersal, but to our knowledge, no efforts have been made to determine what effect this structure has on other research foci, such as larval supply and alongshore dispersal distance (collectively, "larval delivery" to coastal post-larval habitats).

We believe that in some cases, neglecting the cross-shore structure of the environment will lead to erroneous predictions of larval delivery. Fitting a spatially uniform mortality rate to field measurements, or neglecting mortality altogether, can result in substantively different estimates of the fraction of spawned larvae that returns to shore, and may have consequences for local population dynamics. Furthermore, the spatial structure of the mortality rate determines how far offshore settling larvae tend to reside during development. Since alongshore currents are often structured in the cross-shore direction, a heterogeneous mortality rate could influence which alongshore currents larvae experience during development, and consequently, how far alongshore larvae disperse (Largier, 2003, Largier et al, 1993, Nickols et al, 2012).

The trade-off created by near- and offshore hazards may also have evolutionary implications that have not previously been discussed. The diffusivity of an individual larva is the result of both coastal hydrodynamics, which vary on several time scales, and morphology and behavior, which can be shaped over generations by natural selection. Focusing strictly on a population's ability to sustain itself over time, we expect the most favorable phenotypes to be those that maximize the number of larvae that survive until reproduction while minimizing the risk of recruitment failure due to environmental stochasticity. If the mortality risk were equal everywhere, then there would seem to be little reason for larvae to travel long distances, and so evolution would favor phenotypes that reduce diffusivity. On the other hand, a greater risk of death near the shore than elsewhere would select for intermediate or high diffusivity, depending on how this risk compares with that of offshore loss.

Here, we model the passive diffusion of larvae to investigate when and how the cross-shore structure of the mortality rate impacts predictions of larval supply, as measured by the fraction of dispersing larvae that ultimately settles (or equivalently, an individual larva's probability of settling). We also explore how a CBL interacts with the heterogeneous mortality rate, and when a CBL mitigates or exacerbates the offshore loss-mortality trade-off of cross-shore travel. Finally, we address the implications of these findings for alongshore movement of larvae, as represented by the duration of time larvae spend offshore compared with nearshore.

2.2. Methods

We present two models of larval dispersal. The first model is a reaction-diffusion equation describing how the spatial distribution of a population of larvae synchronously spawned from a homogeneous habitat changes over the course of one larval duration. The second model is a stochastic process describing the movement of an individual larva from this population. Because our emphasis is on consequences of cross-shore structuring in the mortality rate and diffusivity, we included the cross-shore spatial dimension only. This is equivalent to modeling dispersal from a long, straight, homogeneous coastline where all cross-sections perpendicular to the shore exhibit the same distribution of larvae.

Both models are non-dimensionalized in order to group together analogous biological and biophysical scenarios while reducing the number of model parameters that must be considered and improving computational efficiency (see 2.2 Non-dimensionalization of the population model).

2.2.1. Reaction-diffusion population model. Let $X \geq 0$ denote cross-shore distance (km) from a coastline located at $X = 0$. We assume that our species of interest has a post-larval habitat (from which larvae spawn and into which larvae settle) occupying a strip of width X_h adjacent to the shore; that is, the habitat is the interval $[0, X_h]$. Typical habitat widths X_h for coastal marine animals range from as narrow as 0.01 km (for animals inhabiting small rocky reefs) to as wide as 5km or more (for animals that can thrive at a variety of depths, such as the dungeness crab) (Rasmuson, 2013).

At time $T = 0$ (days), N_0 larvae are spawned with uniform density over $[0, X_h]$. The total lifespan of a larva is called the larval duration, which we denote by T_{LD}. Larval durations tend to be nearly fixed for individuals of the same species in the same environment, and vary from as short as a few minutes, as in many tunicates, up to many months, as in the dungeness crab or the giant triton, with typical values in the range 5-100 days (Shanks, 2009, Shanks et al, 2003). The larval duration consists of two phases: a pre-competence duration of length T_{PC} during which larvae must become sufficiently developed to undergo metamorphosis, and a competence duration of lenth $T_{LD} - T_{PC}$ during which larvae are ready for metamorphosis but must locate and settle into a suitable habitat. The competence duration is finite because larvae eventually senesce or become inviable for metamorphosis (Levin, 2006, Morgan, 1995b, Shanks, 1995). In our model, settling can only occur when $T \in [T_{PC}, T_{LD}]$, and larvae that have not settled by T_{LD} are considered wasted.

If $N(T, X)$ denotes the density of larvae located X km from shore T days after spawning, then N satisfies the linear reaction-diffusion equation

$$\begin{aligned} &\partial_T N = \partial_X \big[K(X)\partial_X N\big] - \big[R_s(T, X) + R_m(X)\big]N, \\ &N(0, X) = \begin{cases} N_0/X_h & \text{if } X \in [0, X_h], \\ 0 & \text{otherwise.} \end{cases} \end{aligned} \tag{2.1}$$

where $K(X)$ denotes eddy diffusivity in the cross-shore direction, $R_s(T, X)$ denotes the rate at which larvae settle into location X at time T, and $R_m(X)$ denotes the rate at which larvae die at location X. The boundary conditions of this model are discussed in the Appendix 5.2.

To capture the cross-shore structure of the mortality rate with minimal assumptions, we choose $R_m(X)$ to be a time-constant step function that takes one value $m > 0$ over a high mortality zone (HMZ) near the shore, $[0, X_m]$, and a potentially smaller value $n \in [0, m]$ beyond the HMZ:

$$R_m(X) = \begin{cases} m & \text{if } X \in [0, X_m], \\ n & \text{otherwise.} \end{cases} \tag{2.2}$$

Because the HMZ may simply be the habitat range of a predator, X_m has the same typical values as X_h.

We similarly choose the settling rate to be a step function: if larvae settle with rate s into the habitat during the competence duration, but cannot settle at any other time or location, then

$$R_s(T, X) = \begin{cases} s & \text{if } X \in [0, X_h] \text{ and } T \in [T_{PC}, T_{LD}], \\ 0 & \text{otherwise.} \end{cases} \tag{2.3}$$

The cross-shore eddy diffusivity $K(X)$ combines a coastal boundary layer of width $X_b \geq 0$ with a constant diffusion rate $\bar{K} > 0$ attained beyond the coastal boundary layer (CBL). The CBL usually extends as far offshore as the 30m isobath, resulting in typical CBL widths of 1-10 km (Nickols et al, 2015). Empirical results reported by Largier (2003), Okubo and Levin (2001), and Nickols et al (2012) indicate that within the CBL, cross-shore diffusivity increases as a power law with cross-shore distance, $K(X) \propto X^\alpha$. The exponent α ranges from 0.5 to 2, with typical values slightly greater than 1 (Nickols et al, 2012). This produces the cross-shore diffusion rate

$$K(X) = \begin{cases} \bar{K} \cdot (X/X_b)^\alpha & \text{if } X \in [0, X_b] \\ \bar{K} & \text{otherwise.} \end{cases} \tag{2.4}$$

Simulations ignoring the effects of the CBL are run with $X_b = 0$ and a reflecting boundary at $X = 0$.

Model parameters and their typical ranges are summarized in **Table 2.1**.

Table 2.1. Summary of parameter definitions for the dimensional model (2.1). Ranges are meant to capture typical values, but values outside these ranges occur in nature. More information on these parameters and their values can be found from the references provided.

Parameter	Units	Meaning	Range
T_{LD}	d	larval duration (LD)	$5 < T_{LD} \leq 100$[a]
T_{PC}	d	pre-competence duration	10% to 90% of T_{LD}[a]
X_h	km	width of coastal habitat	$0.01 \leq X_h \leq 5$[b]
X_m	km	width of nearshore high-mortality zone (HMZ)	$0.01 \leq X_m \leq 5$[b,c]
X_b	km	width of coastal boundary layer (CBL)	$1 \leq X_b \leq 10$[b,d]
$\bar{K}$	km^2 d^{-1}	eddy diffusivity beyond CBL	$10 \leq \bar{K} \leq 100$[e]
α	—	exponent for diffusivity power-law in CBL	$0.5 \leq \alpha \leq 2$[e]
m	d^{-1}	nearshore mortality rate	$0.002 \leq m \leq 0.2$[f]
n	d^{-1}	offshore mortality rate	$0 \leq n \leq m \leq 0.2$[f]
s	d^{-1}	settling rate in habitat during competence	$0 < s \leq 10$[g]

[a] Shanks (2009), Shanks et al (2003). [b] Nickols et al (2015) [c] Rasmuson (2013).
[d] Morgan and Fisher (2010). [e] Largier (2003), Nickols et al (2012). [f] Rumrill (1990), White et al (2014).
[g] Numerical simulations show that the range $0 < s \leq 10$ captures all variation in model results with respect to s; beyond this range, results are insensitive to s.

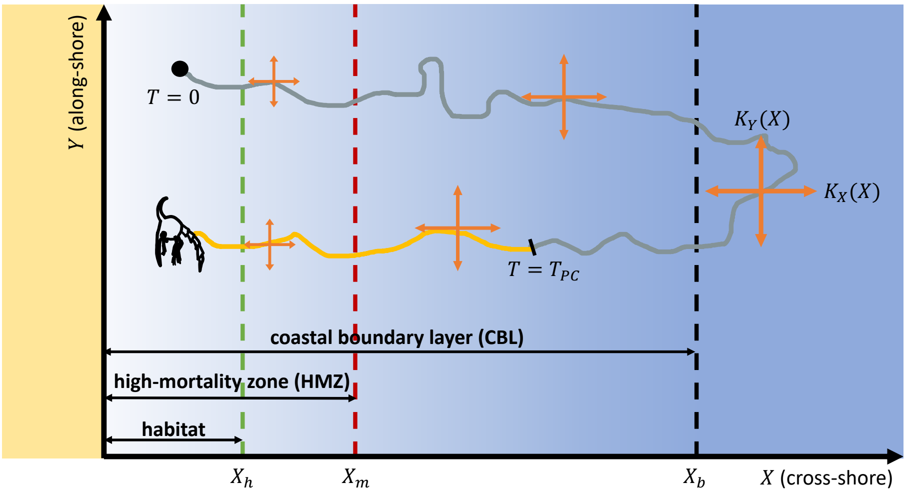

Figure 2.1. A schematic showing the trajectory of a successfully dispersing larva in the structured coastal environment described by model (2.1). Orange arrows indicate the strength of eddy diffusivity in the cross-shore and alongshore directions, $K_X(X)$ and $K_Y(X)$, under the assumption that the environment is homogeneous in the alongshore direction. Our model explicitly considers only cross-shore movement, so K_X is referred to as simply K in the text. The grey part of the larval trajectory takes place during pre-competence, $[0, T_{PC})$, and the yellow part takes place during competence, $[T_{PC}, T_{LD}]$.

2.2.2. Non-dimensionalization of the population model. Non-dimensionalization, or the rescaling of variables and parameters by units (or "scales") characteristic of larval development and dispersal, allows us represent mathematically analogous biological/biophysical scenarios using a single model while reducing the number of parameters we must consider in our analysis. Many rescalings of the model are possible. We choose the one with unitless time variable $t = T/T_{LD}$, length variable $x = X/X_h$, and population density $p(t,x) = N(T,X)/N_0$. The time rescaling allows all simulations to be performed over $t \in [0,1]$. The length rescaling enables us to vary the spatial features of greatest relevance—CBL width, HMZ width, and diffusion—relative to a fixed reference width. Importantly, the rescaled population density $p(t,x)$ can be interpreted as describing the probability density of an individual larva having dimensionless location x at dimensionless time t.

After non-dimensionalization, the model becomes

$$\begin{aligned} &\partial_t p = \partial_x\big[\kappa(x)\partial_x p\big] - \big[\lambda_s(t,x) + \lambda_m(x)\big]p, \\ &p(0,x) = \begin{cases} 1 & \text{if } x \in [0,1], \\ 0 & \text{otherwise.} \end{cases} \end{aligned} \tag{2.5}$$

with dimensionless diffusion rate

$$\kappa(x) = \begin{cases} \bar{\kappa} \cdot (x/x_b)^{\alpha} & \text{if } x \in [0, x_b], \\ \bar{\kappa} & \text{otherwise,} \end{cases} \tag{2.6}$$

and dimensionless settling rate

$$\lambda_s(t,x) = \begin{cases} \sigma & \text{if } x \in [0,1] \text{ and } t \in [t_{pc}, 1], \\ 0 & \text{otherwise} \end{cases} \tag{2.7}$$

(refer to **Table 2.2** for definitions of the dimensionless parameters). In defining the dimensionless mortality rate, $\lambda_m(x)$, it is useful to define the "offshore mortality ratio"

$$\varepsilon = n/m \tag{2.8}$$

Table 2.2. Summary of parameters for the non-dimensionalized model (2.5). As in **Table 2.1**, ranges refer to typical ranges but do not include all possible cases.

Parameter	**Expression**	**Range**	**Default value**[a]
t_{pc}	$T_{LD}^{-1}T_{PC}$	$.1 \le t_{pc} \le .9$	0.5
x_m	$X_h^{-1}X_m$	$0 < x_m \le 2$	1
x_b	$X_h^{-1}X_b$	$0 \le x_b \le 10$	0
$\bar{\kappa}$	$\bar{K}T_{LD}X_h^{-2}$	$1 < \bar{\kappa} < 1000$	100[b]
α	α	$0.5 \le \alpha \le 2$	2
μ	mT_{LD}	$0 \le \mu \le 20$	6
ε	nm^{-1}	$0 \le \varepsilon \le 1$	1
σ	sT_{LD}	$0 < \sigma \le 100$	2

[a] These are the values used in all simulations below, unless different values are specified for particular parameters. The default $x_b = 0$ means that unless otherwise stated, simulations are run with constant diffusivity offshore and no CBL. [b] Many species that travel far enough offshore to experience the extreme diffusivities listed in **Table 2.1** also have long larval durations and large habitats. Therefore, we do not expect $\bar{\kappa}$ to be as large as is theoretically possible from the ranges in **Table 2.1**.

so that we may separately vary near- and offshore mortality rates in our analysis without violating $m \ge n \ge 0$. This gives us the dimensionless mortality rate

$$\lambda_m(x) = \begin{cases} \mu & \text{if } x \in [0, x_m], \\ \varepsilon\mu & \text{otherwise.} \end{cases} \tag{2.9}$$

Note that $\varepsilon \in [0,1]$, with $\varepsilon = 0$ and $\varepsilon = 1$ corresponding to an offshore mortality rate of 0 and a spatially uniform mortality rate of μ, respectively. Parameters from the dimensionless model (2.5) are summarized in **Table 2.2**.

2.2.3. Associated individual stochastic process. It can be shown (see **Appendix 2.5.1**) that the position, ξ_t, of an individual larva governed by model (2.5) satisfies a "killed" stochastic differential equation (Karlin and Taylor, 1981)

$$\begin{aligned} &d\xi_t = f(\xi_t)\ dt + g(\xi_t)\ dB_t, \quad 0 \le t \le \tau, \\ &\xi_0 \sim \text{uniform}([0,1]), \end{aligned} \tag{2.10}$$

where

$$f(\xi) = \frac{d\kappa}{dx}(\xi) \text{ and } g(\xi) = \sqrt{2\kappa(\xi)}. \tag{2.11}$$

In this context, "killing" means that this process terminates at a random time $\tau \leq 1$ if death or settling occurs. Over any short time-step $[t, t+\delta t) \subset [0,1]$, the process located at $\xi_t = x$ terminates due to death or settling, respectively, with probabilities

$$\begin{aligned} &\Pr\{\text{death in } [t, t+\delta t) \mid \xi_t = x\} = \lambda_m(x)\delta t + o(\delta t), \\ &\Pr\{\text{settling in } [t, t+\delta t) \mid \xi_t = x\} = \lambda_s(t,x)\delta t + o(\delta t), \end{aligned} \tag{2.12}$$

where $o(\delta t)$ represents terms that decay faster than δt as $\delta t \searrow 0$ (Karlin and Taylor, 1981). If neither settling nor death occurs before $t = 1$, then $\tau = 1$ and offshore loss occurs. The probability density function of ξ_t on the event that neither form of killing has yet occurred is $p(t,x)$, the solution to model (2.5).

2.2.4. Computing important quantities. The journey of every larva terminates in either settling, offshore loss, or mortality. The probabilities of each outcome can be computed from $p(t,x)$ (see **Appendix 2.5.3**):

$$S = \Pr\{\text{settling}\} = \int_0^1 \int_0^\infty p(t,x)\lambda_s(t,x)\ dx\ dt, \tag{2.13}$$

$$L = \Pr\{\text{offshore loss}\} = \int_0^\infty p(1,x)\ dx, \tag{2.14}$$

$$M = \Pr\{\text{mortality}\} = \int_0^1 \int_0^\infty p(t,x)\lambda_m(x)\ dx\ dt. \tag{2.15}$$

Note that expressions (2.13) and (2.15) are proportional to the average values of the settling and mortality rates over space and time, respectively, weighted by the probability density of the larva's position over time. Also, by definition,

$$S + L + M = 1. \tag{2.16}$$

Adult female benthic invertebrates can spawn anywhere from 10^2 to 10^9 eggs, depending on egg size and fertilization rates (Christiansen and Fenchel, 1979, Levitan, 1995, Rumrill, 1990, Thorson, 1950). Supposing that the number of fertilized eggs falls in the range $10^2 \leq N_0 \leq 10^7$ per adult, and that each adult produces between 1 and 100 successful offspring (so that populations can replace themselves, even after post-larval mortality), we expect S to take very small values, on the order of $10^{-7} \leq S \leq 10^{-2}$ (Rumrill, 1990). S should be regarded as a non-dimensional measurement of larval supply, or the total number of larvae returning to a coastal habitat that may recruit to the reproductive (post-larval) population.

Alongshore currents typically vary and increase in magnitude with offshore distance (Largier, 2003, Largier et al, 1993, Nickols et al, 2012). Therefore, we shall use the amount of time (or, given the nondimensionalization, the fraction of the larval duration) that larvae spend more than distance $x > 0$ offshore prior to settling as a proxy for potential alongshore movement. This quantity is denoted by a random variable depending on x,

$$\theta(x) = \int_0^1 \mathbf{1}_{(x,\infty)}(\hat{\xi}_t)\ dt, \qquad \text{where } \mathbf{1}_A(a) = \begin{cases} 1 & \text{if } a \in A, \\ 0 & \text{if } a \notin A. \end{cases} \tag{2.17}$$

Here, $\hat{\xi}_t$ is the individual process (3.1) conditioned upon dispersal terminating in settling, rather than mortality or offshore loss. We shall approximate the distribution of $\theta(x)$ for $x = 10$ by repeatedly simulating the individual model and computing $\theta(x)$ only for trials in which settling occurs. While this distribution could be computed deterministically from equations resembling (2.5), finer resolution can be attained in far less computation time through stochastic simulations.

2.3. Results

2.3.1. How is larval supply affected by a spatially heterogeneous mortality rate?

We explore the relationship between the probability of settling, S, and the offshore mortality ratio, ε, in **Figure 2.2** in two scenarios: fixed nearshore mortality, and fixed total (or average) mortality.

2.3.1.1. *Fixed nearshore mortality rate.* In this scenario, the dimensionless nearshore mortality rate, μ, is held constant while the offshore mortality ratio, ε, is varied from 0 to 1. This describes the effect of unknown offshore mortality when only a nearshore rate has been measured. The value of S obtained when $\varepsilon = 1$ represents an estimate of larval return obtained by assuming the nearshore

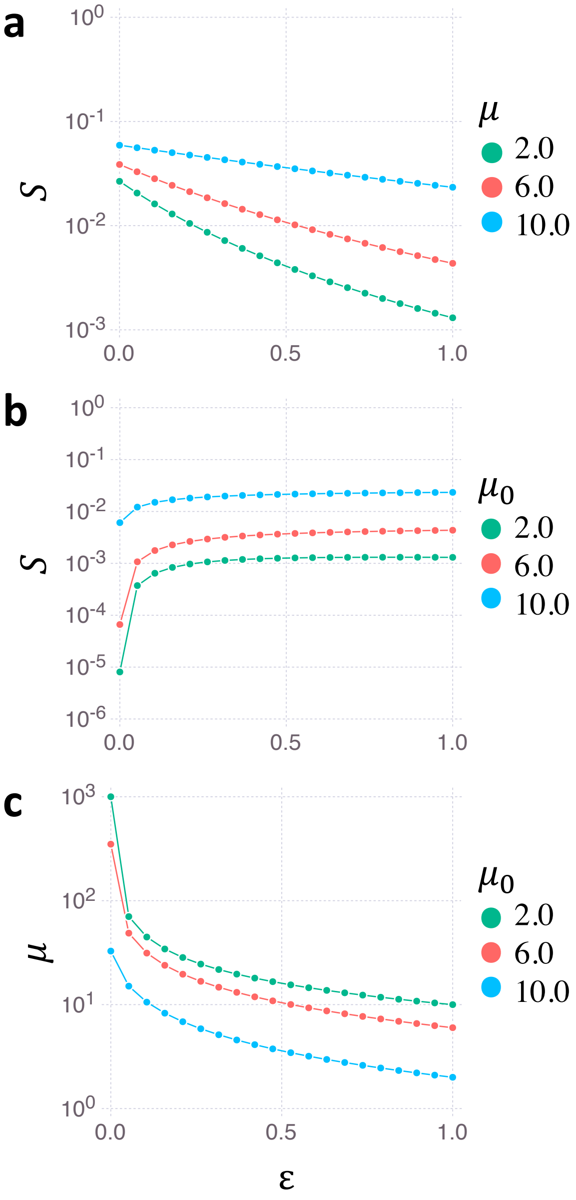

Figure 2.2. Impact of the offshore mortality rate on the estimated probability of settling, S. **(a)** S as a function of the offshore mortality ratio, ε, for fixed nearshore mortality rates $\mu = 2$ (blue), 6 (red), 10 (green). **(b)** S as a function of ε, with probability of mortality, M, fixed at values obtained using uniform mortality rates $\mu_0 = 2$ (blue), 6 (red), 10 (green). **(c)** Nearshore mortality rates, μ, required to keep M constant as ε is varied in (b). Recall that the estimate from a uniform mortality rate appears on the right of (a) and (b), where $\varepsilon = 1$. Note the logarithmic vertical axes used to display S in this figure.

mortality rate holds at all offshore locations. Varying ε alone is also useful for considering the effect of the offshore mortality rate in isolation. However, the following results should be interpreted with the caveat that varying ε also affects the average mortality rate.

The probability of settling, S, strictly decreases with the offshore mortality ratio, ε, when dimensionless nearshore mortality, μ, is fixed (**Figure 2.2a**). This is because increasing ε increases the total mortality rate over the entire coastal environment, $x \in [0, \infty)$. The magnitude of this effect varies positively with the nearshore mortality rate: over the range $\varepsilon = 0$ to 1, S varies by a factor of ~2.5 when $\mu = 2$, compared with ~20 when $\mu = 10$. This increased sensitivity to the offshore mortality ratio as the nearshore mortality rate is increased suggests that when nearshore mortality is high, the risk of offshore loss may be outweighed by the benefit of escaping nearshore predation.

This trend was not qualitatively changed by varying the width x_m of the high mortality zone (HMZ), which lessens the effect of the offshore mortality rate by increasing exposure to the nearshore rate. It was also not qualitatively affected by varying dimensionless eddy diffusivity, $\bar{\kappa}$, although increasing $\bar{\kappa}$ reduces the overall fraction of larvae that settles and steepens the relationship between S and ε. This results in a greater difference between the case $\varepsilon = 1$ and any case with $\varepsilon < 1$.

2.3.1.2. *Fixed total mortality.* In this scenario, the probability of mortality, M, (which is proportional to the total number of larvae that die) is held constant at the value obtained assuming a uniform mortality rate ($\mu = \mu_0$ and $\varepsilon = 1$) while the offshore mortality ratio ε is varied between 0 and 1. To keep M constant, the nearshore mortality rate μ is decreased as ε is increased (**Figure 2.2c**). This describes the effect of unknown offshore mortality when only the fraction of larvae that perish has been estimated. The value of S obtained when $\varepsilon = 1$ represents an estimate of larval return obtained by fitting a uniform mortality rate to measurements of a potentially heterogeneous one.

Generally, S increases slightly with the offshore mortality ratio ε, but is largely insensitive to this parameter while total mortality is constant. In all three mortality schemes considered, S varies by ~4.1 fold or less over the range $0.053 < \varepsilon \leq 1$. However, S is very sensitive to changes in ε when ε is small and total mortality is high. For instance, when $\mu_0 = 10$, S increases by nearly

50-fold over $0 \leq \varepsilon \leq 0.053$ (**Figure 2.2b**). This sharp increase is more likely driven by the decrease in μ possible when even a small amount of offshore mortality is permitted (e.g., the transition from $\varepsilon = 0$ to $\varepsilon > 0$), illustrated in **Figure 2.2c**). These trends are qualitatively unchanged by varying HMZ width, x_m, and eddy diffusivity, $\bar{\kappa}$.

The increasing relationship between the probability of settling, S, and the offshore mortality ratio, ε, when total mortality is fixed may be counter-intuitive, but is clear when considered alongside the relationship between μ and ε shown in **Figure 2.2c**: increasing ε while decreasing μ redistributes the mortality risk from nearshore larvae, which are more likely to locate suitable habitats if they can survive for sufficiently long, to offshore larvae, which are more likely to be wasted.

2.3.2. How is the relationship between diffusivity and larval supply affected by a spatially heterogeneous mortality rate? We varied $\bar{\kappa}$ and ε while holding μ constant to understand the relationship between dimensionless diffusivity, dimensionless mortality, and the probability of settling, S, when mortality risk is elevated nearshore. We did not hold total mortality constant, as was done in the previous section, because we are specifically interested in how a low-mortality region offshore interacts with the rate of movement of the larva.

When the mortality rate is spatially uniform ($\varepsilon = 1$), the probability of settling strictly decreases with diffusivity (**Figure 2.3a**). For instance, when $\mu = 10$, S decreases by a factor of $\sim$18 over the range $1 \leq \bar{\kappa} \leq 1000$. This reflects an increased probability of offshore loss as movement over large distances relative to the size of the habitat becomes more likely. This result holds independently of μ. Qualitatively similar trends appear when the mortality rate is weaker offshore ($\varepsilon < 1$) provided that the nearshore mortality rate is also weak, such that the difference between the HMZ and offshore is small and has little effect on overall mortality. The same trend also appears when the HMZ is narrower (or wider) than the habitat by an order of magnitude or more, such that larvae spend nearly all time prior to settling offshore of (or within) the HMZ, and are thus affected little by the heterogeneous mortality rate (compare, for instance, the blue and red curves in **Figure 2.3a**).

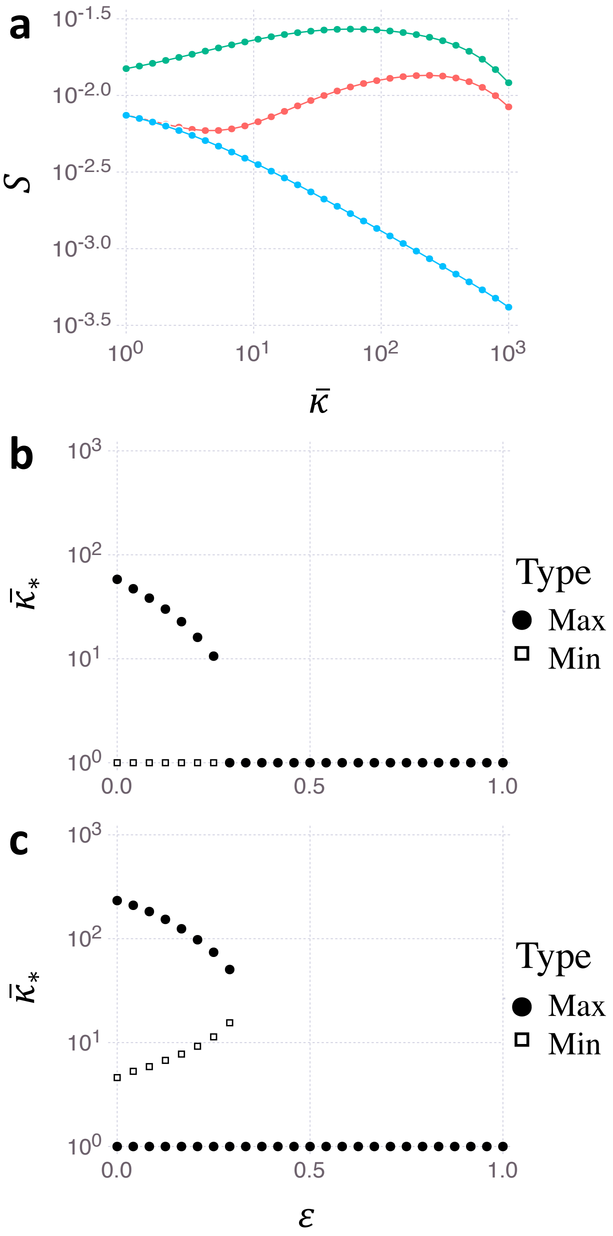

Figure 2.3. The structure of the offshore mortality rate affects how the probability of settling, S, depends on diffusivity, $\bar{\kappa}$. When the mortality rate varies substantially over regions larvae traverse, S may be maximized by intermediate diffusivities. **(a)** S as a function of dimensionless eddy diffusivity, $\bar{\kappa}$, in the following mortality schemes: $\varepsilon = 1$ (blue), $\varepsilon = 0$ and $x_m = 1$ (green), and $\varepsilon = 0$ and $x_m = 2$ (red). **(b)** and **(c)** display the critical value(s) of diffusivity, $\bar{\kappa}_*$, at which S is locally maximized (filled circles) or minimized (open squares) for each $0 \leq \varepsilon \leq 1$ when $x_m = 1$ and $x_m = 2$, respectively.

When the dimensionless mortality rate is high (μ is large) and spatially heterogeneous ($\varepsilon < 1$), and the HMZ is similar in width to the habitat, the probability of settling may vary non-monotonically with diffusivity. The green curve in **Figure 2.3a** illustrates this in the extreme case $x_m = 1$ and $\varepsilon = 0$ (no mortality beyond the habitat), where S attains a global maximum at a dimensionless diffusivity $100 < \bar{\kappa} < 1000$. Importantly, $\bar{\kappa} = 1$ (the smallest tested value of $\bar{\kappa}$) is a local minimum of S in this case, rather than a global maximum as in the uniform mortality case. In the case shown by the green curve in **Figure 2.3a**, S is ~1.8 times larger at its global maximum than at $\bar{\kappa} = 1$. This suggests that despite an increased risk of offshore loss, moderately fast movement relative to the width of the habitat can be beneficial when the nearshore environment is very dangerous compared to the offshore one. The emergence of an intermediate optimal diffusion rate when ε is sufficiently small is shown for $x_m = 1$ in **Figure 2.3b**.

When mortality is high and the HMZ is larger than the habitat, S is maximized by very small and intermediate dimensionless diffusivities, but attains a relative minimum at moderately small diffusivities. In the case shown by the red curve in **Figure 2.3a**, the values of S at its local and global maxima (at $\bar{\kappa} = 1$ and in $100 < \bar{\kappa} < 1000$, respectively), are greater than the value of S at its local minimum at $1 < \bar{\kappa} < 10$ by factors of ~1.3 and ~2.3, respectively. The emergence of both local maxima and minima of S as the offshore mortality ratio decreases is illustrated in **Figure 2.3c**. This trend suggests that high diffusivity relative to the habitat width is beneficial if it is intense enough to transport larvae beyond the HMZ, but deleterious if it merely moves larvae from the habitat into the dangerous region between the offshore edge of the habitat and the offshore edge of the HMZ.

Another important feature of these heterogeneous high mortality cases is that despite these intermediate extrema, S varies little over $1 \leq \bar{\kappa} \leq 1000$ compared with the uniform (or near-uniform) mortality cases considered. In the cases $x_m = 1$ and 2, the maximal and minimal values of S over this range of $\bar{\kappa}$ are within a factor of 3 of each other, compared with the factor of 18 observed in the uniform mortality case. The insensitivity of S to $\bar{\kappa}$ in these cases indicates that reduced offshore mortality ensures that some larvae always survive and settle, even when diffusivity is strong.

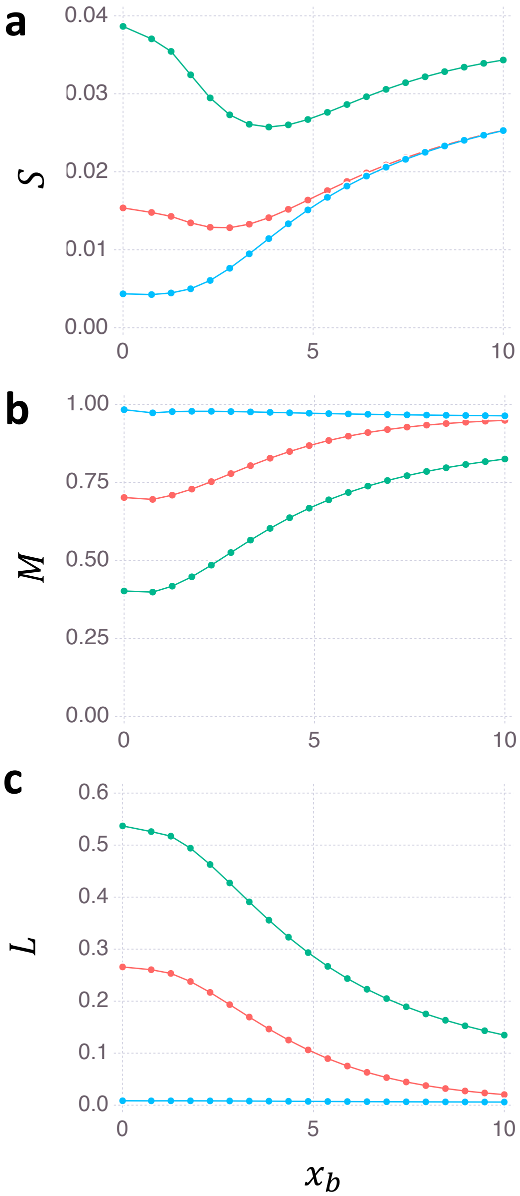

Figure 2.4. Probabilities of **(a)** settling, S, **(b)** mortality, M, and **(c)** offshore loss, L, as functions of coastal boundary layer (CBL) width, x_b, with mortality rate $\mu = 6$ and the following mortality rate structures: $\varepsilon = 1$ (blue), $\varepsilon = 0$ and $x_m = 1$ (green), and $\varepsilon = 0$ and $x_m = 3$ (red). Typically, M increases and L decreases with x_b, such that S may vary non-monotonically with x_b. Note that the vertical axes in this figure are linear, but have different maxima.

2.3.3. How is the relationship between CBL width and larval supply affected by a spatially heterogeneous mortality rate? Here, we introduce a CBL of width between 0 and 10 times that of the habitat ($0 \leq x_b \leq 10$) to explore the interactive effects of low diffusivity and high mortality in the region close to shore. The probability of offshore loss, L, seems always to decrease with respect to CBL width (**Figure 2.4c**), as reduced diffusivity close to shore slows the movement of larvae away from their spawning sites within the habitat. When the mortality rate is spatially uniform, this reduced movement away from the habitat also shortens the mean time larvae spend dispersing prior to settling, causing the probability of mortality, M, to decrease slightly with x_b (**Figure 2.4b**). Combined, these trends result in the probability of settling, S, increasing with respect to CBL width. In the case represented by the blue curve in **Figure 2.4a**, S increases by a factor of 5.9 over $0 \leq x_b \leq 10$.

By contrast, when the mortality rate is higher nearshore than offshore, M increases with x_b (**Figure 2.4b**). This is because a wider CBL reduces the probability of a larva escaping the HMZ to benefit from the safer offshore environment. Due to the relationship (2.16) and the opposite trends of M and W with x_b, S may increase, decrease, or vary non-monotonically with CBL width. If the HMZ is far narrower than the adult habitat or nearshore mortality is weak, then the trend between S and x_b resembles that of the uniform mortality case. However, if the HMZ is similar in size to the habitat, S decreases over smaller CBL widths ($x_b \lessapprox 4$), but increases over greater widths (**Figure 2.4a**). A small to medium CBL increases mortality by retaining larvae in the HMZ, but does not substantially reduce offshore loss. A large CBL also retains larvae in the HMZ, but this cost is outweighed by a large decrease in offshore loss.

2.3.4. How might a spatially heterogeneous mortality rate influence alongshore transport? We simulated the stochastic individual model (3.1) in two mortality schemes, uniform ($\varepsilon = 1$) and heterogeneous ($\varepsilon = 0$), until we obtained 10^4 simulations terminating in settling for each case. These simulations were used to estimate the distribution of $\theta(10)$ (time spent farther offshore than $x = 10$ prior to settling), a proxy for alongshore movement. The resulting histograms are shown in **Figure 2.5**. The reference distance $x = 10$ was chosen because it is far enough offshore that, excluding potential effects of the mortality rate structure, larvae with $\kappa = 100$ are

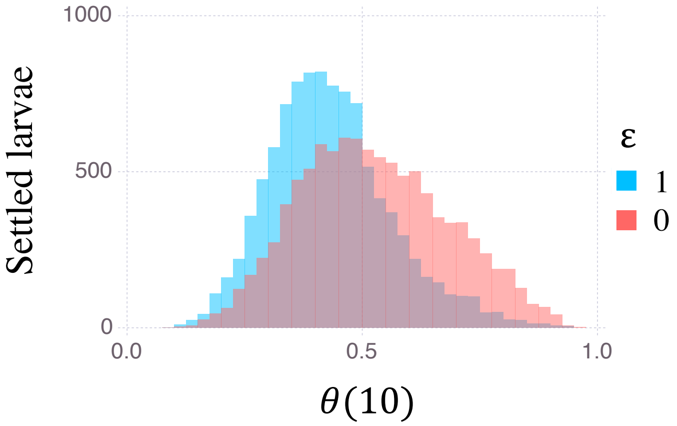

Figure 2.5. Overlapping histograms of $\theta(10)$, the fraction of the larval duration spent offshore of $x = 10$, for 10^4 successful larvae in a uniform mortality rate ($\varepsilon = 1$, blue) and a heterogeneous mortality rate ($\varepsilon = 0$, red). The purple region indicates overlap between these two histograms. All other parameters are set to the default values in **Table 2.2**. In the heterogeneous mortality case, larvae typically spend more time far offshore prior to settling than in the uniform case.

similarly likely to spend a long time within or beyond this distance. However, similar results are obtained using different values of x.

We observed that settling larvae are more likely to spend time far offshore when the mortality rate offshore is weak compared to when the mortality rate is spatially uniform. In particular, the distribution of $\theta(10)$ is has mean 0.51 in the heterogeneous case, compared with 0.42 in the uniform case. Additionally, in the heterogeneous case, 47% of successful larvae spend more than half of the larval duration beyond $x = 10$ (that is, $\theta(10) > 0.5$), compared with only 21% in the heterogeneous case. These results suggest that in an environment where alongshore currents vary in the cross-shore direction, the spatial structure of the mortality rate may have a large effect on the currents to which dispersing larvae are subject.

The differences in the distribution of $\theta(10)$ across mortality rate structure are more pronounced at greater nearshore mortality rates μ, but the overall results are not changed. At lower values of μ, the distributions of $\theta(10)$ are nearly the same, although larvae still spend more time offshore in the heterogeneous case than in the homogeneous case. We did not observe any qualitative changes to these results as the widths of the CBL and HMZ were adjusted.

2.4. Discussion

Our analysis reveals that although the results and intuition provided by several past models appear unchanged by the structure of the coastal environment, there exist conditions in which larval supply may be highly sensitive to changes in the offshore mortality rate. These conditions include high mortality and diffusivity, such that larval supply is severely constrained by death and offshore loss. In such cases, we saw that assuming the nearshore mortality rate applies at all offshore locations can result in a substantial underestimate of larval supply. By contrast, using an average of total observed mortality over all locations, weighted by where larvae spend the most time, results in a more robust estimate of larval supply unless the difference between the near- and offshore mortality rates is extreme.

We affirm the prior result that strong diffusivity often reduces settling by increasing offshore loss. However, this is not necessarily the case when the mortality rate is greater nearshore than offshore. Under this condition, settling can increase or vary non-monotonically with diffusivity due to the trade-off between the high probability of loss larvae face offshore and the potentially higher risk of mortality they face nearshore. The same trade-off results in cases in which a low-diffusion coastal boundary layer (CBL) reduces, rather than increases, the proportion of larvae that settles. Under weak or spatially uniform mortality, the CBL reduces offshore loss and has little effect on mortality, thus increasing settling. When the mortality rate is greater nearshore than offshore, however, this reduction in loss is outweighed by increased mortality due to slow movement in the nearshore high mortality zone (HMZ), unless the CBL is very wide.

Finally, we found that cross-shore heterogeneity in the mortality rate may affect alongshore travel by influencing the proportion of the larval duration a successful larva spends offshore, and, consequently, to which alongshore currents they are exposed. This difference is particularly pronounced when nearshore mortality is moderate or high, and is notable because cross-shore structures are often omitted from studies of alongshore dispersal.

2.4.1. Interpretation of the dimensionless results. Our analysis primarily focused on the relationship between the probability of settling, S, and the unitless parameters describing the structure of the mortality rate and coastal environment in a non-dimensionalized model, (2.5).

We identified the dimensionless nearshore mortality rate, $\mu = mT_{LD}$, and the dimensionless diffusion rate, $\kappa(x) = K(X)T_{LD}/X_h^2$, as two of the most important determinants of whether offshore structure impacts the probability of settling. The exact effects of these parameters depend on the widths of the high mortality zone (HMZ) and the CBL relative to that of the habitat, $x_m = X_m/X_h$ and $x_b = X_b/X_h$, respectively. These dimensionless results should be understood as commenting on the relationship between larval supply and the true parameters from which the dimensionless ones are constructed: larval duration, T_{LD}; nearshore mortality rate, m; diffusion rate, K; and habitat, HMZ, and CBL widths, X_h, X_m, X_b, respectively. A thread that runs through our analysis is the question of which subset of dispersing larvae provides a greater share of the settling population—that which remains close to shore, or that which travels far offshore.

The dimensionless nearshore mortality rate, μ, can be interpreted as mortality exposure because it combines the mortality rate, m, with the duration of the exposure to this rate, T_{LD}. When larvae face little nearshore mortality exposure due to a short larval duration or a low mortality rate, many larvae that remain close to the habitat and HMZ survive until competence and are well-positioned to settle, while larvae traveling far away comprise a smaller fraction of the settling population because comparatively few are diffused back to the habitat before offshore loss occurs. High nearshore mortality exposure due to a long larval duration or a high mortality rate results in far fewer larvae surviving close to shore. This increases the relative fraction of settlers that have been mostly offshore. The size of this latter subpopulation depends on the offshore mortality rate, resulting in greater sensitivity of the overall larval supply to offshore conditions. A wide HMZ reduces sensitivity to offshore conditions simply by reducing the number of larvae that experience reduced mortality exposure offshore.

The dimensionless diffusion rate $\kappa = KT_{LD}/X_h^2$ represents exposure to eddy diffusion (scaled by the width of the habitat, X_h). Our analysis supports prior results in the literature that state that greater exposure to diffusion due to oceanographic conditions or a long larval duration typically increases offshore loss and reduces larval supply in the absence of advection or locomotion (Cowen et al, 2000, Largier, 2003). Increased loss is also achieved by reducing the size of the post-larval habitat, X_h, which increases diffusion exposure in our model. However, we also observed that when larvae experience high mortality exposure over or near post-larval habitat and weaker mortality exposure elsewhere, the probability of settling S is maximized by intermediate diffusion exposure (e.g., just enough to transport larvae away from nearshore hazards without risking excessive offshore loss). This underscores the trade-off larvae face due to the spatial segregation of two forms of larval wastage, mortality and offshore loss. Weak diffusion exposure due to low eddy diffusivity, a short larval duration, or a large habitat (contained in a larger HMZ) prevents individuals from moving far enough offshore to benefit from the heterogeneous mortality rate. On the other hand, strong diffusion exposure due to high eddy diffusivity, a long larval duration, or a small habitat results in too many larvae failing to return to shore before expiration. The optimum is attained when larvae diffuse just fast enough or for just long enough to escape nearshore dangers, but not faster or longer.

When the HMZ is broader than the habitat, one sees a minimum of S at a low diffusion exposure. This indicates that when the habitat is separated from safer offshore conditions by a hazardous non-habitat zone, diffusing too slowly or for too little time is worse than not diffusing at all because it allows larvae to be wasted without sufficient reprieve from nearshore conditions. The maxima at either very low or intermediate diffusivities represent two possible strategies that may appear in nature through selection. Species can feature either short larval durations compared to the size of their habitats or adaptations for weak diffusivity, or else they can have moderately long larval durations or adaptations for moderate diffusivity. This theoretical result supports the observation of Shanks et al (2003) and Shanks (2009) that dispersal distances are bimodally distributed—usually short or long, but rarely intermediate—even though larval durations are continuously distributed.

Another important consequence of S being maximized by intermediate diffusion exposure is that S is also least sensitive to variations in diffusion exposure about the optimal value, due to $dS/d\bar{\kappa} = 0$ at a local optimum. Therefore, intermediate diffusion exposure results in the greatest larval supply possible as well as the least susceptibibility to extinction due to environmental variability. One might expect some species with planktonic larvae to have adaptations for achieving moderate diffusion exposure through body structures, behaviors, and dispersal and developmental duration. This suggests that a long larval duration can be advantageous *per se* in a coastal environment with mortality exposure concentrated nearshore, and is not necessarily the result of development time or an adaptation for alongshore dispersal alone.

2.4.2. Interactive effects of the CBL and mortality rate heterogeneity upon larval supply and loss. Studies that have excluded spatial heterogeneity in the larval mortality rate have previously concluded that nearshore retention zones, such as CBLs, strictly improve larval supply by reducing offshore loss (Largier, 2003, 2004, Nickols et al, 2015). We verified that settling increases with CBL width in the case of a spatially uniform mortality rate, as well as when the mortality rate is heterogeneous but weak. In the low-mortality case, the probability of mortality increases with CBL width because reduced diffusion exposure nearshore prevents larvae from escaping the HMZ. However, this increase in mortality was outweighed by the reduction in offshore loss in all cases we considered. In other words, there is no apparent trade-off between nearshore mortality and offshore loss in the presence of a CBL.

The effect of the CBL is less consistent for heterogeneous mortality with high nearshore mortality. When the habitat and the HMZ have similar widths, reduced offshore loss due to a narrow or medium CBL is offset by increased mortality in the same region. As a result, a narrow or medium CBL reduces larval supply. A CBL extending beyond the HMZ, however, can further reduce offshore loss while only slightly increasing mortality nearshore, resulting in improved larval supply. The trade-off between nearshore mortality and offshore loss is evident when considering the effect of CBL width, as it is impossible for the CBL to reduce loss without increasing mortality simultaneously.

2.4.3. Implications for alongshore movement. Although the focus of this study has been on cross-shore movement, we emphasize that the cross-shore heterogeneity of the mortality rate is likely to have consequences for alongshore movement as well. Advection and diffusion in the alongshore direction frequently increase with distance from the shore, particularly in the presence of a CBL (Largier, 2003, 2004, Largier et al, 1993, Nickols et al, 2012). The modeling study of Largier (2003) showed that alongshore dispersal distance tends to increase nonlinearly with larval duration due to increased exposure to stronger alongshore currents far offshore. We illustrated here that successful larvae with longer larval durations (as well as those facing high nearshore mortality risks) spend more time offshore prior to settling when the mortality rate is weaker offshore. Successful larvae are also likely to experience strong alongshore currents, resulting in greater alongshore dispersal distances than would be predicted using a model with a spatially uniform mortality rate.

2.4.4. When is the cross-shore structure of the mortality rate important (or not)?

Researchers have historically omitted spatial heterogeneity in the mortality rate (or, in some cases, mortality in any form) from mathematical models of larval dispersal because it is poorly quantified, adds model complexity (e.g., increases the number of parameters that must be estimated), and may not seem relevant to the goals of a study, such as those focused on alongshore dispersal (Cowen et al, 2000, Largier, 2003, Nickols et al, 2015, Siegel et al, 2008). Our results indicate that excluding this heterogeneity may be safe in some settings, but may alter model predictions in others. In particular, heterogeneity may be ignored when:

(i) The species of interest has a short larval duration. Since μ and κ both depend linearly on T_{LD}, species with short larval durations will generally experience lower nearshore mortality and diffusivity exposure. Because larval supply and offshore duration vary with the offshore mortality rate and HMZ width only when μ (and secondarily, κ) is sufficiently large, larval supply and alongshore movement will not be substantially affected by mortality rate heterogeneity in species with short larval durations.

(ii) The species of interest has a long larval duration, but experiences weak nearshore predation or weak diffusion (perhaps due to a wide CBL) or can settle into a large region in the environment of interest. If T_{LD} is large, but the nearshore mortality rate m is small, then larvae will face little nearshore mortality exposure. Similarly, larvae will face weaker diffusivity exposure (compared to habitat width) if true diffusivity is weak, or if the habitat is large. These conditions result in small μ and κ, even when T_{LD} is large, with the same outcome as mentioned in the short T_{LD} case. Note that increasing the width, X_b, of the CBL decreases the value of $K(X)$ over each point $X \in [0, X_h]$ for $X_b > X_h$, so a wide CBL has a similar effect to low diffusivity.

(iii) The species of interest experiences high predation nearshore, and its predators occupy a region extending offshore of the species' habitat. Such species experience high nearshore mortality exposure, μ. If the mortality rate is similar offshore over distances larvae are most likely to travel given their larval duration, the diffusion rate, and the size of the CBL, then most larvae may never experience reduced mortality rates offshore, and those that do are unlikely to settle.

Although mortality rates are notoriously difficult to quantify in the field, some of these criteria depend on well-known aspects of the species of interest (e.g., larval duration), measurable features of the coastal environment (e.g., diffusivity and CBL structure), and the habitats of the species of interest and its nearshore predators, rather than away from the shore. Thus, researchers need not directly measure the offshore mortality rate to determine whether that rate will influence model results. Additionally, while measurements of the offshore mortality rate may sometimes be necessary, models using a uniform mortality rate can still provide reasonable estimates of larval supply if measurements are appropriately averaged over locations and time.

In the scenarios in which weak offshore mortality may influence estimates of larval supply and alongshore movement, researchers must decide on a case-by-case basis whether these quantitative differences are important, or whether they may lead to qualitative differences as well. Two examples in which qualitative differences might result from weak offshore mortality arise in coastal population dynamics:

(i) *Complex life cycles:* species with dispersive larvae have "complex" life cycles, in the sense that they have two or more life stages (e.g., larvae and post-larvae) that occupy different habitats (e.g., the plankton and the benthos). Roughgarden et al (1988) observed that while some coastal post-larval populations are relatively stable from year to year, others exhibit large fluctuations. Using a two-life-stage model of coastal population dynamics, the authors showed that larval supply can be subject to annual variability. This results in fluctuations in the post-larval population unless the larval supply is consistently large enough to saturate the post-larval population's carrying capacity. Incorrect estimates of larval supply due to mischaracterization of the larval mortality rate, including its spatial structure, could result in the incorrect classification of a population as limited by larval supply rather than by post-larval carrying capacity.

(ii) *Metapopulation connectivity:* the extent to which alongshore movement allows nearby populations to exchange individuals and act as sources or sinks has long been a focus of the larval ecology and modeling literature (Cowen and Sponaugle, 2008, Cowen et al, 2006, Largier, 2003, O'Connor et al, 2007, Siegel et al, 2008, Swearer et al, 2002, Taylor and Hellberg, 2003). In particular, many studies have sought to estimate the dispersal kernels (probability density functions of where larvae spawned from a given location ultimately settle) of species in particular environments (Shanks, 2009, Shaw et al, 2019, Siegel et al, 2003). We have shown that when the mortality rate is weaker offshore than nearshore, successful larvae tend to spend proportionally more time offshore of the habitat prior to settling than would be estimated with a spatially uniform mortality rate. Given the relationship between offshore distance and alongshore currents (Largier, 2003), this might result in dispersal kernels with heavier tails (i.e., greater variance) than would otherwise be predicted.

2.4.5. Omitted biophysical features and future directions. Several important aspects of marine larval biology and coastal oceanography were omitted from this analysis in order to highlight the effects of cross-shore heterogeneity in the larval mortality rate. For instance, our model considers larvae to be totally passive floaters moved only by random, time-homogeneous diffusion, with net advection due to currents and locomotion ignored. While variability in larvae's positions due to phenomena on length- and timescales shorter than those of dispersal (e.g., day-night cycles) are averaged into the eddy diffusivity, we have not accounted for phenomena that add variance on scales greater than or equal to those of dispersal (e.g., monthly cycles and longer) or that do not average to zero (Largier, 2003, Okubo and Levin, 2001), resulting in nonzero advection or time-varying diffusion.

From the results presented here, we hypothesize that net-offshore advection would result in a lower probability of settling due to fewer larvae returning to shore, more settled larvae arriving after a long offshore duration, and thus greater sensitivity of the larval supply and alongshore movement to the offshore mortality rate. By contrast, net-onshore advection would result in fewer larvae moving offshore. When the mortality rate is higher nearshore than offshore, these larvae would experience high mortality rates, while the exceptionally rare ones diffused offshore would comprise the majority of settlers, just as we observed here in the absence of advection.

Larvae of many species use locomotion to influence their net advection and diffusion, often in different ways during different stages of dispersal (Shanks, 1995, Young, 1995). Organisms with less sophisticated sensory abilities may move randomly to increase their diffusivity, which in turn may increase the probability of moving long distances at times when it is convenient to do so, effectively producing a time-dependent eddy diffusivity (Young, 1995). Pre-competent larvae in species with stronger buoyancy control may reside near-surface at night to exploit an offshore current driven by the land breeze, then descend toward the bottom during the day to escape the opposite sea breeze current, resulting in net-offshore advection. These organisms use an opposite pattern during competence to ensure movement back to the coastal habitat (Shanks, 1995). That some larvae actively move offshore early in development is often attributed to the intense predation risk larvae face near the coast, which was the focus of this paper. We anticipate that by neglecting cross-shore movement due to locomotion, we have underestimated the probability of settling and its sensitivity to the offshore mortality rate.

Finally, we have focused only on larval supply and one proxy measurement for alongshore dispersal, while ignoring other other benefits of dispersal and complex life cycles (including those mentioned in the Introduction). A provocative question in the larval ecology literature is if dispersal is so dangerous, why do some organisms have such long larval durations? Our analysis identified one instance in which a long larval duration might result in a greater larval supply: when the mortality rate is high over the entire habitat and weaker offshore, a longer larval duration may allow larvae to exit the habitat during pre-competence and return before senescence. In other cases, species with long larval durations must experience other benefits that outweigh the reduction in larval supply predicted by most models. Longer larval durations may allow an individual's offspring to spread over a wider range, hedging bets against stochastic events that might wipe out all larvae present in a particular time and location. Another possibility, which has been observed in some species, is that larval durations are coordinated with seasonal changes in the coastal ecosystem: spawning and the larval duration can be timed so that larvae settle in specific locations or at specific times (Donahue et al, 2015, Morgan, 1995b). Incorporating these parent-controlled benefits of larval duration and release timing into models of dispersal is essential for understanding the ecology and evolution of organisms with planktonic larvae. Investigating how these mechanisms interact with offshore heterogeneities presents an interesting direction for future research.

2.5. Appendix

2.5.1. Equivalence of the reaction-diffusion and stochastic individual models. The Fokker-Planck equation is a partial differential equation for the probability density function of a stochastic process of the form in (3.1). For a killed diffusion, like our individual model, the solution to the Fokker-Planck equation gives the probability density of the process on the event that killing has not yet occurred Karlin and Taylor (1981). Suppose that $\tilde{p}(t,x)$ is the probability density of $\xi_t = x$, where ξ_t is the stochastic solution to (3.1). The Fokker-Planck equation for $\tilde{p}$ is

$$\partial_t \tilde{p} = \partial_x \left[\frac{1}{2} \partial_x (g^2(x)\tilde{p}) - f(x)\tilde{p} \right] - [\lambda_s(t,x) + \lambda_m(x)]\tilde{p} \tag{2.18}$$

with the initial condition

$$\tilde{p}(0,x) = \begin{cases} 1 & \text{if } x \in [0,1], \\ 0 & \text{otherwise.} \end{cases} \tag{2.19}$$

reflecting the uniform distribution of ξ_0. No work is needed to see that p (the solution to (2.1)) and $\tilde{p}$ are equal at $t = 0$ for all $x \geq 0$. Expanding the inner derivative in (2.18) and using the definitions of f and g given in (2.11) shows that $\tilde{p}$ also solves (2.1),

$$\begin{aligned} \partial_t \tilde{p} &= \partial_x \left[\frac{1}{2} g^2(x) \partial_x \tilde{p} + \big(g(x) g'(x) - f(x) \big) \tilde{p} \right] - [\lambda_s(t,x) + \lambda_m(x)]\tilde{p} \\ &= \partial_x [\kappa(x) \partial_x \tilde{p}] - [\lambda_s(t,x) + \lambda_m(x)]\tilde{p}, \end{aligned} \tag{2.20}$$

and therefore $p(t,x) = \tilde{p}(t,x)$ for all $t > 0$ and $x \geq 0$.

2.5.2. Boundary conditions of the reaction-diffusion model. All three formulations of the reaction-diffusion model (the dimensional model (2.1), the non-dimensionalization (2.5), and the Fokker-Planck equation (2.18)) require boundary conditions. We always assume that zero larvae travel infinitely far away from shore (or that the probability of doing so is zero),

$$\lim_{X \to \infty} N(T,X) = 0 \text{ for all } T \in [0, T_{LD}], \tag{2.21}$$

$$\lim_{x \to \infty} p(t,x) = 0 \text{ for all } t \in [0,1]. \tag{2.22}$$

In the absence of a coastal boundary layer, the diffusion rate is nonzero over all locations in $[0, \infty)$. This allows larvae to hit the shore, $X = 0$ ($x = 0$ in the non-dimensionalization), and we assert that these larvae are reflected back into the interior of the domain, $(0, \infty)$. This results in no-flux boundary conditions,

$$\partial_X N(T, X)\big|_{X=0} = 0 \text{ for all } T \in [0, T_{LD}], \tag{2.23}$$

$$\partial_x p(t, 0)\big|_{x=0} = 0 \text{ for all } t \in [0, 1]. \tag{2.24}$$

In the presence of a CBL, diffusivity vanishes at the shore $X = 0$ ($x = 0$), and larvae are unable to reach the boundary. In this case, the choice of either a reflecting or absorbing boundary is immaterial; however, we assert that the boundary is absorbing because a no-flux boundary condition would result in division by 0 in our numerical algorithm:

$$N(T, 0) = 0 \text{ for all } T \in [0, T_{LD}], \tag{2.25}$$

$$p(t, 0) = 0 \text{ for all } t \in [0, 1]. \tag{2.26}$$

2.5.3. Derivation of S, L, M. The probability density of the event $\xi_t = x$ (and killing has not yet occurred) is $p(t, x)$. Integrating $p(1, x)$ over all locations x at which the larva could be at time $t = 1$ gives the probability of the event that the larva is located anywhere in the state space, and thus has not settled or died—that is, the probability of offshore loss, L, provided by (2.14).

Let λ_i denote the rate of killing of type i, where $i = s$ (settling) or m (mortality). The probability density of the larva having location x at time t is $p(t, x)$. From (2.12), the probability density of killing of either kind occurring at time t given location x is

$$\begin{aligned}
&\lim_{\delta t \searrow 0} \frac{\Pr\{\text{death or settling in } [t, t + \delta t) \mid \xi_t = x\}}{\delta t} \\
&= \lim_{\delta t \searrow 0} \frac{\big(\lambda_s(t, x)\delta t + o(\delta t)\big)\big(\lambda_m(x)\delta t + o(\delta t)\big)}{\delta t} \\
&= \lambda_s(t, x) + \lambda_m(x) + \lim_{\delta t \searrow 0} \frac{o(\delta t)}{\delta t} \\
&= \lambda_s(t, x) + \lambda_m(x).
\end{aligned} \tag{2.27}$$

Finally, the probability that the type of killing that occurs is type i is $\lambda_i/(\lambda_s + \lambda_m)$. Combining these results, we get the probability densities of settling and killing occurring at location x and time t: respectively, they are

$$\begin{aligned} \phi_s(t,x) &= p(t,x) \cdot (\lambda_s(t,x) + \lambda_m(x)) \cdot \frac{\lambda_s(t,x)}{\lambda_s(t,x) + \lambda_m(x)} = p(t,x)\lambda_s(t,x), \\ \phi_m(t,x) &= p(t,x) \cdot (\lambda_s(t,x) + \lambda_m(x)) \cdot \frac{\lambda_m(x)}{\lambda_s(t,x) + \lambda_m(x)} = p(t,x)\lambda_m(t,x). \end{aligned} \tag{2.28}$$

Integrating ϕ_m over the locations $[0, \infty)$ and the times $[0, 1]$ at which death may occur gives the expression for M in (2.15). Integrating ϕ_s over the locations $[0, 1]$ and times $[t_{pc}, 1]$ at which settling can occur (or simply over all locations $[0, \infty)$ and all times $[0, 1]$, since $\lambda_s \equiv 0$ outside of this set) gives the expression for S in (2.13).

CHAPTER 3

Larvae of coastal marine invertebrates may sacrifice dispersal success for other benefits through active swimming

Abstract

The planktonic larvae of many coastal marine invertebrates swim vertically to exploit variation in current strength and direction, food abundance, and mortality rate throughout the water column. The consequences of this behavior upon larval delivery to coastal habitats have been explored using computational models, but concurrent effects upon predation risk, feeding opportunities, and energy expenditure are not well characterized. We use a simple mathematical model to investigate how a general class of vertical swimming behaviors, including diel vertical migrations, simultaneously affect these aspects of larval biology in a coastal environment with upwelling circulation. We identify two viable categories among these behaviors, "advection-driven" and "diffusion-compensated," that result in mean-onshore and mean-offshore movement, respectively. Advection-driven behaviors result in a large larval supply but few additional benefits. By contrast, diffusion-compensated behaviors offer greater alongshore dispersal, feeding opportunities, and predator avoidance at the expense of larval supply. We hypothesize that advection-driven behaviors are favorable for species with non-feeding larvae and short development times, while diffusion-compensated behaviors are beneficial for feeding larvae. Our analysis underscores the need for further research connecting larval locomotion to other processes occurring during dispersal. More broadly, we emphasize the importance of considering behavior, environmental structure, and several aspects of individual biology when studying dispersal in marine and other settings.

3.1. Introduction

Many coastal marine invertebrates and benthic fish begin life as planktonic larvae (Gerber et al, 2014, Levin and Bridges, 1995, Pechenik, 1999) that can be transported dozens or hundreds of kilometers from their parents' habitat by coastal currents (Largier, 2003, Shanks, 2009, Shanks et al, 2003). 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"; Morgan (1995a), Rumrill (1990), Shanks (1995)). Because metamorphosis is energetically expensive, larvae of many species feed during development or are endowed with a maternally derived energy source (Levin and Bridges, 1995, Shanks et al, 2003). Regardless of their nutritional mode, larvae must ensure they settle and begin metamorphosis with sufficient energy; those that fail to do so may experience reduced fitness later in life (Elkin and Marshall, 2007, Pechenik, 2006, Pechenik and Cerulli, 1991) or may not complete metamorphosis at all (Boidron-Metairon, 1988, Lucas et al, 1979). Finally, larvae must evade predation and other hazards as they develop and feed (Morgan, 1995a, Rumrill, 1990, White et al, 2014, Young, 1995). In summary, planktonic development is a delicate balancing act during which individuals must meet often-conflicting needs.

Larvae of several species improve their likelihood of completing development, defying death, and locating habitats while conserving energy through vertical, rather than horizontal, swimming and other forms of depth control (Chia et al, 1984, Levin and Bridges, 1995, Young, 1995). Depth control is particularly important because while most larvae are slow swimmers (0.1-2 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 meters compared with several kilometers (Cowen et al, 2000, Morgan, 1995a, Shanks, 1995, Sherr et al, 2005, Young, 1995)). Swimming vertically to exploit depth-varying cross-shore currents with speeds of 1-30 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 (Cowen et al, 2000, 2006, James et al, 2019, Marta-Almeida et al, 2006, Rothlisberg et al, 1983). 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).

Vertical swimming behaviors are often matched to the structure of the environment in which larvae develop. In tidal estuaries, for instance, larvae may effect 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 (see **Table 3.1**). 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 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-moving surface layer atop an onshore moving lower layer (see **Figure 3.1a**). Newly spawned larvae may reside in the surface layer 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 lower layer (Shanks, 1995). This behavior, known as an ontogenetic vertical migration (OVM), has been observed in larvae of many species, including the barnacle *Balanus nubilus* by Tapia et al (2010) off Southern California, as well as in the sponge *Rhopaloeides odorabile* by Whalan et al (2008) in laboratory experiments. Changes in depth or vertical swimming behavior can also coincide with changes in nutritional mode (Butler et al, 2011, Tapia et al, 2010) as well as movement between open-coast and estuarine environments during dispersal (Morgan et al, 2014, Queiroga et al, 2007).

Vertical swimming is energetically costly (Sprung, 1984b) 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 an upwelling regime forgo feeding opportunities during daylight, and expose themselves to strong offshore currents while feeding during darkness. These currents transport larvae away from shore, potentially preventing larvae from locating nearshore habitats later in development. Diel vertical migrations therefore have dramatic (and not necessarily advantageous) effects on larval supply and transport in addition to food gathering and predator avoidance. Because larvae must balance dispersal with feeding, predator avoidance, and energy conservation, 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 used mathematical models to investigate the effects of vertical swimming behaviors upon larval supply and alongshore dispersal (reviewed by Metaxas and Saunders (2009); for examples, see Cowen et al (2000, 2006), James et al (2019), Marta-Almeida et al (2006), Owens and Rothlisberg (1991), Rothlisberg et al (1983), Sundelöf and Jonsson (2012)). These studies argue that vertical migration results in greater nearshore retention and less alongshore movement of larvae than would be achieved by passive floating. 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, the precise details of vertical swimming behaviors can have unexpected effects on larval transport (Sundelöf and Jonsson, 2012), yet most studies consider just a few prescribed behaviors with fixed parameters.

We use a simple model to examine the advantages and disadvantages of a broad class of vertical swimming behaviors. We focus on five aspects of larval ecology and biology influenced by vertical swimming: larval supply, potential for alongshore dispersal, predation risk, potential feeding opportunities, and energy expenditure. We consider passive floating alongside a continuous set of active behaviors that includes diel vertical migrations, an ontogenetic migration from the surface to the bottom, and an ontogenetic switch from diel vertical migrations to residing in the bottom only. We limit our analysis to larvae dispersing in the two-layer flow typical of upwelling, since many field and laboratory studies of vertical swimming focus on larvae in or from this type of environment (see **Table 3.1**).

In this paper, we present our model and a classification scheme for vertical swimming behaviors based on the net direction of advection they produce. We then use stochastic simulations of the model to justify the use of this classification and compare the behaviors within these classes, as well as the broader trait-space, against each other and passive floating. Finally, we discuss the ecological, biological, and environmental features that may favor one set of behaviors over another. Our work underscores the importance of considering several behaviors and many aspects of individual biology when modeling the dispersal of marine invertebrate larvae and other organisms.

Table 3.1. 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					
Atelecyclus rotundatus	45-90[a]	F[a]	dos Santos et al (2008)	Open coast with upwelling—Portugal	DVM
Balanus glandula	21-28[b]	F/NF[b]	Morgan and Fisher (2010)	Upwelling shadow—Northern California, US	Reverse OVM (deep then shallow)
Balanus nubilus	14-28[c]	F/NF[b]	Tapia et al (2010)	Southern California, US	OVM
Cancer spp.	60-150[d]	F[e]	Shanks (1986)	Southern California, US	DVM, then RDVM
Carcinus maenas	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
Chthamalus spp.	30-50 [j]	F/NF[j]	Queiroga et al (2007)	Open coast with upwelling—Portugal	DVM (cyprids only)
			Tapia et al (2010)	Southern California, US	Passive (nauplii only)
Hemigrapsus oregonensis	$\leq$ 58[k]	F[e]	Miller and Morgan (2013a)	*Experimental column—Northern California, US*	TVM
Hemigrapsus spp.	15-55[g,o]	F[g,o]	Morgan and Fisher (2010)	Upwelling shadow—Northern California, US	DVM
Jehlius cirratus	22-41[l]	F [m]	Bonicelli et al (2016)	Open coast with upwelling—El Quisco Bay, Chile	Shallow DVM, then deep DVM
Nihonotrypaea harmandi	20-30	F	Tamaki et al (2010)	Tidal estuary—Ariake Sound, Kyushu, Japan	Mixed TVM and DVM
Notobalanus flosculus	39[l]	F/NF[m]	Bonicelli et al (2016)	Open coast with upwelling—El Quisco Bay, Chile	DVM, then reside in surface
Notochthamalus scabrosus	22-41[l]	F/NF[m]	Bonicelli et al (2016)	Open coast with upwelling—El Quisco Bay, Chile	Shallow DVM, then deep DVM
Pachygrapsus crassipes	$<$ 100[n]	F[n]	Morgan and Fisher (2010)	Northern California, US	DVM
Pagurus spp.	13-100[o]	F[o]	Morgan and Fisher (2010)	Upwelling shadow—Northern California, US	OVM and DVM
Panulirus argus	180	NF/F/NF	Butler et al (2011)	*Experimental column—Florida Keys, Florida, US*	Shallow DVM, then deep DVM
Petrolisthes cinctipes	45[p]	F[p]	Miller and Morgan (2013a)	*Experimental column—Northern California, US*	DVM
ECHINODERMS					
Amphiura filiformis	21-42	F	Guillam et al (2020)	Stratified bay—Bay of Douarnenez, Brittany, France	Deep
Dendraster excentricus	2-9[o]	F	Pennington and Emlet (1986)	*Lab/mesocosm—East Sound, Washington, US*	DVM
			Pennington and Emlet (1986)	Weak-current embayment—East Sound, Washington, US	Near surface
Ophiocomina nigra	21-42	F	Guillam et al (2020)	Stratified bay—Bay of Douarnenez, Brittany, France	Hybrid: DVM then deep
Ophiothrix fragilis	21-42	F	Guillam et al (2020)	Stratified bay—Bay of Douarnenez, Brittany, France	DVM near-surface
MOLLUSKS					
Brachidontes granula	$\geq$ 55[q]	F[q]	Bonicelli et al (2016)	Open coast with upwelling—El Quisco Bay, Chile	Late stages near surface
Concholepas concholepas	90[r]	F	Poulin et al (2002b)	Open coast with upwelling—El Quisco Bay, Chile	RDVM during competence
Kelletia kelletii	$\geq$ 35	F	Romero et al (2012)	Southern California, US	DVM then deeper, less pronounced DVM
Mytilus edulis	32[d]	F	Dobretsov and Miron (2001)	Kandalakshsky Gulf, White Sea, Russia	Reverse OVM (deep, then shallow)
Perumytilus purpuratus	14-18[s]	NF[t]	Bonicelli et al (2016)	Open coast with upwelling—El Quisco Bay, Chile	Late stages near surface
Semimytilus algosus	27[u]	F[t]	Bonicelli et al (2016)	Open coast with upwelling—El Quisco Bay, Chile	Late stages near surface
Strombus gigas	35[v]	F	Barile et al (1994)	*Lab/mesocosm—Caribbean*	Possibly DVM
OTHER INVERTEBRATES					
Limulus polyphemus	20-50[w]	F[x]	Ehlinger and Tankersley (2006)	*Experimental column—New Jersey, US*	Endogenously cued TVM
Owenia fusiformis	30	F[y]	Thiébaut et al (1992)	Partially mixed estuary—Bay of Siene, English Channel, France	OVM
Rhopaloeides odorabile	$\leq$ 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] Schlotterbeck1976 (1976). [o] O'Connor et al (2007). [p] Ceballos-Osuna et al (2013). [q] Campos and Ramorino (1980). [r] Poulin et al (2002a).
[s] Śmietanka et al (2018). [t] Lagos et al (2007) report feeding, but Campos and Ramorino (1980) and Śmietanka 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).

3.2. Methods

We use a stochastic process to describe the movement of an individual larva in an environment with sustained upwelling circulation. Because we are primarily interested in the interaction of vertical swimming with the cross-shore and vertical structure of the environment, we explicitly model the larva's cross-shore position, X_t (km), and depth, Z_t, over time, t. Alongshore position, Y_t (km), is modeled implicitly to estimate the effect of cross-shore and vertical movement upon dispersal between coastal habitats. See **3.2.2.1** and **Appendix 3.5.3** for details.

The modeled environment, illustrated in **Figure 3.1a**, consists of two layers: a surface layer with an offshore current and a lower layer with a compensatory onshore current. Within each layer, currents vary over timescales shorter than a typical larval duration; these variations are incorporated into layer-specific eddy diffusivities. We also treat the mortality rate and food abundance as independent of depth within each layer, such that Z_t need only take two values: $Z_t = \ell$ when the larva is in the lower layer and $Z_t = s$ when the larva is in the surface layer. Previous versions of our model allowed Z_t to vary continuously, but produced qualitatively similar results.

The larva's cross-shore position, X_t, while in layer Z_t changes over time according to the stochastic differential equation

$$\begin{aligned} &dX_t = u_x(Z_t)\ dt + \sqrt{2K_x(Z_t)}\ dW_t, \quad X_0 = x_0 > 0, \\ &\text{where } x = 0 \text{ is a reflecting boundary,} \end{aligned} \tag{3.1}$$

where W_t is a standard Brownian motion and u_x and K_x are the cross-shore advective velocity (away from shore) and eddy diffusivity, respectively, that appear in standard reaction-diffusion models. The expression $\sqrt{2K_x}$ arises due to subtle differences in the formulation of reaction-diffusion equations and the stochastic processes they describe (Meyer et al, 2021). In general, we have $u_x(s) > 0$ (offshore movement) and $u_x(\ell) < 0$ (onshore movement). The relative magnitudes of $u_x(s)$ and $u_x(\ell)$ and $K_x(s)$ and $K_x(\ell)$ depend on the relative thickness of the surface and bottom layers, but generally $|u_x(s)| > |u_x(\ell)|$ and $K_x(s) > K_x(\ell) > 0$.

Modeled larvae have a larval duration of T hours. Individuals may only initiate metamorphosis if they encounter a suitable habitat during a finite competence duration. In our model, this habitat occupies the interval $[0, x_h]$ adjacent to the coast, representing a long, homogeneous habitable region along the shore. Larvae are competent from $t = T_C$ until $t = T$. If a larva is delivered to the nearshore habitat during competence, the stochastic process terminates; the time at which this occurs is denoted T_* (see **Figure 3.1b**).

We assume the cross-shore advection and diffusion rates, u_x and K_x, do not vary with offshore distance. However, the effects on larval dispersal of oceanographic features resulting in spatially heterogeneous currents, such as a slow-moving nearshore coastal boundary layer, have been discussed extensively in the literature (Largier, 2004, Meyer et al, 2021, Nickols et al, 2012, 2013, Shanks, 2009). In a separate paper, we show that the coastal boundary layer limits offshore movement of larvae, reducing offshore loss but potentially increasing nearshore predation (Meyer et al, 2021). An analysis of the interaction of vertical swimming with the coastal boundary layer and other oceanographic features is beyond the scope of this paper. However, preliminary simulations suggest the effects of swimming may overshadow those of the coastal boundary layer.

3.2.1. Swimming Behaviors. We consider a continuous trait-space of swimming behaviors in which larvae initially reside in the surface layer or exhibit diel vertical migrations and may eventually migrate to the lower layer for the remainder of the larval duration. These behaviors can be described using two parameters: the nightly number of hours spent at the surface during the first phase of dispersal, $A \in [0, 24]$; and the fraction of the larval duration that elapses before the ontogenetic migration to the bottom layer, $B \in [0, 1]$ (see **Figure 3.1b**). The nightly period spent at the surface lasts from $A/2$ hours before midnight to $A/2$ hours after midnight. Note that $A = 24$ h means that larvae reside continuously in the surface layer during the first phase of development (i.e., a single ontogenetic vertical migration), and $B = 1$ means that larvae exhibit diel vertical migrations (if $0 < A < 24$ h) or remain at the surface (if $A = 24$ h) for the entirety of the larval duration.

We highlight how behaviors in this trait-space differ in their advantages by also focusing on three specific examples: OVM (ontogenetic vertical migration), DVM (diel vertical migrations), and HYBRID (a combination thereof). The values of A and B for these behaviors, as well as plots showing their typical outputs X_t and Z_t, are presented in **Figure 3.2**. Parameters were selected to illustrate key differences in performance, rather than to capture the behaviors of any particular

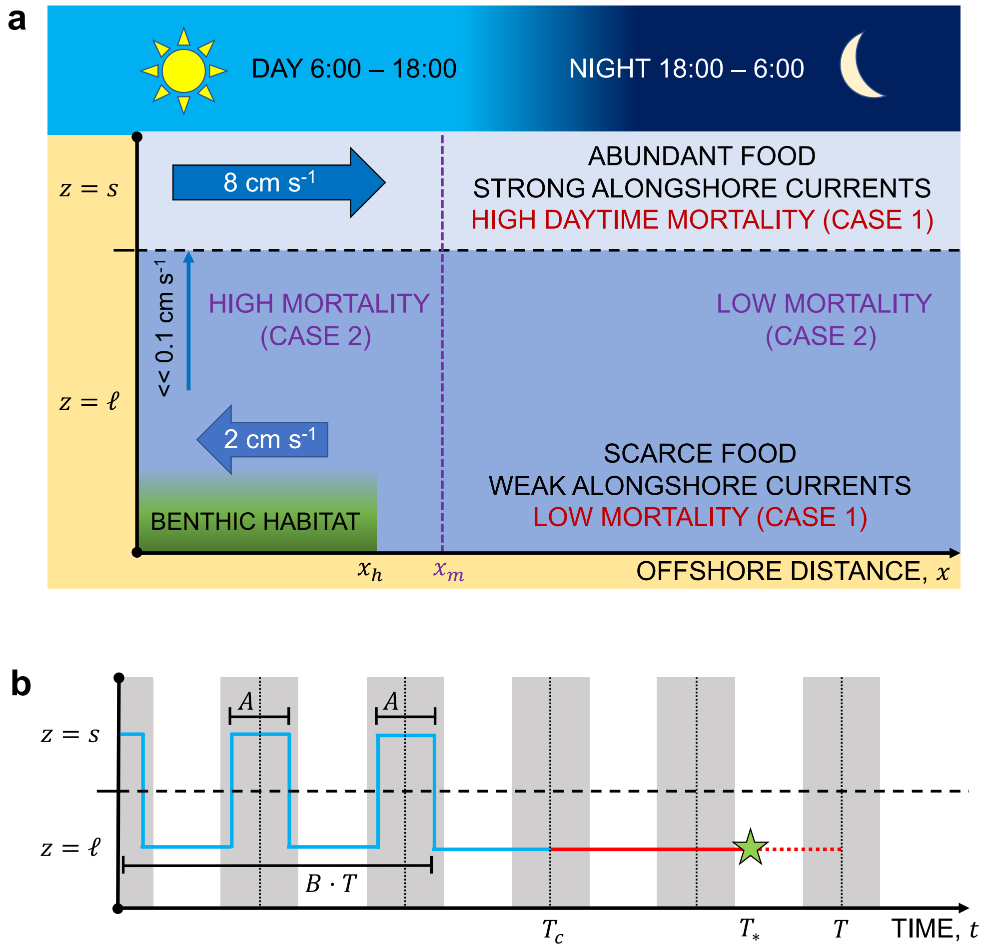

Figure 3.1. Schematic diagrams illustrating the model design. **(a)** A cross-section of the offshore environment. Cases 1 (red) and 2 (purple) refer to the two mortality schemes described in *3.2.2.2*. Larvae can only settle while above the benthic habitat (green) during their competence window. **(b)** An example vertical trajectory of a larva exhibiting a swimming behaviors in the (A, B) trait-space. White and gray regions correspond with periods of light and darkness. The larva spends A h (centered about midnight) in the surface each night during the first $B \cdot T$ hours of development, then resides in the bottom for the remainder. The larva is pre-competent (blue) until time $t = T_C$ and competent (red) thereafter. In this example, the larva encounters the habitat during competence at T_* (green star) before the end of its larval duration T. The dashed red path following T_* shows the depth of the larva if it continued to disperse after encountering the habitat.

organism. For comparison, we also consider a passive floating behavior, PASSIVE, in which the modeled larva switches between the surface and lower layers according to a Markov process. The mean residence times in the lower and surface layers are $\lambda_\ell = 14$ h and $\lambda_s = 1$ h, respectively.

These quantities are derived from the assumption that the lower and upper layers have thickness 40 m and 10 m, respectively, and that vertical eddy diffusivity is approximately 20 cm^2 s^{-1} (see **Appendix 3.5.1**).

We assume that swimming larvae are moved only by locomotion, and not vertical diffusion. Additionally, we ignore vertical advection in all scenarios. Although upwelling circulation typically results in upward currents close to shore, these currents are generally very slow compared with the velocities of larval swimming and sinking ($\ll 0.1$ cm s^{-1}, Liang et al (2017), compared with 0.1-2 cm s^{-1}, Chia et al (1984)).

3.2.1.1. *Classification of Swimming Behaviors.* To facilitate analysis of the (A, B) trait-space, we classify behaviors based on the net direction of advection they produce. Grouping behaviors in this way is useful for two reasons. First, whether or not larvae are, on average, transported on- or offshore has a large effect on whether larvae locate nearshore habitats, how long it takes to locate those habitats, and the extent to which larvae experience offshore conditions during dispersal. Second, the net direction of advection depends on how much time larvae spend in the offshore-flowing surface layer compared with the onshore-flowing bottom layer, which in turn informs how larvae are affected by vertical variation in alongshore currents, predation rate, and food abundance.

Behaviors in the (A, B) trait-space that result in net-onshore (offshore) advection lie below (above) the hyperbola

$$B = \left(-\frac{24u_x(\ell)}{u_x(s) - u_x(\ell)}\right) A^{-1}, \tag{3.2}$$

along which net advection is 0 (see **Appendix 3.5.2**). Under the parameter values in **Table 4.1**, this becomes

$$B = 4.8A^{-1}. \tag{3.3}$$

We give the resulting classes the following descriptive names:

(i) *Advection-driven behaviors* for which net advection is onshore. These behaviors lie below the hyperbola (3.2). Ignoring mortality, the most common outcome for larvae exhibiting these behaviors is transport toward the coast and delivery to the nearshore habitat during competence. Offshore loss is mainly due to random diffusion against the onshore mean.

(ii) *Diffusion-compensated behaviors* for which net advection is offshore, but random diffusion against this mean returns an appreciable fraction of larvae to the nearshore habitat. These behaviors lie above the hyperbola (3.2). Ignoring mortality, the most common outcome for larvae exhibiting these behaviors is offshore loss.

A third class contains *inviable behaviors* for which net advection is so strongly offshore that shoreward diffusion cannot compensate. More precisely, these behaviors fail to deliver any larvae to the nearshore habitat during competence in the course of the analysis detailed in **3.2.3** below.

3.2.2. Performance Metrics.

Larval swimming behaviors are scored using five performance metrics, which are explained below and summarized in **Table 3.2**.

3.2.2.1. *Dispersal Efficiency and Potential.* We define the *dispersal efficiency*, DE, of a vertical swimming behavior to be the fraction of larvae exhibiting that behavior that return to shore during competence when mortality, which we model separately, is ignored:

$$DE = \frac{\#\text{ of larvae delivered to habitat}}{\#\text{ of larvae simulated}}. \tag{3.4}$$

Dispersal efficiency is a proxy for larval supply and provides an upper bound on the fraction of spawned larvae (or the probability of an individual larva being) delivered to the nearshore habitat.

Dispersal potential, DP, measures how far alongshore the larvae that ultimately encounter habitats typically travel during dispersal. Alongshore currents usually increase in strength with offshore distance and are stronger near the surface than below (Largier, 2003). We assume that the alongshore diffusivity at location (x, z) takes the form

$$K_y(x, z) = \frac{K_y^\infty(z)x}{\hat{x} + x}, \tag{3.5}$$

where $K_y^\infty(z)$ is the alongshore diffusivity far from shore in layer z and $\hat{x}$ is the offshore distance at which alongshore diffusivity $K_y^\infty(z)/2$ is attained. In the absence of other alongshore currents, the alongshore position of a larva after T_* time units follows a normal distribution with the following standard deviation, which we use to estimate alongshore dispersal potential:

$$DP = \sqrt{\mathbf{E}_D \left[\int_0^{T_*} 2K_y(X_t, Z_t)\, dt \right]} \tag{3.6}$$

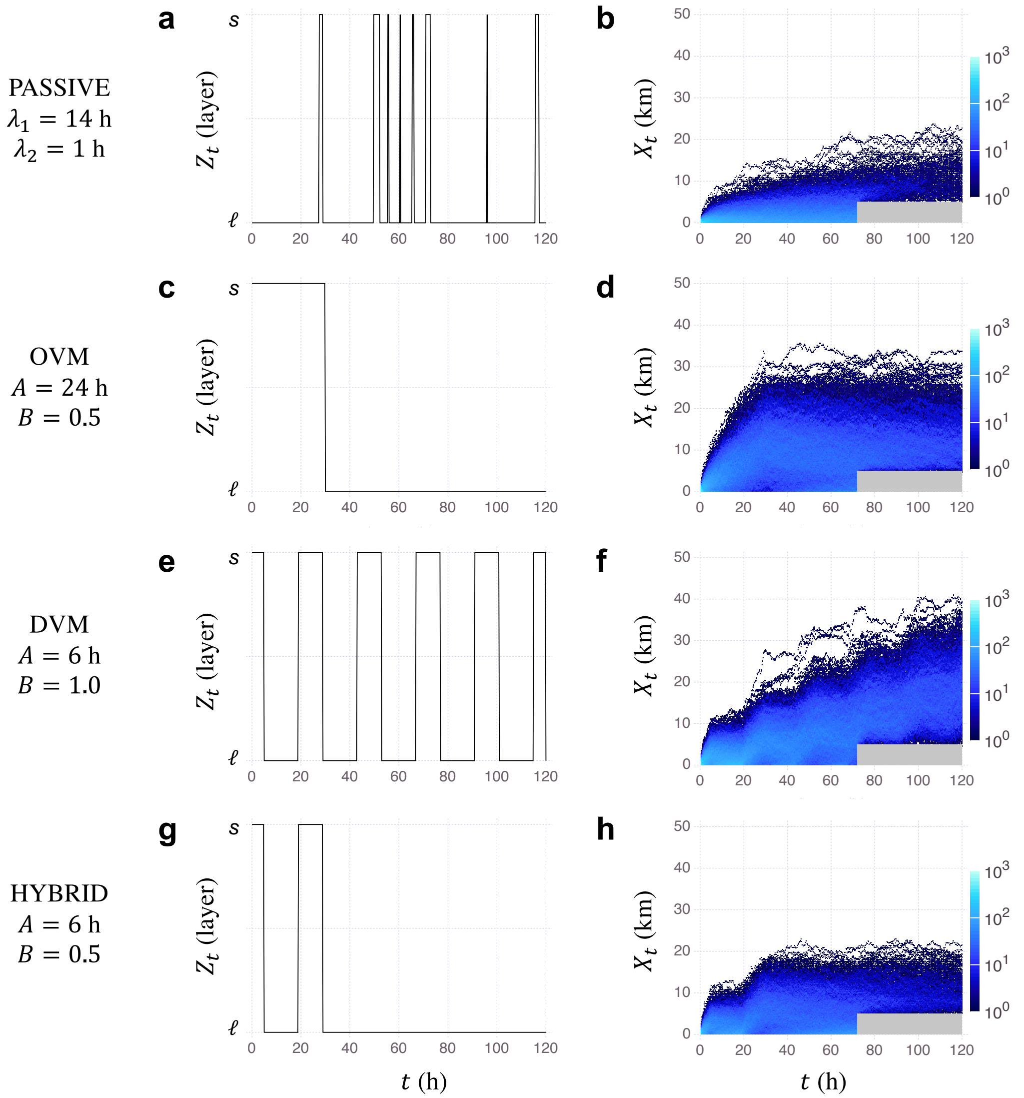

Figure 3.2. Sample simulations using each of the four example behaviors: PASSIVE (first row), OVM (second row), DVM (third row), and HYBRID (fourth row). **(a)**, **(c)**, **(e)**, and **(g)** show single instances of vertical position, Z_t, for each behavior. **(b)**, **(d)**, **(f)**, and **(h)** are 2d histograms showing the number of larvae, out of 2000 simulated individuals, passing through each offshore location $x > 0$ at each time $t \in [0, T]$. Larvae end dispersal if they encounter the nearshore habitat region, $[0, x_h]$, during a competence window, $[T_C, T]$, shown by the gray box in the lower right of these histograms.

(see **Appendix 3.5.3**). The operator $\mathbf{E}_D$ represents an average of only larvae that are delivered to nearshore habitats during their competence window (that is, expected value conditioned upon delivery). The performance of larvae that are not delivered to habitats during competence is usually irrelevant and, as noted later, sometimes misleading.

3.2.2.2. *Mortality Risk.* If $\delta(x,z)$ denotes the larval mortality rate at offshore distance x in layer z, then the probability of a larva surviving its path (X_t, Z_t) is

$$\exp\left(-\int_0^{T_*} \delta(X_t, Z_t)\ dt\right) \tag{3.7}$$

(Karlin and Taylor, 1981). We quantify the mortality risk of a behavior using the geometric mean probability of survival along paths that ultimately deliver larvae to the nearshore habitat during competence,

$$S = \exp\left(-\mathbf{E}_D\left[\int_0^{T_*} \delta(X_t, Z_t)\ dt\right]\right). \tag{3.8}$$

The geometric mean is more appropriate for averaging probabilities than the arithmetic mean; however, the choice of mean has no qualitative impact on our results.

We consider two mortality schemes:

(i) *Diurnal Predation.* The mortality rate is δ_1 in the upper layer during daylight (6:00 to 18:00), δ_0 in the upper layer during darkness (18:00 to 6:00 the following morning), and δ_0 in the lower layer at all times, where $\delta_0 < \delta_1$.

(ii) *Nearshore Predation.* The mortality rate is δ_1 within a nearshore region occupying the interval $[0, x_m]$, and δ_0 at all locations offshore of x_m, where $\delta_0 < \delta_1$.

We do not directly combine these structures because it is not clear how the nearshore and surface mortality rates compare in magnitude. However, their combined effects can be gleaned from examining each in isolation.

3.2.2.3. *Energy Expenditure and Feeding.* Larvae use energy for maintenance, development and locomotion. In our analysis, we use the rates of maintenance and swimming energy consumption reported by Sprung (1984b) for the mussel *Mytilus edulis.* Although rates vary across species and with environmental conditions (Lucas et al, 1979, Rodriguez et al, 1990, Sprung, 1984b, Thiyagarajan et al, 2003, Videla et al, 1998, Wendt, 2000), their exact values are less important than their relative magnitudes. We assume that the rate of maintenance energy consumption is constant, c_0 (μJ h^{-1}). Transitioning from the lower layer to the surface layer costs a fixed amount of energy, C_+

(μJ); similarly, transitioning from the surface layer to the lower layer costs C_- (μJ). The expected energy spent on locomotion by a larva that makes N_+ trips from the lower to the surface layer and N_- trips from the surface to the lower layer before arriving in the nearshore habitat is

$$E_L = \mathbf{E}_D[C_+N_+ + C_-N_-], \tag{3.9}$$

and the expected energy spent on maintenance is

$$E_M = \mathbf{E}_D[c_0T_*] = c_0\mathbf{E}_D[T_*]. \tag{3.10}$$

The total expected energy expenditure is $E = E_L + E_M$. For *M. edulis*, locomotion is only a small fraction of the total energy budget of a larva (Sprung, 1984b), so $E_M \gg E_L$ and total expenditure, E, is nearly proportional to the expected dispersal time of larvae delivered to the nearshore habitat during competence, $\mathbf{E}_D[T_*]$. However, it is useful to consider E and E_L separately because this may not be true for all organisms.

Let $f(x, z)$ denote the density of a food source, such as phytoplankton, at offshore distance x in layer z. We measure the feeding opportunities provided by a vertical swimming behavior using the expected total amount of food encountered by larvae that are delivered to the nearshore habitat during competence

$$F = \mathbf{E}_D\left[\int_0^{T_*} f(X_t, Z_t)\; dt\right]. \tag{3.11}$$

We assume that food abundance in the surface layer, f_s is greater than food abundance in the lower layer, f_ℓ, and that neither varies with cross-shore distance. By using food encountered as a proxy for food consumed, we are also assuming that larvae feed constantly and that their rate of consumption is proportional to local food density. We acknowledge, however, that larvae of many species have both feeding and non-feeding stages (Butler et al, 2011, Levin and Bridges, 1995, Pechenik, 1999, Tapia et al, 2010), and that feeding rates sometimes vary nonlinearly with food density (Sprung, 1984a).

3.2.3. Simulations.

We approximated the five performance metrics in **Table 3.2** through numerical simulations of the stochastic model (3.1). Using the default parameter set in **Table 4.1**

Table 3.2. Definitions of the five performance metrics used to assess vertical swimming behaviors. All referenced probabilities and expected values are conditioned upon successful delivery of larvae to the nearshore habitat during competence.

Quantity	**Symbol**	**Units**	**Description**	**Expression**
Dispersal efficiency	DE	—	Fraction of larvae successfully delivered	$\frac{\#\text{ of larvae delivered to habitat}}{\#\text{ of larvae simulated}}$
Dispersal potential	DP	km	Typical alongshore dispersal distance	$\sqrt{\mathbf{E}_D\left[\int_0^{T_*} 2K_y(X_t, Z_t)\ dt\right]}$
Probability of survival	S	—	Probability of escaping predation	$\exp\left(-\mathbf{E}_D\left[\int_0^{T_*} \delta(X_t, Z_t)\ dt\right]\right)$
Energetic costs:				
Locomotion	E_L	μJ	Expected energy spent on vertical swimming	$\mathbf{E}_D\left[C_+N_+ + C_-N_-\right]$
Maintenance	E_M	μJ	Expected energy spent on maintenance/growth	$c_0\mathbf{E}_D\left[T_*\right]$
Total	E	μJ	Expected energy spent for any purpose	$E_M + E_L \approx E_M$
Feeding opportunities	F	cells mL^{-1} h	Expected total phytoplankton density encountered	$\mathbf{E}_D\left[\int_0^{T_*} f(X_t, Z_t)\ dt\right]$

and looping over each swimming behavior (A, B) in a 49×21 uniform mesh of $[0, 24] \times [0, 1]$, as well as passive floating, we simulated the model 5000 times using the Euler-Maruyama method. Dispersal efficiency, DE, is estimated as the fraction of those simulations that terminate with the larva being delivered to the nearshore habitat during competence. The other four metrics are conditional expectations containing the operator $\mathbf{E}_D$, which we approximated by averaging over only those simulations ending in delivery to the nearshore habitat during competence.

We performed additional simulations to illustrate the success of our classification of behaviors and the sensitivity of dispersal efficiency, DE, to larval duration, T, and the strengths of advection and diffusion, u_x and K_x. This included performing the same analysis described above using a shorter larval duration, $T = 120$ h, as well as using only the example behaviors in **Figure 3.2** while sweeping over ranges of T, $u_x(s)$, and $K_x(s)$ one at a time. Finally, we determined the direction of change of DE with respect to T, $u_x(s)$, and $K_x(s)$ by performing the analysis described above three additional times, each with a perturbation to one of these three parameters: $T = 360$ h instead of 600 h, $u_x(s) = 0.5$ km h^{-1} instead of 0.288 km h^{-1}, and $K_x(s) = 1$ km^2 h^{-1} instead of 0.72 km^2

Table 3.3. Summary of symbols used in the formulation of the model, along with their default values and ranges (where applicable).

Variable	Meaning	Units	Default	Range
x	Offshore distance	km	—	$[0, \infty)$
z	Depth	layer	—	s or ℓ
t	Time since spawning	d	—	$[0, T]$
T	Total larval duration	h	600 (25d)	up to 180d[a]
T_C	Pre-competence duration	h	360 (15d)	10-90% of T[a,b]
h_{light}	Time of sunrise	—	6:00	—
h_{dark}	Time of sunset	—	18:00	—
x_h	Width of post-larval habitat	km	5	0.01 to 10km[c]
$u_x(\ell)$	Horizontal advection in lower layer of water column	km h^{-1}	-0.072	-0.036 to -1.08[d]
$u_x(s)$	Horizontal advection in upper layer of water column	km h^{-1}	0.288	0.036 to 1.08[d]
$K_x(\ell)$	Cross-shore eddy diffusivity of larvae in lower layer	km^2 h^{-1}	0.18	0.036 to 3.6[e]
$K_x(s)$	Cross-shore eddy diffusivity of larvae in upper layer	km^2 h^{-1}	0.72	0.036 to 3.6[e]
$K_y^{\infty}(\ell)$	Max alongshore eddy diffusivity of larvae in lower layer	km^2 h^{-1}	0.18	0.036 to 3.6[e]
$K_y^{\infty}(s)$	Max alongshore eddy diffusivity of larvae in upper layer	km^2 h^{-1}	3.6	0.036 to 3.6[e]
$\hat{x}$	Offshore dist. where alongshore diff. attain half maximum	km	10	5-10[f]
δ_0	Baseline (far offshore and during darkness) larval mortality rate	h^{-1}	0.005	0.001 to 0.14[g]
δ_1	Elevated mortality rate nearshore/at surface during daylight	h^{-1}	0.025	0.001 to 0.14[g]
x_m	Width of nearshore high-mortality zone	km	5	0 to 10[d]
c_0	Baseline rate of energy consumption	mJ h^{-1}	15	1 to 36[h]
C_+	Energy cost of moving from lower to upper layer	mJ	10	[i]
C_-	Energy cost of moving from upper to lower layer	mJ	0	[i]
λ_0	Expected time spent in lower layer while passively floating	h	14	[j]
λ_0	Expected time spent in upper layer while passively floating	h	1	[j]
f_ℓ	Phytoplankton density in lower layer	cells mL^{-1}	10^4	0 to 10^4 [k]
f_s	Phytoplankton density in surface layer/food-rich patch	cells mL^{-1}	10^5	10^2 to $3 \cdot 10^5$ [k]

[a] Shanks (2009), Shanks et al (2003). [b] Wang and Widdows (1991). [c] Nickols et al (2015), Rasmuson (2013).
[d] Shanks (1995). [e] Largier (2003). [f] Assumed range. [g] White et al (2014). [h] Sprung (1984b).
[i] See **Appendix 3.5.4**. [j] See **Appendix 3.5.1**. [k] Fehling et al (2012), Sherr et al (2005).

h^{-1}. While varying T, we kept the onset of competence as $T_C = 0.6T$, and while varying surface advection and diffusion, we kept lower layer advection and diffusion as $u_x(\ell) = -0.25 u_x(s)$ and $K_x(\ell) = 0.25 K_x(s)$, respectively, preserving the ratios in the default parameter set.

Finally, we performed 10^4 simulations using the behaviors DVM, OVM, and HYBRID from **Figure 3.2**, but allowed larvae to continue dispersing until $t = T$ even if they arrived in the nearshore habitat during competence. We recorded the final cross-shore position, X_T, of each simulated larva, as well as whether the larva successfully reached the nearshore habitat during competence.

3.3. Results

3.3.1. Classification of Behaviors. We classified vertical swimming behaviors in the (A, B) trait-space as advection-driven or diffusion-compensated if they result in net-onshore or net-offshore advection, respectively. We found that at the default parameter set in **Table 4.1**, dispersal efficiency, DE, increases (decreases) with respect to the strength of advection, $u_x(s)$, for every advection-driven (diffusion-compensated) behavior (**Figure 3.3a**). Among the example behaviors in **Figure 3.2**, HYBRID is advection-driven while DVM and OVM are diffusion-compensated. Accordingly, the efficiency of HYBRID increases with the advective velocity while the efficiencies of DVM and OVM decrease with advective velocity (**Figure 3.3d**). The PASSIVE behavior cannot formally be classified as advection-driven or diffusion-compensated because it does not depend on A and B, but performs similarly to advection-driven behaviors by most metrics. This is because in our default parameter set, PASSIVE larvae average 14 times more time in the bottom layer than the surface (see **Appendix 3.5.1**). The only inviable behaviors, which did not result in any larvae being delivered to the nearshore habitat during competence, lie in the upper-right corner of the (A, B) plane.

The nomenclature "advection-driven" and "diffusion-compensated" is justified in **Figure 3.4**, which illustrates how far offshore larvae finish dispersal, X_T, when they do not stop dispersing even if delivered to the nearshore habitat during competence. According to classical diffusion theory, these histograms approximate normal distributions, except that larvae are reflected at $x = 0$ and accumulate there if experiencing net-onshore advection. The mean of this distribution represents how far larvae are moved by advection, while the variance about this mean represents the dispersion (spreading out) of a group of larvae due to diffusion (Okubo and Levin, 2001). The HYBRID behavior results in most larvae being delivered to shore during competence and accumulating there, indicating net-onshore advection (**Figure 3.4a**). Generally, HYBRID larvae finish dispersal less than 25 km from shore. On the other hand, for the DVM behavior larvae are transported more than 100 km offshore, with only a small fraction arriving nearshore during competence (**Figure 3.4c**). The red portion of the histogram in **Figure 3.4c** showing larvae that returned to shore during competence is the left tail of a normal distribution reflected at $x = 0$, indicating that settling occurs due to variance, or diffusion, about an offshore-moving mean. OVM results in a distribution of final positions in between these two extremes, (**Figure 3.4b**) highlighting that although we use advection-driven and diffusion-compensated as a convenient binary classification, they should be regarded as the two ends of a spectrum of behaviors.

We found good agreement between the curve (3.2) separating advection-driven and diffusion-compensated behaviors and the boundary between behaviors that decrease or increase in efficiency with respect to cross-shore eddy diffusivity, K_x (**Figures 3.3b,e**). In particular, all advection-driven behaviors and some diffusion-compensated behaviors close to the curve decrease in efficiency with respect to diffusivity. By contrast, most diffusion-compensated behaviors increase in efficiency with diffusivity. This curve also approximately separates behaviors that increase or decrease in efficiency with respect to larval duration, T (**Figures 3.3c,f**), although the boundary separating these classes is fuzzier: the dispersal efficiency of most advection-driven (diffusion-compensated) behaviors increases (decreases) with the length of the larval duration.

Because our behavioral classes are tied to time spent in the surface layer compared with the bottom layer—and because the surface layer flows offshore while the bottom layer flows onshore—our categorization roughly predicts the performance of some behaviors, as measured by the performance metrics in **Table 3.2**. These results are discussed below.

3.3.2. Dispersal Efficiency. Vertical swimming behavior has a large impact on dispersal efficiency, DE. As A and B are varied, DE ranges from 0 to over 0.999 (**Figures 3.5a,b**). The greatest dispersal efficiencies were attained by advection-driven behaviors that spend little time in the surface layer. This includes diel vertical migrations with a short nightly duration at the surface (e.g., $B = 1$ and A small), an early ontogenetic switch from the surface to the bottom ($A = 24$ h and B small), and hybrid behaviors with one or both of these features. This also includes PASSIVE, the dispersal efficiency of which is shown by the white contour in **Figures 3.5a,b**. Diffusion-compensated behaviors that spend many hours per night in the surface or have a late ontogenetic switch to the bottom result in low dispersal efficiency and, at the extreme, may be inviable (e.g., $DE = 0$ over 5000 simulations).

The transition between high- and low-efficiency behaviors is gradual with a short larval duration, but sharp with a medium or long larval duration (compare **Figures 3.5a,b**). This suggests that the longer the larval duration, the greater impact small changes in behavior have upon dispersal efficiency. **Figure 3.3d** supports this observation, illustrating that the dispersal efficiencies of behaviors in **Figure 3.2** diverge as T is increased. We also noted that the dispersal efficiencies of these behaviors diverge as advection is strengthened with diffusivity held constant, but

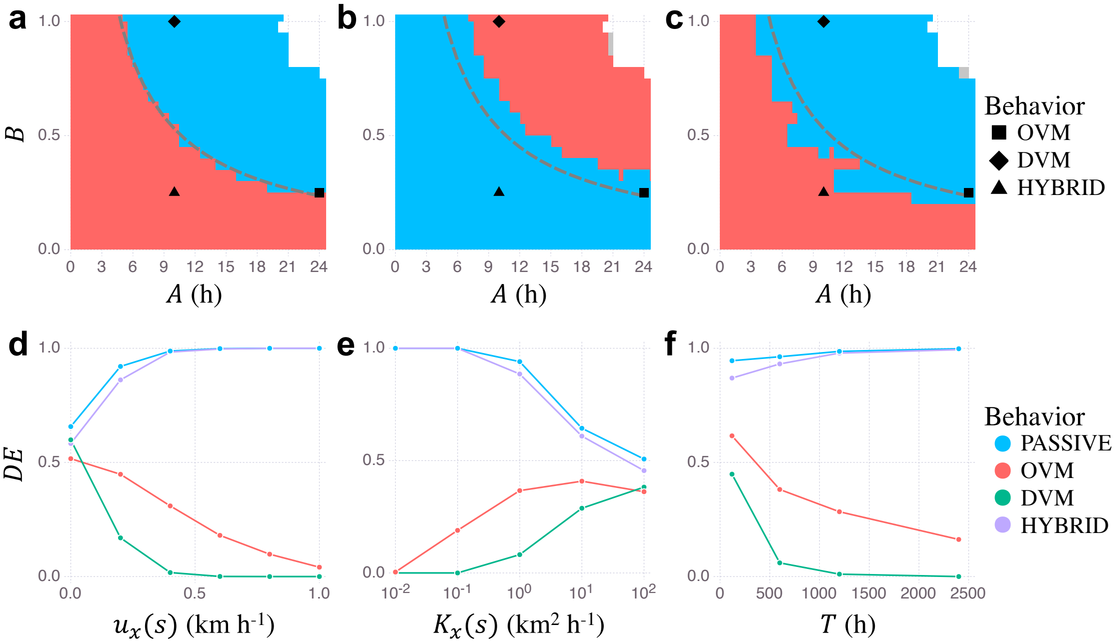

Figure 3.3. The sensitivity of dispersal efficiency, DE, to advection and diffusion strength and larval duration differs between advection-driven and diffusion-compensated behaviors. Top row: direction of change of DE with respect to **(a)** surface advection velocity, $u_x(s)$, **(b)** surface eddy diffusivity, $K_x(s)$, and **(c)** larval duration, T, from the default parameter values in **Table 4.1**. Red and blue indicate increasing and decreasing relationships, respectively, while the white region in the upper right indicates that $DE = 0$ at the default parameters (inviable behavior). Gray regions indicate no change; such instances are random artifacts due to the stochasticity of the numerical model. The locations of the behaviors OVM, DVM, and HYBRID from **Figure 3.2** in the (A, B) trait-space are shown as a square, a diamond, and a triangle, respectively, and the dashed gray curve shows the hyperbola $B = 4.8A^{-1}$ separating advection-driven and diffusion-compensated behaviors. Bottom row: DE as functions of **(d)** surface advection velocity, **(e)** surface eddy diffusivity, and **(f)** larval duration for the four behaviors in **Figure 3.2**.

converge as diffusivity is strengthened with advection held constant (**Figures 3.3e,f**, respectively). Because advection is deterministic while diffusion is stochastic, this suggests that the behaviors considered have a greater impact on dispersal efficiency when the environment is more predictable.

3.3.3. Dispersal Time and Potential. The expected dispersal time of larvae that ultimately arrive in the habitat during competence, $\mathbf{E}_D[T_*]$, is a good predictor of some performance metrics. Diffusion-compensated behaviors and advection-driven behaviors near the hyperbola (3.2) generally result in longer dispersal times than advection-driven behaviors below (3.2) or passive floating (**Figure 3.5c**). Larvae exhibiting diffusion-compensated behaviors generally travel farther offshore and

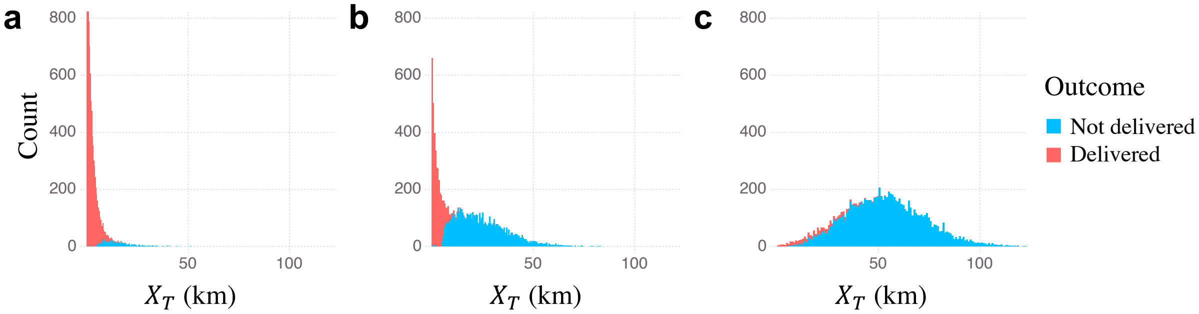

Figure 3.4. Final offshore positions, X_T, of 10^4 simulated larvae exhibiting the behaviors **(a)** HYBRID, **(b)** OVM, and **(c)** DVM described in **Figure 3.2**. HYBRID is advection-driven, DVM is diffusion-compensated, and OVM is diffusion-compensated but lies close to the boundary between the two classes. Simulated larvae were allowed to disperse until the end of the larval duration, T, even if delivered to the nearshore habitat at some time T_* during competence. In the stacked histograms above, the distribution of final positions of successfully delivered larvae are shown (in red) atop the distribution of final positions of unsuccessful larvae (in blue).

require more time to return, while larvae performing advection-driven behaviors or passive floating are retained close to shore and encounter suitable habitats near the beginning of their competence window. On the other hand, advection-driven behaviors and passive floating offer less potential for alongshore dispersal, DP, than diffusion-compensated behaviors (**Figure 3.5d**). Advection-driven behaviors simultaneously prevent larvae from experiencing strong alongshore currents in the surface and far offshore, and also limit the duration of exposure to even weak nearshore and bottom currents through early delivery to the nearshore habitat (smaller $\mathbf{E}_D[T_*]$).

We observed an unusual trend between behavior and dispersal time among diffusion-compensated behaviors. As shown in **Figure 3.5c** in the region with approximately $5 \leq A \leq 18$ and $0.75 \leq B \leq 1$, the expected dispersal time for settling larvae is actually shorter for larvae exhibiting pure diel vertical migrations than for larvae that undergo a late ontogenetic switch to the bottom layer. Intuitively, however, even a late switch should decrease dispersal time by subjecting larvae to a current that moves toward the nearshore habitat. We speculate that this is because the larvae delivered to shore by very low-efficiency diffusion-compensated behaviors are, in a sense, outliers. Intuition for how behaviors affect typical larvae—which may finish dispersal far offshore—does not apply to the few larvae that return to shore during competence. The outlying nature of successful larvae using diffusion-compensated behaviors is illustrated by **Figure 3.4c**, in which most larvae delivered to shore during competence are in the reflected left tail of the distribution of final positions.

3.3.4. Mortality Risk. The two mortality schemes we considered generally favor different swimming behaviors. Unsurprisingly, high mortality in the surface layer during daylight due to visually guided predators results in a low probability of survival, S, for behaviors that do not actively avoid the surface layer during daylight (**Figure 3.5e**). This includes all behaviors that either continually reside in the surface layer for a non-negligible portion of the larval duration ($A = 24$ and $B \gtrapprox 0.15$) or exhibit diel vertical migration-like behavior but spend a portion of the photoperiod in the surface ($A > 12$). These behaviors are diffusion-compensated, although surface-avoiding diffusion-compensated behaviors result in a greater probability of survival. Nearly all advection-driven behaviors, as well as passive-floating, result in a high probability of survival by spending little time in the surface layer. Among these behaviors that avoid the surface during daylight, we noted a small difference in S which can be explained by dispersal time. Prolonged exposure to even the lower mortality rate in the bottom or the surface at night results in a lower probability of settling.

By contrast, high mortality nearshore due to coastal and benthic predators results in a low probability of survival for behaviors with little offshore movement. This includes passive floating and most advection-driven behaviors, which permit little exposure to the offshore-moving surface layer. We observed the greatest probabilities of survival among diffusion-compensated behaviors that either move larvae far offshore but reliably return them to shore during competence (for instance, the example behavior OVM, shown as an orange square in **Figure 3.5f**) or somewhat limit offshore movement but deliver larvae to shore as early as possible (for instance, diel vertical migrations with a long nightly period in the surface layer). Due to the non-monotonic relationship between B and dispersal time described in the previous section, diffusion-compensated behaviors between these two categories (that is, diel vertical migration-like behaviors with medium-late ontogenetic switches to the bottom layer) result in a lower probability of settling than these two extreme behaviors.

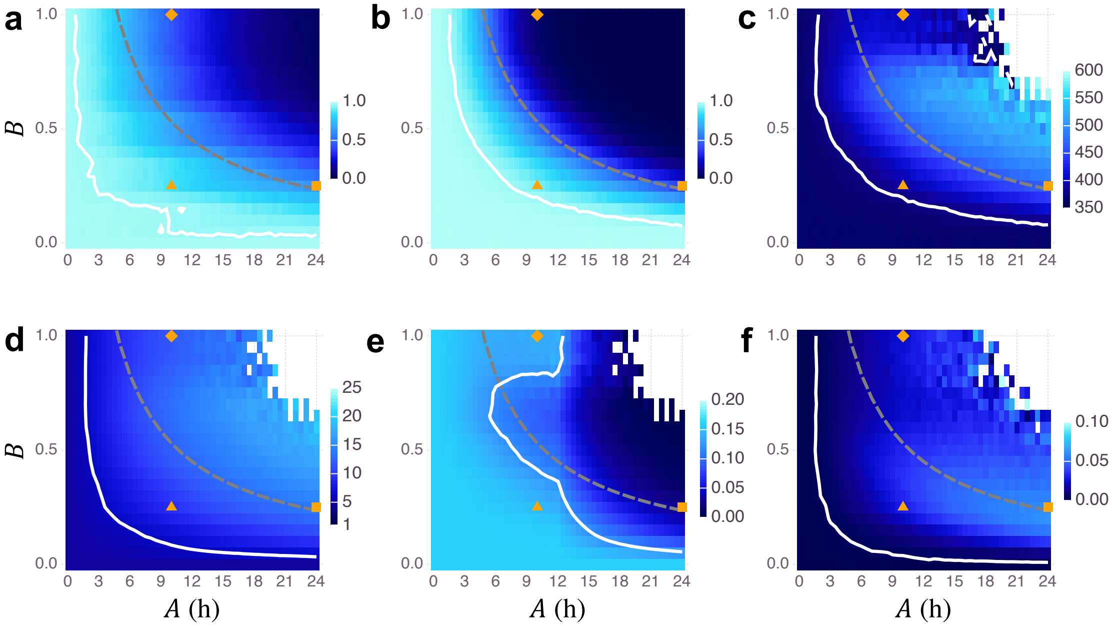

Figure 3.5. Performance of vertical swimming behaviors in the (A, B) trait-space (heatmaps) and passive floating (white contour lines), as measured by metrics from **Table 3.2**. **(a)** and **(b)** show dispersal efficiency, DE, for larval durations $T = 120$ h and 600 h, respectively; **(c)** shows mean dispersal time of successful larvae, $\mathbf{E}_D[T_*]$ (h); **(d)** shows alongshore dispersal potential of successful larvae, DP (km); and **(e)** and **(f)** show the probability of survival, S, for successfully delivered larvae subject to diurnal and nearshore predation, respectively. Meanings of the gray dashed curve, the white regions, and the orange plotted points are as in **Figure 3.3**, and the white contour lines shows values attained by passive floating.

3.3.5. Energy and Feeding. We found that the expected amount of energy larvae spend on locomotion, E_L, is small compared with that spent on other processes, E_M. This is illustrated by the scales of the heatmaps in **Figures 3.6a,b**: for every behavior (A, B), E_L is on the order of hundreds, but $E = E_M + E_L$ is on the order of thousands. An expected consequence is that E mirrors the relationship between behavior and expected dispersal time, $\mathbf{E}_D[T_*]$, even though E_L does not (compare with **Figure 3.5c**).

The most expensive behavior based on locomotion alone is diel vertical migration due to frequent costly trips between the surface and bottom layers (**Figure 3.6a**). Other than passive floating (for which $E_L = 0$ μJ by construction), the cheapest viable behaviors are either a single ontogenetic migration from the surface to the bottom layer ($A = 24$ h)—which only costs as much as that single migration, C_-—or residing in the bottom layer for the entirety of dispersal ($B = 0$).

The classes of advection-driven and diffusion-compensated behaviors contain both extremes of energy expenditure on locomotion. However, the number of vertical migrations performed by a larva generally increases with dispersal time, and dispersal times are typically longer for diffusion-compensated behaviors. Thus, diffusion-compensated behaviors tend to be slightly more expensive.

The most expensive behaviors based on total energy, E, are not pure diel vertical migrations ($A < 24$ h and $B = 1$), but instead feature an ontogenetic switch to the bottom layer after about $B \approx 0.7$ of the larval duration has elapsed (**Figure 3.6b**). This is due to the close relationship between E and dispersal time and the unexpected observation that these behaviors result in longer dispersal times than pure diel vertical migrations. Another consequence is that advection-driven behaviors tend to be cheaper than diffusion-compensated ones. Passive floating is among the cheapest behaviors due to both early delivery to the coastal habitat and no expenditure on locomotion. However, behaviors that deliberately remain in the lower layer for most of dispersal and undergo few vertical migrations are even cheaper.

Under the assumption that food is more abundant in the surface layer than the bottom layer, the food encountered prior to returning to shore, F, is greatest for behaviors that either spend a long time in the surface layer or have long dispersal times in general. Both of these trends favor diffusion-compensated behaviors. Passive floating and advection-driven behaviors that switch to the bottom layer early in dispersal (that is, with small B) or spend very little time at the surface (with small A) offer minimal feeding opportunities. Like alongshore dispersal potential, DP, and total energy expenditure, E, total food encountered closely reflects expected dispersal time, $\mathbf{E}_D[T_*]$.

3.4. Discussion

We used a mathematical model of larval dispersal in an upwelling regime to assess how a wide range of vertical swimming behaviors affect dispersal efficiency (a proxy for larval supply), potential for alongshore movement, predation risk, feeding opportunities, and energy expenditure. Among the behaviors considered were passive floating, diel vertical migrations (DVM), an ontogenetic vertical migration (OVM) from the offshore-moving layer to the onshore-moving bottom, and many behaviors combining diel vertical migrations with such an ontogenetic shift (Hybrid). Our results support previous modeling studies' conclusion that vertical swimming in a stratified current can

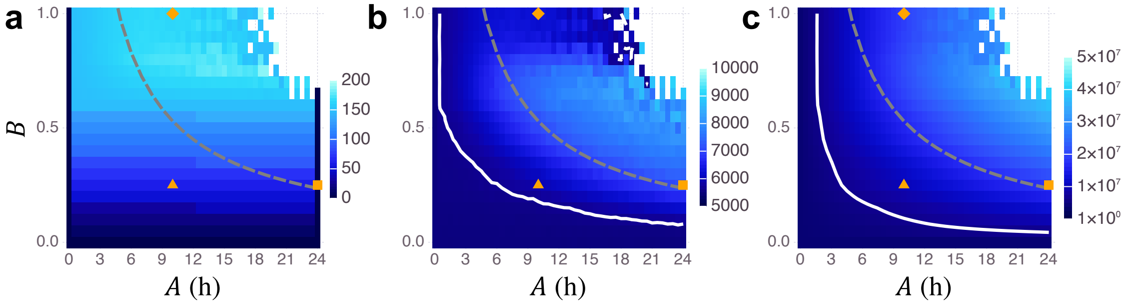

Figure 3.6. Mean energy used by successful larvae for **(a)** locomotion, E_L (μJ), and **(b)** for all processes, E (μJ), for each vertical swimming behavior in the (A, B) trait-space and passive floating. **(c)** Total food encountered by successful larvae, F (cells mL^{-1} h), during dispersal for each swimming behavior and passive floating. Meanings of the gray dashed curve, the white regions, and the orange plotted points are as in **Figure 3.3**, and the white contour lines shows values attained by passive floating. No contour appears in (a) because passive floating expends no energy on swimming, $E_L = 0$.

significantly alter larval supply and dispersal, and therefore that accurate predictions of coastal population dynamics require behavior to be included alongside oceanographic factors (Cowen et al, 2000, 2006, James et al, 2019, Marta-Almeida et al, 2006, Metaxas and Saunders, 2009, Owens and Rothlisberg, 1991, Rothlisberg et al, 1983, Sundelöf and Jonsson, 2012). The longer the larval duration or the greater the strength of cross-shore advection relative to cross-shore diffusion, the greater the effect of swimming upon dispersal. On the other hand, we observed that 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 rough categories of viable behaviors for larvae: advection-driven behaviors where larvae are delivered to the coastal habitat by net-onshore advection, and diffusion-compensated behaviors where advection is net-offshore and delivery occurs due to random movement toward shore. While our analysis focuses on dispersal in upwelling circulation, these behavioral classes should appear in any other current regime where larvae rely on directed and variable currents for delivery to coastal habitats. Different behaviors could be used to exploit tides, internal waves, wind-driven currents, and other phenomena known to affect the cross-shelf migration of

Table 3.4. A comparison of advection-driven (larvae delivered to nearshore habitats by net-onshore transport) and diffusion-compensated (larvae delivered to nearshore habitats by stochastic diffusion that opposes net-offshore advection) behaviors. We note the types of behaviors in each class, their performance based on the metrics considered above, and the biological and environmental attributes which favor each class. The right column of this table lists figures from this chapter to support each observation. DVM = diel vertical migration and OVM = ontogenetic vertical migration.

	Advection-driven	**Diffusion-compensated**	**Figure**
Example behaviors	Early OVM DVM, short surface period Hybrid, early OVM or short surface period Passive floating[a]	Medium/late OVM DVM, medium/long surface period Hybrid, moderate OVM and medium surface period	3.3,3.4
Dispersal efficiency	High	Low	3.5a,b
Trend with larval duration	Increasing	Decreasing	3.3a,d
Trend with surface velocity	Increasing	Decreasing	3.3b,e
Trend with eddy diffusivity	Decreasing	Increasing	3.3c,f
Dispersal time	Short	Long	3.5c
Dispersal potential	Low	High	3.5d
Probability of survival			
Due to diurnal predation	Low	High	3.5e
Due to nearshore predation	High	Varies	3.5f
Energetic cost			
Total	Low	High	3.6b
Due to locomotion	Varies	Varies	3.6a
Due to maintenance	Low	High	3.5c[b]
Feeding opportunities	Low	High	3.6e
Favorable species attributes	Non-feeding Fewer expensive larvae High maintenance cost Cheap metamorphosis Pop. dynamics limited by larval supply	Feeding Many cheap larvae Low maintenance cost Expensive metamorphosis Pop. dynamics limited by adult interactions	
Favorable environmental attributes	Advection stronger than diffusion High mortality rate Scarce food	Advection weaker than diffusion Low mortality rate Abundant food	

[a] As noted in Results, passive floating performs similarly to the advection-driven behaviors by most metrics even though it cannot be classified using our scheme. [b] Figure **3.5c** displays $\mathbf{E}_D[T_*]$, and $E_M \propto \mathbf{E}_D[T_*]$.

larvae (Shanks, 1995). More generally, the concept that organisms can successfully disperse by behaving in ways that alter their net transport or its variance can be applied to any system, including non-marine ones, where movement is well-approximated by an advection-diffusion process.

In upwelling, the key difference between advection-driven and diffusion-compensated behaviors is how much time they spend in the surface layer compared with the bottom layer. This determines how larvae are impacted by the vertical structure and cross-shore currents—and, consequently, cross-shore structure—of the upwelling environment. Cross-shore transport and mean current direction also affect total dispersal time, or the duration of exposure of the larvae to these offshore conditions. Together, time in the surface layer and total dispersal time explain most of the variation in food access, mortality risk, and energy expenditure we observed across swimming behaviors. The correlation between these two quantities made our classification system useful: all advection-driven or diffusion-compensated behaviors tend to result in similar outcomes, despite apparent differences in how they move larvae over time. Generally, advection-driven behaviors improve larval supply but provide limited opportunities for feeding and alongshore transport. By contrast, diffusion-compensated ones enhance feeding opportunities, promote alongshore movement, and allow larvae to escape nearshore hazards including benthic predators, but at the cost of greater offshore loss and a lower larval supply.

Advection-driven behaviors should be considered “low risk, low reward”: individuals exhibiting such behaviors have a high probability of returning to shore (neglecting premature death due to predation), but receive few potential benefits of planktonic development. Such behaviors may be advantageous for non-feeding larvae that are unaffected by limited food access. Non-feeding larvae are more expensive to produce and spawned in fewer numbers than feeding larvae (Christiansen and Fenchel, 1979, Levin and Bridges, 1995, Levitan, 2000, Perron and Carrier, 1981, Rumrill, 1990, Vance, 1973), so species with non-feeding larvae may also benefit more from the higher efficiency of advection-driven behaviors, assuming that reduced offshore loss is not outweighed by increased exposure to nearshore predators (Meyer et al, 2021). On the other hand, diffusion-compensated behaviors are “high risk, high reward,” resulting in a low dispersal efficiency but greater food access, alongshore movement, and offshore movement (which may offer safety from nearshore predators during development). The increased food access afforded by diffusion-compensated behaviors would benefit species with feeding larvae. Adults of these species may also spawn sufficiently many larvae to offset the greater offshore loss that diffusion-compensated behaviors produce (Christiansen and Fenchel, 1979, Levin and Bridges, 1995, Levitan, 2000, Perron and Carrier, 1981, Rumrill, 1990, Vance, 1973).

Given this hypothesized link between nutritional mode and behavioral type, we can further constrain the behaviors we expect to see in nature based on their energetic costs (**Figures 3.6a,b**). If advection-driven behaviors are favorable for non-feeding larvae with no means of replenishing their energy supply during dispersal, then we expect to see mainly cheap advection-driven behaviors that result in shorter dispersal times, fewer vertical migrations, and greater dispersal efficiency. This includes a single ontogenetic vertical migration from the surface to the bottom early in development. Although we could not find sufficiently many examples of vertical swimming behavior by non-feeding larvae in the literature to test this hypothesis, we note that Whalan et al (2008) did observe this behavior in the non-feeding larvae of the sponge *Rhopaloeides odorabile.* This may also include passive floating, although this strategy is less reliable than active behaviors at returning larvae to shore and escaping diurnal predation.

If diffusion-compensated behaviors are favorable for feeding larvae, then more costly behaviors involving long dispersal times and many trips between layers—including diel vertical migrations and, in tidally forced environments, tidal vertical migrations (see **Table 3.1**)—are permissible, provided they result in greater feeding opportunities without excessive exposure to predation. Diel vertical migration-like behaviors are particularly advantageous when the mortality rate in the surface varies on a day-night cycle, while undergoing a single ontogenetic vertical migrations from the surface to the bottom near the middle of the larval duration may be advantageous when the mortality rate is concentrated nearshore. While the relative importance of vertical and cross-shore heterogeneity in the larval mortality rate is not well resolved, we note that few behaviors considered here achieve a low mortality risk in both settings. Diel vertical migrations with a surface period of less than 12 hours followed by a permanent migration to the lower layer in the first half of the larval duration achieves moderate mortality in both settings, which may be more favorable in environments with variable mortality rate structure than optimizing for either high nearshore or high surface predation alone.

Another biotic factor that may affect the favorability of certain behaviors is the ecology of benthic post-larval stages. Roughgarden et al (1988) observed that some coastal populations have relatively constant size over time while others 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, which varies with offshore conditions. A population limited by larval supply could benefit more from advection-driven behaviors that boost larval supply (**Figure 3.5a,b**). On the other hand, a population close to its carrying capacity might benefit from diffusion-compensated behaviors for two reasons. First, the increased larval supply resulting from advection-driven behaviors would be unnecessary if larval supply already meets the needs of the adult population. Second, diffusion-compensated 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 (2006), Pechenik and Cerulli (1991), Videla et al (1998).

We observed that diffusion-compensated behaviors typically result in greater potential for alongshore dispersal, an important driver of coastal metapopulation connectivity. Connectivity can have both positive and negative effects in metapopulations subject to local extinction events, aiding both wastage of propagules when a habitat is disrupted and recolonization if the habitat recovers (Hanski, 1998). It is tempting to argue, as Strathmann (1974) did, that the connectivity resulting from diffusion-compensated provides an advantage in coastal environments subject to random local perturbations. However, Palmer and Strathmann (1981) later showed that random disturbances cannot select for dispersal because good colonizers inevitably disperse to worse habitats. Thus, while diffusion-compensated behaviors may offer a short-term advantage in volatile metapopulations, they do not necessarily emerge through natural selection.

We found that, theoretically, advection-driven behaviors result in greater dispersal efficiency than diffusion-compensated ones over long larval durations (**Figure 3.3f**). Although this suggests that advection-driven behaviors are advantageous for long-lived larvae, we are not aware of empirical evidence supporting this idea. Long-lived larvae generally acquire energy through feeding (Rumrill, 1990, Shanks et al, 2003), and the surface-avoiding advection-driven behaviors considered here offer few opportunities to do so. Additionally, if nearshore mortality is intense, then advection-driven behaviors that fail to deliver larvae into safer offshore waters would trade high offshore loss for high mortality nearshore (Meyer et al, 2021). Thus, advection-driven behaviors appear disadvantageous for long-lived larvae by most metrics besides the most obvious one: that is, the fraction of larvae that would arrive in nearshore habitats if mortality were a non-issue.

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 highlights 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. While larval mortality rates are notoriously difficult to measure in the field (Morgan, 1995a, Rumrill, 1990, White et al, 2014), even a uniform mortality rate interacts with vertical swimming due to the effect of behavior on dispersal time.

Although we described movement as deterministic and pre-programmed, real larvae do not move in lockstep. Variation in the timing of vertical migrations results in a spreading out of larvae which seem to exhibit the "same" behavior, some of which is captured in our model and others by eddy diffusivity (Largier, 2003). We further explored the effects of this variation by considering a continuum of behaviors alongside specific examples, since the behavior of by a given species is more likely to comprise a region, rather than a point, in the (A, B) trait-space. We described behaviors as being either advection-driven or diffusion-compensated, but it is possible for larvae to exhibit a set of behaviors that straddles the boundary between these classes. This creates an opportunity for bet-hedging: a single individual could produce some offspring that receive the risks and rewards of offshore travel associated with diffusion-compensated behaviors, and others that enjoy the nearshore retention resulting from advection-driven behaviors.

Unexpectedly, we observed that behaviors like diel vertical migrations with a late ontogenetic migration to the bottom layer result in longer dispersal times than pure diel vertical migrations, despite greater exposure to the shoreward moving current. We attribute this to the fact that larvae have a low probability of returning to the nearshore habitat using both behaviors and are essentially outliers within the overall population of spawned larvae. Because dispersal time can only be calculated for the few larvae that arrive in the habitat during competence (rather than all larvae), intuition based on the paths followed by typical larvae may fail when applied to these outliers. This is particularly important because in some cases, the post-larval population may be composed entirely of these outliers. This caveat should be noted by researchers studying how the the structure of the offshore environment could affect populations with dispersive larvae, and may apply to non-marine organisms with a dispersive stage as well.

While our results offer a cursory look at the relationship between vertical swimming and larval supply, dispersal, survival, and energetics, a systematic analysis of data presented in the literature is needed to establish definitive relationships connecting larval duration, nutritional mode, adult ecology, and environmental features to larval behaviors. Although researchers have examined the swimming speeds and metabolic rates of non-feeding larvae (Chia et al, 1984, Wendt, 2000, Young, 1986), few descriptions exist of swimming behavior by non-feeding larvae over the entirety of dispersal. A literature review or meta-analysis of biotic and abiotic features determining vertical swimming behavior will require descriptions of a greater diversity of organisms in a wider range of habitats than has previously been studied, as well as analytical methods for inferring behaviors from field-measured depth profiles.

3.5. Appendix

3.5.1. Residence times in each layer for passive floating. We assume that the water column has depth $L < 0$, and the layers are separated by some $z_* \in (L, 0)$. Suppose that the larva's depth evolves according to a reflected Brownian motion $\tilde{Z}_t$ in $[L, 0]$ with diffusivity $2D > 0$, e.g.,

$$d\tilde{Z}_t = \sqrt{2D}\, dW_t, \tag{3.12}$$

and that the larva's initial depth is uniformly distributed in $(0, L)$ (i.e., the process starts from its stationary distribution). The constant D is equivalent to the larva's vertical eddy diffusivity.

Based on results presented by Karlin and Taylor (1981), the expected time a Brownian motion with diffusivity $2D$ spends in the interval (a, b) when starting from $z \in (a, b)$ is

$$\phi(z, a, b) = \frac{(z-a)(b-z)}{2D}. \tag{3.13}$$

The expected time when starting from any point in (a, b) is then

$$\Phi(a, b) = \frac{1}{b-a}\int_a^b \phi(z, a, b)\ dz = \frac{(b-a)^2}{12D} \tag{3.14}$$

The value λ_0 is the expected time the process $\tilde{Z}_t$ spends in the lower layer, $[L, z_*]$, before crossing into the upper layer. This is equivalent to the expected time until a (non-reflected) Brownian motion with diffusivity $2D$ hits $\pm(z_* - L)$ starting from any point in $\big(-(z_* - L), z_* - L\big)$:

$$\lambda_0 = \frac{(z_* - L)^2}{3D}. \tag{3.15}$$

Similarly, λ_1 is the expected time the process $\tilde{Z}_t$ spends in the upper layer, $[z_*, 0]$, before crossing into the lower layer, which is equivalent to the expected time until a (non-reflected) Brownian motion with diffusivity $2D$ hits $\pm z_*$ when starting at any point in $(z_*, -z_*)$:

$$\lambda_1 = \frac{z_*^2}{3D}. \tag{3.16}$$

The default parameter values $\lambda_0 = 14$ h and $\lambda_1 = 1$ h from **Table 4.1** are obtained by assuming the water column has uniform depth $L = -50$ m, the upper layer extends to depth $z_* = -10$ m, and that vertical diffusivity is $D \approx 40\ \mathrm{m}^2\ \mathrm{h}^{-1}$.

3.5.2. Curve separating advection-driven and diffusion-compensated behaviors. By net advection, we mean the integral of the larva's advection over the entire larval duration (excluding, for simplicity, settling before $t = T$):

$$\text{Net Advection} = \int_0^T u(Z_t)\,dt. \tag{3.17}$$

Because $u(z)$ only takes two values—u_0 (u_1) when the larva is in the lower (upper) layer—this integral simplifies to

$$\text{Net Advection} = u_0[\text{total time in lower layer}] + u_1[\text{total time in upper layer}]. \tag{3.18}$$

The total times in each layer over the entire larval duration (again, ignoring early settling) are deterministic:

$$\text{total time in lower layer} = \left(1 - \frac{A}{24}\right) BT + (1 - B)T, \tag{3.19}$$

$$\text{total time in upper layer} = \frac{A}{24} BT. \tag{3.20}$$

A behavior is advection-driven if its net advection is negative (e.g., toward shore):

$$0 > u_0 \left(1 - \frac{A}{24}\right) BT + u_0(1 - B)T + u_1 \frac{A}{24} BT \tag{3.21}$$

$$= u_0 T + \frac{ABT(u_1 - u_0)}{24} \tag{3.22}$$

$$\implies \frac{ABT(u_1 - u_0)}{24} < -u_0 T \tag{3.23}$$

$$\implies B < \left(-\frac{24u_0}{u_1 - u_0}\right) A^{-1}. \tag{3.24}$$

diffusion-compensated behaviors satisfy the opposite inequality, with net advection positive, and the two categories are separated by the hyperbola obtained when equality holds

3.5.3. Alongshore dispersal potential. We define the dispersal potential of a behavior, DP, to be the standard deviation of how far alongshore larvae travel, under the assumptions that alongshore advection is negligible and alongshore eddy diffusivity $K_y(x, z)$ does not vary with alongshore position. In this case, the alongshore position, Y_t, of a larva changes according to the stochastic differential equation

$$dY_t = \sqrt{2K_y(X_t, Z_t)}\ dW_t', \quad Y_0 = 0 \tag{3.25}$$

where W_t' is a Brownian motion independent from the one used in equation (3.1) for X_t. We have assumed, without loss of generality, that the larva's initial alongshore position is 0. Integrating both sides (in the Itô sense, on the right) and using the initial condition produces

$$Y_t = \int_0^t \sqrt{2K_y(X_s, Z_s)}\ dW_s'. \tag{3.26}$$

The variance in the larva's alongshore position when it reaches the nearshore habitat during competence (conditioned on the event that this happens at all) is

$$\mathbf{E}_D[Y_{T_*}^2] = \mathbf{E}_D\left[\left(\int_0^{T_*} \sqrt{2K_y(X_t, Z_t)}\ dW_t'\right)^2\right] = \mathbf{E}_D\left[\int_0^{T_*} 2K_y(X_t, Z_t)\ dt\right], \tag{3.27}$$

where we have invoked the Itô isometry in the last step (Steele, 2001). Taking the square root of this expression gives us the standard deviation, DP, of Y_{T_*}.

3.5.4. Energetic costs of maintenance and vertical migrations. Our estimates of the energetic costs of maintenance and vertical migrations are based on Sprung (1984b). Sprung measured the swimming, sinking, and metabolic rates of larvae of the mussel *Mytilus edulis* throughout development and at several temperatures. On average, *M. edulis* larvae swim and sink at 2 mm s^{-1}. If we assume that larvae switch between depths of approximately -5 m (middle of the surface layer) and -30 m (middle of the bottom layer), then vertical trips are approximately 25 m and take approximately 3.5 h.

Sprung estimates the metabolic rate of *M. edulis* larvae as between 1 and 36 μJ h^{-1} and the energy required per unit time to move a larva's weight through seawater at 2 mm s^{-1} as 0.15 μJ h^{-1}. However, Sprung conjectures that the actual cost of locomotion is about 20 times greater than the cost of moving the larva's weight (3 μJ h^{-1}) and that the total metabolic rate is about 100 times greater (which agrees with the range 1-36 μJ h^{-1}). Given these measurements, we assume the metabolic rate of a larva is $c_0 = 15$ μJ h^{-1} and that the cost of swimming from the lower layer to the upper layer is

$$C_+ = 3.5\ \mathrm{h} \cdot 3\ \mu\mathrm{J}\ \mathrm{h}^{-1} \approx 10\ \mu\mathrm{J}. \tag{3.28}$$

We assume that larvae sink, rather than swim, downward, such that the cost of switching from the surface layer to the bottom layer is $C_- = 0\ \mu$J. While larvae of some species to expend energy to swim downward Chia et al (1984), this assumption has little qualitative impact on our results because (a) the cost of swimming downward should be less than or comparable to the cost of swimming upward, and (b) the number of trips upward and downward made by a larva differs by at most 1. Thus, the effect of including active downward swimming would be similar to increasing the value of C_+.

CHAPTER 4

Coastal marine larvae optimally or robustly balance habitat-finding, predator avoidance, and energy use through vertical swimming

Abstract

Dispersive early life stages are common in nature. Although many dispersing organisms (“propagules”) are passively moved by outside forces, some can improve their chances of successfully dispersing through weak movements that exploit the structure of the environment for large effects. The planktonic larvae of many coastal marine invertebrates, for instance, swim vertically through the water column to take advantage of depth-varying currents, food abundance, and predation risk. Past work has characterized several larval swimming behaviors and their potential effects on larval transport between coastal habitats. However, it is unclear why certain behaviors are advantageous compared with others and how they affect predation risk and energy use. We address this gap with a mathematical model of larval dispersal that assigns a score to behaviors based on how they balance the needs of habitat-finding, predator avoidance, and energy conservation. Using dynamic programming, we compute vertical swimming behaviors that optimize this score under several conditions. Concurrently, we use the same score to assess how non-optimal behaviors perform across multiple conditions. Our model predicts that some observed behaviors are optimal in certain scenarios. Furthermore, while optimal behaviors are sensitive to current velocity, energetic needs, and predation risk, some observed behaviors are robust against changes in these conditions. Our results highlight the importance of carefully examining the weak behaviors of otherwise passive propagules, especially when making population dynamical predictions.

4.1. Introduction

Many plants, animals, and fungi have dispersive early life stages where individuals are transported relatively long distances by outside forces (Cowen and Sponaugle, 2008, Levin et al, 2003, Okubo and Levin, 2001). Familiar examples include the wind-borne seeds of the common dandelion, *Taraxacum officinale* (Nathan et al, 2008); the the hatchlings of ballooning spiders that sail through the air on gossamer parachutes (Suter, 1999); and the planktonic spores or larvae of many marine kelps, fish, and invertebrates (Shanks et al, 2003). The distances traveled by these dispersive entities, or "propagules," range from a few meters up to several hundred kilometers (Aylor, 2003, Aylor et al, 1982, Nathan et al, 2008, Shanks, 2009, Shanks et al, 2003, Suter, 1999). Because adults of these species are usually sedentary or sessile (Levin et al, 2003), understanding how these propagules disperse is critical for predicting the spatial and temporal dynamics of their populations.

The propagules of many organisms are passive, at the mercy of the media in which they disperse (Okubo and Levin, 2001). However, the propagules of some animals exhibit surprising control over their fates through behavior. The larvae of several coastal marine invertebrates, for example, regulate their depths during dispersal to exploit vertical variations in currents, food abundance, and predation risk (Largier, 2003, Levin, 2006, Morgan, 1995a, Shanks, 1986, 1995). Larval swimming speeds are typically less than 2 cm s^{-1} (Chia et al, 1984), but conditions in the water column vary on length scales of 1 to 100 m (Cowen et al, 2000, Morgan, 1995a, Shanks, 1995, Sherr et al, 2005). Thus, swimming for just a few hours can move larvae from food-poor depths to food-rich ones, or from offshore currents to onshore ones. These cross-shore currents usually flow faster than larvae can swim (1 to 30 cm s^{-1}), so vertical swimming also provides an efficient mechanism by which larvae can regulate their cross-shore movement (Shanks, 1995). Therefore, despite their poor locomotive abilities, larvae dramatically alter their dispersal outcomes through interactions with the structure of their environment.

In principle, many of the pressures that shape the behaviors of coastal invertebrate larvae are easily understood, making them ideal subjects for exploring how propagule behavior influences dispersal. Larvae are spawned in vast quantities from nearshore habitats (Gerber et al, 2014, Rumrill, 1990), and develop in the water column for a species-specific period of time called the larval duration (Levin and Bridges, 1995). They are simultaneously transported off- and alongshore by ocean currents, enabling dispersal between coastal habitats (Shanks, 1995, 2009, Shanks et al, 2003) and an escape from nearshore predators (Morgan, 1995a, Pechenik, 1999). Some larvae feed during dispersal, while others, supplied with a maternal energy source, do not (Levin and Bridges, 1995). However, all larvae must settle into nearshore habitats at the end of the larval duration and perform a costly metamorphosis to their post-larval forms (Elkin and Marshall, 2007, Pechenik, 1999, Shanks, 1995). This is a perilous journey during which most larvae succumb to predation or are lost asea (Morgan, 1995a, Rumrill, 1990). Larval behaviors are, at least in the short term, driven by the requirements that individuals return to shore, escape predation, and reserve energy for metamorphosis (Morgan, 1995a, Shanks, 1995). It is less clear how behaviors might be shaped by the long-term benefits of dispersal between populations.

Behaviors observed in the field and laboratory seem to reflect predictable elements of the environment in which dispersal occurs, as well as features of larvae themselves. Diel vertical migrations (DVM), in which larvae visit the surface at night and descend to the bottom during the day, are frequently reported by laboratory and field studies of species with feeding larvae, such as the crabs *Atelecyclus rotundus* (dos Santos et al, 2008), *Carcinus maenas* (Queiroga et al, 2007), and *Cancer* spp. (Shanks, 1986). This behavior allows larvae to exploit abundant food near the surface while escaping visually guided predators during the photoperiod. Another common behavior is ontogenetic vertical migration (OVM), in which larvae vary their depths throughout development according to their changing needs over time. For example, larvae of the barnacle *Balanus nubilus* are only able to feed during the first part of dispersal, so they begin in the food-rich surface layer and then migrate to the food-poor bottom (Tapia et al, 2010). In upwelling circulation, which results in an offshore-moving surface layer atop an onshore-moving bottom layer (**Figure 4.1a**), this behavior also achieves transport away from nearshore hazards at the start of dispersal, then toward nearshore habitats at the end (Shanks, 1995).

While these behaviors seem likely to exert some effect on the fates of dispersing larvae, it is not obvious what this effect is. Swimming requires energy and the food-rich surface may also feature elevated predation and offshore currents, and it is unclear how larvae should prioritize feeding, predator avoidance, and onshore transport. Furthermore, changes in current regime, food abundance, predation, and other variables across both locations and time suggest that behaviors should be adapted to a range of conditions, and it is difficult to predict how the performance of these behaviors can be affected by these variables *per se* or in tandem. Consequently, mathematical models have been frequently used to explore how larval swimming might affect the dispersal of larvae between coastal habitats (Cowen et al, 2006, Marta-Almeida et al, 2006, Owens and Rothlisberg, 1991, Paris et al, 2007, Rothlisberg et al, 1983, Sundelöf and Jonsson, 2012). These studies support the hypothesis that observed vertical swimming patterns result in nearshore retention of larvae in realistic habitats, but consider only a few prescribed behaviors (e.g., diel vertical migrations) and are rarely validated by data. James et al (2019) instead attempted to construct behaviors that could recreate vertical distributions of larvae measured in the field, assuming only that larvae change their swimming velocity at key moments throughout the tidal cycle. The authors found that some, but not all, observed distributions could be reproduced by such behaviors, underscoring the importance of considering more than one type of swimming behavior and validating the results of dispersal models.

None of the studies listed above consider the effects of vertical swimming behaviors upon mortality risk and energy use. In Chapter 3 of this dissertation, we address this gap by modeling how larval delivery, predation risk, energy use, and food access are affected by a broad class of behaviors, including diel vertical migrations and ontogenetic depth changes. We showed that while some behaviors successfully retain larvae nearshore and others improve feeding opportunities, no behaviors we considered were able to do both simultaneously in the idealized environment of our model. In other words, remaining nearshore during development and acquiring energy for metamorphosis, escaping nearshore predators, and dispersing between habitats are conflicting needs.

These theoretical results raise simple but intriguing questions. How should larvae swim in order to balance dispersal success, energetics, and long-term resilience? And why do we see behaviors like diel vertical migrations so often and not some other archetypes? We address these questions using a simple mathematical model that describes the cross-shore movement, vertical swimming, and energy content of a single larva. We do not assume that larvae perform any specific type of vertical swimming behavior. Instead, we use dynamic programming, an optimization technique commonly applied in behavioral ecology (Mangel and Clark, 1988), to compute behaviors *de novo* that maximize a performance metric under several conditions. After this, we prescribe behaviors inspired by the optima, the results of Chapter 3 of this dissertation, and the literature to assess their robustness against large changes in current strength and food abundance.

4.2. Methods

4.2.1. Model Development. We model the dispersal and energetics of a coastal marine larva in an environment with upwelling circulation. The model is a discrete-time stochastic process with three state-variables: the larva's depth, $Z_t \in \{0, 1\}$, distance from shore, $X_t \geq 0$ (km), and energy content, $E_t \geq 0$ (mJ), after t days of dispersal. While continuous-time models are often preferable for describing movement, Mangel and Clark (1988) explain that discrete-time models are more amenable to optimization by dynamic programming and can usually approximate continuous-time processes sufficiently well if a small enough time-step, Δt, is used. The model we describe below is analogous to the continuous-time one we developed in Chapter 3, but augmented to include the energy content of the simulated larva over time.

The simulated larva spawns from a nearshore habitat extending from the coastline, $x = 0$, to an offshore location, $x = X_*$ (km). After spawning, the larva disperses for a fixed larval duration of T days. The environment in which the larva disperses consists of two layers: a surface layer, $z = 1$, featuring an offshore current with velocity $U_1 \geq 0$ (km d^{-1}) and a large eddy diffusivity $K_1 > 0$ (km^2 d^{-1}); and a bottom layer, $z = 0$, featuring a compensatory onshore current with velocity $U_0 \leq 0$ (km d^{-1}) and weaker eddy diffusivity $0 < K_0 < K_1$ (km^2 d^{-1}). This two-layer construction provides a tractable approximation to the stratified flow typical of upwelling circulation. Under these assumptions, the larva's offshore distance is governed by

$$X_0 \sim \text{uniform}([0, X_*]), \tag{4.1}$$

$$X_{t+\Delta t} = X_t + U_{Z_t}\Delta t + \xi_t\sqrt{2K_{Z_t}\Delta t}, \quad t = 0, \Delta t, \ldots, T - \Delta t, \tag{4.2}$$

where $\xi_0, \ldots, \xi_{T-\Delta t}$ are independent standard normal random variables.

The larva regulates its depth, Z_t, through a sequence of vertical migrations $\Delta Z = \{\Delta Z_0, \ldots, \Delta Z_{T-\Delta t}\}$. A larva in the bottom layer, $Z_t = 0$, can either maintain its depth, $\Delta Z_t = 0$, or migrate to the upper layer, $\Delta Z_t = +1$. Similarly, a larva in the surface, $Z_t = 1$, can maintain its depth or migrate to the lower layer, $\Delta Z_t = -1$. A larva with no energy, $E_t = 0$, has no choice but to maintain its depth. The larva's depth over time is simply

$$Z_0 = 0, \tag{4.3}$$

$$Z_{t+\Delta t} = Z_t + \Delta Z_t, \quad t = 0, \Delta t, \ldots, T - \Delta t. \tag{4.4}$$

The sequence of depth changes, ΔZ, is the control by which we will optimize our metric of the larva's dispersal success, formulated in **4.2.2**.

We aim to provide a simple treatment of energy that makes clear how constraints imposed by feeding, maintenance and growth, and locomotion coalesce to influence vertical swimming behaviors. We assume that the simulated larva uses energy for maintenance and growth at a constant rate, $G > 0$ (mJ d^{-1}). Additionally, each vertical migration $\delta z = -1, 0, +1$ incurs a fixed cost, $C_{\delta z} \geq 0$ (mJ).

We are interested in both feeding and non-feeding larvae. We assume that feeding larvae in layer z assimilate energy from their surroundings at rate F_z (mJ d^{-1}). While F_z captures the larva's feeding rate as well as its local food abundance, we almost exclusively interpret F_z in the latter sense; to make this clear, we refer to F_z as food abundance throughout this chapter. We simplify the problem by assuming that food is only present in the surface layer, $F_0 = 0$. For non-feeding larvae, we set $F_1 = 0$ as well. Finally, we assume that larvae cannot store more than $E_{\max}$ mJ at any instant, and assert that the larva's energy content must always be non-negative. The energy content of the modeled larva changes according to

$$E_{t+\Delta t} = \max\left\{0, \min\left\{E_{\max}, E_t + (F_{Z_t} - G)\Delta t - C_{\Delta Z_t}\right\}\right\}. \tag{4.5}$$

Suppose that a larva initiating metamorphosis with at least $E_* > 0$ mJ of energy is usually able to complete metamorphosis. We assume that feeding larvae spawn with only enough energy for maintenance and must gather additional energy for movement and metamorphosis,

$$E_0 = GT. \tag{4.6}$$

Non-feeding larvae spawn with enough energy for growth and metamorphosis, plus a maternally supplied surplus for movement, $S \geq 0$ (mJ):

$$E_0 = GT + E_* + S. \tag{4.7}$$

These assumptions and the values of G, $C_{\delta z}$, and E_* are based on the energy budget for *Balanus balanoides* presented by Lucas et al (1979) and the respiration rates for *Mytilus edulis* reported by Sprung (1984b).

4.2.2. Optimization.

4.2.2. Optimization. Our goal is to compute vertical swimming "policies" that maximize a performance score, J, combining the larva's exposure to predators during dispersal, the suitability of its final offshore position, and its ability to complete metamorphosis. By policies, we mean a sequence of functions $\Delta Z_t = f(t, X_t, Z_t, E_t)$ for choosing the depth change ΔZ_t based on a larva's state in time t, rather than a prescribed sequence of depth changes. These policies are the standard output of dynamic programming and highlight a range of possible behaviors individuals could perform under various circumstances (Clark, 1990, Mangel and Clark, 1988).

Let $(X, Z, E) = \{(X_t, Z_t, E_t) : 0 \leq t \leq T\}$ denote the movement trajectory and energy content of a simulated larva. The performance score $J[X, Z, E]$ is the sum of three terms,

$$J[X, Z, E] = J_m[X, Z] + J_s(X_T) + J_e(E_T). \tag{4.8}$$

The first term, $J_m[X, Z]$, expresses the total mortality risk encountered by a larva during dispersal. If the mortality rate at time t and location (x, z) is $\mu(t, x, z)$ (d^{-1}), then the total mortality risk is

$$J_m[X, Z] = -\sum_t \mu(t, X_t, Z_t)\Delta t. \tag{4.9}$$

We consider two different scenarios for the mortality rate (see **Figure 4.1a**):

(i) *Nearshore mortality (NS).* Larvae experience elevated mortality over a region adjacent to shore. That is, $\mu(t, x, z) = \mu_1$ if $x \leq X_m$ and $\mu(t, x, z) = \mu_0$ if $x > X_m$, where $\mu_1 > \mu_0$.

(ii) *Surface/diurnal mortality (SD).* Larvae experience elevated mortality in the surface during periods of light. That is, $\mu(t, x, z) = \mu_1$ if $z = 1$ and t is a time between 6:00 and 18:00, and $\mu(t, x, z) = \mu_0$ otherwise, where $\mu_1 > \mu_0$.

Without empirical data regarding how survival through metamorphosis is affected by the larva's settling site or final energy content, we cannot rigorously formulate $J_s(X_T)$ or $J_e(E_T)$. We opt for simplicity instead. We assume that larvae finishing dispersal in the habitat $[0, X_*]$ are not penalized; however, the penalty for finishing at $X_T > X_*$ grows as a power law with distance from X_*:

$$J_s(X_T) = \begin{cases} 0 & \text{if } X_T \leq X_*, \\ -\sigma(X - X_*)^\alpha & \text{if } X_T > X_* \end{cases} \tag{4.10}$$

where $\sigma > 0$ and $\alpha \geq 1$ are constants determining the severity of the penalty. Similarly, we assume that larvae finishing dispersal with at least E_* mJ of energy are not penalized, but the penalty for finishing with $E_T < E_*$ grows as a power law with the size of this deficit:

$$J_e(E_T) = \begin{cases} 0 & \text{if } E_T \geq E_*, \\ -\lambda(E_* - E_T)^\beta & \text{if } E_T < E_* \end{cases} \tag{4.11}$$

where $\lambda > 0$ and $\beta \geq 1$. Numerical experiments suggest that the optimization is qualitatively unaffected by the choice of α and β, so we use $\alpha = \beta = 1$.

The resulting optimization problem is to

$$\underset{\Delta Z}{\text{maximize}}\, \mathbf{E}\left(J[X, Z, E] \;\middle|\; \Delta Z\right) \tag{4.12}$$

subject to the dynamics described in **4.2.1**. This type of problem is solved by working backwards through a recursion relation known as the Bellman equations (Mangel and Clark, 1988):

$$V_T(x, z, e) = -\mu(T, x, z)\Delta t - \sigma R(x - X_*) - \lambda R(E_* - e), \tag{4.13}$$

$$V_{t-\Delta t}(x, z, e) =$$

$$\max_{\delta z} \left\{-\mu(t, x, z)\Delta t + \mathbf{E}\left[V_t(X_t, z + \delta z, E_t) \;\middle|\; (X_{t-\Delta t}, Z_{t-\Delta t}, E_{t-\Delta t}) = (x, z, e)\right]\right\}. \tag{4.14}$$

The "value-to-go" functions $V_0, \ldots, V_T$ are defined so that $V_t(x, z, e)$ is the greatest expected increase in J possible between times t and T when $(X_t, Z_t, E_t) = (x, z, e)$. The maximizing values of

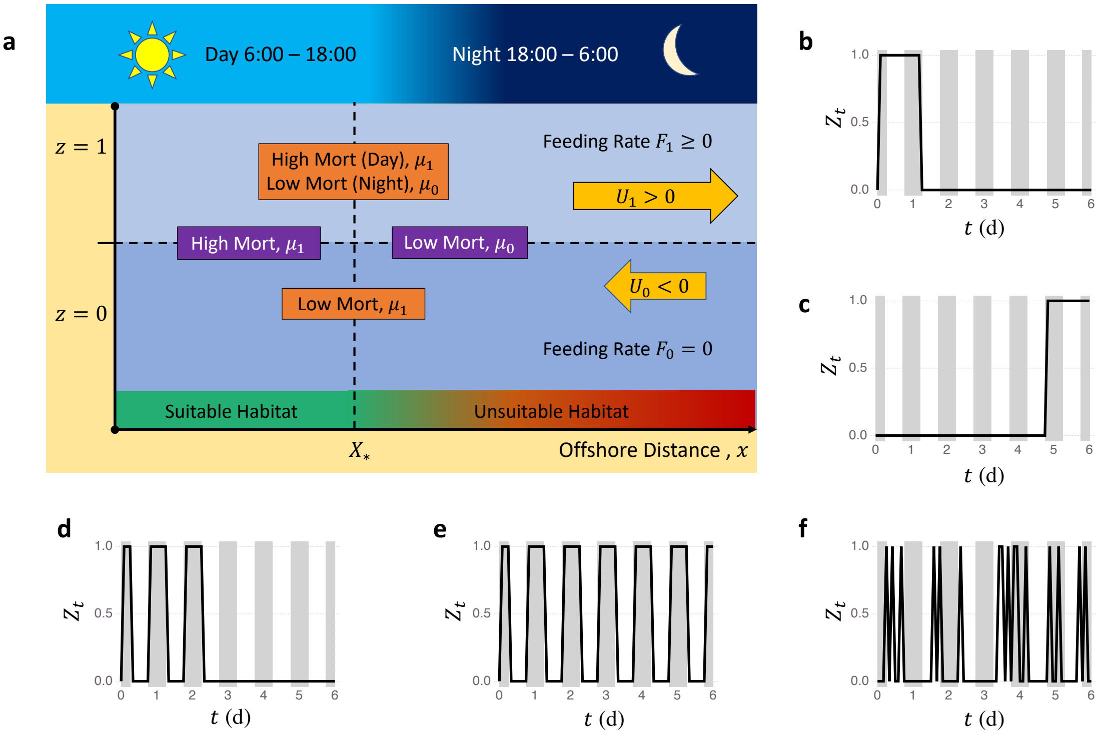

Figure 4.1. Schematic diagrams of **(a)** the modeled environment and the five prescribed vertical swimming behaviors we shall study: **(b)** classical ontogenetic vertical migration (OVM), **(c)** reverse ontogenetic vertical migration (ROVM), **(d)** diel vertical migrations (DVM) for the first half of the larval duration, **(e)** DVM for the entire larval duration, and **(f)** passive floating, as approximated for the two-layer scheme in Chapter 3. Gray bars in panels (b-f) indicate periods of darkness.

δz chosen in the recursive step (4.14) depend on (t, x, z, e), and form the optimal swimming policy we seek, $\Delta Z_t(x, z, e) = \delta z$.

4.2.3. Simulations, Scenarios, and Non-Optimal Behaviors. We computed the optimal behaviors of feeding and non-feeding larvae in two current schemes, strong upwelling, $U_1 = 10$ km d^{-1} and $U_0 = -2.5$ km d^{-1}, and still water, $U_1 = U_0 = 0$ km d^{-1}; two mortality schemes, nearshore and diurnal (see previous section and **Figure 4.1a**); and two energy levels, low and high (i.e., food abundance F and surplus size S small or large for feeding and non-feeding larvae, respectively). See **Table 4.1** for parameter values used in each scenario. After computing the optimal swimming policy in each case, we simulated the resulting dispersal trajectories 1000 times each. We repeated this process while sweeping over current speeds $0 \leq U_1 \leq 12$ km d^{-1} and, for feeding larvae only, food abundances $1.5G \leq F_1 \leq 12G$ mJ d^{-1}, where G is the rate of energy use for maintenance. We fixed $U_0 = -0.25U_1$ while varying U_1 to preserve the ratio from the default parameter set, which represents a scenario where the surface layer is 25% as thick as the bottom layer.

Finally, we simulated larval dispersal and computed scores J for 1000 larvae using each of five archetypal behaviors, shown in **Figures 4.1b-f**, for both nutritional modes, both energy levels, both mortality schemes, and both current strengths. These five behaviors are:

(b) Classical ontogenetic vertical migration (OVM), wherein a larva spends the first part of the larval duration in the surface layer and the second part in the bottom, as observed in *B. nubilus* (Tapia et al, 2010).

(c) Reverse OVM (ROVM), wherein a larva spends the first part of the larval duration in the bottom layer and the second part in the surface, as observed in *Balanus glandula* (Morgan and Fisher, 2010).

(d) Half diel vertical migrations (DVM), wherein a larva visits the surface nightly during the first half of the larval duration and remains in the bottom for the second half, as observed in *Ophiocomina nigra* (Guillam et al, 2020).

(e) Full DVM, wherein a larva visits the surface every night throughout the larval duration. This strict behavior has not been reported in the literature, but is often implemented in modeling studies, such as (Sundelöf and Jonsson, 2012).

(f) Passive floating, wherein a larva randomly switches between layers according to a Markov process where the mean length of each visit to the surface (bottom) layer is $\tau_1 = 1/24$ d ($\tau_0 = 14/24$ d), as estimated in **Appendix 3.5.1** of Chapter 3.

4.3. Results

4.3.1. Nutritional Mode. In the modeled environment, visiting the surface is a risk. Even with nearshore mortality only and no upwelling current ($U_1 = 0$), the elevated diffusivity of the surface, $K_1 > K_0$, reduces the probability of individuals visiting the surface being close to shore at the end of the larval duration. Non-feeding larvae have no cause to visit the surface besides achieving transport away from nearshore hazards. Thus, our model predicts no movement from the bottom for non-feeding larvae subject to diurnal predation only (**Table 4.2**). When mortality is instead

Table 4.1. Summary of state variables, parameters, and their default values. Abbreviations for different scenarios: feeding (F), non-feeding (NF), upwelling (UW), still water (SW). Values without footnotes for references are assumed values chosen through numerical experiments.

State Var.	**Unit**	**Meaning**	**Range**
t	d	Time from spawning	0 to T
X_t	km	Larva's distance from shore at time t	non-negative
Z_t	none	Larva's layer at time t	0 or 1
E_t	mJ	Larva's energy content at time t	0 to $E_{\max}$

Parameter	**Unit**	**Meaning**	**Default**
Δt	d	Time-step in discrete-time model	1/24
T	d	Larval duration	20[a]
U_0	km d^{-1}	Advective velocity of bottom layer	
		Upwelling	-2.5[b]
		Still water	0
U_1	km d^{-1}	Advective velocity of surface layer	
		Upwelling	10[b]
		Still water	0
K_0	km^2 d^{-1}	Eddy diffusivity in bottom layer	4[c]
K_1	km^2 d^{-1}	Eddy diffusivity in surface layer	16[c]
X_*	km	Offshore edge of ideal nearshore habitat	10[d]
G	mJ d^{-1}	Rate of energy use for maintenance and growth	15[e]
F_0	mJ d^{-1}	Rate of energy intake in bottom layer	0
F_1	mJ d^{-1}	Rate of energy intake in surface layer	
		Feeding, food-poor	22.5
		Feeding, food-rich	112.5
		Non-feeding	0
S	mJ	Size of maternally supplied energy surplus	
		Non-feeding, low energy	0
		Non-feeding, high energy	420
C_{-1}	mJ	Cost of migrating from surface to bottom layer	10[f]
C_{+1}	mJ	Cost of migrating from bottom to surface layer	10[f]
C_0	mJ	Cost of maintaining position within a layer	0
E_*	mJ	Minimum energy needed to ensure successful metamorphosis	120[e]
$E_{\max}$	mJ	Maximum possible energy content of larva	
		Feeding	330[e]
		Non-feeding, low energy	420
		Non-feeding, high energy	840
σ	km^{-1}	Decrease of log-probability of survival per km settled beyond X_*	0.069
λ	mJ^{-1}	Decrease of log-probability of survival per mJ below E_* at settling	0.038
μ_0	d^{-1}	Mortality rate in low-mortality regions and times	0.05[g]
μ_0	d^{-1}	Mortality rate in high-mortality regions and times	0.1[g]
X_m	km	Offshore edge of nearshore high-mortality region	10[d]
τ_0	d	Mean stay in bottom layer while passively floating	0.583[h]
τ_1	d	Mean stay in surface layer while passively floating	0.042[h]

[a] Shanks (2009), Shanks et al (2003). [b] Shanks (1995). [c] Largier (2003). [d] Nickols et al (2013), Rasmuson (2013).
[e] Lucas et al (1979). [f] See **Appendix 3.5.4** of Chapter 3. [g] Rumrill (1990), White et al (2014).
[h] See **Appendix 3.5.1** of Chapter 3.

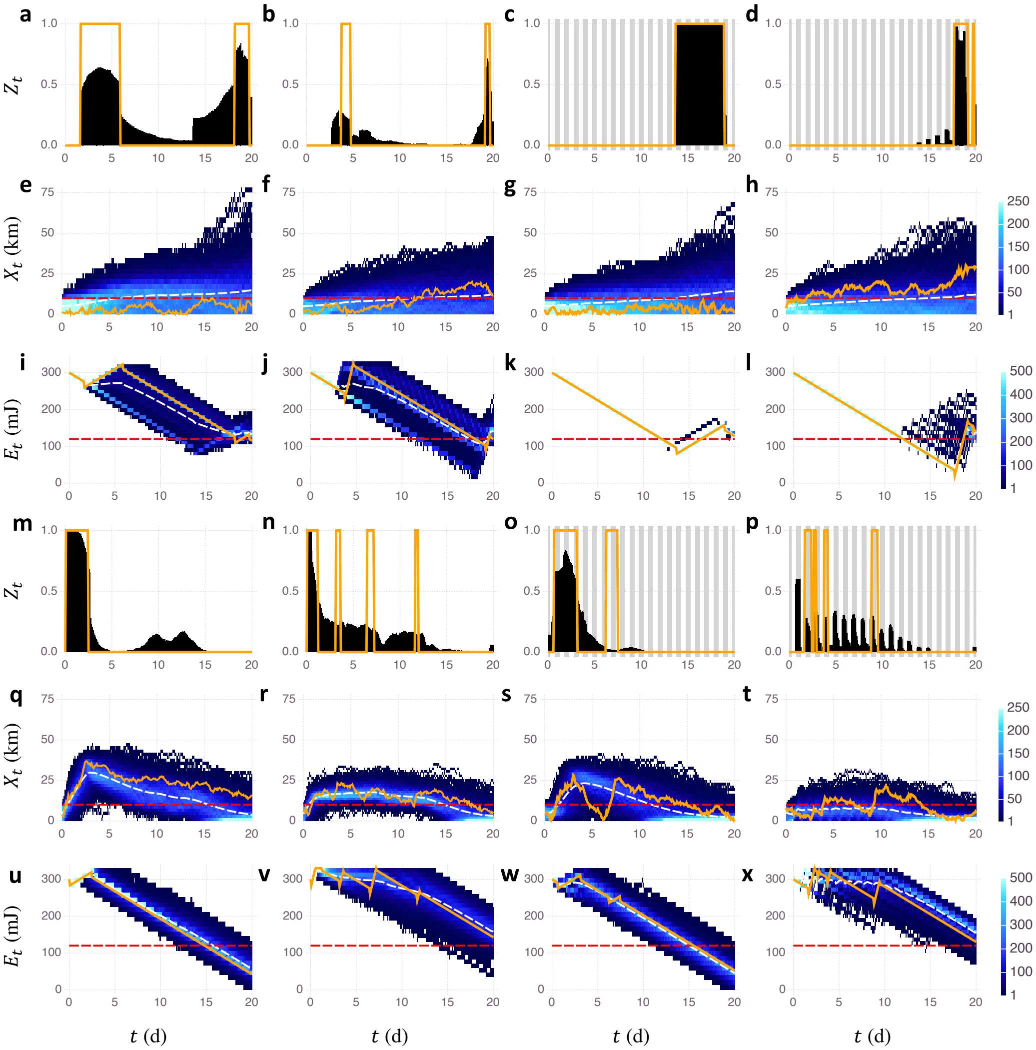

Figure 4.2. Optimal larval behaviors and trajectories simulated 1000 times in each of the following conditions: still water, nearshore mortality, low food **(a,e,i)** and high food **(b,f,j)**; still water, diurnal mortality, low food **(c,g,k)** and high food **(d,h,l)**; strong upwelling, nearshore mortality, low food **(m,q,u)** and high food **(n,r,v)**; strong upwelling, diurnal mortality, low food **(o,s,w)** and high food **(p,t,x)**. Rows (a-d) and (m-p) show optimal simulations of depth, Z_t (orange), and the fraction of larvae across all trials in the surface, $\mathbf{E}[Z_t]$ (black), over time. In the diurnal mortality cases (c,d,o,p), gray bars indicate periods of darkness. Rows (e-h) and (q-t) show optimal simulations of cross-shore position, X_t (orange), a 2d histogram of the position of all larvae over time (blue), the mean position over all trials, $\mathbf{E}[X_t]$ (white), and the edge of the nearshore habitat region, X_* (red). Similarly, rows (i-l) and (u-x) show a single simulation of energy content, E_t (orange), a 2d histogram of the energy contents of all larvae (blue), the mean energy content over all trials, $\mathbf{E}[E_t]$ (white), and the energy required to ensure successful metamorphosis, E_* (red).

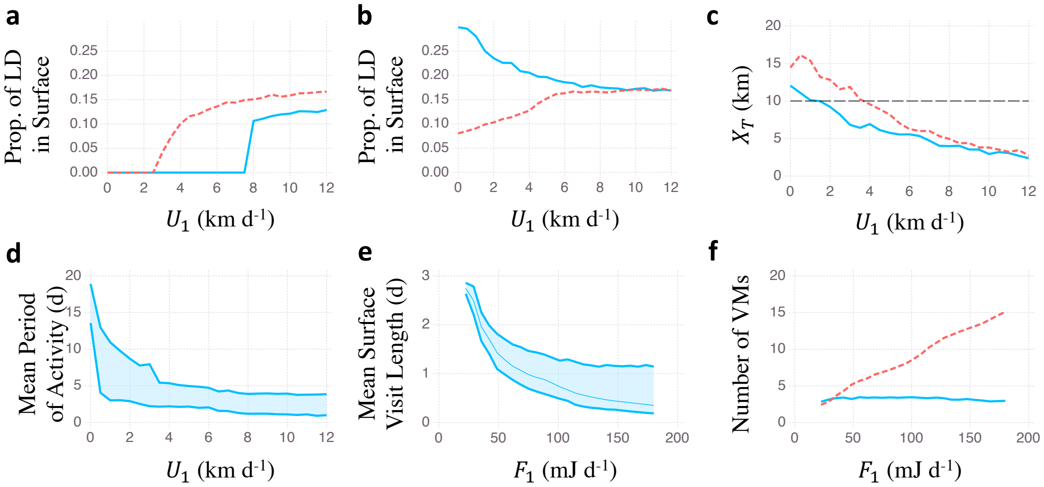

Figure 4.3. Effects of current strength and food abundance upon various aspects of the optimal vertical swimming behaviors. Mean fraction of time spent in the surface as a function of surface current velocity, U_1, for **(a)** non-feeding and **(b)** feeding larvae. The blue and red curves show low and high energy scenarios, respectively. **(c)** Mean final offshore distance, $\mathbf{E}[X_T]$, of feeding (blue) and non-feeding (red) larvae with excess energy as functions of U_1. The black dashed line represents the edge of the nearshore habitat, X_*. **(d)** Mean period of vertical swimming activity during dispersal as a function of U_1 for feeding larva with low food. **(e)** Mean maximum, minimum, and median duration of visits to the surface as a function of food abundance in the surface, F_1. **(f)** Mean number of vertical migrations performed in still water (blue) and upwelling (red) as functions of F_1. All examples presented here except for (d) feature nearshore, rather than diurnal, mortality; however, results are qualitatively similar across mortality schemes.

concentrated nearshore, our model predicts that non-feeding larvae should not visit the surface unless they have a surplus of energy, the nearshore mortality rate is sufficiently high, or upwelling is sufficiently strong (i.e., U_1 sufficiently large) to ensure offshore transport (**Figure 4.3a**). This movement mainly occurs at the beginning of the larval duration (Supplemental **Figure 4.5a**), such that individuals have sufficient time to be transported toward shore by the current in the bottom layer (see **4.3.2**).

Feeding larvae must visit the surface to gather energy for metamorphosis and swimming, since they spawn with only enough for maintenance. This encourages swimming regardless of mortality rate structure or current conditions (**Figures 4.2a-d** and **m-p**), even though it may result in incidental offshore transport (as in **Figure 4.2s**, for example). Our model predicts that in upwelling, feeding larvae with limited food are more likely to visit the surface late in the larval duration than non-feeding larvae with little or no energy surplus. This is because feeding larvae may need to procure more energy ahead of metamorphosis and can offset the costs of these late vertical migrations through the resulting feeding opportunities (compare **Figure 4.2m** with Supplemental **Figure 4.5a**). Despite the differences listed above, however, our model predicts very similar behaviors for feeding and non-feeding larvae in strong upwelling with nearshore mortality.

4.3.2. Upwelling Strength. The directed currents of the upwelling regime allow larvae to efficiently regulate their cross-shore positions through depth control (**Figures 4.2q-t**). By contrast, larvae in still water have little agency over their cross-shore movement (**Figures 4.2e-h** and **4.3c**). Feeding larvae in upwelling may visit the surface to feed, escape nearshore predation, or both; consequently, larvae subject to nearshore predation visit the surface immediately after spawning in upwelling (**Figures 4.2m,n**), but not in still water (**Figures 4.2a,b**). Our model also predicts that larvae with sufficient energy (i.e., feeding larvae in food-rich conditions or non-feeding larvae with large energy surpluses) can achieve nearshore retention in upwelling by migrating frequently between layers (compare vertical behaviors in **Figures 4.2n,p** to resulting cross-shore trajectories in **r,t**). This is not possible in still water. However, note that in both still water and strong upwelling, many larvae fail to reach the nearshore habitat by the end of the larval duration (**Figures 4.2e-h** and **q-t**).

In still water, feeding larvae tend to be active either throughout the larval duration or exclusively near its end (**Figures 4.2a-d**). Feeding and non-feeding larvae in upwelling circulation, however, either maintain a position close to shore if they have sufficient energy, or else concentrate their movements at the start of the larval duration (**Figures 4.2m-p**). In doing so, energy-constrained larvae move far offshore soon after spawning but allocate time for the onshore current of the bottom layer return them to coastal habitats. The need (and ability) to return to shore in upwelling explains the transition from the reverse ontogenetic vertical migration (ROVM)-like optimum in still water (compare **Figures 4.1c** and **4.2c**) to the standard ontogenetic vertical migration (OVM)-like one in upwelling (**Figures 4.1b** and **4.2o**). This transition occurs abruptly as current strength increases from 0, but the timing of movement is insensitive to changes in the strength of sufficiently strong upwelling (**Figure 4.3d**).

Feeding larvae in still water visit the surface to gather energy, but otherwise avoid it for the reasons stated in **4.3.1**. For example, the optimal behavior for food-limited larvae subject to nearshore mortality is to spend as little time as possible in the surface: individuals migrate to the surface, feed until they have $E_t = E_{\max}$, and then return to the bottom (**Figures 4.2a,i**). This visit is usually timed so that larvae returning to the bottom have at least $E_T = E_*$ at the end of dispersal; otherwise, larvae visit the surface again at the end of dispersal to achieve $E_T = E_*$. In diurnal mortality, larvae also minimize their time in the surface; however, they visit the surface exclusively at the end of dispersal (**Figures 4.2c,k**).

4.3.3. Energy Availability. Our model predicts that larvae with limited energy should spend more time in the surface per visit than larvae with excess energy (see **Figure 4.3e**, and compare **Figures 4.2a** to **b**, **c** to **d**, **m** to **n**, and **o** to **p**). These multi-day visits allow more time for feeding and require fewer costly vertical migrations. Interestingly, the model predicts that these long surface stays are optimal even for larvae subject to diurnal predation in the surface (**Figure 4.2o**). Also, observe that despite the influence of energetics upon these optimal behaviors, many larvae in food-poor upwelling conditions still fail to complete dispersal with E_* mJ of energy reserved for metamorphosis (**Figures 4.2u,w**).

Larvae with more energy perform shorter visits to the surface, but the number and timing of those visits depends on the mortality scheme and current (**Figure 4.3f**). In still water, feeding larvae in food-rich conditions and nearshore predation usually perform only one or two surface visits that last no more than two days each and are timed to ensure that $E_T \geq E_*$ at the end of dispersal (**Figures 4.2b,j**). Subject to diurnal predation instead, larvae perform one or a couple of surface visits near the end of dispersal (**Figures 4.2d,l**). Although these visits typically begin and end at sunset and sunrise, respectively, they may last 1.5 days (as in the example in **Figure 4.2d**) and do not occur throughout dispersal. In other words, this optimal behavior is quite far from the archetypal DVM behavior illustrated in **Figure 4.1e**.

In upwelling, our model predicts that the surface visits of larvae in high-energy conditions are more frequent, in addition to being shorter, than in low-energy conditions (**Figures 4.2m-p** and **4.3f**). Feeding and non-feeding larvae with excess energy in upwelling with nearshore mortality perform an initial surface visit of up to about five days and subsequently visit the surface

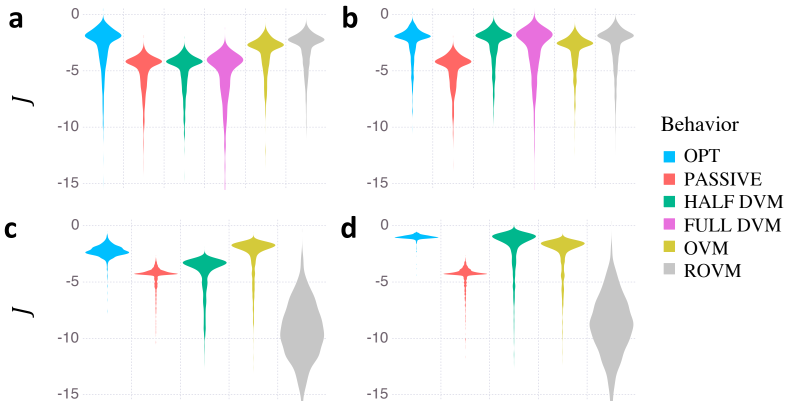

Figure 4.4. Performance scores, J, of feeding larvae subject to nearshore predation exhibiting the archetypal behaviors from **Figure 4.1** in **(a)** still water with low food, **(b)** still water with high food, **(c)** upwelling with low food, and **(d)** upwelling with high food, all with nearshore mortality. The behavior "Full DVM" is omitted from the upwelling cases because it achieves far lower performance scores ($-10 > J > -30$) than the other three archetypes. This figure is recreated for non-feeding larvae and feeding larvae with diurnal mortality in Supplemental **Figure 4.8**.

several times (**Figure 4.2n**). These visits appear intended to keep larvae away from the dangerous nearshore region and, for feeding larvae, to gather additional energy for metamorphosis (**Figures 4.2r,v**, respectively). In diurnal predation, the optimal behavior also switches from a single or a few long surface visits to several short ones throughout dispersal (**Figures 4.2o,p**). These visits almost exclusively occur at night, suggesting a behavior like diel vertical migrations. However, adherence to DVM is not perfect: only some larvae visit the surface each night, and fewer do so as time elapses (**Figure 4.2p**).

4.3.4. Performance of Prescribed Behaviors. The relative performance of the five behavioral archetypes from **Figures 4.1b-f** is insensitive to mortality scheme. Additionally, the only notable effect of nutritional mode is that for non-feeding larvae, full diel vertical migrations (DVM) performs substantially worse than all other behaviors (including passive floating) in all cases considered, rather than just in upwelling (as in the feeding case in **Figure 4.4**). See Supplemental **Figure 4.8** for these results.

The ontogenetic vertical migration (OVM) archetype is the only one that performs better than passive floating regardless of current strength and food availability (as well as nutritional mode and mortality scheme; see **Figure 4.4** and Supplemental **Figure 4.8**). In still water, OVM and the reverse ontogenetic vertical migration (ROVM) archetype perform similarly, and both outperform half and full DVM (**Figure 4.4a**). That ROVM performs well in this scenario somewhat agrees with the optimal behaviors in low food conditions and still water shown in **Figures 4.2a,c**, both of which feature a long, late visit to the surface. The poor performance of half and full DVM (even when subject to diurnal predation; see Supplemental **Figures 4.8a-d**) reflects the large energetic costs of these behaviors. However, these costs are offset by increased feeding opportunities when food is abundant, as shown by the success of these behaviors in **Figure 4.4b**.

In strong upwelling with limited food, OVM performs nearly optimally, and better than all other archetypes (**Figure 4.4c**). This agrees with the optimal behaviors shown in **Figures 4.2m,o**. Full DVM and ROVM, on the other hand, perform worse than even passive floating. This is due to excessive exposure to the offshore current of the surface layer, especially at the end of the larval duration, which prevents larvae remaining close to the habitat, $X_T < X_*$. By contrast, when food is abundant, half DVM performs nearly optimally and outperforms OVM, which still beats passive floating (**Figure 4.4d**). This result makes sense given the optimal behaviors of high energy larvae in upwelling shown in **Figures 4.2r,t**, which feature frequent surface visits of about 1 d in length throughout dispersal (although these visits need not occur at night in nearshore mortality).

4.4. Discussion

We used a simple model of larval dispersal, vertical swimming, and energy use in an idealized coastal environment to determine vertical swimming behaviors that maximize a performance score balancing predation risk, habitat choice, and energy reserved for metamorphosis. Under many of the scenarios we considered, the model predicted behaviors that share important features with some behaviors characterized in the literature (see **Table 4.2** and **Figures 4.1b-f**). These promising results suggest that some of the pressures shaping larval swimming behavior in nature are captured by our model. Additionally, while these optimal behaviors are sensitive to environmental conditions and larval biology, we showed that idealized behaviors resembling these optima are successful in a multitude of settings.

Table 4.2. Summary of vertical migration behaviors computed in different settings by maximizing $\mathbf{E}[J|\Delta Z]$. We consider two current schemes (upwelling or no current), two nutritional modes (feeding, F, or non-feeding, NF), two mortality schemes (nearshore, NS, and surface/diurnal, SD), and two scenarios for energy availability (low: food-poor for feeding, no surplus for non-feeding; high: food-rich for feeding, large surplus for non-feeding). Parameter values for each case are presented in **Table 4.1**. Where possible, we list the archetypes from **Figure 4.1** that these optima most resemble.

Current	**Mode**	**Mort.**	**Energy**	**Description of Behavior**	**Archetype**	**Fig.**
Upwelling	F	NS	Low	Long surface visit at start, possible short visits later	OVM	4.2m
			High	Medium surface visit at start of dispersal, sporadic short visits throughout	Half DVM[a]	4.2n
		SD	Low	Long surface visit at start of dispersal	OVM	4.2o
			High	Nocturnal visits to surface	Half DVM	4.2p
	NF	NS	Low	Long surface visit at start of dispersal	OVM	4.5a[b]
			High	Medium surface visit at start of dispersal; sporadic short visits throughout	—	4.5d
		SD	Low	Bottom only: no incentive to visit surface	—	—
			High	Bottom only: no incentive to visit surface	—	—
No current	F	NS	Low	Long surface visit near start of dispersal, possible medium/long visits near end of dispersal	—	4.2a
			High	Short surface visits only near the beginning and end of dispersal	—	4.2b
		SD	Low	Long surface visit at end of dispersal	ROVM	4.2c
			High	One or a few nocturnal surface visits at the end of dispersal	—	4.2d
	NF	NS	Low	Bottom only: offshore transport not reliable enough to justify cost and risk	—	—
			High	Bottom only: offshore transport not reliable enough to justify cost and risk	—	—
		SD	Low	Bottom only: no incentive to visit surface	—	—
			High	Bottom only: no incentive to visit surface	—	—

[a] Resembles half DVM in frequency of surface visits, even though visits do not occur on a day-night cycle. [b] **Figure 4.5** is in **Appendix 4.5.2**.

Our analysis indicates that the most important factor shaping the optimal swimming behavior of larvae in strong upwelling is access to energy, which determines the extent to which individuals can regulate their offshore distance. Our model predicts that non-feeding larvae with no surplus in nearshore mortality and feeding larvae in food-poor conditions with any mortality structure should make just one prolonged visit to the surface at the start of dispersal, similar to the classical ontogenetic vertical migration (OVM) shown in **Figure 4.1b**. By contrast, non-feeding larvae with large surpluses and feeding larvae in food-rich conditions may visit the surface frequently throughout dispersal, using the difference in current direction across layers to remain close to shore. That this result depends only on energy availability suggests that efforts to explain differences in larval behavior using nutritional mode or mortality scheme may be misdirected. Furthermore, while we agree with previous modeling studies that nearshore retention is an important objective of vertical swimming (Cowen et al, 2000, 2006, Marta-Almeida et al, 2006, Sundelöf and Jonsson, 2012), our results suggest that larvae may also exhibit behaviors that sacrifice nearshore retention for feeding opportunities and predator avoidance.

Directed currents are a double-edged sword. In strong upwelling, depth-varying directed currents allow larvae to regulate their cross-shore positions through vertical migrations, but the co-occurrence of food and an offshore current in the surface layer means that larvae visiting the surface to feed must risk offshore transport. This danger is removed for larvae in still water and weak upwelling, but they are unable to effect predictable changes in their offshore distance through vertical migrations. Because our model decouples cross-shore and vertical movement in still water (except for the effects of diffusivity, or undirected currents), it predicts swimming behaviors that are primarily shaped by feeding and, when possible, predator avoidance. In nearshore mortality, larvae can increase their probability of leaving shore by visiting the surface, where diffusivity is elevated, but are not guaranteed to return to shore. Thus, it may be advantageous to stay nearshore despite predation. Under our default mortality rate parameters, we saw this was indeed the case for non-feeding larvae.

Food abundance and the strength of upwelling vary geographically, and our model predicts strong effects of both of these factors upon the optimal swimming behaviors of larvae. We therefore expect the locations where adult organisms thrive to shape the swimming behaviors of their larvae. For instance, megalopae (late larvae) of the estuarine crab *Carcinus maenas* exhibit flood-phased tidal vertical migrations to facilitate transport into estuaries (Queiroga et al, 2007, Zeng and Naylor, 1996b), while younger larvae perform ebb-phased vertical migrations in the bays of North Wales, UK, (Zeng and Naylor, 1996a) but diel vertical migrations in the western Iberia upwelling system off the coast of Portugal (Queiroga et al, 2007). For other species, we theorize that the geographical ranges of adults could be determined, in part, by the range of vertical swimming behaviors of their larvae. Conditions also vary locally over time, both predictably (e.g., seasonally) and unpredictably. Larvae of some species can cope with this variability through behavioral plasticity (Miller and Morgan, 2013b), and adults can further limit the effects of predictable variability by timing their reproduction to favorable local conditions (Donahue et al, 2015, Morgan, 1995b).

As pointed out by Donahue et al (2015), the most beneficial behaviors surrounding reproduction are those that perform well in extreme years, rather than typical ones. Our analysis of non-optimal vertical swimming patterns showed that OVM and half-DVM (that is, diel vertical migrations for only the first half of dispersal; see **Figure 4.1d**) are two such behaviors. OVM offers an advantage over passive floating regardless of current strength, food abundance, and mortality scheme. Half-DVM can offer a greater advantage, but only if food is abundant. Thus, the larvae of species that thrive in highly variable conditions may be best served in the long-term by OVM, with half-DVM preferred for species in locations where current strengths are variable but food abundance is reliably high. We note, however, that the "best" behavior in a given environment or set of environments varies across species due to developmental timing and costs, locomotive abilities, and possibly several other factors not included in our model. This is evidenced by the different behaviors observed across species living within the same environments (Bonicelli et al, 2016).

Our model does not predict that larvae should perform diel vertical migrations throughout the entire larval duration under any of the cases we presented in this paper. This is because visiting the surface near the end of the larval duration necessarily increases a larva's chance of being lost offshore due to increased diffusivity and, in upwelling, offshore advection. Additional numerical experiments revealed only two cases where sustained DVM is optimal. The first case is when the penalty for finishing dispersal far from shore is small compared with potential benefits of predator avoidance and energy conservation (i.e., $\sigma \ll \lambda, \mu_i$). This could apply for species where adults can thrive in a wide range of depths and conditions, such as the dungeness crab, *Cancer magister* (Rasmuson, 2013). The second case is when currents flow in the opposite direction of what we considered here (i.e., $U_0 > 0 > U_1$), such as in regions with downwelling-favorable currents like the east coast of North Carolina (Shanks et al, 2002) and the Beaufort Sea (Yang, 2009). Downwelling is also possible in some regions that are typically characterized by upwelling, such as the west coasts of Oregon (Shanks and Shearman, 2009) and Chile (Narváez et al, 2006); the dramatic differences in optimal behaviors across up- and downwelling regimes underscore the importance of seasonal release timing.

If sustained DVM truly is common even in regions with upwelling or still water, then there exist several possible explanations for why our model does not predict it, including:

(i) The optimization objective, J, does not include benefits of offshore transport, such as potential for alongshore dispersal, that could favor DVM.

(ii) Our idealized model of upwelling circulation does not accurately capture how DVM interacts with currents in nature.

(iii) There are scenarios that favor DVM, such as downwelling, that our analysis does not consider.

Alternatively, sustained DVM may be less common in nature than is currently believed. Data on larval depth control in the laboratory and field are usually noisy (Queiroga et al, 2002, dos Santos et al, 2008, Shanks, 1986, Tapia et al, 2010), and are frequently averaged into a single DVM-like mean to facilitate visualization or interpretation. This average can be easily misunderstood as a suggestion that most larvae perform DVM in unison, but our simulation results illustrate that DVM-like means appear even when no individual reliably performs this behavior (see **Figure 4.2p**). Indeed, Kunze et al (2013) found that in the Hudson River estuary, fish and invertebrate larvae achieve retention in the upper estuary by only roughly adhering to diel and tidal vertical migrations, and that their ability to perform these migrations depends on the strength of tidal mixing.

Behaviors must be inferred cautiously from laboratory and field observations, particularly when they are to appear in predictive modeling studies. When considering larval dispersal only, unreliable adherence of larvae to behavioral archetypes would result in greater variance in larval positions and less correlated movement across individuals than strict adherence, effectively increasing eddy diffusivity and decreasing advection (Largier, 2003). Studies implementing strict larval behaviors probably overstate the extent to which larval movement differs from passive diffusion on a population level. The consequences of this for population dynamical predictions are not clear, but as emphasized by James et al (2019), the resulting error could be quite large after several modeled generations. Because behaviors cannot easily be identified and may vary within populations of larvae, it may be preferable to interpret field-derived larval depth profiles as probability densities for the locations of larvae, rather than as indicating their variance about a single mean depth.

Dynamic programming is a powerful method for determining whether a given set of assumptions (e.g., that returning to shore, reserving energy, and escaping predation are important) are sufficient to explain behaviors observed in nature (e.g., diel vertical migrations). However, our use of this approach has limitations that must be recognized. For one, dynamic programming and other optimization approaches cannot predict the behaviors and traits that might emerge through natural selection. In the context of our study, our emphasis on the performance of an individual larva does not capture the long-term and population-scale benefits of planktonic development, such as range expansion, metapopulation connectivity, and gene flow (Burgess et al, 2016, Hedgecock, 1986, Levin, 2006, Pechenik, 1999, Shaw et al, 2019, Strathmann, 1974). It is possible that these factors incentivize vertical migrations in some of the cases where our model predicted no movement, such as for non-feeding larvae subject to diurnal predation.

On a technical note, it is generally preferable to apply dynamic programming using optimization objectives with clear interpretations, such as the expected lifetime reproductive output of an individual. However, because dynamic programming requires objectives to take a specific form (Mangel and Clark, 1988), this is not always possible. Our objective $\mathbf{E}[J|\Delta Z]$, defined in (4.8), heuristically balances the costs of mortality, habitat choice, and energy use, but lacks a concrete biological meaning: while $J[X, Z, E]$ can be regarded as the log-probability of surviving through metamorphosis conditioned on the trajectory (X, Z, E) and behavior ΔZ,

$$\Pr\{\text{survive through metamorphosis} \mid X, Z, E, \Delta Z\} = \exp(J[X, Z, E]), \tag{4.15}$$

(see **Appendix 4.5.1**) the probability of doing so regardless of trajectory is

$$\Pr\{\text{survive through metamorphosis} \mid \Delta Z\} = \mathbf{E}[\exp(J[X, Z, E])|\Delta Z]. \tag{4.16}$$

From Jensen's inequality,

$$\mathbf{E}[\exp(J[X, Z, E])|\Delta Z] \geq \exp\big(\mathbf{E}[J[X, Z, E]|\Delta Z)]\big). \tag{4.17}$$

In other words, our optimization maximizes the (logarithm of) a lower bound on the probability of survival through metamorphosis, rather than that probability itself. The consequences of substituting one expression for the other on the results of our optimization are not clear, but we expect that optima computed using the objective on the left-hand side of (4.17) would be more (less) influenced by outliers above (below) the mean of J, since the exponential inside of the expectation weights those cases more (less) heavily. Better resolving this difference is an interesting direction for further investigation.

Despite these limitations, our results compellingly illustrate how propagules with a limited capacity for locomotion can use environmental conditions to their advantage during dispersal. Regarding the biology of coastal marine larvae, our analysis suggests that behaviors commonly reported in the literature are robust attempts by larvae to improve their chances of survival in potentially variable conditions. More broadly, we argue that both the assumption that propagules are completely passive and the methods by which active behaviors are inferred must be carefully examined, especially when trying to predict population dynamics.

4.5. Appendix

4.5.1. Rough Interpretation of the Optimization Objective. Here, we discuss non-rigorously how J can be interpreted as the logarithm of the probability of a larva surviving through metamorphosis, conditioned upon its trajectory, $(X, Z, E) = \{(X_t, Z_t, E_t) : 0 \leq t \leq T\}$, and its sequence of depth changes, $\Delta Z = \Delta Z_0, \ldots, \Delta Z_T$. As mentioned in the Discussion, however, we cannot interpret the expectation of J as the logarithm of the overall probability of survival because the order of operations (taking the logarithm and integration/averaging is incorrect).

Let

$$P[X, Z, E] = \Pr\{\text{survive through metamorphosis} \mid X, Z, E, \Delta Z\}, \tag{4.18}$$

and assume that this quantity can be decomposed into four factors,

$$P[X, Z, E] = P_0 \cdot P_m[X, Z] \cdot P_s(X_T) \cdot P_e(E_t), \tag{4.19}$$

where P_m is the probability of surviving the trajectory (X, Z), P_s is the probability of initiating and surviving metamorphosis at the final offshore position, X_T, and P_e is the probability of surviving metamorphosis given final energy content E_T (all conditioned on $X, Z, E, \Delta Z$). P_0 contains all parts of the probability P that do not depend on the larva's path or behavior.

From Karlin and Taylor (1981), the probability of surviving dispersal conditioned upon the path X, Z and behavior ΔZ is

$$P_m[X, Z] = \exp\left(-\sum_t \mu(t, X_t, Z_t)\Delta t\right). \tag{4.20}$$

For initiating and surviving metamorphosis, we assume that the effects of settling site and energy content are independent. For the larva's chosen settling site, we assume that the probability of survival decays exponentially with distance beyond the ideal habitat,

$$P_s(X_T) = \exp(-\sigma R(X_T - X_*)), \tag{4.21}$$

where R is the "ramp" function,

$$R(a) = \begin{cases} 0 & \text{if } a \leq 0, \\ a & \text{if } a > 0. \end{cases} \tag{4.22}$$

Similarly, we assume that the larva's probability of completing metamorphosis decays exponentially with the amount it falls short of E_* mJ of energy:

$$P_e(E_T) = \exp(-\lambda R(E_* - E_T)). \tag{4.23}$$

The logarithm of the resulting expression for $P[X, Z, E]$ is $J[X, Z, E]$, after normalizing by P_0:

$$\begin{aligned} J[X, Z, E] &= \log\left(\frac{P[X, Z, E]}{P_0}\right) \\ &= -\sum_t \mu(t, X_t, Z_t)\Delta t - \sigma R(X_T - X_*) - \lambda R(E_* - E_T). \end{aligned} \tag{4.24}$$

The probability of surviving metamorphosis given a sequence of depth changes ΔZ and any trajectory is

$$\begin{aligned} \Pr\{\text{survive through metamorphosis} \mid \Delta Z\} &= \mathbf{E}(P[X, Z, E] | \Delta Z) \\ &= \mathbf{E}\left(P_0 \cdot P_m[X, Z] \cdot P_s(X_T) \cdot P_e(E_T) \mid \Delta Z\right). \end{aligned} \tag{4.25}$$

However, the expectation of J is not equivalent to the logarithm of this expression.

4.5.2. Supplemental Figures. The supplemental figures on the following pages show:

(i) Optimal trajectories for non-feeding larvae in strong upwelling in **Figure 4.5**, which is similar to **Figure 4.2**. Recall that our model predicts that non-feeding larvae simply remain in the bottom layer in still water.

(ii) Additional simulations of Z_t for all cases shown in **Figure 4.2** and **Figure 4.5**. Simulations in still water are in **Figure 4.6** and in simulations in upwelling are in Figure 4.7.

(iii) Performance scores, J, for the optimal behavior, passive floating, and the four prescribed archetypes from **Figure 4.1** for feeding larvae subject to diurnal predation and non-feeding larvae subject to nearshore predation are in **Figure 4.8**.

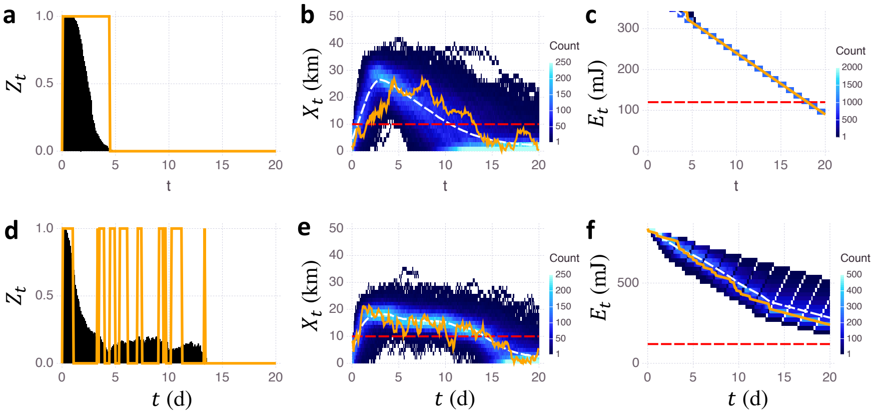

Figure 4.5. Optimal dispersal trajectories of non-feeding larvae subject to nearshore mortality in strong upwelling. The top and bottom rows each illustrate simulations of 1000 non-feeding larvae with no energy surplus or a large energy surplus, respectively. **(a)** and **(d)** Single optimal simulations of Z_t (orange) and the fraction of optimal larvae in the surface over time, $\mathbf{E}[Z_t]$ (black). **(b)** and **(e)** The simulated cross-shore distances, X_t (blue), a single simulation (orange), the mean cross-shore position over all trials, $\mathbf{E}[X_t]$ (white dashed), and the offshore edge of the coastal habitat, X_* (red dashed). **(c)** and **(f)** Simulated energy contents, E_t (blue), a single simulation (orange), the mean of all simulations, $\mathbf{E}[E_t]$ (white dashed), and the minimum energy required to safely complete metamorphosis, E_* (red dashed).

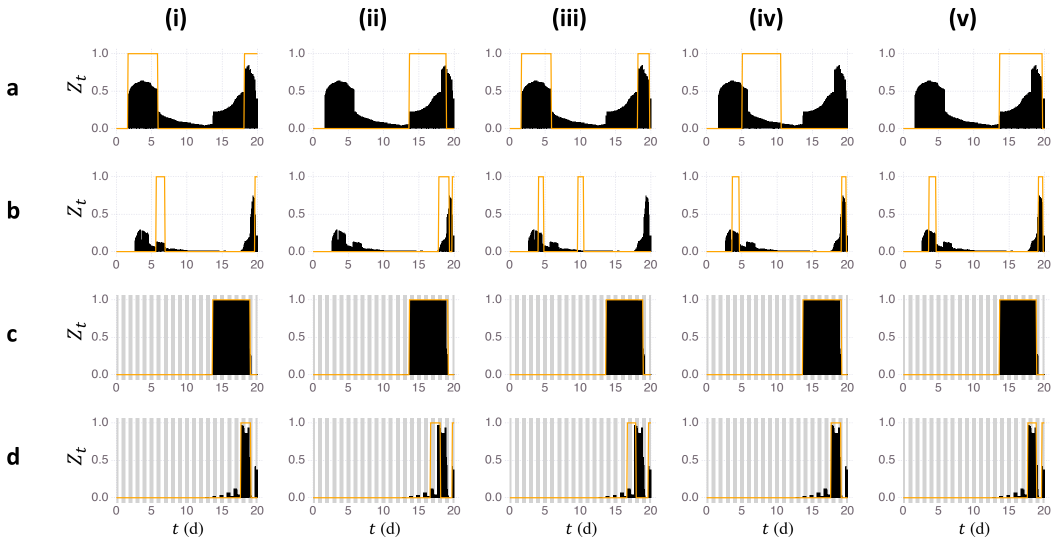

Figure 4.6. Simulations of larval depth over time, Z_t, for feeding larvae obeying the optimal behaviors computed in still water. For each row, (i)-(v) show different simulations of Z_t (orange) and the fraction of all larvae in the surface, $\mathbf{E}[Z_t]$ (black). Each row represents a different case. **(a)** Nearshore mortality, food-poor; **(b)** nearshore mortality, food-rich; **(c)** diurnal mortality, food-poor; **(d)** diurnal mortality, food-rich. Gray bars in rows (c) and (d) indicate periods of darkness.

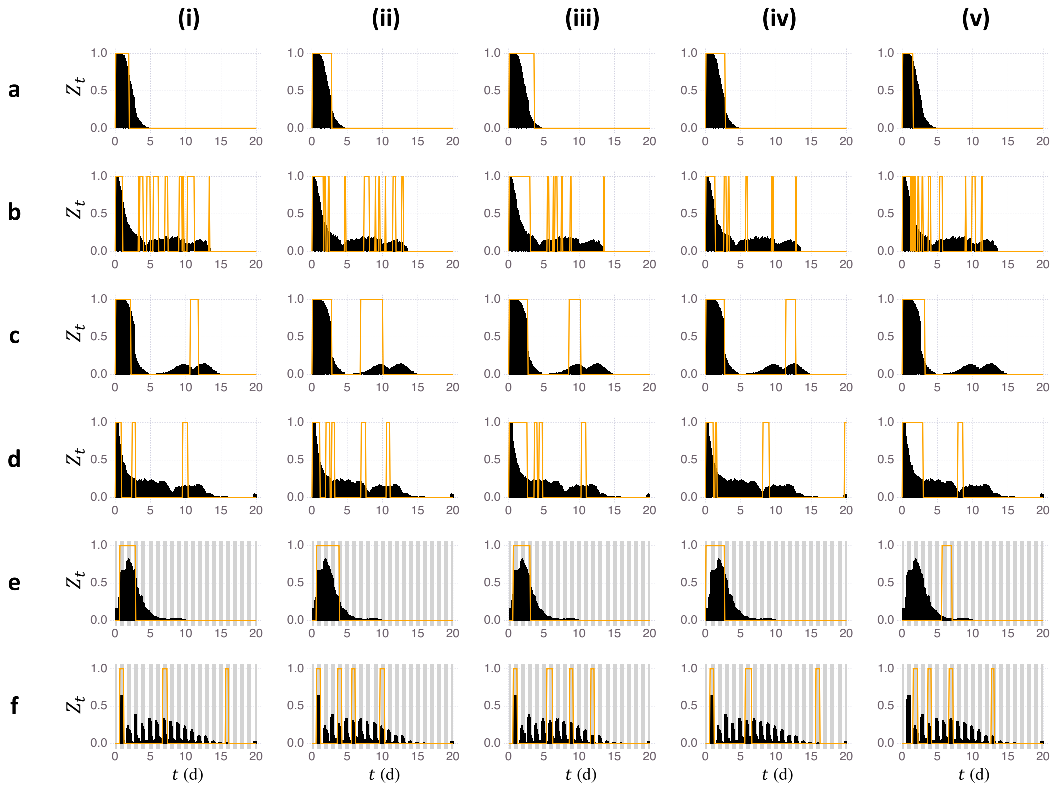

Figure 4.7. Simulations of larval depth over time, Z_t, for larvae obeying the optimal behaviors computed in strong upwelling. For each row, (i)-(v) show different simulations of Z_t (orange) and the fraction of all larvae in the surface, $\mathbf{E}[Z_t]$, (black). Each row represents a different case. **(a)** Non-feeding larva, nearshore mortality, no surplus; **(b)** non-feeding larva, nearshore mortality, large surplus; **(c)** feeding larva, nearshore mortality, food-poor; **(d)** feeding larva, nearshore mortality, food-rich; **(e)** feeding larva, diurnal mortalilty, food-poor; **(f)** feeding larva, diurnal mortality, food-rich. Gray bars in rows (e) and (f) indicate periods of darkness.

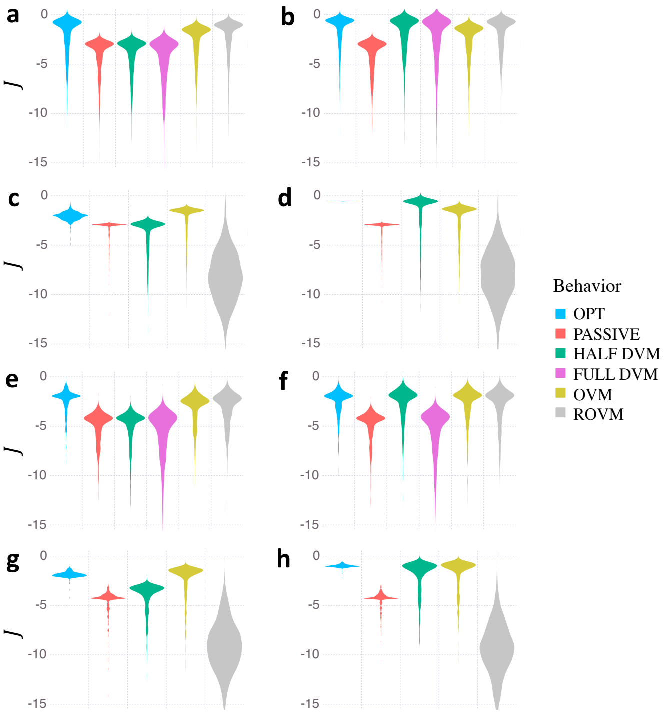

Figure 4.8. Performance, J, of simulated larvae using the following behaviors: optimal (blue), passive floating (red), half DVM (green), full DVM (purple), OVM (yellow), and reverse OVM (gray). Each panel presents a different case. **(a-d)** capture feeding larvae subject to diurnal predation, with (a) and (b) showing food-poor/food-rich (respectively) still water and (c) and (d) showing food-poor/food-rich water with strong upwelling. **(e-h)** capture non-feeding larvae subject to nearshore predation. (e) and (f) show the performance of larvae with no surplus or a large surplus, respectively, in still water. (g) and (h) show the performance of non-feeding larvae with no surplus or a large surplus, respectively, in strong upwelling.

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