

Larval Transport in the Coastal Zone: Biological and Physical Processes

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But the most frequent mode of transportation, probably, consists in their buoyancy of their eggs... These... may be swept along by a wave that breaks upon a coral-reef, and may then be borne by a current to a distance.

Charles Lyell, 1832, p.112

11.1 Introduction

The life cycle of most benthic marine metazoans is characterized by large fecundities and a two-phase life cycle, where individuals produce hundreds to millions of eggs. Typically, fertilized zygotes develop into minute, swimming larvae, and larvae travel away from adult habitats as they develop. After developing for minutes to several months, larvae must return to suitable adult habitats to settle, grow, and reproduce; this migration is mediated by larval transport (see review of concepts by Young, 1990).

Larval transport can play a key role in population dynamics by determining settlement rates (Roughgarden et al., 1988). Further, the local circulation regime (Zimmer et al., 2012), in conjunction with behavioral and morphological characteristics of the larvae, may cause local population fecundities to decouple from local settlement rates (reviewed in Pineda et al., 2010), such as when larvae produced at one location are advected away from natal habitats and must settle on distant habitats. Thus, larval transport is a [fundamental](#) biological-physical process in the ecology of benthic populations and communities. Further, larval transport is fundamental to the dynamics of metapopulations (Botsford et al., 2001), with implications for fisheries management and conservation.

Larval transport is a concept that can also be described as a measurement and, more specifically, quantified as a flux, a quantity flowing across a surface per area and time (e.g., an “Eulerian” approach). For example, larval flux across a lagoon’s mouth during the incoming tide (e.g., DiBacco and Chadwick, 2001) can be quantified using fixed nets at the lagoon’s mouth, together with measurements of flow across the mouth (with units # larvae/L² · time).

To be most relevant to understanding population processes, larval transport should be measured during the entire settlement season, including periods when the bulk of larvae are transported. Measuring larval transport as larval flux in these cases is not typically practical, because larval transport tends to be sporadic, larvae are patchily distributed (Haury et al., 1978; Natunewicz and Epifanio, 2001), and the settlement season may be long (several months). For example, ~~crab, bivalve, gastropod, and polychaete settlement and plankton pump data~~ (Reyns and Sponaugle, 1999; Queiroga et al., 2006) [suggest](#) that larval transport [tends](#) to be unpredictable, including long periods of negligible transport (weeks to months) punctuated by daily or even hourly events (Garland et al., 2002; Porri et al., 2006; Reyns et al., unpub.) when the bulk of the larvae are transported. For measures of larval flux to be effective in demarcating the relevant components

of larval transport, continuous measurements resolving short timescales (minutes to hours) and sustained for months would be necessary. For most open coastline applications, however, such time-series biological measurements would be impractical, requiring fixed sampling structures to measure larval fluxes through a depth layer or the entire water column. Moreover, with current methodologies, the effort required to process larval samples would be ~~very great~~. Despite the potential advantages of measuring larval transport as larval flux, so far these measurements are prohibitively taxing for the majority of benthic systems, and therefore marine ecologists have resorted to other descriptions of larval transport.

Larval transport has been defined simply as “the horizontal translocation of a larva between points x_1, y_1 and x_2, y_2 , where x and y are horizontal axes, say, perpendicular and parallel to the coastline” (Pineda et al., 2007). In this definition, larval transport is measured in length units (e.g., meters). To more closely relate the meaning of larval transport to “Lagrangian” descriptions of flow, which describe the trajectory of a parcel of water with respect to a temporal dimension, a more refined definition is needed.

We define larval transport as *the mean horizontal translocation of larvae between points along a specified one-dimensional axis per unit time* (with units L/time). This definition does not consider timing and magnitude of spawning, larval abundance, mortality, or settlement (discussed in Pineda et al., 2007). It acknowledges the separation of pelagic and benthic habitats, and accommodates the mechanistic resolution of the fundamental biological-physical processes accounting for larval translocation along a spatial dimension of interest (e.g., alongshore, cross-shore).

11.2 Scales of Larval Transport

While understanding the processes that account for larval translocation appears straightforward, several processes are involved which range over vast spatial and temporal scales. At one extreme, biological-physical accumulation processes with scales of centimeters to meters and seconds to minutes play an important role. At the other extreme, processes with thousands of kilometers and interannual scales, such as the El Niño–Southern Oscillation,

modulate local biological and physical processes that can determine larval transport, including surface gravity waves (Seymour et al., 1989) and thermocline depth (Filonov and Tereshchenko, 2000). The spatial scales of larval transport—that is, the horizontal distances covered by the larvae—must vary in different systems (e.g., tropical estuaries, seamounts, temperate intertidal). However, the dominant scales of larval transport are imperfectly known. There is some consensus that dispersal distances in many coastal invertebrates are on the order of 5–25 km (Shanks, 2009), but transport distance over hundreds to thousands of kilometers have been inferred in species with a long larval duration (Scheltema, 1968). Temporally, lunar and seasonal variability in larval transport, inferred from settlement data, are important in many systems, but in most cases, the relative contribution of biological (reproductive cycles) and physical (e.g., water stratification, seasonal variability) processes is not well resolved, since rarely has larval transport and timing of reproduction been measured concurrently (but see Hurlbut, 1992; Barbosa et al., 2016). One exception is for many hermatypic corals and other reef fauna that spawn according to the lunar cycle and season (Harrison et al., 1984), and thus predictably initiate larval transport. A further complication to understanding larval transport is that the physical processes that might be involved are themselves imperfectly known (Lentz and Fewings, 2012). For these reasons, a mechanistic understanding of the processes involved in larval transport is challenging, and the variability among systems is likely high.

This chapter reviews larval transport, emphasizing the advances in the last 25 years. A full discussion of the different processes and oceanic regions is beyond the scope of this chapter. Thus, we emphasize first-order phenomena, where mechanistic understanding has been achieved and on the topics that may need more attention. Whereas the processes we discuss apply to most habitats, we focus on open coastal environments, which the bulk of studies on invertebrates are concerned with and for which process-oriented understanding is most advanced. We use literature for fish larvae and other environments when it helps clarify the issues at hand.

11.3 Components of Larval Transport and Other Relevant Phenomena

What are the components of “larval transport”—the first-order processes responsible for the translocation of a larva from point *a* to point *b*? And what other general processes are relevant to larval transport itself, and to benthic population dynamics, including processes determining how many larvae transport, and the spatial and temporal variability in the number of larvae that transport? We suggest that the components of larval transport include the following: (1) larval behavior, particularly behaviors influencing vertical distribution, and (2) the physical transport mechanisms accounting for advection, diffusion, and their variability. In instances where larval transport is associated with propagating fronts, an additional component is (3) the mechanism of larval accumulation in those features. Knowledge of all the components is necessary. For example, if one knows that the cross-shore physical transport mechanism *a* features an accumulation mechanism *b* which requires a behavior *c* for accumulation and transport, then one could make a larval transport prediction depending on whether an untested species possesses behavior *c*.

11.3.1 Larval Behavior

Horizontal flow velocities vary with depth, from slowing down toward the bottom due to friction, to current reversals in different layers in some flows, and larvae may exploit this variability by swimming vertically. The hypothesis that minute planktonic larvae can control their horizontal transport by exploiting behaviorally the layered vertical structure of marine flows was suggested over a century ago by J. Nelson (1912):

The swimming powers of the fry are too feeble to change their distribution in the current directly. But they have the power to change this distribution indirectly. For they can rise and sink, they have the power to seek the bottom and to rise to the top. . . . Then the larvae could control their own distribution. (p. 307)

Thus, the essence of the “behavioral control of larval transport” hypothesis is (a) given that horizontal ocean current magnitudes are much larger

than non-oscillatory vertical flows (e.g., cm/s vs. mm/s), and that (b) small invertebrate larvae are weak swimmers and cannot generally determine their horizontal distribution by swimming against horizontal currents, then (c) by swimming vertically, larvae can exploit the layered structure of the horizontal currents, and in this way control their horizontal distribution.

In its simplest and best-known version, a larva encounters a layer where the flow is predominantly in one direction, resulting in transport in that direction. This concept has been applied to two-layer estuarine and coastal lagoon (Nelson, 1912; Bousfield, 1955), nearshore and coastal (Rothlisberg and Miller, 1983; Cowen et al., 2000; Paris and Cowen, 2004), and open-ocean (Scheltema, 1968) flows.

What triggers larvae to swim vertically to exploit depth-dependent flows? Studies invoking horizontal control of larval transport by vertical swimming often explain vertical positioning as a fixed-schedule behavior promoting return to natal habitats. For example, crab larvae can migrate vertically by entering the water column during one phase of the tidal cycle and remaining near bottom during the other tidal phases, resulting in horizontal movement termed selective tidal stream transport (Forward and Tankersley, 2001). Another frequently invoked view in coastal lagoons and other systems is ontogenetic vertical positioning, where early stage larvae occupy a depth layer promoting their transport away from shallow adult habitats, followed by migration of developing larvae to another depth layer with flows promoting their return to adult habitats (Bousfield, 1955). In each case, behavioral responses to environmental cues, in the form of taxis or kinesis, mediate vertical larval migrations. Cues may include changes in temperature, salinity, gravity, light, turbulence, currents, chemicals, and sound, among other factors, and have been extensively addressed elsewhere (Metaxas, 2001; Fuchs et al., 2004; Weidberg et al., 2015; Epifanio and Cohen, 2016).

Given the times scales of larval development, which vary from minutes to years, with a mode of ~1–8 weeks for temperate species (Levin and Bridges, 1995), the implication is that there must exist mean Eulerian flows connecting juvenile and adult benthic habitats to the “larval pool,” the pelagic grounds where larvae develop. Moreover, the

temporal scales of these flows should be of similar order or longer than those of invertebrate larval duration. However, whereas these assumptions may hold in some estuarine systems and oceanic islands and reefs, they are problematic for most continental open-coast nearshore systems, because mean cross-shore currents are small or negligible. While vertical migration at fixed tidal and ontogenetic schedules may work in many systems, settlement data (a proxy for larval transport) indicate that at least some larval transport is associated with rapid and unpredictable (in the short term) changes in hydrodynamic conditions, sometimes associated with small-scale frontal features (Garland et al., 2002).

How can larvae exploit depth-dependent flows in unpredictable features? Pineda (1999) found that the vertical distribution of barnacle larvae switched from a deeper distribution at sites away from an internal bore warm front to a near-surface distribution at the front. It was speculated that cyprid larvae responded to the convergent frontal downwelling currents by swimming up against the downwelling circulation, and in this way accumulated and translocated with the front. A later study found that cyprid larvae indeed respond to downwelling currents by swimming up, indicating that this mechanism is plausible (DiBacco et al., 2011). Here we use “adaptive behavior” in the context of larval transport to denote near-instantaneous individual responses to

a change in a physical field (Figure 11.1). Adaptive behavior could lead to shifts in vertical distribution or to swimming that reduces vertical displacement. The appearance of adaptive behaviors might coincide with developmental changes in morphology and could be used to exploit event-type processes with short temporal scales, such as increased wave height, sea-level change (pressure), intensification of winds, upwelling relaxation, and internal tidal bores. Larvae possessing adaptive behaviors would have a higher success rate in reaching the juvenile habitat, settling, and growing to reproduce.

11.3.2 Physical Transport Mechanisms and Hydrodynamic Variability

Ecologists aspire to identify the advective physical mechanisms associated with larval transport to understand the spatial and temporal modulation of larval supply, settlement, recruitment, and population dynamics by physical processes, as well as the larval traits that mediate transport. Advection and diffusion determine planktonic larvae separation with time (Scheltema, 1986), and a plethora of small- to large-scale physical processes cause the water to move, from eddy diffusion, to the slow Stokes drift associated with surface gravity waves (but see Lentz and Fewings, 2012), to fast western boundary currents such as the Gulf Stream.

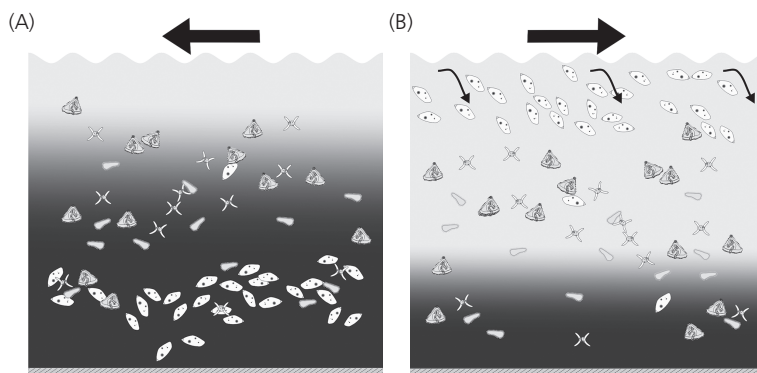


Figure 11.1 Hypothesis of adaptive behavior. A rapid change in an environmental property, for example, currents (arrows on top of the panels) leads to a sudden change in larval behavior in barnacle cyprids, such as swimming up in response to downwelling currents (DiBacco et al., 2011), influencing vertical distribution and leading to larval transport in some taxonomic groups. Panels A and B are Time 1 and Time 2. Short-term changes in vertical distribution in barnacle cyprids have been observed in response to internal tidal bore warm fronts and alongshore current reversals (Reyns et al., unpub.). In this example, other type *to* larvae, bryozoan cyphonautes, gastropod veligers, and anemone planulae, do not change behavior; shade gradients represent stratification (see Plate 8).

The fundamental attribute of advection in larval transport is variability. If currents would flow in only one direction, with similar magnitude at all depths and no temporal variability, weak larval swimmers would have no chance to return to their natal habitats. Temporal current variability is frequently associated with tides, but wind-forced, buoyancy-driven flows and other processes (e.g., waves, internal waves) also cause current fluctuations. Thus, spatial and temporal hydrodynamic variability are fundamental in larval transport.

Is larval transport intrinsically linked to certain processes? Are mass transport, diffusion, and behavior necessary for larval transport to occur? In principle, it appears that larval transport has no strict dependencies, as it can occur with or without mass transport and diffusion in the case of strong larval swimmers, and in the absence of any particular behavior, when transport would be entirely dependent on advection and diffusion.

It is impossible for maximum larval distance to exceed the limits set by two factors: the upper limits of larval duration and the maximum separation between initial and ending positions set by advection and diffusion (i.e., maximum horizontal particle dispersion), plus distance added by horizontal larval swimming. Further, larvae must be present to be transported; yet this obvious consideration becomes non-trivial when testing links between physical transport and larval supply or settlement using time-series analyses (discussed in Pineda, 2000). Diffusion is often used as an important source of larval loss (Hill, 1991), and it also plays a role in the distribution and transport of invertebrate larvae (Okubo, 1994); however, its role remains to be investigated in field conditions. In one of the few observational studies addressing horizontal larval distributions, Natunewicz and Epifanio (2001) tracked larval crab patches and hypothesized that patch coherence was maintained behaviorally. Larvae may aggregate in convergences, and these features limit larval dispersion. Given that swarming behavior may be associated with proficiency in swimming capabilities and that larger larvae tend to be better swimmers, diffusion may be more important in larval transport of the smallest and weakest swimmers.

11.4 Advective Physical Mechanisms in the Coastal Ocean Associated With Larval Transport

Winds, tides, and buoyancy-driven flows (flows associated with horizontal differences in water density) are the three main forcing mechanisms in the coastal ocean, and, unsurprisingly, most physical mechanisms associated with larval transport invoke flows forced by these processes, a perception that has changed little in the past 25 years (Epifanio and Garvine, 2001). What has changed is a broader use of physical measurements to study larval transport, more attention to nearshore and small-scale flows in observational studies, and increased sophistication in considering potential mechanisms at work. Waves, the main forcing mechanism in the surf zone (Lentz and Fewings 2012), have only been recently considered by larval ecologists as a component of larval transport (Fujimura et al., 2014; Röhrs et al., 2014).

The importance of the three main forcing mechanisms varies depending on the domain (i.e., cross- vs. alongshore). Some of the coastal physical processes that tend to be energetic in the alongshore axis, such as tidal currents, tend to have smaller variability in the cross-shore (Figure 11.2). Conversely, the internal tide can have larger cross-shore variability (Winant and Bratkovich, 1981). This asymmetry in cross- and alongshore processes, however, does not always hold in other systems where larval transport is studied, including coral reefs, where tidal currents play an important role (Wolanski et al., 1989), and in coastal lagoon mouths and channels, where tidal currents are energetic (Epifanio, 1988; DiBacco and Chadwick, 2001). Much interest in larval ecology in coastal areas is focused on larval transport perpendicular to the shoreline. Nearshore water cooling during winter (Checkley et al., 1988), thermocline shallowing associated with the internal tide (Pineda, 1994), and strong offshore winds can lead to the appearance of a cool, dense body of water in the nearshore with corresponding cross-shore density gradients. If the density field relaxes on short timescales, these density gradients can create gravity currents, where the dense nearshore water flows and sinks offshore, while a buoyant, lighter parcel of water advances shoreward.

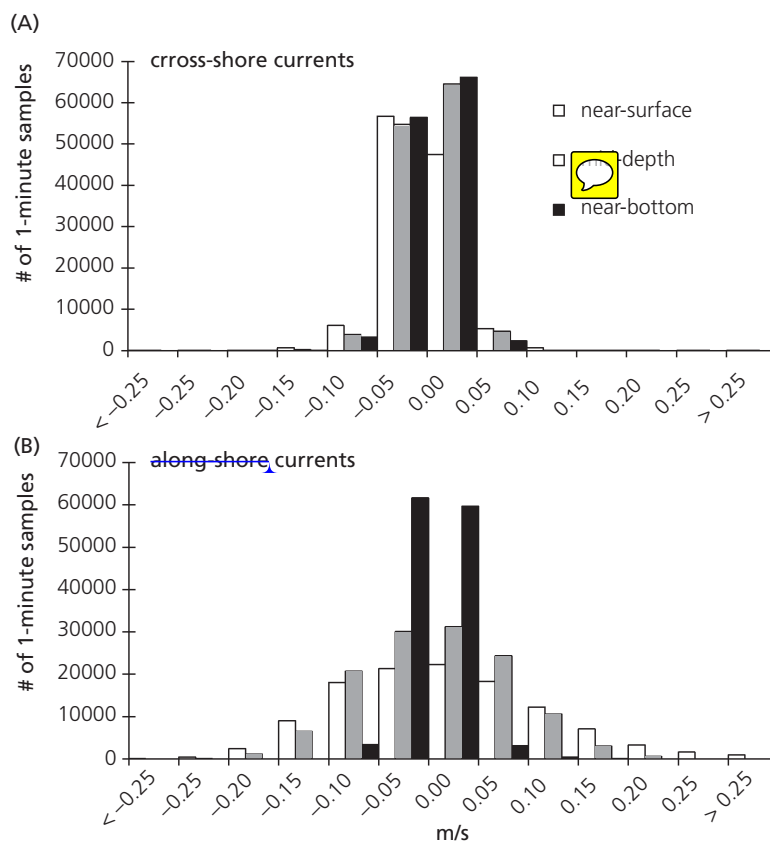


Figure 11.2 Frequency distribution of 1-minute averaged cross-shore (A) and alongshore (B) currents (m/s), collected in an open-coast nearshore environment using an Acoustic Doppler Current Profiler deployed at an 8m, ~ 900m from Bird Rock, La Jolla, California, USA, during April–July 2014. Positive are southward and onshore currents. Near-surface, mid-depth, and near-bottom currents were collected at 6.7, 4.7, and 1.5 m above bottom, respectively. Cross-shore currents are less energetic and have a narrower distribution in speed than alongshore currents. Additionally, near-surface currents have the largest range, and speeds decrease with depth (mid-depth and near-bottom have progressively smaller ranges in currents), particularly in the alongshore domain (Reyns et al., unpub.).

During the past 25 years, studies have highlighted evidence of larval transport or settlement associated with upwelling relaxation/downwelling (Farrell et al., 1991; Wing et al., 1995; Shanks et al., 2000; Garland et al., 2002), internal tides (Pineda, 1994; 1999), storm systems (Eggleston et al., 1998; 2010), mesoscale eddies (Sponaugle et al., 2005), and surface gravity waves (Pfaff et al., 2015). Many of these studies underscore the switch in focus from consideration of open-ocean processes to nearshore processes (discussed in Pineda, 2000), such as surface gravity waves (Pfaff et al., 2015) and shallowing of the internal tide (MacTavish et al., 2016). Moving forward, there need to be more studies examining systems where the previously mentioned

physical processes are not dominant (Hrycik et al., 2013; Daigle et al., 2014).

Another recent development is the realization that large-scale and remote physical processes may modulate nearshore flows and larval transport (discussed in Pineda et al., 2007). For example, both coastally trapped waves (Brink, 1991) and mesoscale rings (Sponaugle et al., 2005) influence nearshore thermocline depth. The thermocline can shallow in response to these processes, allowing the internal tide to penetrate the nearshore and settlement to increase (Pineda and López, 2002; Sponaugle et al., 2005). Thus, modulation of small-scale nearshore flows by large-scale and remote processes provides a way for linking small to larger scales (Mullin, 1993).

11.5 Other First-order Phenomena and Processes Relevant to Larval Transport

11.5.1 Swimming Proficiency and Size

Larval swimming proficiency, a potentially key trait for the behavioral control of larval transport, is partially dependent on whether larvae use cilia or muscles for locomotion (Young, 1995), and how this varies with respect to phylogeny, size (from microns to a few centimeters), and ontogenetic stage. For example, late-stage bivalve larvae tend to be small (less than a few hundreds of microns), with some exceptions (e.g., teleplanic *Planktomya henseni* maximum size 1.5 mm; Allen and Scheltema, 1972). Viscous forces dominate the environment of the smallest plankton, so while these larvae may attain relatively large horizontal swimming speeds in body-lengths per second, these speeds may be insignificant for larval transport because they are negligible relative to the ambient flow velocity (see Hodin et al., this volume). Even for the larger larvae (e.g., \sim 1 millimeters to few centimeters), swimming efficiency ranges from excellent (e.g., crustacean larvae; Phillips and McWilliam, 1986) to weak and at the mercy of the flows (e.g., ascidian larvae; Olson, 1985).

11.5.2 Larval Duration

Is there a simple relationship between larval transport distance and larval duration? Most marine invertebrates develop through either a lecithotrophic (nonfeeding) or planktotrophic (feeding) larval phase, and it is generally accepted that feeding larvae spend more time in the plankton than nonfeeding larvae (e.g., Strathmann, 1985). This development time, or larval duration (we use larval duration instead of the commonly used pelagic larval duration because many invertebrate larvae are demersal and neritic, not pelagic), constrains the upper limit of larval transport, with potentially greater spatial scales of larval transport for longer-lived species (Scheltema, 1989), and, clearly, species with very short larval life cannot translocate long distances (Gerrodette, 1981). Therefore, a simple relationship between larval duration and dispersal distance is expected (Scheltema 1989), and plots describing such relationships have been offered in the literature (Siegel et al., 2003; Shanks,

2009) and used in modeling studies (discussed in Shanks, 2009; Leis et al., 2011). Scheltema (1989) asked whether “these assumptions and intuitions are really correct” and tested whether geographic range correlated with larval duration in coastal larvae. Although he found no correlations, long-lived teleplanic larvae tended to have distributions on both sides of the Atlantic Ocean, whereas species with 2–4 week larval duration did not. Several biological and physical factors negate a simple relationship between larval transport distance and larval duration. These include larval behavior; taxon-specific swimming capabilities; physiological condition; impacts of variable environmental conditions, such as temperature; capacity for delaying settlement; as well as sheared flows, including reduced velocities at the bottom of the benthic boundary layer; local physiography; the coastal boundary (Shanks, 2009); and regional circulation singularities.

Further, recent research indicates that larvae of some invertebrate and fish taxa may disperse less from adult habitats and have more constrained distributions (Jones et al., 1999; Tapia and Pineda, 2007; Morgan et al., 2009) than anticipated by larval duration (Efford, 1970); these findings could not have been anticipated by simple relationships between larval transport scale and larval duration. Thus, the existence of an upper limit in larval transport distance determined by maximum larval duration is arguably a useful construct; however, there is a need for rigorous observational data on larval transport and dispersal distance, and larval duration.

11.5.3 Accumulation

Several studies have suggested that larval transport is associated with front propagation, including internal bore warm fronts and upwelling-relaxation fronts (Pineda, 1999; Shanks et al., 2000). Accumulation processes are likely particularly important in buoyancy-driven flows. For example, accumulation and transport associated with the propagation of gravity currents have been considered in the case of larval transport by internal tidal bore warm fronts. In these gravity flows, surface currents behind the leading edge of the gravity current, the front, are faster than the propagating speed of the front (Simpson and Britter, 1979; Helfrich and Pineda, 2003).

As fronts propagate, buoyant particles and plankton behind the front reach the downwelling convergent frontal area, and those that swim up in response to the frontal downwelling convergent currents will accumulate near the surface and transport in the direction of front propagation. Those lacking the swim-up behavioral response will also be transported, but to a lesser extent. Larval transport with accumulation in fronts can be more efficient than pure advection in cases where the buoyant body advances all the way to near the juvenile benthic habitat. After the front reaches the juvenile habitat, mean distance between juvenile habitat and larvae that accumulated in the

front would be shorter than for those larvae that are advected but did not accumulate (Figure 11.3). Importantly, a variety of phenomena can result in gravity current propagation, including nearshore cooling by cold fronts (Checkley et al., 1988), internal tidal bores (Pineda 1994), and relaxation from cross-shore winds (Shanks et al., 2000; Tilburg, 2003). In all cases, as well as in transport in trapped cores of depression and elevation, where current speed can be larger than the propagation speed (White and Helfrich, 2008), relevant larval behavior to transport efficiently is to swim against the dominant vertical currents (Figure 11.4).

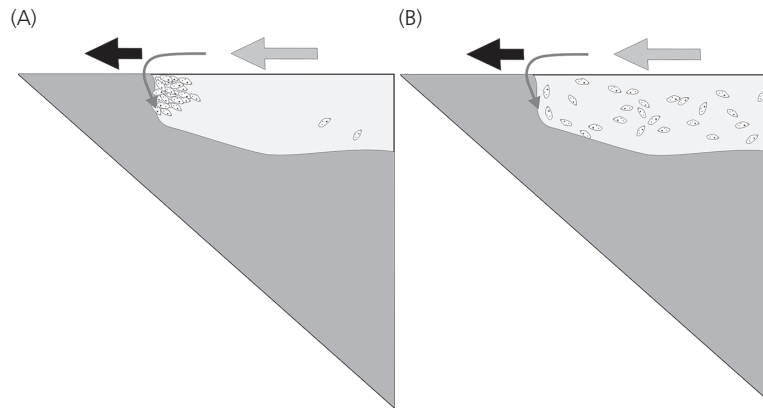


Figure 11.3 Representation of larval transport associated with advection, with accumulation (panel A) and without accumulation (B). The shallow adult habitat is on the left side of each diagram. Accumulation can occur when the current speed u associated with a parcel of water behind (seaward side) a front (i.e., light arrows on the top of the panels) is faster than the propagation speed C of the front (thick black arrows), and larvae swim against the dominant vertical current (curved arrows). Larvae that do not swim against the dominant vertical currents at the front will also be advected and swept toward the front, but they will not accumulate at the front (panel B). Larvae that accumulate will reach the vicinity of the adult habitat, while larvae that do not accumulate will be, on average, more distant (Pineda, 1999) (see Plate 9).

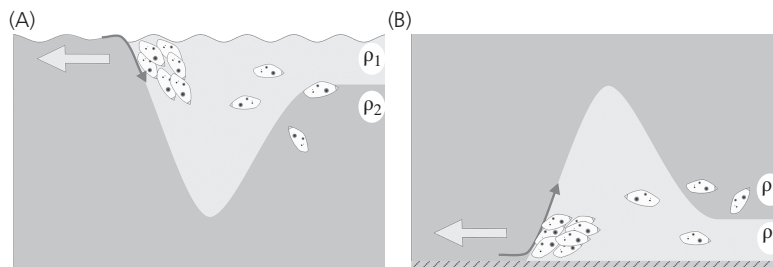


Figure 11.4 Hypothesis that swimming behavior against vertical currents can lead to more efficient larval transport in a variety of physical processes. Panel A: Onshore larval transport associated with gravity currents, including relaxation after nearshore cooling associated with cold fronts (Checkley et al., 1988), in internal bore warm fronts (Pineda, 1999), upwelling relaxation/downwelling (Shanks et al., 2000), and after cross-shore winds (Tilburg, 2003). Panel B: Larval transport associated with bottom-propagating gravity currents (Simpson and Britter 1979), such as internal tidal bore cold surges. Sigma is density, and arrows denote the propagation direction of the gravity currents. Hypothetical onshore larval transport associated with recirculating trapped cores in nonlinear internal waves of depression and elevation (not depicted; White and Helfrich, 2008) would also be aided by the behavior of swimming against the vertical currents (see Plate 10).

11.5.4 Patchiness and Episodic Transport

Patchiness is an aspect of spatial variability and is pervasive in all animal distributions, and in understanding larval transport, the combination of patchy larval distributions and episodic physical transport have conspired for decades against fundamental understanding. Put another way: while analyses of time series of dependent biological variables such as larval settlement and independent physical variables associated with advection can be used to hypothesize functional relationships between larval transport and physical forcing, these correlations may be weak or fail due to larval patchiness (discussed in Pineda, 2000). One way to circumvent this problem is to use statistical analyses that filter the independent variable, keeping instances where there is a response in the dependent variable such as settlement (Prager and Hoenig, 1989). Another, more powerful approach, is using a hypothetic-deductive method and sampling in response of the hypothesized larval transport events.

11.5.5 Spatial Variability in Larval Abundance

As noted previously, elucidating the vertical distribution of larvae is essential to resolve transport processes. Larval transport hypotheses and research that disregards the layered structure of the flows and the dependence of larval transport with depth may eventually prove wrong. Spatial scales of variability are expected to be larger on horizontal scales where larval patches are separated by greater distances (kilometers) than on vertical scales. This is due to the constraining effects of the sea surface and sea floor in addition to physical (e.g., currents, temperature) and chemical (e.g., oxygen) gradients that are much sharper in the vertical than horizontal dimensions. The vertical and horizontal scales of variability might be more comparable in benthic deep-sea environments because vertical gradients near the bottom may be less pronounced than in shallow coastal environments that are influenced by sunlight and surface heating. However, some benthic deep-sea gastropod larvae can be found in surface waters (Killingley and Rex, 1985).

Horizontal variability in larval abundance may relate to proximity of adult habitat, to habitat physiography (e.g., “coastal retention zones”), and to

water column stratification. If increased stratification leads to a more sheared environment, sites with stronger stratification might promote the retention of larvae that behaviorally exploit these flows, as speculated by Pineda and López (2002). Spatial variability in benthic population abundance, another expression of patchiness, is a hallmark of many marine populations, and ecologists have asked for decades whether this variability is related to variability in larval transport, settlement, and recruitment (Efford, 1970; Eggleston et al., 1998). Horizontal variability in larval transport has also been related to coastal physiography (Morgan et al., 2011; von der Meden et al., 2012) and potentially larval swimming proficiency (Daigle et al., 2014).

In coastal environments, cross-shore crustacean larval distributions are sometimes structured by stage (Bousfield, 1955) and reflect distance from natal habitat, with early stages adjacent to nearshore habitats. These distributions might also suggest changes in behavior with stage. For example, Tapia and Pineda (2007) found early nauplii stage intertidal barnacle larvae near the shore with mid-stages further offshore; yet larvae of the terminal cyprid stage were found nearshore, suggesting an ontogenetic change in behavior.

11.6 Challenges and Recent Approaches to Understanding and Measuring Larval Transport

11.6.1 Challenges

The importance of larval movement and dispersal for the ecology of bottom organisms has been acknowledged for over one and a half centuries (Lyell, 1832; Young, 1990). For example, discussing the mechanisms accounting for fish size-class strength, Hjort (1926) offered two explanations, one based on food quality and the other on larval transport.

Despite decades of interest, larval transport mechanisms for the majority of systems remain unresolved. Spatial and temporal scales of variability in chemical and physical variables can be addressed with time-series analyses using off-the-shelf sensors (e.g., temperature loggers and acoustic Doppler current meters) and statistical techniques, such as spectral analyses (discussed in Haury et al., 1978). So far, these approaches are limited for

resolving larval transport and distribution because high-frequency, species-specific sampling and processing capability of up to thousands of samples is practically impossible. Moreover, variability in the larval pool may result in failure in identifying the forcing physical processes, as discussed previously, and zooplankton distributions are non-stationary (Haury et al., 1978), violating the assumptions of spectral analysis.

Ideally, development of high frequency and spatially dense sampling, and development of techniques for analyzing large numbers of samples would resolve dynamic larval distributions, and in this way advance our understanding of the larval transport process. Pragmatically, costs associated with the development of such sampling and analysis techniques at current cost and funding levels may hinder their further development.

The main challenges for resolving larval transport include the following: (a) patchy spatial distributions, (b) episodic larval transport events, (c) enormous ranges of spatial and temporal scales of the potential processes, (d) knowledge of larval behavior during transport, (e) imperfect knowledge of physical transport processes, (f) the arduous nature of observational approaches to measuring and inferring larval transport, and (g) the variety of species and settings to be understood. Later, we discuss these challenges, and contemporary and promising approaches that might help resolve the larval transport processes. We also caution about potential pitfalls of some methodologies.

To address patchiness, episodic transport, and the wide range of scales, (a)–(c), we suggest that, when possible, a hypothesis-based approach and “adaptive sampling” be used to test specific processes. An explicit hypothesis-based approach identifies advective mechanisms underlying larval transport events, with expectation on how physical fields such as temperature and currents behave with or change in response to the advective event. It tests predictions of temporally and spatially constrained larval abundance, and horizontal and vertical distributions. In adaptive sampling, changes in specific environmental conditions initiate larval sampling. Obviously, this approach requires contrasting larval distributions during hypothesized transport against larval distributions in non-transport

circumstances. Ideally, adaptive sampling should be accompanied by other types of measurements, including settlement time series. This sampling approach also requires real-time communication to remote environmental sensors (e.g., temperature or current velocity data). Technology for adaptive sampling, including satellite, radio, and cell network communications, is mature and, because some of this technology is used commercially, it is relatively inexpensive. Adaptive sampling has been used successfully in addressing various event-type phenomena in biological oceanography, including the study of larval transport by internal tidal bore warm fronts (e.g., Pineda, 1999). Adaptive sampling is challenging to research teams because it requires the formulation of a specific hypothesis and a crew to be in standby for extended periods.

Larval behavior during transport, (d), may be more economical to address after other larval transport processes are identified, because the larval behavioral repertoire is very large (Metaxas, 2001; Epifanio and Cohen, 2016). For example, hypotheses of larval behavior during transporting events can be posed after identifying the physical processes and the vertical distributions associated with the event. Improvement in understanding near-shore physical advective processes associated with larval transport, (e), will require progress in understanding fundamental nearshore hydrodynamics (Lentz and Fewings, 2012), as well as knowledge of the nearshore and coastal circulation associated with unpredictable events, such as storms.

Observationally, larval transport can be addressed with field measurements of physical fields, larval distribution, and settlement (f). In situ circulation and larval distribution studies can unambiguously identify larval transport processes, but sustained and targeted studies of larval distributions are very challenging. Thus, researchers often resort to study settlement, where long-term sustained measurements are possible. These observations can reveal characteristic spatial and temporal patterns and suggest larval transport mechanisms (Eggleston et al., 1998; Reyns and Sponaugle, 1999; Pfaff et al., 2015). Settlement, however, is necessarily inferential, and results require cautious interpretation (Pineda, 2000). Simultaneous measurement of larval distribution and settlement is arguably the

most powerful approach to address larval transport processes. Finally, for addressing (g), the large diversity of systems, the hope is that resolution of a number of larval transport cases will lead to some generalities, for example, swimming behavior against the dominant vertical currents (Figure 11.4).

11.6.2 Recent Approaches

Recent technology and methodological approaches, including computer-technology miniaturization, improved computing capability, development of imaging techniques, and remote sensor development (e.g., satellite SAR and spectroradiometer sensors), have revolutionized areas in ecology and oceanography. Some of the recent technology and approaches, including inexpensive sensors with improved endurance, and numerical modeling, have been used to address larval transport. These developments represent opportunities for larval ecologists, yet there are also nagging issues to consider.

11.6.2.1 Autonomous and Remote Sampling

Autonomous and remote observations of physical and biological properties are revolutionizing fields in oceanography (Clark and Isern, 2003). One promising area for larval transport is the development of remote, autonomous sampling of larval distributions by building and mounting larval samplers to autonomous underwater vehicles (AUVs). Researchers have demonstrated AUV sampling of larvae in coastal (Ryan et al., 2014; Govindarajan et al., 2015) and benthic deep-sea environments (Billings et al., 2016). The advantages of these devices over plankton pumps and nets include (a) the ability to sample very close to the bottom; (b) increased spatial resolution (i.e., few meters), particularly for deep sampling, where net resolution is coarse and maneuvering a pump intake is very challenging; and (c) the possibility to sample larvae adaptively, in response to changing physical and biological fields (e.g., temperature, fluorescence). These devices, however, take only a few samples (two to less than a handful; Ryan et al., 2014; Billings et al. 2016), or sample a small volume of water (~2 to 55 L; Ryan et al., 2014; Govindarajan et al., 2015). Further, they are expensive to build and operate. Therefore, while the devices have already

helped resolve larval abundance and distribution fields, improvements in sample number, sampling volume, and cost reduction remain necessary. Other recent advances include the development of drifters that can be tracked and programmed for different vertical positioning (T. Wolcott and S. Morgan, pers. comm.; J. Jaffe, pers. comm.). The next step in AUV development, particularly to address issues of larval patchiness, might include swarms of AUVs that communicate and adaptively sample larval distributions.

11.6.2.2 Imaging in Distributional Studies and Species Identification

Imaging of plankton using towed vehicles can reveal fine- to large-scale (centimeters to thousands of kilometers) field distributions, and a variety of approaches have been developed in the last 25 years (Wiebe and Benfield, 2003). Use of this approach has revealed small (few centimeters) to basin-scale variability in plankton distribution (Davis et al., 1992; Davis and McGillicuddy, 2006), including distributions of diverse trophic groups (Greer et al., 2013), and spacing among and orientation of individual zooplankton (Cowen and Guigand, 2008). A caveat of some of these devices, small sample size, has been addressed with new systems that can sample larger volumes (Cowen and Guigand, 2008), although at the expense of sampling rate, towing speed, and plankton size resolution. These approaches have enormous potential for resolving plankton and larval distribution, but automatized identification of rare or small and “difficult” invertebrate larvae remain a problem (Wiebe and Benfield, 2003), and the cost of the technology makes it prohibitive for large segments of the research community.

Automated larval species recognition in field samples, one of the nagging issues in larval studies, was addressed with the development of an imaging approach based on automated recognition of species-specific coloration of larval bivalve shells (Tiwari and Gallager, 2003; Thompson et al., 2012a). This approach has been used successfully in field studies using larval bivalve dynamics (Thompson et al. 2012b; Goodwin et al. 2014). This system is, so far, limited to bivalve shells and requires a reference library with the exact set of known species to be identified (Thompson et al., 2012a).

11.6.2.3 In Situ Species Identification and Robotic Techniques

The -omics approaches are revolutionizing the biological sciences, including select areas in marine ecology, which are addressed in Williams and Carrier (this volume). Here, we point to two developments. First, use of barcoding to identify minute larvae to species (Ryan et al., 2014; Govindarajan et al., 2015; Billings et al., 2016). This development is particularly important for identifying problematic larvae (e.g., small bivalve larvae). A related approach is in situ species identification using robotic systems and sandwich hybridization methods (Goffredi et al., 2006). With improvement in sample processing time, necessary for resolving high-frequency transporting events, these devices will be able to remotely detect species of interest and perhaps initiate adaptive sampling. The widespread use of these devices might only be feasible once costs decrease.

11.6.2.4 Numerical-Modeling and Observational Approaches to Larval Transport

Taking observations to measure larval transport is arduous and expensive, equipment can be lost and vandalized, and researchers get seasick. Moreover, biological observations in systems where processes at multiple spatial and temporal scales operate tend to be sparse. Despite these impediments, observational approaches have revealed almost all phenomena relevant to larval transport and dispersal, including the following: (a) the realization that larval vertical migration is the main mechanism determining horizontal transport (Nelson, 1912); (b) awareness of “wastage” during the larval phase, including a geometric decrease of larval concentration with distance from natal habitat related to mortality and diffusion (e.g., Hjort, 1926; Scheltema, 1986), and the role of large-scale features in larval wastage (Porri et al., 2014); (c) the existence of long-lived larvae and potentially large dispersal distances (Scheltema, 1968); (d) that upwelling (Garland et al., 2002), upwelling relaxation/downwelling (Farrell et al., 1991; Wing et al., 1995), internal tidal bore warm fronts (Pineda, 1999), and eddies (Sponaugle et al., 2005) are associated with onshore larval transport to adult habitats; (e) unambiguous evidence that larvae can return to natal habitats (Jones et al. 1999); and (f) the

finding of constrained larval distributions in near-shore temperate settings (Barnett and Jahn, 1987; Tapia and Pineda, 2007; Morgan et al., 2009).

Simulation numerical models of larval transport and dispersal, on the other hand, are relatively inexpensive to run, can readily fill any spatiotemporal domain and simulate larval transport and dispersal processes at regional scales, link a variety of disparate processes (Werner et al., 2007), and rapidly generate results for unsuspecting researchers. Here, we restrict our discussion to numerical simulation models at geophysical scales in the sense of Oreskes et al. (1994), where these models are used “to evaluate large-scale or complex physical processes” (p. 641). We do not deal with models based on interpolated observations (Paris and Cowen, 2004), with “heuristic” models (Cowen et al., 2000; Botsford et al., 2001; Tilburg, 2003; Pringle et al., 2011), where fundamental relationships are used to illustrate a given dynamics, or with models of small-scale domains (Scotti and Pineda, 2007), where the physical processes are relatively well understood and the parameter space is constrained.

Compared to observational approaches, however, fundamental new insights by numerical models are very rare, even considering their relatively recent emergence in oceanography (late 1960s; Kantha and Clayson, 2000). For example, combined numerical modeling and observational studies have suggested that dispersal among coral reefs could be both limited and feasible (Wolanski et al., 1989; cited in Black et al., 1991). Other types of modeling (e.g., “heuristic” models, not simulation models), have also contributed. A heuristic model highlighted that diffusive and mortality processes caused larval abundance to decrease geometrically with distance from larval release, contributing to the realization that marine populations were more closed than originally thought (Cowen et al., 2000).

Researchers are gravitating toward regional simulation numerical models, such as the regional ocean modeling system (ROMS) and the finite volume community ocean model (FVCOM) to link hydrodynamic and larval behavior processes with larval transport and dispersal patterns. Simulation of physical fields (e.g., density, currents) by numerical modeling is a key component in many disciplines, and these models are well accepted in situations

where the systems to model are relatively simple and the processes involved well understood and parameterized (e.g., White and Helfrich, 2008). In systems where models have been thoroughly tested (Gilg and Hilbish, 2003), or the behavioral and distributional processes accounting for the transport of larvae are understood, and the hydrodynamic processes relatively well resolved (North et al., 2008), numerical modeling can offer valuable insights to larval transport and dispersal issues. Research comparing model predictions and field observations is also valuable, as modeling results can be tested against some observable property (Wolanski et al., 1989; Sponaugle et al., 2012).

Unfortunately, many systems studied by marine ecologists are complex (e.g., nearshore open-coast), biological and physical processes are understudied or unknown, and models go untested. Ecologists should hold numerical-modeling studies to the same standards as experimental and observational studies, but this practice is very rare. Simulation numerical models, like other hypotheses, should be tested observationally, against “Lagrangian” observations (e.g., Hrycik et al., 2013), or at least against other observed properties (Trindade et al., 2016). Further, in some larval transport and connectivity studies, numerical output is equated to an accurate depiction of the physical fields, with little objective evaluation of the assumptions or validity of this premise. In other cases, modeled and observed “Eulerian” fields are compared, and if the comparison is favorable, the model is said to be “validated,” justifying using the numerical output as observations. However, simulation numerical models *cannot* be validated (Oreskes et al., 1994); they remain hypotheses. As such, it is untenable to use them to test other observational data. Another complication is the many and poorly characterized biological variables integrated in these models (Metaxas and Saunders, 2009). Finally, because model parameters can be tweaked to represent a range of results (e.g., limited or wide dispersal distance), research reporting modeling results should present a clear description of the iterative parameter choice or a range of results (e.g., Ross et al., 2016).

No simulation numerical model features all the potentially relevant mechanisms that move the water and are associated with larval transport in coastal

and nearshore settings—another issue that is not often addressed in the larval transport and connectivity literature. For example, these models often do not capture the small-scale processes that may account for nearshore larval transport (e.g., transport by surface waves and propagating convergences such as upwelling fronts and internal tidal bore warm fronts). This is highlighted by recent advances in our understanding of the dominant processes driving the cross-shelf circulation over the nearshore region (for a review, Lentz and Fewings, 2012). Historically, studies of wind-driven shelf circulation have focused on along-shelf wind forcing and coastal upwelling or downwelling. The dominant role of surface waves and cross-shelf winds in driving cross-shelf circulation over the nearshore has been highlighted in a sequence of process-oriented studies (Tilburg, 2003; Lentz et al., 2008), and, notably, surface wave forcing has only recently been incorporated into regional hydrostatic circulation models (e.g., Newberger and Allen, 2007). Thus, the commonly invoked premise that numerical models can be used to test the role of larval behavior in larval transport and dispersal by comparing numerical model output with observations of dispersal obtained by other means does not hold, because the numerical model does not include all relevant processes that account for passive dispersal, and therefore the “real” dispersal of passive particles is unknown.

Regional hydrostatic models are not a substitute for process-oriented understanding. Particularly for research addressing complex settings such as the nearshore and coastal ocean, with a large range of scales and where multiple mechanisms might play a role, it should be obvious that some level of process-understanding of larval transport should be achieved first, followed by simulations by numerical modeling. Knowledge of the process reduces the dimensional complexity of the modeling problem, limiting the number of possible scenarios, and focusing the modeling research. Blind modeling is risky and inefficient, yet, to date, few modeling studies addressing larval transport and dispersal operate with knowledge of the specific larval transport processes involved, and even fewer compare model predictions with observations.

In summary, process-oriented understanding of larval transport and model testing is key for

achieving an understanding of larval dispersal and connectivity, and basic process understanding of biological and physical processes is necessary before simulation numerical modeling.

11.7 Conclusion and Next Steps

Understanding larval transport processes in the coastal ocean has increased considerably during the past 25 years, due to improvements and cost reduction in technology, approaches often based in hypothesis testing, a more sophisticated understanding of the behavioral and physical processes, a more critical appraisal of the evidence in observational studies, and a mechanistic resolution of a handful of larval transport cases. Advances include an understanding that larval supply and settlement observations measure different processes, appreciation of the importance of accumulation processes and of how larger-scale processes might modulate local factors that influence larval transport, a realization that propagules and larvae have generally a more constrained distribution than originally thought, and insight about the distinction of the nearshore and open-ocean domains. Although process-oriented understanding of larval transport has increased incrementally, more understanding of the dominant mechanisms of larval transport is needed.

On the other hand, interest and necessity in understanding larval transport and connectivity at regional scales, coupled with the difficulty in resolving observationally these processes, has led to the growth of simulation numerical modeling. So far, this growth has been disproportionate relative to model testing and fundamental knowledge of the processes. Thus, if these models are to be useful to understanding natural systems, simulation numerical models should be accompanied by testing (e.g., Hrycik et al., 2013) and constrained by understanding of specific larval transport processes at work.

Technological development, broader sensor usage, and reduction of costs foretell a future where the coastal ocean will be seeded with a multitude of sensors that aid in resolving larval transport. Nonetheless, intensive field and laboratory studies addressing process-level understanding of larval transport will still be sorely needed. Simulation numerical models are growing in sophistication, yet our understanding

of physical processes in complex systems is still incomplete, and our knowledge of the relevant larval processes to include in these models is meager.

We conclude by suggesting that the next step in larval transport understanding should include wider use of emergent technologies and mechanistic resolution of larval transport in multiple systems. Numerical models will be useful if they incorporate the relevant larval transport processes, and are well tested; unfortunately, so far these studies are sorely lacking.

11.8 Summary

1. Larval transport is defined and discussed, both as a concept and as a measurement.
2. The components of larval transport include larval behavior, primarily those behaviors influencing larval vertical distribution, physical advective and diffusive processes, and their variability.
3. Other first-order phenomena in larval transport include larval accumulation in propagating fronts, larval swimming proficiency and size, larval duration, larval patchiness and episodic larval transport, and spatial variability in larval transport.
4. There are multiple challenges for understanding larval transport: (a) patchy spatial distributions, (b) episodic larval transport, (c) enormous range of spatial and temporal scales of the potential processes, (d) knowledge of larval behavior, (e) imperfect knowledge of physical transport processes, (f) the arduous nature of observational approaches, and (g) the multitude of species and settings to be understood.
5. Recent approaches addressing larval transport include autonomous and remote sampling, imaging approaches, in situ species identification and robotic techniques, and numerical models.
6. The advantages of simulation numerical models are minimal cost and the ability to address regional scales and link disparate processes. Some drawbacks include lack of testing, use of numerical output as observations, and uncertainty surrounding whether relevant larval transport processes are included.

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