

Larval Transport and Dispersal in the Coastal Ocean and Consequences for Population Connectivity

BY JESÚS PINEDA, JONATHAN A. HARE, AND SU SPONAUGLE

MANY MARINE SPECIES have small, pelagic early life stages. For those species, knowledge of population connectivity requires understanding the origin and trajectories of dispersing eggs and larvae among subpopulations. Researchers have used various terms to describe the movement of eggs and larvae in the marine environment, including larval dispersal, dispersion, drift, export, retention, and larval transport. Though these terms are intuitive and relevant for understanding the spatial dynamics of populations, some may be nonoperational (i.e., not measurable), and the variety of descriptors and approaches used makes studies difficult to compare. Furthermore, the assumptions that underlie some of these concepts are rarely identified and tested. Here, we describe two phenomenologically relevant concepts, larval transport and larval dispersal.

These concepts have corresponding operational definitions, are relevant to understanding population connectivity, and have a long history in the literature, although they are sometimes confused and used interchangeably. After defining and discussing larval transport and dispersal, we consider the relative importance of planktonic processes to the overall understanding and measurement of population connectivity. The ideas considered in this contribution are applicable to most benthic and pelagic species that undergo transformations among life stages. In this review, however, we focus on coastal and nearshore benthic invertebrates and fishes.



Larval transport is defined 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. In larval transport, only the spatial dimensions matter. Although this definition ignores the vertical axis (z) for simplicity, this dimension is critical for larval transport because larvae can modify their horizontal distribution by swimming vertically, thereby encountering different currents (Nelson, 1912; Crisp, 1976). To transfer from point x_1, y_1 to point x_2, y_2 , a larva can swim horizontally and may be transported by diffusive and advective processes (Scheltema, 1986). Defined as the translocation of a larva between two points, larval transport appears deceptively simple. However, the wide range of larval behaviors and physical mechanisms, together with their variability at multiple scales, makes larval transport exceedingly difficult to measure. The temporal and spatial scales of variability are enormous (Scheltema, 1986), even when considering a single physical transport mechanism (see Box 1).

In contrast, **larval dispersal** refers to the spread of larvae from a spawning source to a settlement site. This definition is consistent with the terrestrial literature (natal dispersal in Clobert et al., 2001; Begon et al., 2006) that describes seed dispersal as the probability density function of the number of seeds versus distance from the adult source (i.e., the dispersal kernel) (Nathan and Muller-Landau, 2000; see Gerrodette, 1981, for a rare marine example). Using the dispersal kernel, dispersal can be viewed as a probability that a released zygote will make it to settlement over

a certain distance, herein referred to as dispersal distance. Larval transport is an important component of larval dispersal, and broad dispersal requires significant larval transport. Restricted dispersal, however, does not imply little larval transport (Figure 1). Further, processes and factors associated with the end of larval transport (i.e., settlement) also influence dispersal, including settlement behavior, distribution of suitable settlement sites, and refuge availability (Figure 2). Similarly, because spawning initiates larval dispersal, spawning time and location are important, as are factors influencing spawning, including season and synchronicity of spawning, age and condition of spawners, and fertilization success. In addition to the spatial dimensions inherent in larval transport, larval dispersal involves a survival probability, and thus food availability and predation are important. The highest mortality in marine populations occurs

invasive species, and other phenomena (Cowen et al., 2006, this issue; Levin, 2006). By this definition, if the exchange is measured at the time of settlement, connectivity is essentially larval dispersal from one population to another (e.g., Webster et al., 2002). Not all settlers will survive, however, and survival may be influenced by larval experience. Thus, connectivity is frequently measured at some point after settlement, once settlers survive to enter, or recruit to, the juvenile population. Functionally, however, this point is somewhat arbitrary and differs among taxa. A more precise demographic milestone is reproduction. If settlers die without reproducing, dispersal is of questionable importance to population growth or spread of invasive species. In this contribution we differentiate between population connectivity, measured at the time of settlement, and **reproductive population connectivity**, defined as the dispersal of individu-

The fundamental challenge in population connectivity studies is to determine the source populations of settling larvae and the settlement sites of dispersing larvae.

during the early life stages, so mortality plays a large, but understudied, role in larval dispersal.

Population connectivity has been defined as the exchange of individuals among geographically separated subpopulations (see Cowen et al., this issue) and is thought to be a key process for population replenishment, genetics, spread of

als among subpopulations that survive to reproduce. Reproductive population connectivity encompasses larval dispersal but is also influenced by post-settlement mortality (e.g., Hunt and Scheibling, 1997; Doherty et al., 2004), growth, and condition from settlement to successful reproduction. By the definition above, although dispersal of larvae

that do not survive to reproduce can play a role in population and community ecology, their contributions to reproductive population connectivity are minimal (Figures 1 and 2).

LARVAL TRANSPORT

Reconsideration of the Scales of Larval Transport

The term larval transport brings to mind small, passive larvae being moved throughout the ocean by meso- and large-scale physical processes (Johnson, 1939). This view has become a paradigm—larvae are released, transported by mesoscale processes, mixed in a larval pool, and then randomly recruited to juvenile or adult habitat

(e.g., Roughgarden et al., 1988; Siegel et al., 2003). An increasing number of studies, however, conclude that a significant amount of self-recruitment occurs in marine populations (Jones et al., 2005; Almany et al., 2007). These conclusions are not in and of themselves surprising: a population is defined as a self-sustaining component of a species, and thus self-recruitment is a defining attribute of a population (Sinclair, 1988). What is surprising is the relatively small spatial scales over which self-recruitment has been observed. For example, despite a planktonic stage of 9–12 days, approximately 30% of settling panda clownfish self-recruited to an area of 0.5 km² (Jones et al., 2005). The implication of

this and similar observations, combined with recent modeling and genetic studies (Cowen et al., 2000; Gerlach et al., 2007)

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BOX 1. VARIABILITY IN SPATIAL AND TEMPORAL SCALES OF LARVAL TRANSPORT

The movement of larvae in internal bores is an example of the variety of spatial and temporal scales involved in larval transport. Larval accumulation at surface-propagating convergences is critical for effective transport in internal bore warm fronts, and the time scales of these convergences are from a few seconds to a few hours. On the other hand, water-column stratification, a seasonal phenomenon, modulates the energy of internal bores and therefore also impacts larval transport (Pineda and López, 2002). At even larger scales, stratification and internal bores are modulated by El Niño, an interannual phenomenon (Zimmerman and

Robertson, 1985). Thus, temporal scales relevant for understanding larval transport by internal tidal bores range from seconds to years. Other temporal scales important to internal tidal bore larval transport that are not depicted here include fortnightly periodicity (~ 14.4 days), and the periodicity of coastally trapped waves (a few weeks; Pineda and López, 2002). In the literature, larval transport generally encompasses horizontal distances ranging from tens to hundreds of kilometers, a usage we follow in this contribution.



and the constrained nearshore larval distributions of littoral species (Barnett and Jahn, 1987; Tapia and Pineda, 2007), is that the spatial scales of larval transport may be much smaller than previously recognized. These results indicate that small-scale and nearshore physical processes play an important role in larval transport (Kingsford, 1990; Willis and Oliver, 1990; Pineda, 1999).

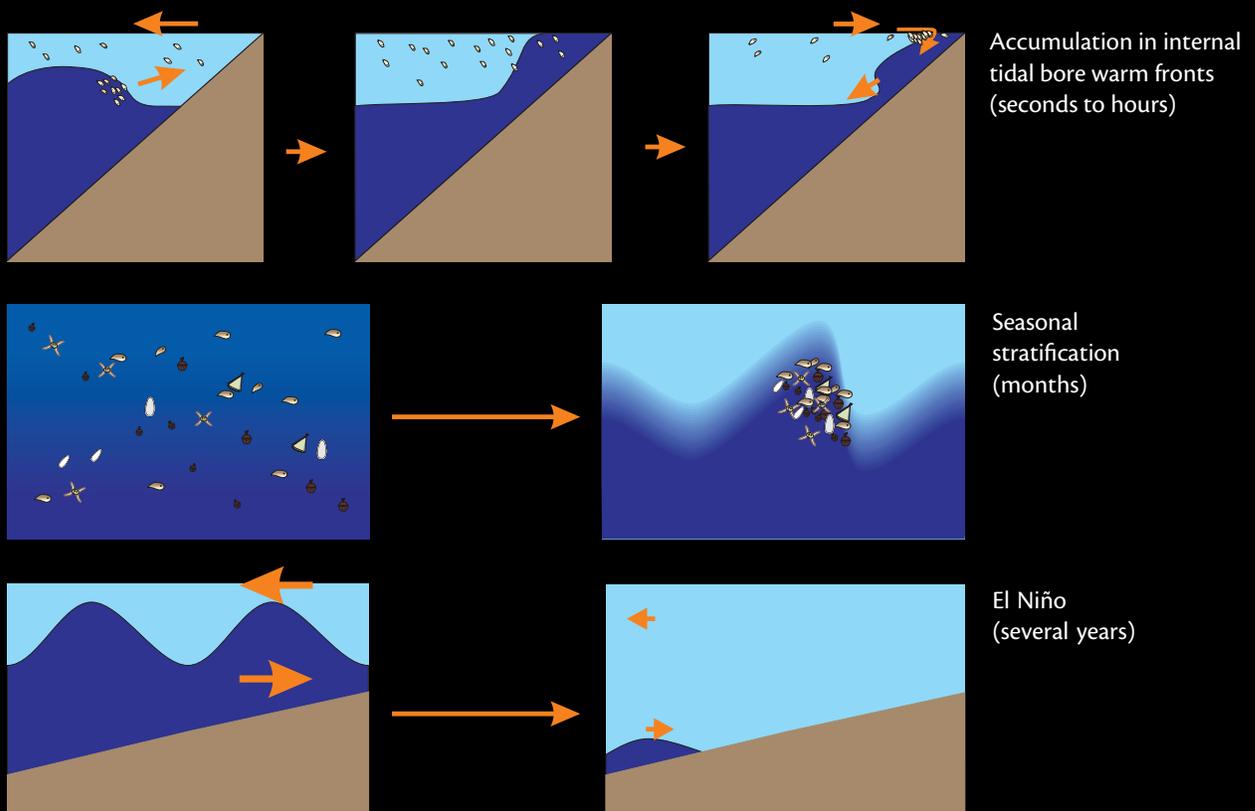
Nearshore, Coastal, and Oceanic Currents

Flows in nearshore, shallow environments, including the surf zone, are different from coastal and deep-ocean

flows mainly because of the shoreline barrier, shallow depths, bathymetric features associated with the continental shelf, and nearshore inputs of freshwater.¹ Moreover, flows in nearshore waters tend to be more complex than in the deep and coastal ocean because many processes operate there, including surface gravity waves, buoyancy-driven flows, wind-forcing, surface and internal tides, large-amplitude internal waves and bores, and boundary-layer effects. These differences between nearshore and coastal/open ocean hydrodynamics are important for larval transport. The shoreline barrier serves as a

topographic guide for coastally trapped waves and tends to steer flows in the alongshore direction (see Box 2). Tidal ellipses that tend to be isomorphic in the open ocean become compressed near the coast, and large-scale flows such as the Gulf Stream and the Humboldt Current flow parallel to the shoreline, not perpendicular. Freshwater runoff and large-scale currents running parallel to the coastline produce characteristic stratification in the nearshore, such as shallowing of the thermocline near the coastline in response to the California Current (Hickey, 1979) and the Florida Current/Gulf Stream (Leaman et al.,

¹In this contribution we use the term nearshore to describe (a) the shallow waters where surface and bottom Ekman layers interact, the nearshore of Mitchum and Clarke (1986), and the inner shelf of Lentz (1995), and (b) the surfzone, while the coastal region includes mid- and outer-shelf areas.



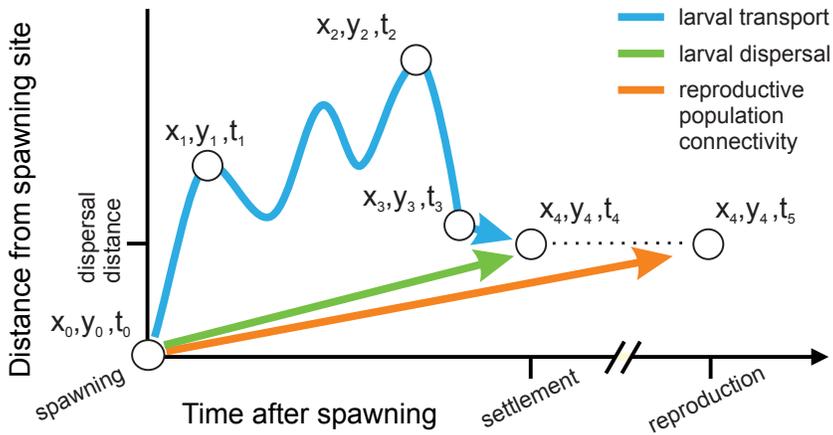


Figure 1. Relationship between the spatial and temporal components of larval transport, larval dispersal, and reproductive population connectivity for a sessile species. Survivorship is not depicted. Note that the sum of larval transport distances can be larger than the dispersal distance. White circles are locations in space with coordinates x - y at times t . All locations are pelagic except x_0, y_0 and x_4 and y_4 which are benthic. Distance could also be represented in two dimensions (e.g., x, y as cross- and alongshore axes.)

1989). Salinity (Thièbaut et al., 1992) and water-column stratification (Pineda and López, 2002) contribute to larval transport because sharper stratification in shallow waters (e.g., Hickey, 1979) allows larvae of coastal species to exploit vertically sheared flow to control horizontal distributions (Paris and Cowen, 2004), and internal motions such as internal tidal bores may transport larvae onshore. Surface waves that break near the shore produce some mass transport, and storm systems that originate in the deep ocean sometimes move onshore. Flows in the nearshore are broken by coastline topographic features such as bays and capes, resulting in complex flows with smaller spatial coherence (see discussion in Okubo, 1994). This is true for cross-shore coastal flows, whose coherence scales are much smaller than the alongshore coastal flows (Brink, 1999). The relative importance of these processes varies with depth and distance

from the shoreline (e.g., Lentz et al., 1999; Largier, 2003).

Modulation of Nearshore Cross-Shore Transport by Large-Scale Processes

Clearly meso- and large-scale processes affect larval transport, and most studies emphasize these effects. Large-scale physical processes also influence the smaller-scale processes discussed above. Many large-scale circulation systems and processes, such as eastern and western boundary currents, El Niño, coastal upwelling, and coastally trapped waves, are energetic and coherent in the alongshore direction, but can also modulate smaller-scale processes in ways that enhance or suppress larval transport. For example, as pointed out above, the strength of the California Current determines the depth of the thermocline in shallow nearshore waters, with a stronger current resulting in a shallow ther-

mocline. A shallow thermocline creates vertically sheared environments that may restrict larval transport for species with diel vertical migration; thus, interannual variability in the strength of these large-scale current systems might lead to variability in dispersal, an untested speculation. Consider the effects of coastal upwelling, El Niño, and coastally trapped waves on shallow water stratification and cross-shore transport along the west coasts of North and South America. The combination of strong coastal upwelling and El Niño produces weak nearshore stratification due to the upwelling of unstratified cold waters and the piling up of mixed surface warm waters in the nearshore (Simpson, 1984; Zimmerman and Robertson, 1985). Both upwelling and El Niño result in decreased water-column stratification, suppressing the shallowing of the thermocline by the internal tide and the internal tidal bores, which, in turn, may result in decreased onshore larval transport (recent work of author Pineda and Manuel López, Centro de Investigación Científica y de Educación Superior de Ensenada). In contrast, coastally trapped waves produce a transient, small drop in sea level that is compensated by a large uplifting of the nearshore thermocline. This results in the shallowing of the thermocline by the internal tide and larval transport by internal bore warm fronts (Pineda and López, 2002).

Small-Scale Processes and Event-Type Larval Transport

Spatial and temporal scales are linked in the ocean (Stommel, 1963), so the importance of small-spatial-scale processes underscores the significance of

small-temporal-scale processes to larval transport. Moreover, meso- and large-scale processes can exhibit small-temporal-scale variability (Stommel, 1963) and be episodic (e.g., hurricanes). Larval settlement from the plankton for many marine organisms is episodic, and it is not uncommon to have the majority of a season's settlement occur in a handful of days (Forward et al., 2004; Sponaugle et al., 2005). Even though settlement records imply transport events and are often correlated with various physical factors, the observation of event-driven larval transport remains elusive. Similarly, larval distributions are often used to infer transport and the influence of events (e.g., the occurrence of an eddy; Limouzy-Paris et al., 1997), but few studies have measured the movement of larvae in the water over time by event-type processes. When larval distributions are sampled repeatedly over time, they offer excellent views of the processes involved in larval transport (Pepin and Helbig, 1997; Natunewicz and Epifanio, 2001), but due to sampling limitations, such studies are rarely able to observe the influence of smaller-scale processes. Examining the effect of events on transport is more straightforward in a modeling context—a well-modeled example is the effect of wind-driven events on settlement (Garvine et al., 1997; Brown et al., 2004)—but most circulation models do not capture smaller-scale physical processes, frontogenesis, frontal convergence and divergence, intrusions, internal waves, and topographic effects, particularly in the nearshore.

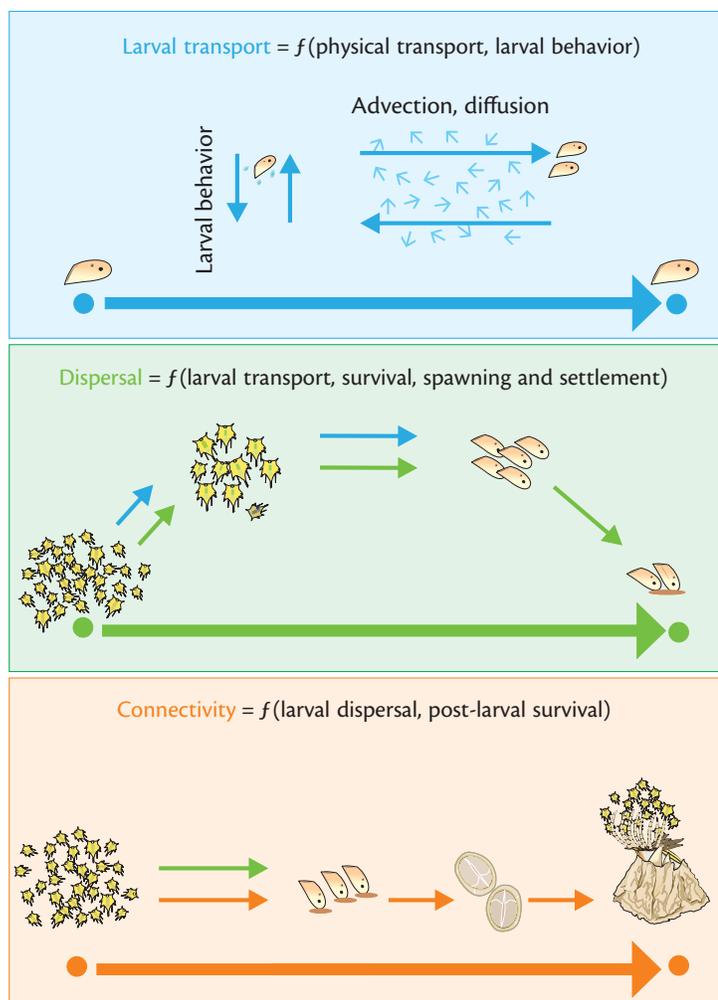


Figure 2. The concepts of larval transport, larval dispersal, and reproductive population connectivity. Colors of arrows distinguish each concept. For example, the green arrow in the connectivity box means dispersal is involved in reproductive population connectivity.

Behavior and Larval Transport

As our appreciation of small-scale physical processes grows, so does our appreciation for the role of larval behavior in influencing larval transport. For many years, larvae were considered planktonic, that is, moving at the whim of ocean currents but using feeding and predator avoidance behaviors that resulted in small-scale (millimeters to centimeters) movements (Blaxter, 1969). The view of passive larvae gave way to the con-

cept that vertical swimming behavior, changes in buoyancy, and ontogenetic changes in vertical position influence the horizontal movement of larvae; this view was adopted early in estuarine and coastal lagoon systems (Nelson, 1912; Pritchard, 1953; Bousfield, 1955) and later in shelf and open-ocean systems (Kelly et al., 1982; Cowen et al., 1993). Additionally, the influence of larval settlement behavior on the specific location of settlement, at scales of meters to tens

of meters, was recognized as important (e.g., Crisp, 1976; Raimondi, 1991).

More recent research shows that larvae also have horizontal swimming capabilities that improve with development (see review by Leis, 2006). For example, larvae of a damselfish swam continuously for 39 hours without food, covering a distance equivalent to 19 km (Stobutzki, 1997). Similarly, larval lobsters and early pelagic stages of cephalopods are good swimmers (Villanueva et al., 1996; Jeffs and Holland, 2000). In combination with the capability to swim vertically and horizontally, larvae of both invertebrates and vertebrates can orient and potentially navigate over short (meter-to-kilometer) to long (10-to-100-km) distances, using light,

sound, smell, and possibly magnetism, electric fields, and wave swell (e.g., Kingsford et al., 2002; Gerlach et al., 2007). Clearly, larvae are complex and capable organisms that develop the ability to feed, avoid predation, and move within the pelagic environment. Thus, in the equation of larval transport, behavior plays an equally important role as advection and diffusion.

LARVAL TRANSPORT: RESEARCH NEEDS

Identification of Nearshore Larval Transport Mechanisms

Knowledge of larval transport in nearshore environments is very limited. Major drawbacks include lack of rigorous knowledge of the suspected physical

mechanisms involved in larval transport, and ignorance of other potential transport mechanisms (see Cowen, 2002, for a review). Physical mechanisms that could affect transport include surface gravity waves (Monismith and Fong, 2004), submeso- and mesoscale eddies (Bassin et al., 2005; Sponaugle et al., 2005), barotropic tidal currents (Hare et al., 2005; Queiroga et al., 2006), and cross-shore winds (Tapia et al., 2004).

Some proposed mechanisms have not been tested rigorously in field conditions. Moreover, the logistical difficulty of studying transport sometimes can push researchers to use weak inferential approaches, such as inferring larval transport mechanisms from settlement data (Pineda, 2000; Queiroga et al.,

BOX 2. ALONG- AND CROSS-SHORE PHYSICAL TRANSPORT PROCESSES

Larval transport in nearshore and shelf species is often split into cross- and alongshore components (e.g., Hare et al., 1999; Ma and Grassle, 2005). This distinction follows a convention in coastal physical oceanography and is convenient because cross- and alongshore hydrodynamic processes have different temporal and spatial scales (Winant, 1983), different physical processes dominate cross- and alongshore transport (e.g., Winant and Bratkovich, 1981), and momentum balances in these two axes are accounted for by different terms (e.g., Lentz et al., 1999). Also, plankton patches have widely different dimensions in the two axes (Mullin, 1993). Because the strongest gradients in water properties and ecological variables are in the cross-shore dimension, transport on this axis has a disproportionately large effect on the distribution of larvae. For nearshore species whose later developmental stages move progressively offshore with time, such as the southern California barnacle nauplii (Tapia and Pineda, 2007), cross-shore transport is the most critical process, as older larvae tend to be farther away from the shore and must return nearshore to settle and reproduce. Similarly, for species that move offshore to spawn but have nearshore settlement habitats, such

as Atlantic menhaden (Quinlan et al., 1999), larvae must move onshore to recruit to juvenile habitats. Although cross-shelf transport is often emphasized in studies of larval transport, it is obvious that alongshore processes also play a role (Hare et al., 1999), particularly in population connectivity. Nearshore and coastal marine populations are generally arrayed along coasts, and the alongshore movement of larvae between these populations can keep these geographically isolated populations connected.



2006). The lure of mesoscale processes and satellite oceanography has proved irresistible for some shallow-water ecologists, resulting in an overemphasis on explanations based on mesoscale processes while disregarding nearshore processes and mechanisms that cannot be studied remotely. Unambiguous identification of the mechanisms of larval transport is rare, and testing alternative explanations is almost unheard of. Thus, there is a serious need to follow up some of these weakly founded hypotheses with rigorous tests. With limited knowledge of nearshore larval transport, it seems that assessing the relative contributions of various physical transport mechanisms in larval transport for a given case study is, so far, only a utopian hope. The field will be mature when such a study can be proposed and accomplished.

Understanding the role of small-scale processes in larval transport is also limited by modeling capabilities. Large-scale and mesoscale models forced by winds and the surface tide are now commonplace (see Werner et al., this issue). The spatial resolution of these models is increasing and extending into nearshore areas (e.g., Chen et al., 2006). Decreased grid size, however, is only one aspect of resolving smaller-scale processes. Small-scale processes, such as surface waves, internal waves, and propagating convergences, need to be included. Currently, no numerical model appears capable of simultaneously resolving Lagrangian transport caused by, for example, shallowing internal tides, sea breeze, large-amplitude internal waves, and surface gravity waves. Further, accurately modeling larval transport will require embedding these small-scale processes

in larger-scale models, thereby capturing the large-scale aspects of larval transport, the modulation of small-scale processes by large-scale forcing, and the very small-scale processes (e.g., turbulence) where larval swimming capabilities and behavior become overly important (see discussion in Metaxas, 2001). Even modeling a single, relatively straightforward process, such as the accumulation of particles in gravity currents, can be extremely complex (e.g., Scotti and Pineda, 2007). Thus, using numerical models for inferring larval transport when poorly studied processes may be important, or where the physical forcing is unknown, is dire. On the other hand, it is clear that numerical models are powerful tools in settings where processes are well known and in cases where field hydrodynamics are well simulated by the model (e.g., Reynolds et al., 2006). Thus, we suggest that bottlenecks in understanding larval transport are less related to numerical modeling than to the mechanistic knowledge of larval transport.

Challenges of Adaptive Sampling

It is unclear how much larval transport occurs during episodic events and how much occurs during “mean” conditions. Sharp peaks in settlement time series and studies of larval transport by wind and internal motions suggest that transport can be sporadic, larvae extremely patchy, or both (see Pineda, 2000, for discussion). Time-series measurements of relevant hydrodynamics and larval distributions during larval transport are of limited use when measurements cannot be taken with the necessary frequency and spatial resolution to describe the processes with sufficient

detail. Furthermore, surveys by research vessels diligently planned in advance do not guarantee that larval-transport events will happen during the surveys. Adaptive sampling, defined as sampling in response to an event, is a solution to these dilemmas; it has been used successfully to sample hydrodynamics and larval distributions during transport by internal tidal bores (Pineda, 1994, 1999). Adaptive sampling is challenging, however, because it is hypothesis based; sampling is initiated in response to a real-time change in a time-dependent variable, such as temperature or wind direction, that is integral to the hypothesized larval transport mechanism. Adaptive sampling is therefore a stringent hypothesis test, because if larval transport does not occur as expected, the hypothesis is rejected. Adaptive sampling is also logistically difficult. If the events are sporadic, and the sampling is shipboard, adaptive sampling requires having a vessel and crew on standby ready to sample for long periods, an expensive prospect for anxious researchers. Conceivably, remote sampling systems initiated in response to events could be constructed with off-the-shelf gear and new technologies currently under development such as in situ molecular detection of larvae (e.g., Goffredi et al., 2006). Thus, similar to the limitations in modeling larval transport, adaptive sampling is limited in part by technology and in part by the development of testable, mechanistic hypotheses.

Breaking the Behavioral Black Box

The incorporation of larval behavior fully into the larval transport equation requires several important advances.

First, hypotheses on the role of behavior in transport need to be developed and tested. Colby (1988) argued that passive *advection* and *diffusion* should be the null hypothesis for studies of larval transport. In an early example of this approach, Woods and Hargis (1971) compared the distribution of coal particles with that of similarly sized oyster larvae and concluded that larvae were not being transported passively. A study on ascidian tadpole larvae found that dispersal distance was shorter in swimming larvae than in nonswimming individuals of similar size and shape (Bingham and Young, 1991). Similarly, Arnold et al. (2005) followed a cohort of larval hard clams and found their distribution differed from dye distributions and from modeled distributions based on passive particles. There are other examples of the use of a hypothesis-testing approach for evaluating the processes that affect larval transport (e.g., Hare et al., 2002). This approach should be expanded to take advantage of advances in modeling as well as in field and laboratory studies. Behavioral hypotheses from laboratory studies are attractive because quantification of hydrodynamics and behavior is feasible, but these hypotheses should be tested in field conditions, and vice versa.

Second, the incorporation of behaviors into models of transport needs to be rule-based rather than deterministic, and individual variability should be considered. Most transport models that include larval behavior use population-level descriptions of distributions or swimming speeds and apply them to particles released in the model (Hare et al., 1999). Another approach is to provide a set of behavioral rules that attempt to capture

the trade-offs between feeding and predation; these rules result in vertical (and potentially horizontal) responses to various cues (Titelman and Fiksen, 2004; Fiksen et al., in press). Although the importance of time-dependent behaviors, such as diel, tidal, and ontogenetic, is well recognized, little is known about “adaptive” behavior on scales of seconds to minutes, where larvae might respond to transient physical and biological features. We know that larvae respond behaviorally to a number of factors, such as time of day, light, temperature, turbulence, pressure, and food availability, and that some of these responses influence transport, but only a few behaviors facilitating transport have been identified (e.g., Boehlert and Mundy, 1988; DiBacco et al., 2001). For example, field observations, modeling, and laboratory experiments imply that “swimming up” behaviors in response to transient downwelling flows in propagating features determine efficient larval transport (Pineda, 1999; Scotti and Pineda, 2007). To incorporate our understanding of behavior into rule-based models will require a hypothesis-based approach. Without hypotheses, we run the risk of evaluating the effect of multiple irrelevant behavioral scenarios on larval transport. This rule-based approach coupled with more studies on adaptive behavior and well-developed biophysical, individual-based models (e.g., Lough et al., 2005, and recent observations of Claudio DiBacco of Bedford Institute of Oceanography, author Pineda, and Karl Helfrich of WHOI), will greatly advance our understanding of the combined roles of advection, diffusion, and larval behavior.

Third, most research has focused on how larval behavior affects advection, but the influence of behavior on diffusion requires more emphasis. Using an advection-diffusion-mortality model, Cowen et al. (2000) estimate that successful larval transport to coral reef habitats diminishes sharply when diffusion rates increase from 0 to $100 \text{ m}^2 \text{ s}^{-1}$ (the latter is a typical diffusion rate used in larval transport studies; see also Okubo, 1994). However, the assumption that larvae diffuse passively in the marine environment likely does not hold, particularly for older larval stages. Peaks in settlement must result from high-density patches of larvae reaching adult habitats, and these coherent patches run counter to hypothesized diffusion. Natunewicz and Epifanio (2001) followed discrete patches of crab larvae for up to six days and hypothesized that associative swimming behaviors might be responsible for patch maintenance. A U-shaped patchiness-at-age function has been described for the larval stages of several fish species, and this shape has been interpreted as initial diffusion with subsequent schooling (Matsuura and Hewitt, 1995). In addition, larvae may remain in thin layers of food (Lasker, 1975) and reduce their diffusion owing to vertical differences in flow (shear diffusion). Larvae can also accumulate at upwelling and downwelling fronts by swimming into the current (e.g., Franks, 1992; Metaxas, 2001), thereby reducing diffusion. Thus, small-scale vertical and horizontal larval behavioral responses may limit diffusion and greatly affect larval transport. Consequently, the use of advection-diffusion models to understand larval transport requires great

care. For example, Hill (1991) underscored the limitations of an advection-diffusion-mortality model in cases when active vertical positioning of larvae was expected, and Okubo (1994) warned that a horizontal diffusive model would not work in settings with strong convergent flows, a widespread phenomenon in coastal and nearshore settings.

LARVAL DISPERSAL

Defining Dispersal Kernels

Most attempts to describe dispersal kernels have emphasized larval transport (e.g., Botsford et al., 1994), but other processes such as spawning, settlement, pelagic larval duration, and survival also influence larval dispersal (Edwards et al., in press). Many marine species release their offspring at specific locations and times, using specific behaviors. For example, relatively sedentary bluehead wrasse spawn daily at particular reef spawning sites that have been used for years (Warner, 1988). Similarly, several fish species spawn in circular motions that may create hydrodynamic vortices (Okubo, 1988; Heyman et al., 2005). The influence of these small-scale events on larval dispersal over periods of weeks is unknown. On a larger scale, a number of motile species, including snappers, herring, and blue crabs, move to particular locations for spawning (Carr et al., 2004; Heyman et al., 2005). In the temporal domain, many coral species participate in annual mass spawning events, with more than 60% of species spawning over the course of several days (Babcock et al., 1994), and crabs and barnacles tend to release their larvae at certain phases of the tide or the day (Morgan, 1995; Macho et al., 2005). While such spawn-

ing behaviors have long been thought to maximize larval survival (e.g., Hughes et al., 2000), the overall effect of localized and punctuated spawning on larval dispersal is unclear.

Moreover, where individuals end their planktonic stage is also an important

component of larval dispersal. Larval durations of some species are fixed while others are flexible (Pechenik, 1986; Cowen, 1991). Some species have very narrow habitat requirements for the continuation of the life cycle, such as river mouths on isolated oceanic islands for some gobies, wave-beaten rocky points for gooseneck barnacles, and specific species of anemones for some reef fish (Radtke et al., 1988; Cruz, 2000; Jones et al., 2005). Other species have broad habitat requirements such as eurytopic *Pachygrapsus* crabs (Hiatt, 1948) and flounders of the genus *Etropus* (Walsh et al., 2006). For most species, only a subset of locations will support the continuation of the life cycle; these locations must be reached within the time window of possible settlement. Understanding these habitat and time constraints will be necessary to observe and model dispersal kernels. A number of models have included such considerations at a relatively large scale, for example, assuming modeled larvae that arrive within

10–15 km of known habitat have successfully settled (Hare et al., 1999; Paris et al., 2005). How larvae transverse these last 10 km is unknown largely because of the exclusion of smaller-scale processes in models and the inability to include realistic behaviors (see above).

...all the research needs identified under the larval transport and dispersal sections sum together as research needs for population connectivity.

The dispersal kernel also is dependent on larval mortality. Most studies of larval dispersal, however, either do not consider larval mortality (Hare et al., 1999), consider spatially homogenous mortality (Cowen et al., 2000), or assume low mortality (Gaylord and Gaines, 2000). Modeling studies that assume low mortalities should be reconsidered in light of observed higher mortalities (e.g., Rumrill, 1990); use of high mortalities in dispersal models frequently yields lower maximum dispersal estimates than those obtained assuming low mortality (Cowen et al., 2000; Ellien et al., 2004; Tapia and Pineda, 2007). Differential survival of larvae during transport contributes to defining the dispersal kernel in potentially numerous species-specific ways. The ecological literature is rich with examples and models in which the role of spatial heterogeneity in mortality shapes subsequent patterns in abundance, distribution, and demographics. These concepts, however, have yet to be applied to mortality in pelagic early life

stages. It is also clear that not all larvae are equal, and the range of traits will result in selective survival (see later section on Population Connectivity).

Larval duration also influences survival probability. Pelagic larval duration (PLD) must be correlated with the dispersal kernel for the simple reason that species with short PLD must have reduced larval transport and relatively “short” dispersal kernels; PLD is a constraining variable for dispersal. In contrast, long PLDs do not necessarily yield broad dispersal kernels, as larval behavior breaks the direct-proportional relationship between PLD and dispersal distance, both for fish and invertebrates (Sponaugle et al., 2002). Of course, long PLD yields higher cumulative mortalities than short PLD when everything

else is equal (i.e., same daily mortality for species with short and long PLD; see Hare and Cowen, 1997). It is also unclear how variables influencing PLD, such as temperature and food (Scheltema and Williams, 1982), may influence the dispersal kernel (see O’Connor et al., 2007, for model predictions). Thus, the relationship between PLD and dispersal is ambiguous except for species with very short larval durations (see discussion in Sponaugle et al., 2002).

Dispersal Estimates in the Coastal Ocean

Given the complexity of larval dispersal, it is not surprising that measurement of a dispersal kernel in the marine environment is extraordinarily rare (Shanks et al., 2003). Gerrodette (1981) measured

the dispersal of planula larvae from adults in a temperate solitary coral and found that mean dispersal distance from the parent was < 50 cm. Similar work with ascidians quantified dispersal from spawning to settlement, but the pelagic stage of ascidians is short (hours), larvae are large (millimeters), and mortality is low (< 90%) (Olson and McPherson, 1987), making it possible to follow individuals from the beginning to the end of the pelagic stage (see also Bingham and Young, 1991). Work on an isolated reef indicated that most acroporid and pocilloporid corals recruited in experimental moorings within 300 m from the reef, and that spat mortality decreased with distance from the reef (Sammarco and Andrews, 1989). Several studies followed patches of more typical marine larvae

Eventually, long-term, labor-intensive studies will be needed to increase our understanding of reproductive population connectivity of longer-lived mobile species.



(PLD of weeks, size < 1–10 mm, and high mortality), but these efforts are not true measures of larval dispersal because the spawning and ending locations were inferred (Pepin and Helbig, 1997; Natunewicz and Epifanio, 2001; Paris and Cowen, 2004). Other studies marked spawned eggs and then collected offspring at the end of their planktonic stage (Jones et al., 2005; Almany et al., 2007); these studies provide a partial measure, but not a complete description, of the dispersal kernel because all potential ending locations could not be sampled. Although dispersal kernels will eventually be fully quantified for some species in some systems, the measurement of these probability distributions in the marine environment will remain extremely rare.

It is easier to obtain dispersal kernels with models than with field measurements. Some models consider simplified situations using advection-diffusion models. More complex numerical circulation models coupled with Lagrangian particle-tracking algorithms follow particles released at multiple locations and multiple times and have proven instrumental in estimating dispersal kernels in the marine environment (Cowen et al., 2000; see also Werner et al., this issue). Edwards et al. (in press) used a fully orthogonal approach to examine the effects of different factors on generic two-dimensional dispersal kernels estimated from a three-dimensional circulation model of the Southeast United States shelf. This study found that time and place of initial release were most important in determining the position of the dispersal kernel, and that dispersion and PLD were most critical in determining the spread of the dispersal kernel.

Larval behavior was not as important, but horizontal swimming behavior was not included and depth-stratified currents were minimal through most of the modeling domain, limiting the effect of different vertical positions.

LARVAL DISPERSAL: RESEARCH NEEDS

Field Observations of Dispersal

The paradigm of broad dispersal of fish and invertebrate larvae is giving way to the notion of restricted dispersal, mainly because of studies finding: (1) unexpected high levels of self-recruitment, (2) high larval mortality rates, and (3) restricted scales of larval transport (see above). Still, the dominant scales of dispersal are not known. Solid empirical estimates of dispersal are needed to guide field and numerical modeling studies to address questions such as: What regions of the ocean should researchers focus on? What processes must be included in the models? Studying dispersal is challenging, and for fish and invertebrate species with long and typical larval durations (i.e., about four weeks for temperate invertebrates; Levin and Bridges, 1995), knowledge will be gained incrementally by using multiple approaches, including: (1) empirical estimates of larval origin, such as natural and artificial tags and genetic distance and structure, (2) a mechanistic understanding of larval transport, (3) assessment of how the space and time of spawning and settlement influence dispersal, (4) trophodynamic studies to address the influence of pelagic patchiness and structure on the larval journey from spawning to settlement, and (5) improved mortality estimates in dis-

persal models in locations where physical processes are well known.

When empirical estimates of dispersal are obtained, it is crucial that they be used to test the assumptions and hypotheses resulting from both simple and complex models. Robust measurements of dispersal will be rare and opportunities to evaluate and test models must not be lost. In this way, the skill of models can be assessed and improved through an iterative process of observation and modeling, and the resulting dispersal kernels can be part of larger studies of connectivity with increasing confidence. Although the challenges are immense, we emphasize that solid empirical estimates of dispersal are necessary to guide further field studies and numerical modeling; theoretical developments and modeling of spatial population processes and connectivity may be futile unless we gain more observationally based knowledge of larval dispersal.

POPULATION CONNECTIVITY The Concept of Population Connectivity

A mechanistic understanding of larval dispersal is sufficient for determining population connectivity at time of settlement. Knowledge of population connectivity at the time of settlement or shortly thereafter may be adequate for some objectives because subadult individuals use resources, interact with adults and other members of the community and in some instances, sustain fisheries. *Reproductive population connectivity*, on the other hand, is the exchange of individuals that eventually reproduce. Accordingly, for benthic marine species, it is not only a function of larval dispersal

(including survivorship of larvae during transit), but also of post-settlement and juvenile survival to the point of reproduction (Figures 1 and 2). Reproductive population connectivity can be expressed as the number of individuals from site a and population A that disperse to site b containing population B and reproduce there per unit time. Thus, during development to the adult stage (which varies greatly among species, from days to multiple years), juveniles must survive, grow, mature, and reproduce. As characteristics of settlers are often variable and those surviving to reproduce may not be a random sample of the settlers, simply tracking larval trajectories from spawning to settlement is insufficient to quantify reproductive population connectivity. The remainder of this discussion considers the ecological processes contributing to reproductive population connectivity.

For a population to be ecologically sustained, a minimum number of offspring must mature and reproduce over time intervals dictated by species' longevity. Identifying this number is essential to parameterize population models, but an equally important consideration is the *composition* of the survivors that make up this number: What are the characteristics of dispersers that lead to successful recruitment? Which of those recruits will then survive to reproduce? Recent evidence points to important influences of spawning patterns, maternal effects, and pelagic experience on larval size, growth, condition, and survival. Furthermore, many of these larval traits “carry over” and influence juvenile survival. However, comparatively little is known about the linkages between these early life phenomena and adult survival and reproduction.

Variation in Larval Traits and Survival During the Pelagic Stage

Most larvae exhibit variation in early life history (ELH) traits, such as size at a given age and growth rate. This variation can be introduced as early as the egg stage, when differential size, age, condition, or stress level of the mother can influence quality of the spawned eggs (Berkeley et al., 2004; McCormick, 2006). Larval encounter with variable pelagic environments also influences larval growth and survival. Water temperature plays a central role in regulating metabolism and growth (Houde, 1989), with larvae in different temperatures exhibiting variable ELH traits (Meekan et al., 2003; Sponaugle et al., 2006). Sustained growth requires adequate food; therefore, variable access to food also affects larval traits and survival. Transit across nutrient-poor open oceans may be particularly difficult for species with high growth rates. Access to food and avoidance of predation or other developmental conditions may be related to the timing of spawning, such that particular “windows” of time result in higher larval survivorship (Cushing, 1990; Baumann et al., 2006). Encounter with oceanographic features such as fronts or meso-scale eddies can also influence food supply and exposure to predators (Grimes and Kingsford, 1996; Sponaugle and Pinkard, 2004). Thus, a complex oceanographic environment coupled with variable egg quality at spawning results in a pool of larvae with variable traits (Jarrett, 2003; Lee et al., 2006; Sponaugle and Grorud-Colvert, 2006).

Survival of pelagic larvae is typically nonrandom and proceeds according to three general concepts of the “growth-

mortality hypotheses” (reviewed in Anderson, 1988). Theoretically, survivors should be those larvae that are larger at a given age (“bigger is better” hypothesis; Miller et al., 1988), grow faster (“growth-rate” hypothesis; Bailey and Houde, 1989), and/or move through an early stage more rapidly (“stage-duration” hypothesis; Anderson, 1988). Larvae of a diversity of marine fish (e.g., Meekan and Fortier, 1996; Hare and Cowen, 1997; Meekan et al., 2006) appear to adhere (to varying degrees) to aspects of these overarching concepts. Differential survival of larvae due to their pelagic experience and ELH traits can influence the magnitude of larval settlement pulses. Variation in the magnitude of settlement events has been related to variable larval growth throughout or during particular periods of larval life (e.g., Bergenius et al., 2002; Jenkins and King, 2006; Sponaugle et al., 2006)

Influence of Larval Traits on Juvenile Survival

Settlement of larvae to the benthos is a risky event plagued with high levels of predation mortality (e.g., Hunt and Scheibling, 1997; Doherty et al., 2004); thus, additional selective loss typically occurs during this period. Most marine species undergo a metamorphosis between the larval and juvenile stages as they move between radically different environments. While metamorphosis enables closer adaptation to stage-specific environments (Wilbur, 1980), larval history is not erased and accompanies this transition (Pechenik et al., 1998). Importantly, recent studies have begun linking these two stages and investigating how larval traits influence juvenile sur-

vival. Traits exhibited by settling larvae as a consequence of pelagic constraints and selective pressures have the potential to “carry over” and influence survival of juveniles. For example, larval growth, size, and condition influence the survivorship of juvenile sponges, molluscs, barnacles, bryozoans, and fishes (e.g., Searcy and Sponaugle, 2001; Pechenik et al., 2002; Jarrett, 2003; McCormick and Hoey, 2004; Phillips, 2004; Marshall et al., 2006; Sponaugle and Grorud-Colvert, 2006). The potential exists for some traits that are advantageous to larvae to become subsequently detrimental to juveniles or vice versa. For example, crab zoeae reared at reduced salinities suffer higher mortality as larvae, but metamorphose into larger juveniles (Giménez and Anger, 2003), and a short pelagic larval duration enables fish larvae to escape the predation in the plankton, but results in smaller settlers (e.g., Sponaugle et al. 2006), which in some cases may be more susceptible to predation (Anderson, 1988). Most studies have focused on consequences to juveniles and somewhat less on the trade offs associated with conflicting constraints in complex life histories.

Survivorship Beyond the Juvenile Stage

Although events during larval life can play an important role in early juvenile survival, much less is known about how these traits are carried through or lost from individuals that survive to reproduce. Studies on larval dispersal or population connectivity typically define recruitment as entry into the juvenile population, not to the adult population. Thus, settlers are tracked at most to the point of settlement or through the

first few days or weeks as juveniles. We know little about the settlers that eventually survive to reproduce. It is generally substantially more time-consuming and logistically challenging to track cohorts of settlers all the way to reproduction. A few recent studies have had some success following species that mature rapidly.

Pineda et al. (2006) sampled barnacles that settled over an 89-day period until they reproduced 11 months later and found that survivors settled during a narrow 21-day “recruitment window.” Meekan et al. (2006) tracked a single cohort of a fast-growing coastal fish and found that despite strong selective loss during early stages, there was no additional selective mortality between the juvenile and adult stages. For bryozoans in an experimental manipulation, however, adults that were larger as larvae had higher survival rates and produced larger larvae themselves than those that were smaller as larvae, although delaying metamorphosis erased this relationship (Marshall and Keough, 2006). Optimal traits may vary with the environment encountered by the larval, juvenile, or adult stages, as evident for a snail (Moran and Emler, 2001) and colonial ascidian (Marshall et al., 2006). Thus, traits obtained during early stages have the potential for long-term effects on later stages, but many complex interrelation-

ships likely influence the outcome. When carryover effects occur, they may persist, become amplified, or, instead, be compensated for during subsequent stages (Podolsky and Moran, 2006). In short, simply reaching a settlement site does not guarantee that larvae will possess the necessary traits to survive to reproduce.

...simply reaching a settlement site does not guarantee that larvae will possess the necessary traits to survive to reproduce.

POPULATION CONNECTIVITY: RESEARCH NEEDS

The fundamental challenge in population connectivity studies is to determine the source populations of settling larvae and the settlement sites of dispersing larvae. In short, all the research needs identified under the larval transport and dispersal sections sum together as research needs for population connectivity. In addition, there is a need to link maternal effects and larval processes to early juvenile survival and, in the case of reproductive population connectivity, to the point of reproduction. Because reproductive population connectivity per se is defined as the exchange of individuals that eventually reproduce, tracking dispersing larvae to the point of settlement or juvenile recruitment, while important for some purposes, is functionally insufficient. New efforts to track settlers to reproduction will initially advance with shorter-lived sessile species. Eventually, long-term, labor-intensive studies will be needed to increase our understanding

of reproductive population connectivity of longer-lived mobile species. There is a rich history of marine ecological work examining the relative importance of recruitment versus density-dependent, post-settlement processes in structuring benthic populations (Caley et al., 1996), but we need to move beyond numeri-

if settlers that survive to reproduction are only spawned at time t and site x,y , or if successful individuals only settle in recruitment windows coinciding with physical-transport processes p and feeding and prey environments e , the vast parameter space that potentially affects pelagic eggs and larvae, and vexes

Real measures of reproductive population connectivity require an understanding of who is surviving to reproduce and why.

cal responses and refine the question to focus on trait-based ecological linkages among all stages. Real measures of reproductive population connectivity require an understanding of who is surviving to reproduce and why.

As there is ample evidence that larval growth and condition can influence performance in later stages, from a practical point of view we need more reliable measures of condition. The coarsest measures of condition often use size as a proxy (e.g., many invertebrates), while others measure organic (Jarrett, 2003) or lipid content (Hentschel and Emlet, 2000), RNA/DNA ratios (Suthers et al., 1996; Lee et al., 2006), or (for fishes) otolith-based measures (e.g., Sponaugle et al., 2006), all of which have some limitations. As new genomic techniques are developed, perhaps new measures of performance can be incorporated into both observational and manipulative studies.

Finally, focusing on the individuals that survive to reproduce may guide larval transport and dispersal studies;

researchers, may be effectively reduced to a more manageable set.

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