Larval Dispersal and Marine Population Connectivity

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Abstract

Connectivity, or the exchange of individuals among marine populations, is a
central topic in marine ecology. For most benthic marine species with com-
plex life cycles, this exchange occurs primarily during the pelagic larval stage.
The small size of larvae coupled with the vast and complex fluid environment
they occupy hamper our ability to quantify dispersal and connectivity. Ev-
idence from direct and indirect approaches using geochemical and genetic
techniques suggests that populations range from fully open to fully closed.
Understanding the biophysical processes that contribute to observed disper-
sal patterns requires integrated interdisciplinary approaches that incorporate
high-resolution biophysical modeling and empirical data. Further, differen-
tial postsettlement survival of larvae may add complexity to measurements of
connectivity. The degree to which populations self recruit or receive subsidy
from other populations has consequences for a number of fundamental eco-
logical processes that affect population regulation and persistence. Finally,
a full understanding of population connectivity has important applications
for management and conservation.

INTRODUCTION

The fluid environment in which marine populations live offers a wide variety of means to disperse individuals within and among populations. For benthic species (termed demersal or sessile), the primary dispersal phase is typically associated with the earliest life history stage (spore, egg, or larva). For more mobile species, the juveniles and adults may also disperse. Importantly, the extent of successful dispersal, especially among subpopulations (see Glossary of Terms), is a major determinant of the dynamics of populations (along with overall birth and death rates), but one in which details are poorly understood for most marine species. When dispersal is combined with factors leading to survival of the dispersed organisms, the concept of population connectivity emerges. An underlying and critical component of population connectivity is the spatial (and temporal) context in which population dynamics are placed from both a cause and an effect perspective.

For most coastal marine species, the larval phase is the dominant dispersal stage, and therefore considerable focus is placed on this stage and the processes that influence it in addressing issues of population connectivity in marine systems. Understanding the drivers of larval dispersal is an inherently biophysical problem: biological in the sense of processes that influence offspring production, growth, development, and survival; physical in the sense of advection and diffusion properties of water circulation; and biophysical in the sense of interactions between certain larval traits (e.g., vertical swimming behavior) and physical properties of the environment that operate at various scales. The core challenges fall within four categories: observation (determination of spatial-temporal scaling of connectivity), explanation (resolution of the processes underlying larval

GLOSSARY OF TERMS

Connectivity matrix: provides the probability of exchange of individuals between patches; if the matrix is row-normalized, then the matrix element rij gives the probability that an individual in population i came from population j

Dispersal kernel: the distribution of dispersal distances based on repeated events (i.e., the probability density function of the number of propagules from the adult source) that theoretically captures the temporal variability in dispersal processes (e.g., variation in current direction and strength)

Larval dispersal: the intergenerational spread of larvae away from a source to the destination or settlement site at the end of the larval stage

Local or subpopulation: a set of individuals that live in the same habitat patch and interact with each other

Metapopulations: an assemblage of discrete local populations with some measure of shared migration among them

Open versus closed populations: open populations receive and export individuals to other local populations; closed populations do not exchange individuals to an appreciable extent

Population connectivity: the exchange of individuals among geographically separated subpopulations that comprise a metapopulation; set in the context of benthic-oriented marine species, population connectivity encompasses the dispersal phase from reproduction to the completion of the settlement process (including habitat choice and metamorphosis)

Reproductive connectivity: dispersal of individuals among subpopulations that survive to reproduce

Self recruitment: also called local replenishment; recruitment into a population from itself

Source versus sink: a source is population in which the net export of individuals is greater than the net import of individuals; the reverse is a sink

Subsidy: recruitment into a population from a nonlocal population source

(Definitions are modified from the following sources: Hanski & Simberloff 1997, Nathan & Mueller-Landau 2000, Cowen et al. 2007, Pineda et al. 2007)

dispersal and connectivity), consequences (impact of connectivity on population structure and dynamics), and application (issues of conservation and resource management; Cowen et al. 2007). These components can only be addressed with interdisciplinary approaches that utilize a variety of research tools, many of which promise exciting new results.

Here we provide an overview of the recent developments relevant to larval dispersal and population connectivity in marine systems, methods of study, including new and promising technologies, and application to societal issues such as fisheries and conservation. We attempt to cover the rapid increase in both studies that address the observed patterns that relate to population connectivity as well as studies that explore the biological and physical processes that create the observed patterns. We also include discussion of recent work on the implications of population connectivity patterns to population and metapopulation dynamics and genetics. The field is expanding rapidly, and the confines of this review limit our abilities to be comprehensive, but our intention is to introduce the relevant topics and literature to serve as a solid launching point for more detailed studies of this topic. Additional accounts of the literature are available in a series of related reviews and special journal issues (e.g., reviews: Cowen & Sponaugle 1997, Bradbury & Snelgrove 2001, Cowen 2002, Leis & McCormick 2002, Leis 2006, Levin 2006; special issues: Warner & Cowen 2002, Lubchenco et al. 2003, Cowen et al. 2007).

The parallel between larval disperal and terrestrial seed dispersal is worth comment. Terrestrial botanists have been studying dispersal of seeds for many years (see Nathan & Muller-Landau 2000), utilizing similar methods (e.g., genetic markers to establish source of seeds) to understand the spatial extent of dispersal. Although some methods of study may be similar, the variety of processes that influence dispersal and population connectivity likely differs significantly between terrestrial and marine systems. For example, larvae of marine organisms possess biological traits, including behaviors, variable growth, and condition, that interact with physical dispersal processes and influence successful dispersal; such interactions are not as apparent in terrestrial systems. However, the consequences of spatial dispersal patterns on the structure and dynamics of populations, whether terrestrial or marine, may be quite similar.

POPULATION CONNECTIVITY: SOME GUIDELINES

Although connectivity can refer to the flux of any material (e.g., organisms, gametes, genes, disease vectors, nutrients) between locations, here we focus explicitly on the movement of individuals within and among local or subpopulations. Implicit in this definition is that the level of exchange, when referring to population connectivity, must be sufficient to impact the demographic rates of the local population(s). The level of such ecologically relevant exchange is several orders of magnitude larger than the level of exchange required for the maintenance of genetic homogeneity among subpopulations (which requires only a few individuals per generation; Slatkin 1993). Thus, when viewing a dispersal kernel, ecologically relevant dispersal does not necessarily extend out to include the tails of the distribution. Determination of the distances over which dispersal from a given source has direct ecological impact and thus contributes to the persistence and structure of distant populations is a critical area of research.

Populations persist when births + immigration equal or exceed deaths + emigration. When examining the relevant spatial scales over which subsidy from a source is sufficient to contribute to a receiving population's persistence, a decision must be made regarding the appropriate subsidy contribution. This contribution cutoff can be established arbitrarily—for example, defining demographically significant subsidy to be that which contributes at least 10% of the total recruitment to a population. Alternatively, more dynamical approaches might be utilized to establish the point at which additional subsidy no longer significantly influences the stability of the local population (e.g.,

population viability analysis; see Beissinger & McCullough 2002). Similarly, the demographically effective dispersal kernel may be determined for a given source site (i.e., how far out on the tail of the distribution do propagules contribute significantly to downstream populations?). Note, however, that even as the numbers of propagules decrease with distance from the source, it is the conditions at the receiving population that will determine what level of subsidy is significant (for a more thorough and quantitative discussion see Beissinger & McCullough 2002 and Hastings & Botsford 2006).

Linked to this discussion is the issue of the extent to which marine populations (of predominantly coastal species) are open or closed (Cowen et al. 2000, Warner & Cowen 2002, Mora & Sale 2002). The concept of larvae settling into a local population from a well-mixed larval pool (i.e., larvae from all potential sites mixed together into a single source pool) led to the belief that marine populations are demographically open, potentially over hundreds to thousands of kilometers. This perspective was supported by studies that found little genetic structure over large spatial scales. However, within the past decade, evidence that contradicts this concept of routinely broad larval dispersal has mounted at ever-increasing rates (e.g., Swearer et al. 2002, Jones et al. 2005, Almany et al. 2007). This new evidence points to the existence of fine-scale structure in dispersal patterns among locations, which leads to the view that marine populations may be less open than we thought. More explicitly, the findings couch the argument as one of identifying where along the continuum from completely open to completely closed marine populations lie, and how different populations and species vary in this extent. This can be viewed conceptually as a comparison among different connectivity matrices (**Figure 1a**).
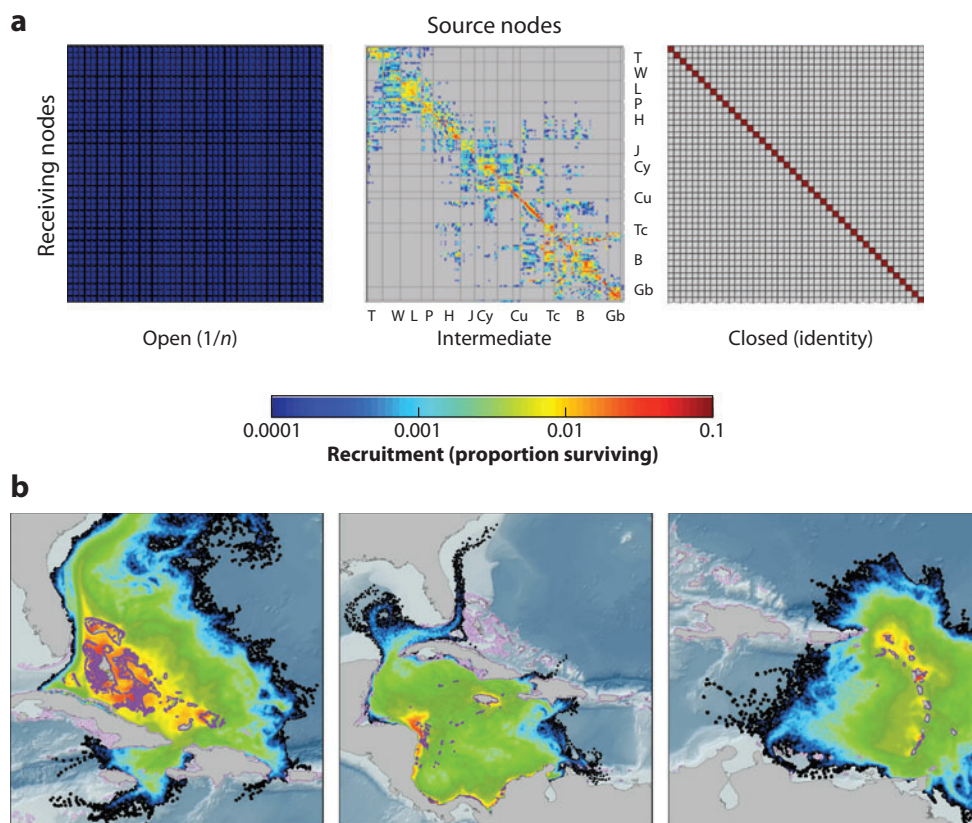
OBSERVATION: EVIDENCE OF DISPERSAL DISTANCE

Information on the true scale of larval dispersal was for many years limited, and larval dispersal was inferred to be extensive based on the collection of larvae of coastal species far out at sea (e.g., Scheltema 1986). The root of the problem is that dispersal distances are notoriously difficult to measure directly. For one, the number of larvae diminishes rapidly with distance from the spawning location and time owing to advective and diffusive properties of the mixing and stirring of currents as well as naturally high mortality rates. Additionally, the young must be located at their settlement site to identify the successful dispersers. Yet, for the relatively few organisms for which such distances have been obtained or estimated, a pattern is emerging regarding the scaling of typical larval dispersal distances that contribute to population connectivity. Sinclair (1988) provided an early summary that suggested significant subpopulation structure. A recent survey of estimated dispersal distances across a variety of taxa yielded a wide range (m to 1000 km) of distances, but with modal distances closer to the tens to hundreds of kilometers range for many fish species, and even less for coastal invertebrates and plants (Kinlan & Gaines 2003).

For many of these organisms, dispersal distance scales directly with the time larvae spend in the plankton, the pelagic larval duration (PLD) (Shanks et al. 2003), and consequently, PLD is frequently used in modeling or estimating dispersal. Yet, because PLD is taxon specific and influenced by environmental conditions such as temperature, dispersal distances likewise can be

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Figure 1

(*a*) Comparison of open to closed population continuum. The degree to which a set of local populations (or nodes) might be connected to each other via larval dispersal can be expressed as a connectivity matrix where nodes are distributed along both the vertical and horizontal axes. In the fully open case, where all populations within a given domain contribute propagules equally to each other, all cells within the connectivity matrix are populated similarly (1/n where n is the total number of local populations, i.e., source locations). This extreme case signifies what might be expected if all propagules were equally mixed and then settled at random back to the source sites. In the completely closed case, all propagules return directly to their source location, all cells along the diagonal would be populated with probability of 1 (i.e., 100% self recruitment), and all other cells not along the diagonal would be populated by zero. This case would be expected if all populations were completely isolated from any other location through dispersal processes. The intermediate situation is represented by a matrix constructed from biophysical modeling data with some variation of probabilities along both the diagonal and subsidy cells (modified from Cowen et al. 2006). Where the sample domain lies along this continuum can be defined by the relative strength of the probabilities along the self-recruitment diagonal as compared with the subsidy cells. Note that by using connectivity matrices in this way, null models can be determined, either by using the extreme cases (fully open or fully closed) or through bootstrapping from a set of modeled dispersal kernels that define explicit properties under study. The scale represents a range in cumulative abundance of successful recruits, where red/orange represents ecologically significant levels of exchange and green/blue represents very low levels of genetically relevant exchange. Explicitly, the scale bar represents the probability with which larvae (from sources) survive to recruit at settlement sites, depicting order of magnitude changes. Note that since the values are probabilities, they are unitless. Letters indicate Caribbean populations: T, Trinidad; W, Windward Islands; L, Leeward Islands; P, Puerto Rico; H, Hispaniola; J, Jamaica; Cy, Cayman Islands; Cu, Cuba; Tc, Turks and Caicos Islands; B, Bahamas; Gb, Grand Bahamas. (*b*) Translation of connectivity matrices into geographical representation of dispersal. Regional dispersal kernels were taken from the intermediate connectivity matrix example in (*a*). Source nodes in each example are shown in purple; potential receiving nodes are shown in pink (but also include all source nodes). The Caribbean region is divided into separate zones simply for clarity of presentation. Cumulative dispersal distribution is color coded per the same scaling as used in (*a*). Note the relatively confined dispersal distances in all regions with respect to an ecologically relevant level of successful dispersal (*red and orange*) leading to population connectivity. (*Left*) Source locations include the greater Bahamas and Turks and Caicos Islands; (*center*) central Caribbean source locations including Jamaica, Cayman Islands, Nicaragua, Panama, and Colombia; (*right*) Lesser Antilles source locations.

species, season, and location specific as well. Further, because many additional factors contribute to dispersal distance, simply setting dispersal distance as a direct function of PLD is insufficient (Sponaugle et al. 2002). To help resolve the various sources of variation in scaling of dispersal distances, and ultimately, population connectivity, a need remains for measures of dispersal distances across species and systems (e.g., Bradbury et al. 2008).

Several means of determining dispersal distances exist, ranging from studies of single spawning events and subsequent dispersal of the young to more synthetic estimations over multiple generations. Both direct and indirect methods using geochemical and genetic markers (see reviews by Planes 2002; Thorrold et al. 2002, 2007; Hedgecock et al. 2007; Hellberg 2007), as well as sophisticated coupled biophysical models (Werner et al. 2007, Gallego et al. 2007), are available. Direct methods range from identification of island endemics (Robertson 2001), to in situ observation of the individual propagules and mapping of their trajectories (Gerrodette 1981), to tagging propagules at release and then surveying (recapturing) them at a later date (e.g., after settlement) to determine the dispersal pattern from a given event (e.g., Jones et al. 2005, Almany et al. 2007). These labor-intensive efforts can yield unequivocal empirical evidence of the scale and success of a dispersal event, with the potential to examine the role of physical forcing mechanisms (see below). However, this approach typically does not allow an estimation of a dispersal kernel because it only provides evidence of a single event; nor does it allow for direct inference of likely dispersal patterns for other locations.

One highly promising new technique of marking the otoliths of larval fishes (and potentially larval shells in mollusks) is via injection of enriched stable isotopes (e.g., ^{137}Ba) into mature females prior to their production of eggs (Thorrold et al. 2006). The enriched isotope is passed to each egg, which provides a unique isotopic signature that is permanently incorporated into the core of the embryonic otolith. This transgenerational tagging approach significantly reduces the effort involved (e.g., one female is more easily injected in situ than immersion of a clutch of eggs into oxytetracycline), which allows for the tagging of a greater proportion of the population. The potential to use different isotopes to mark several different sources, though labor intensive, could provide unique direct empirical evidence of both the scaling of dispersal and levels of population exchange within specific systems.

Indirect methods have the advantage that they provide insight on the spatial scales of population connectivity among multiple populations, but with some limitation on the temporal and spatial resolution. Depending on the methods used, either individual events (i.e., for a given year) or long-term patterns (integrated over many generations) can be resolved, but usually with fairly coarse spatial resolution, due in part to sampling limitations. Indirect methods typically utilize naturally occurring markers, eliminating the need to apply some sort of artificial tag to individuals. These markers are of two basic kinds: microchemical signatures in hard parts (e.g., otoliths and shells) and genetic markers [e.g., mitochondrial DNA (mtDNA), microsatellites]. The latter approach is broader taxonomically, but both have the advantage that every individual within the population is marked (see Hellberg et al. 2002; Planes 2002; Thorrold et al. 2002, 2007; Palumbi 2003; Hellberg 2007; Hedgecock et al. 2007). These two approaches are discussed separately below.

Geochemical signatures (based on stable isotopes, elemental ratios, or both) retained within the hard parts of certain taxa (e.g., otoliths in fishes, shells and statoliths in mollusks) have been used with varying levels of success to identify spatial variation in potential source locations of larvae, especially in estuarine systems (e.g., Thorrold et al. 2001, 2007) and even nursery habitats over relatively short spatial scales (e.g., Gillanders & Kingsford 2000). Demonstration of similar spatial variance along coastal environments is also mounting (e.g., Warner et al. 2005, Becker et al. 2007). The underlying principle is that environmentally available elements and stable isotope concentrations are spatially variable; remaining questions ask over what spatial and

temporal scales does this variation occur and what drives it (from both a physical and biological perspective).

Variation in geochemical signatures through time can limit the success of predictions of source locations among years (i.e., sampling must be repeated for all potential source locations each year recruits are measured), even though within-year spatial assignment can be high (e.g., Warner et al. 2005, Zacherl 2005). Assigning likely source locations of larvae/recruits with specific geochemical signatures requires knowledge of samples of young at time of production from all potential source locations. In lieu of such data, assumptions must be made as to potential source locations (e.g., Swearer et al. 1999, Hamilton et al. 2008). One means of refining the accuracy of source-location determination using microchemistry is to outplant young larvae (e.g., mollusks) along the coastal domain under study and compare the assimilated microchemical signatures of their shells with those of wild collected larvae/recruits (sensu Becker et al. 2007). Another approach is to establish an atlas of geochemical properties from potential source sites. Warner and colleagues (2005) attempted to establish such an atlas of geochemical signatures using proxies (e.g., water chemistry, adult otoliths, and resin). Though this approach has so far met with limited success, increased knowledge of the assimilation process (e.g., Bath et al. 2000) will help to identify the best proxies. Once appropriate proxies are established, large areas could be rapidly surveyed as potential source locations to be compared with geochemical signatures found at the core of newly recruiting young.

An alternative method is the application of genetic markers, which have escalated thanks to improved laboratory protocols for analyzing genetic data. Hedgecock and coworkers (2007) and Hellberg (2007) provide recent reviews of these techniques, point to promising new approaches (e.g., Monte Carlo, maximum likelihood, and Bayesian analyses; Neilsen & Wakeley 2001, Manel et al. 2005, Beerli 2006), and note important limitations of using genetic markers to differentiate population structure at various spatial scales. Two primary analytical approaches for measuring demographic rates of exchange in marine organisms have dominated the recent literature: utilization of the stepping-stone model (Wright 1943, Slatkin 1993) via estimation of isolation-by-distance, and more recently, the use of assignment tests (Manel et al. 2005) to more directly link dispersal of young to known adult populations. These indirect and direct genetics-based approaches are sensitive to many of the same issues as are geochemical approaches (above) in that the indirect approach provides a view of genetic connectivity taking place over many generations, whereas the direct approach records event (or near-event) scale exchange, making it difficult to link patterns to processes that drive the direction and scale of exchange (Hedgecock et al. 2007). Moreover, separating historical from recent exchange is often difficult (Benzie 1999, Neilsen & Wakeley 2001). Nonetheless, these approaches have provided considerable evidence for the modal spatial scales of exchange that often fall within tens to hundreds of kilometers across a range of species and marine coastal environments (see review by Palumbi 2003) and recent applications of Bayesian analytical techniques have demonstrated the potential to discern small spatial patterns in demographically relevant connectivity (e.g., Baums et al. 2005, Hare et al. 2006, Richards et al. 2007, Underwood et al. 2007).

Given the extensive effort that often must be expended to complete the tracking of a single reproductive event from a single source location, alternative means must be sought to identify realistic dispersal kernels. One alternative approach to estimate dispersal distances, with the potential to calculate dispersal kernels, is the utilization of high-resolution biophysical models (e.g., James et al. 2002, Cowen et al. 2006, Aiken et al. 2007). Although considerable qualifications are warranted in the use of models, one obvious advantage over the above indirect and direct methods is that the models allow for multiple releases of virtual larvae. Thus, although each individual run of the model is equivalent to an isolated measurement of a dispersal event, the modeling approach allows repeated measures through time and space, thereby capturing the expected environmental

variability and allowing construction of a connectivity matrix (**Figure 1**). Models are also powerful tools when combined with field/empirical methods (Werner et al. 2007). Besides their utility in resolving spatial scaling patterns, models are also critically important in resolution of the processes contributing to the patterns, and thus are discussed in greater detail below.

EXPLANATION: PROCESSES THAT DRIVE LARVAL DISPERSAL AND POPULATION CONNECTIVITY

High spatial and temporal variability in the abundance of early life history stages through settlement and recruitment implies a complex set of interacting processes that operate across various scales to establish the seemingly stochastic patterns observed (**Figure 2**). Fundamentally, we need to understand the processes that drive dispersal patterns before we can fully describe patterns of population connectivity. In doing so, the link from larval dispersal to population connectivity is obvious because the processes that control the dispersal of individuals from one location to another demographically connect many benthic marine populations. However, the influence of
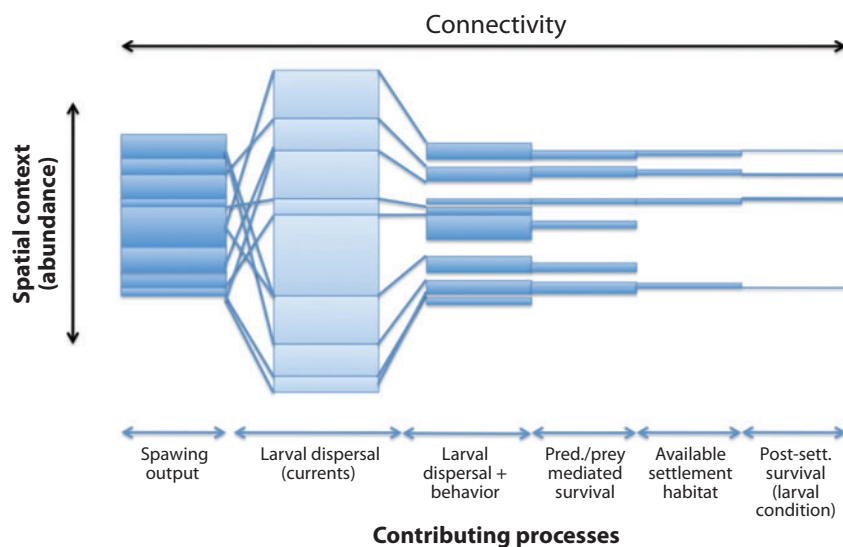

Figure 2

A representation of the combined processes that act to determine the spatial connections among populations via larval dispersal and survival. The spatial context is depicted by a series of populations (each represented by a single band on the left). The spawning output of those populations is dependent on the size, fecundity, etc. of each population; hence the relative size of each band indicates spatial variability in reproductive output. The larval physical dispersal process (advection and diffusion) acts to mix the young (*the crossing lines to different bars*), expand the spatial distribution of the larvae (*expanded size of the bands*), and consequently dilute the concentration (*lighter color*). With the inclusion of larval behaviors (e.g., vertical migration, horizontal swimming), the diffusive nature of the physical processes may be counteracted through biophysical interactions; hence the constriction of the spatial extent and increase in density (*smaller bands and darker color*). In addition to physical dispersal, various biological and physical factors operate to extract a spatially varying loss (mortality) as depicted by a continual reduction in available survivors (*smaller bands*) due to predator/prey interactions, availability of settlement habitat, and postsettlement survivorship, in part driven by larval condition at time of settlement (e.g., carryover effects). Comparison of the two extremes of this figure (the source and receiving locations) provides an idea of the pattern of connectivity, or the scale of successful dispersal. The steps between these two ends provide an overview of the processes that contribute to the dispersal kernel.

additional nondispersal processes results in population connectivity not being identical to larval dispersal. For example, the availability of suitable settlement and nursery habitat is important, as are the factors that affect the success of metamorphosis from larvae into benthic juveniles (e.g., larval condition, benthic predation).

Larvae (and spores) are dispersed in the ocean via an interplay between physical and biological processes. Certainly, for the very smallest and youngest propagules (e.g., spores and pelagic eggs), the biological contribution to the dispersal process is limited to the timing and location of the starting point for each propagule. This contribution may be as simple as release from the sessile adult on a regular basis, or aggregation of adults for spawning at specific sites once or twice a year (e.g., groupers, snappers, and lobsters). More complex biophysical interactions can and do occur when more complex behavioral traits are expressed, such as vertical migration and oriented horizontal swimming, as well as physiological and developmental traits, such as growth rates and PLD. How such biological traits mediate dispersal driven by the advective-diffusive field the larvae encounter is a critical area of research that requires a coordinated, interdisciplinary approach. Though much of the progress and many of the challenges lie at the interface of these biological/physical interactions (for reviews see Shanks 1995, Cowen 2002, Sponaugle et al. 2002, Largier 2003, Pineda et al. 2007), some of the following discussion, for simplicity, addresses the biological/physical mechanisms separately, with a final call for examination of the interactions of both sets of processes.

Physical Processes

In many respects, some of the largest challenges to studying population connectivity mechanistically lie within physical oceanography. Although knowledge of the drivers and responses of the deep ocean is extensive, the same is not so for the shallow nearshore environment. Yet, the nearshore is the primary starting and ending point for larval dispersal of coastal species, and one where cross-shelf and along-shelf flow change rapidly over short distances owing to strong interactions of frictional forces of coastal topography, stratified water columns, tidal forces, wind, buoyancy, surface waves, and turbulence (Largier 2003, Gawarkiewicz et al. 2007). The high level of variability within this zone across multiple scales creates the challenges. The transition from small spatial and temporal scales within coastal environments to larger scales offshore requires a balance of fine-scaled sampling strategies nearshore and more extensive spatial and temporal domains offshore. Variation across scales of specific processes is also a challenge to modelers because resolving mesoscale and small to intermediate scales simultaneously is currently problematic (Werner et al. 2007), though recent advancements in model nesting techniques are helping (e.g., Sheng et al. 2005).

Retention mechanisms in coastal environments have been relatively well described for estuarine-dominated coasts (e.g., Epifanio & Garvine 2001), but less so for other coastlines. Coastal topography creates regions of reduced flow and/or retention, especially in the vicinity of headlands (e.g., Graham & Largier 1997, Lipphardt et al. 2006, Mace & Morgan 2006). Higher bottom topography similarly adds to retention potential as shallow nearshore flow is reduced due to bed friction. This reduced nearshore flow potentially limits cross-shore dispersion of nearshore-spawned propagules, and thus access to stronger along-shore flows offshore (Largier 2003). Frontal convergences, such as those that occur at coastal boundaries, may further minimize offshore transport of larvae. Similarly, submesoscale eddies may enhance retention of larvae, as well as increase variability in the spatial and temporal pattern of larval and nutrient delivery to the coast (e.g., Bassin et al. 2005, Sponaugle et al. 2005). These are just a few examples of processes within the coastal environment that require relatively fine spatial and temporal measurement to

resolve. Moreover, the interactions among processes need resolution. For example, to what extent are the above mechanisms moderated by tides?

Biological Traits

The above coastal processes can have direct and indirect effects on larval transport and survival that lead to diverse patterns of connectivity. Not only are various flow features critical to dispersal, but many of the drivers (e.g., wind, temperature, salinity) can also interact to influence nutrient availability, physiological rates, and behavioral responses. The interaction of biological responses and behaviors with the physical environment can serve to moderate dispersal and connectivity such that the outcomes are quite different from those predicted on the basis of physics alone.

At the onset of the dispersal process, production of offspring requires that adults have access to sufficient nutrition. Seasonal changes in water temperature and productivity frequently underlie seasonal production of young. Not only do such environmental conditions influence adult spawning behavior and thus the starting point of pelagic life, but maternal condition also influences egg and larval quality, and thus survival (Berkeley et al. 2004, McCormick 2006). Larvae that survive to hatch pass through various ontogenetic stages that can exhibit increasingly complex behaviors. Whereas larvae of some invertebrates and plants may be largely passive throughout their pelagic period, other larvae such as those of fishes and lobsters are capable of large vertical migrations and directed horizontal swimming (reviewed in Cowen 2002, Leis & McCormick 2002, Leis 2006, Montgomery et al. 2006). Larvae must, of course, be near suitable settlement habitat at the time that they are competent to settle or they presumably die. Larvae can be passively transported to such habitats by ocean currents (see above), or they can actively orient and navigate to such habitat using various auditory, olfactory, or other potential cues (e.g., reviewed in Kingsford et al. 2002, Montgomery et al. 2006).

The amount of time that larvae remain in the water prior to settlement to the benthos and/or metamorphosis into a juvenile clearly has an important effect on the distance larvae are dispersed. PLD is thus one of the fundamental components examined in the study of population connectivity (Cowen et al. 2000, Shanks et al. 2003, Kinlan & Gaines 2003). Depending on the taxa and the environment encountered, PLD can be relatively invariant or highly flexible. Water temperature and available nutrients play a critical role in dictating PLD of some species (Houde 1989, Pepin 1991, McCormick & Molony 1995, Rombough 1997). Predicted increases in water temperature with global climate change therefore may have a real effect on population connectivity (O'Connor et al. 2007).

Events that occur during larval transit can have important consequences for larval survival to settlement. Beyond transport in association with particular physical features such as fronts (Grimes & Kingsford 1996) or mesoscale eddies (Sponaugle et al. 2005), water masses encountered by larvae can influence their growth and survival through temperature-mediated effects or potential prey availability (Bergenius et al. 2002, Meekan et al. 2003, Sponaugle & Pinkard 2004, Phillips 2005, Jenkins & King 2006, Sponaugle et al. 2006). Although these processes are not well known, even less is known about variability in larval predator fields and how larval encounter with different water masses may influence rates of predation. Theory predicts that there should be fewer predators offshore than in nearshore waters, but direct measurement of larval predation is rare. Larvae are potentially faced with tradeoffs between maximizing growth at the expense of higher predation in nutrient-rich waters versus avoiding high predation while tolerating lower growth in nutrient-poor waters (Fiksen et al. 2007). In addition to the potential effects of spatial variation in prey on larval growth and mortality, behavior associated with foraging may also influence dispersal and hence, connectivity (Woodson & McManus 2007).

Faster-growing larvae generally experience higher survivorship in the plankton (Meekan & Fortier 1996, Hare & Cowen 1997), and are thus more likely to be transported to a suitable settlement habitat (Wilson & Meekan 2002). Such faster growers also are usually in better condition at the time of settlement, which leads to their further success as juveniles (Searcy & Sponaugle 2001, Shima & Findlay 2002, McCormick & Hoey 2004). That all larvae do not settle at a constant physiological condition and that larval traits carry over to influence juvenile survival (Sogard 1997, Pechenik 2006) are demographically important. New settlers are usually susceptible to high predation (Caley et al. 1996, Hunt & Scheibling 1997) and their survival can be related to their condition at settlement. Higher-condition individuals preferentially survive metamorphosis and early juvenile life (Phillips 2002, Vigliola & Meekan 2002, Thiyagarajan et al. 2003, Sponaugle & Grorud-Colvert 2006) and thus potentially contribute disproportionately to the population. Whether the traits from early life continue to influence performance through to reproduction is unknown for species with long times to maturity. For a few shorter-lived species, quality of early stages may (Marshall & Keough 2006) or may not (Meekan et al. 2006) influence later reproductive performance.

The increased integration of studies across life stages is beginning to demonstrate that selective loss of individuals with particular traits may not remain consistent or linear throughout life (Gagliano et al. 2007). Traits that are advantageous in the larval stage may even be detrimental to juvenile survival (Gimenez & Anger 2003). Further, optimal traits may shift with environmental or demographic conditions (Moran & Emlet 2001, Gagliano et al. 2007). Differential survival of settlers has the potential to either reduce or increase population connectivity. In St. Croix, where self recruitment is thought to be high (~60%), differential survival of long-distance versus potentially self-seeded recruits may reduce this rate of self recruitment (Hamilton et al. 2008).

In short, environmental and oceanographic variation inserts high variance into the spatial and temporal distributions and physiological composition of pelagic larvae. This variance interacts with physically and biologically mediated larval transport to result in variable patterns of settlement. Carry over effects and variable benthic conditions interject differential postsettlement survival and, ultimately, reproductive success. Together, these various processes generate specific patterns of realized (sensu Hamilton et al. 2008) or reproductive (sensu Pineda et al. 2007) connectivity. Clearly, attempts to dissect the processes that drive connectivity patterns require greater integration of biology and physics, and thus, interdisciplinary empirical and modeling approaches are required.

Biophysical Integration

Multiple studies utilize an interdisciplinary approach to link larval transport to physical flow features, though often these studies are limited in their temporal or spatial resolution (i.e., they do not cover the full larval life history and/or they do not encompass the spatial extent of the dispersal process). One reason for these limitations is that obtaining the necessary temporal and spatial resolution while simultaneously sampling over the full duration and spatial domain can be prohibitively time consuming and expensive. When the full range of biological responses is considered, empirical studies become complex, multi-investigator efforts that require models to provide the necessary synthesis, hypothesis generation, and sampling design. Attempts to complete the entire integration are probably premature at this time. However, studies that optimize sampling to examine subsets of biological and physical processes that contribute to specific transport outcomes and eventually, dispersal kernels, are possible and preferred.

Multiple approaches to model larval dispersal exist, and choosing among them depends on the goal. At the base of these models, some sort of physical flow model is necessary to place larval

dispersal into an oceanographic context. For example, use of advection-diffusion models can serve important heuristic goals. Cowen and colleagues (2000) used a simple advection-diffusion model that incorporated larval mortality to demonstrate the significant dilution and loss of larvae with distance from source locations, and concluded that biophysical mechanisms must be operating to reduce the loss of larvae from the vicinity of the source location. Similarly, Largier (2003) used a 1-D advection-diffusion model to demonstrate, among other things, how small changes in cross-shelf dispersal can create large differences in along-shore dispersal distance. More realistic, though still idealized, flow models can be used to examine the role of spatial heterogeneity in flow dynamics on dispersal patterns, or how certain larval behaviors may mediate the effect of the flow field on the dispersal outcome (Siegel et al. 2003, Byer & Pringle 2006, Mitarai et al. 2008). One trade-off between these two approaches is illustrated in a modeling study (S. Mitarai, D.A. Siegel, K.B. Winters, R.R. Warner & S.D. Gaines, manuscript in preparation), where spatial heterogeneity in flow versus averaged (smoothed) flow conditions (i.e., diffusion model case) is critical for population persistence in the case of two competing species (**Figure 3**).

Such modeling approaches are critical for the examination of consequences of certain processes, but are not ideal for the determination of which processes may be explicitly operating within specific locations. Here, higher resolution numerical models are increasingly available, and provide the opportunity for more realistic renditions of spatial and temporal variation of flow within regions of particular interest. Werner and colleagues (2007) and Gallego and coworkers (2007) review recent advances in modeling relevant to population connectivity in marine systems, noting not only significant advances in model structure, but also distinct challenges for linking shallow water coastal domains to shelf and offshore environments. With the advent of highly resolved flow fields in hydrodynamic models, it becomes possible to embed behavioral models to assess biophysical interactions. Biophysical models ultimately need to be built that allow for individual variation in larval decisions/reactions to the modeled environmental parameters—i.e., ruled-based models. Individual-based models (IBM) allow such parameterization of biological variables (e.g., Werner et al. 2001, Siegel et al. 2003). Paris et al. (2007) and North et al. (2008) recently used an IBM approach to show how variation in certain behavioral traits can affect Lagrangian transport outcomes (i.e., particle trajectories) (**Figure 4**). Ultimately, when biological models are combined with regional and local hydrodynamic models, repeated scenarios can be computed under variable forcing (e.g., real wind fields) to generate spatially explicit connectivity matrices (e.g., James et al. 2002, Bode et al. 2006, Cowen et al. 2006, Huret et al. 2007). Inclusion of spawning and settlement habitat, and biological traits such as mortality and growth, especially when ruled-based, can generate predictions about the relative importance of certain environmental conditions (e.g., temperature fields or ocean productivity). Overall, no single model will serve all species, biological responses, or locations, but many examples exist of regional models that address a diverse set of biological responses to the physical environment.

Hand in hand with the building of models is the need to evaluate their validity at predicting outcomes. Validation must operate at a variety of levels, and focus on individual parameters and model processes (e.g., vertical distributions) to overall outcome (transition matrix). Validation is an iterative process whereby models can be used to make field predictions/hypotheses that are then empirically tested. Following that, models are modified to respond to differences between model predictions and field measurements, and then the cycle is repeated (see Lynch & Davies 1995). As biophysical models become more complex, validation is increasingly complicated (Arhonditsis & Brett 2004). Sensitivity studies using the models themselves can help determine which parameters are most responsive to variation, thereby suggesting where to initially focus validation efforts.

Similarly, models can be used to guide sampling by predicting specific outcomes or likely spatial scales of a given event to which a specific sampling strategy can be matched. With greater

a Three independent spawning seasons   **b** Smoothed
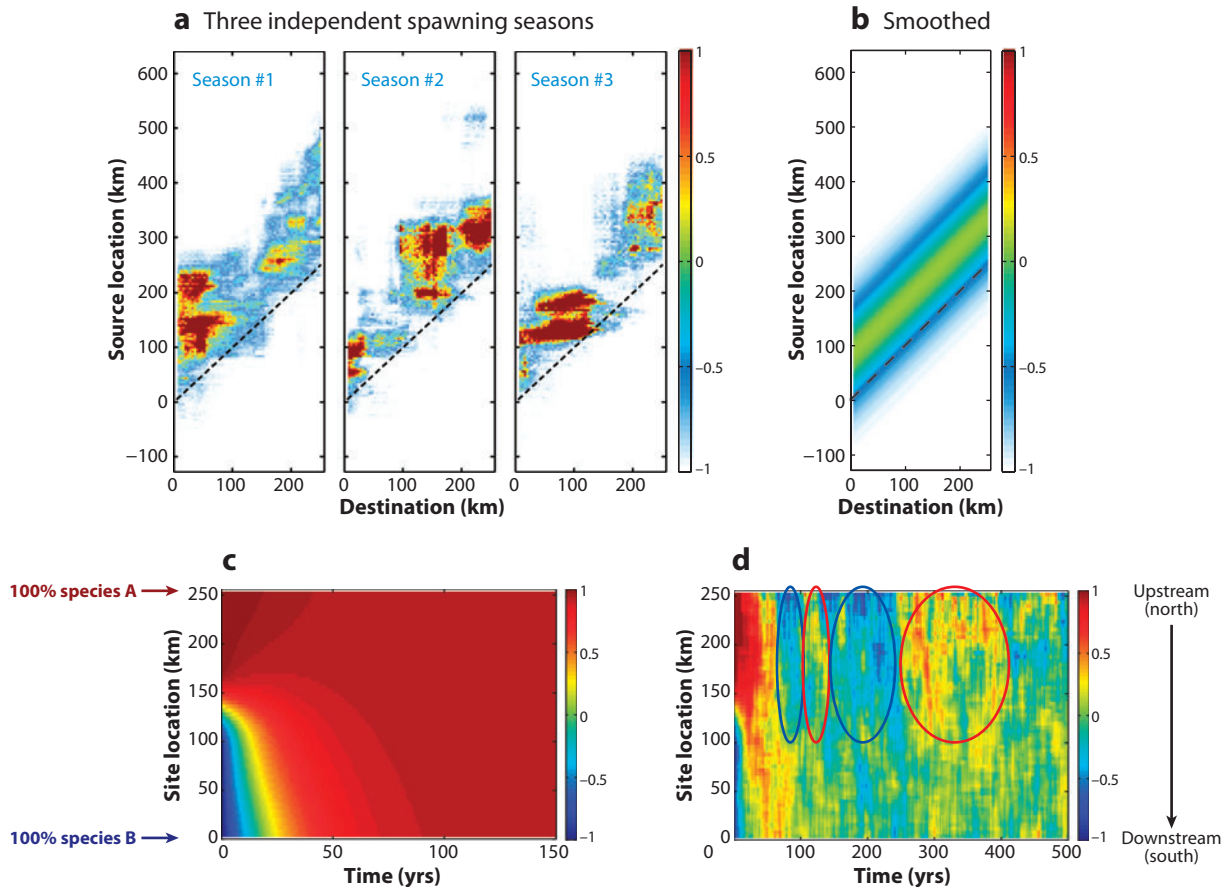
c   **d**

Figure 3

Stochasticity experiment. Utilizing an idealized coastal circulation model (Mitarai et al. 2008) coupled to a Lagrangian particle (larva) tracking model, a connectivity matrix was estimated for multiple spawning seasons (*a*). Each individual spawning season resulted in unique connectivity patterns that represent stochastic variability in the flow regime introduced by high spatial heterogeneity in eddying motions. When the individual connectivity matrices are averaged over many seasons, a smoothed matrix resembling a simple diffusion model is obtained (*b*) (i.e., eddies are ignored). The scale bar represents a proportion of total number of released particles from all sites, and is therefore dimensionless. To examine the importance of stochasticity as introduced by eddies in driving marine population dynamics, a simple two-species (spatial competitors) model was run within these two connectivity conditions (stochastic versus diffusive or smoothed). In each case, one species was introduced at the upstream location, and the other species was introduced downstream. Red (+1) indicates that 100% of the population consists of the species A; blue (−1) indicates 100% of population consists of species B; green (0) indicates half and half. In the diffusion model case, only the upstream species persisted after a short time (*c*), whereas when stochastic connectivity was maintained by running the model each season with a different seasonal connectivity matrix, both species persisted through time (*d*). Moreover, eddy-scale variation was evident in the distribution of the species, which apparently resulted in multidecadal oscillations in species dominance along certain portions of the model domain (*alternating blue/red oval in d*). After a modeling study by S. Mitarai, D.A. Siegel, K.B. Winters, R.R. Warner & S.D. Gaines (manuscript in preparation), with permission of the authors.

predictability of where, for example, larval dispersal patches may exist, focused sampling with new rapid plankton imaging systems and analysis (e.g., Benfield et al. 2007) (**Figure 5**) could target larval trajectories to correspond to model outputs. Combining multiple sampling approaches, both physical and biological, to capture the various stages and processes that operate along the full spawning/dispersal/settlement continuum is tractable when appropriately constrained via models.
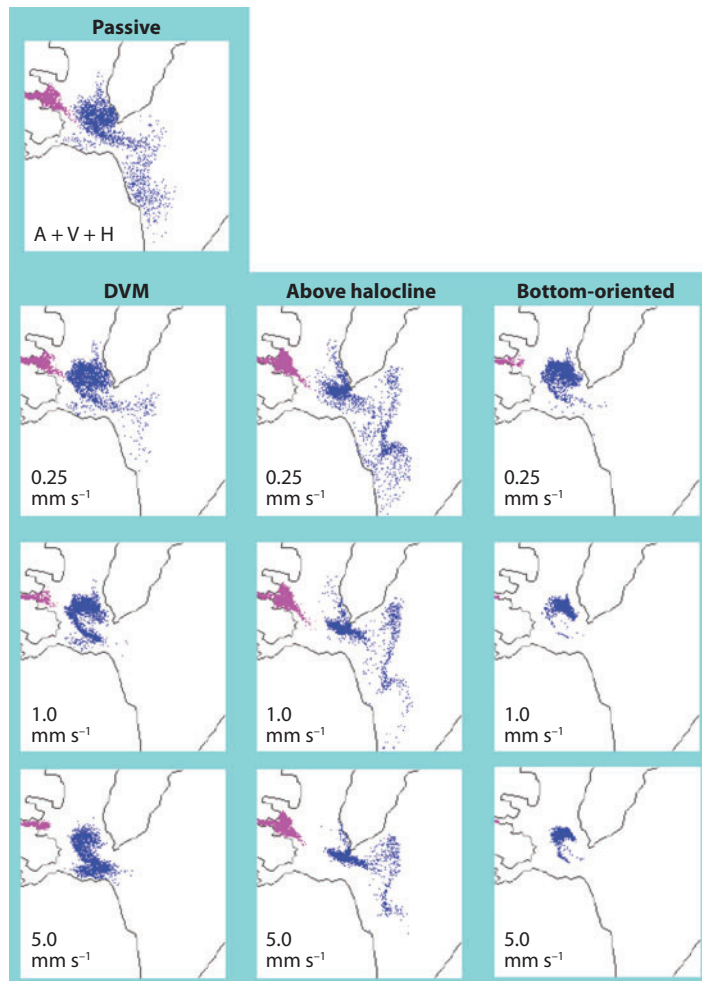
Figure 4

Example of the influence of vertical swimming behavior on dispersal outcomes as compared with passive
(non-swimming) scenarios for minimal swimmers (e.g., dinoflagellates) to moderate swimmers (e.g., fish
larvae) at the mouth of the Chesapeake Bay. In the model simulations, four behavioral scenarios are
compared: passive, diel vertical migration (DVM), surface-oriented (salinity gradient cueing; staying above
the halocline), and bottom-oriented swimming. In the three swimming scenarios, three vertical swimming
speeds were compared (0.25 mm s^{-1}, 1.0 mm s^{-1}, and 5 mm s^{-1}). All scenarios have advective (A) model
output coupled with both horizontal (H) and vertical (V) turbulence components using random walk and
random displacement models, respectively. 2500 particles were released in each scenario within 1 m^3 at
0.5–1.5 m depth, and then tracked for seven days. Note that many nonpassive scenarios resulted in a greater
proportion of particles retained within the bay mouth than for the passive scenario. Further, although even
minimal swimming speeds enhanced retention, the fastest speeds (5 mm s^{-1}) resulted in the most retention.
From E.W. North, Z. Schlag, M. Li & L. Zhong, unpublished results.

With the expanded availability of environmental data through ocean observation networks, the
need for proper design of field deployments can also benefit from model scenarios and data as-
similation (Walstad & McGillicuddy 2000). Observation system simulation experiments (OSSEs)
may be of use for designing studies of population connectivity and expanding the time and spatial
domain over which empirical measurements are regularly available (Werner et al. 2007).
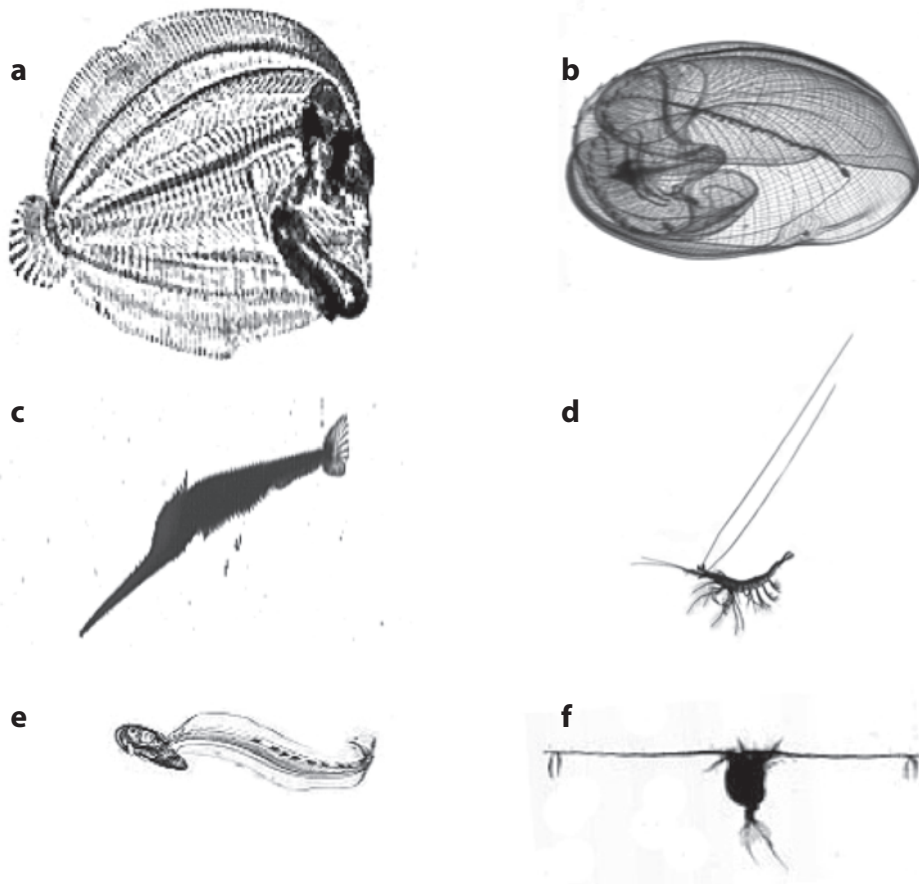
Figure 5

Example images from In Situ Ichthyoplankton Imaging System (ISIIS) (Cowen & Guigand 2008). Images were taken while towing ISIIS at 2.5 m s^{-1} (5 knots) between the surface and 40 m. All images shown were taken within the Florida Current, between 1 and 10 km of the reef track, approximately 15 km south of Miami, FL. ISIIS records images continuously via a linescan camera and shadow lighting technique that builds images with ∼60 μm pixel resolution, while scanning at a rate of ∼36 kHz. All organisms are imaged in situ with minimal turbulence. Simultaneous data on temperature, salinity, fluorometry, downwelled light, depth, and speed through water are also collected. Imaged organisms range in size from 4–20 mm: (*a*) Bothidae (flounder) larva, (*b*) ctenophore, (*c*) Xiphiidae (swordfish) larva, (*d*) Euphausiacea (krill), (*e*) appendicularian (larvacean), (*f*) calanoid copepod.

CONSEQUENCES: ECOLOGICAL CONTEXT OF POPULATION CONNECTIVITY

The field of marine ecology has long focused on the role of larval dispersal in influencing population dynamics (Roughgarden et al. 1988, Underwood & Fairweather 1989), largely from the perspective of whether or not young entering the population are from nearby or farther away. Mechanisms of density-dependent population regulation, a cornerstone of ecology, differ among populations depending on their degree of self-recruitment versus subsidy (reviewed in Hixon et al. 2002). Historically, larvae entering a benthic population were treated as independent of

the local production, or sourced from a homogenous pool of mixed-source larvae (Gaines & Roughgarden 1985). However, beyond this numerical response, the composition of larvae that settle into a benthic population can determine the characteristics of the future population as well as potentially influence existing individuals. As discussed earlier, traits of larval settlers can, via carryover, influence their likelihood of survival and even reproduction. Because such traits may differ owing to genetics and/or the larval pelagic environment, diverse population sources (with or without different genetic compositions) may spawn larvae that travel different routes and encounter contrasting pelagic conditions. Thus, recruits from diverse sources (with different traits) may vary in their benthic success (e.g., Hamilton et al. 2008). By extension, the outcomes of competitive and predator-prey interactions in a local subpopulation may vary according to the natal source of settlers. In locations with temporally variable compositions of settlers, the mechanisms underlying observed ecological interactions may be difficult to identify without factoring in larval source. More recent population modeling efforts now include explicit components related to larval dispersal (e.g., Gaines et al. 2003), and this is increasingly refined to include dispersal not merely as a function of diffusion, but also in a directional and temporally and spatially heterogeneous manner (Amarasekare 2003, Snyder & Chesson 2003, Gerber et al. 2005). Unfortunately, because larval sources are largely unknown for most settlers, few empirical data exist to test theoretical concepts in nature. In one example, although true larval sources were unknown, Wieters and colleagues (2008) broadly classified subpopulations of a suite of intertidal predators and prey as open or closed on the basis of their dispersal potential, and demonstrated that predator abundance tracked prey recruitment only where predator dispersal was limited (closed populations).

On longer timescales, the degree of exchange of propagules among subpopulations influences their likelihood of extinction (Hastings & Botsford 2006). Relative demographic isolation of a population is particularly important in light of increasingly fragmented habitats and changing global climate (see Jones et al. 2007). Population persistence is fundamentally linked to rates of larval delivery and recruitment, and thus connectivity, among subpopulations. Population connectivity therefore also underlies the rates of successful population establishment and expansion of introduced species (reviewed in Swearer et al. 2002). Over evolutionary scales, the degree of geographic isolation among subpopulations may impose selective pressures for particular larval dispersal distances (e.g., Strathmann et al. 2002), as may the implementation of marine protected areas (MPAs; see below) of particular configurations (i.e., short larval dispersal distances; Botsford et al. 2001; see also Gaines et al. 2007).

APPLICATIONS: IMPORTANCE OF UNDERSTANDING POPULATION CONNECTIVITY IN A CHANGING WORLD

Recent environmental and anthropogenic threats have led to the call for increased spatial management of populations and ecosystems, and much effort with regard to population modeling is currently directed at designing effective marine reserves. Roberts (1997) brought the issue of marine population connectivity to the forefront with respect to its implications for spatial management. Though the predicted outcomes of his simplified model were problematic, the concept of spatially complex linkages (or connections) among populations has been recognized in the value and design of MPA networks (e.g., Crowder et al. 2000, Botsford et al. 2001, Lipcius et al. 2001, Russ 2002, Sala et al. 2002, Gaines et al. 2003, Hastings & Botsford 2003, Halpern & Warner 2003, Kritzer & Sale 2004, Gaylord et al. 2005, Fogarty & Botsford 2007). With the ultimate goal of conserving biodiversity or maximizing fishery yields, most theoretical efforts to design maximally effective reserves now consider the role of connectivity via larval exchange and, in some cases, adult movement (e.g., Guichard et al. 2004, Gerber et al. 2005; reviewed in Gaines et al.

2007). Some efforts have collected what limited empirical data are available on potential larval dispersal distances to make explicit recommendations regarding reserve size and spacing (Kinlan & Gaines 2003, Palumbi 2003, Shanks et al. 2003). Of course, given the often wide diversity of taxa (with highly diverse life history strategies) to be protected in an equally wide range of habitat types and oceanographic environments, a single solution is unlikely. Consideration of multiple interacting organisms in a complex environment necessitates incorporation of community processes (e.g., larval dispersal, recruitment, colonization, succession, competition, predation) into the increasingly complex population models (i.e., metacommunity models; Guichard et al. 2004). Reserve design and planning further require that economic and sociological aspects be factored in (Sale et al. 2005). Finally, population genetics also plays an important role in the conservation of marine populations and the spatial context of population connectivity provides a more realistic, if not complex, framework to evaluate genetic exchange theory (e.g., Galindo et al. 2006, Pringle & Wares 2007). Although the task at hand may be daunting, the more we can learn about population connectivity, the more nuanced and integrated these theoretical treatments will become, which will ultimately lead to better design of MPAs.

Of course, the world as we know it is not static and an increasing number of stressors are affecting marine populations. Perhaps the largest threat, global climate change, has the very real potential of disrupting existing larval dispersal pathways and thus patterns of population connectivity. Increasing ocean temperatures and changing weather patterns are projected to change the speed and direction of major currents, which will clearly impact the physical transport of propagules. In addition, because basal metabolic rates, growth, development, and energetic costs of larvae are determined in large part by water temperature, increasing ocean temperatures will generally reduce larval durations and thus dispersal potentials (e.g., O'Connor et al. 2007, Munday et al. 2008). More rapid larval growth will require more food or mortality rates will increase (Houde 1989). Assuming plankton distributions remain patchy or experience greater fluctuations with increasing water temperatures (e.g., Hays et al. 2005), recruitment of many organisms with planktivorous larvae will become more variable (reviewed in Munday et al. 2008), which will contribute to further reductions in connectivity. Rising sea levels and habitat modification (e.g., coral beaching) also will likely alter the availability of benthic habitats for juveniles and adults, and moderate their ecological interactions therein, potentially impacting reproductive success. Because the suite of potentially interacting variables and processes is complex, uncertainty exists regarding the synergistic impacts of climate change on population connectivity (Munday et al. 2008). The changing nature of the environment reinforces the need to understand the processes that contribute to observed patterns in population connectivity. Only a complete understanding of the underlying processes will enable us to eventually predict outcomes of particular environmentally induced changes or human-imposed management scenarios, let alone the explicit patterns in marine population connectivity occurring today.

FUTURE ISSUES

1. The nearshore environment represents a core challenge for physical oceanographers because of the confluence of multiple drivers that interact at fine to mesoscales. Similarly, biologists need to better resolve processes that operate within this zone because it represents critical starting and ending points (and perhaps, for many species, encompasses the entire period) of the pelagic dispersal phase. Relevant to both disciplines, horizontal and vertical stratification in the ocean can be extensive, and the potential interactions are complex, which requires a concerted research effort to resolve.

2. Advances in computing power and model frameworks are allowing ever more complex models to be developed. The community will therefore need to focus extensive field effort on the task of model validation and parameter evaluation to ensure model accuracy and utility. Modelers and empiricists will need to forge strong and regular collaborations to test assumptions and hypothesis predictions, understand modeled processes, and identify critical knowledge gaps.

3. Development of novel technologies or modification of technologies from other fields will continue to provide expanded sampling opportunities. Development of rapid and/or automated samplers (or postsampling analyses) will serve to increase sampling resolution and extent, which is critically important for resolving many of the smaller-scale processes that operate within the coastal domain. Molecular tools developed in other fields may have direct application toward examining genetic consequences, as well as larval tracking and physiological responses relevant to population connectivity.

4. Bringing the theoretical and fundamental understanding of the processes that underpin larval dispersal and population connectivity into the management mainstream within a useful framework will require direct interaction between scientists and managers. Development of useful decision-support tools will require input from managers to both realistically constrain what input they can provide to these tools and maximize the utility of the outputs. Applications to a variety of problems must be anticipated (e.g., management of single and multiple species, spread of invasive species, ecosystem-based scenarios).

5. Exploration of the potential impacts of increasing temperature and ocean acidity on larval survival and dispersal will require more work on the influence of stress on ecological interactions and selective mortality. Similarly, forecasting hydrodynamic ocean models that incorporate future climate scenarios will need to be linked to biological models with explicit, individual-based response rules to dissect physiological from strict dispersal response outcomes.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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Errata

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