Recent progress in understanding larval dispersal: new directions and digressions

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Synopsis Larvae have been difficult to study because their small size limits our ability to understand their behavior and the conditions they experience. Questions about larval transport focus largely on (a) where they go [dispersal] and (b) where they come from [connectivity]. Mechanisms of transport have been intensively studied in recent decades. As our ability to identify larval sources develops, the consequences of connectivity are garnering more consideration. Attention to transport and connectivity issues has increased dramatically in the past decade, fueled by changing motivations that now include management of fisheries resources, understanding of the spread of invasive species, conservation through the design of marine reserves, and prediction of climate-change effects. Current progress involves both technological advances and the integration of disciplines and approaches. This review focuses on insights gained from physical modeling, chemical tracking, and genetic approaches. I consider how new findings are motivating paradigm shifts concerning (1) life-history consequences; (2) the openness of marine populations, self-recruitment, and population connectivity; (3) the role of behavior; and (4) the significance of variability in space and time. A challenge for the future will be to integrate methods that address dispersal on short (intragenerational) timescales such as elemental fingerprinting and numerical simulations with those that reflect longer timescales such as gene flow estimates and demographic modeling. Recognition and treatment of the continuum between ecological and evolutionary timescales will be necessary to advance the mechanistic understanding of larval and population dynamics.

Introduction

Interest in the dispersal of larvae dates back to the seminal ideas of Hjort (1926) and Thorson (1946), who advocated the importance of larval transport and survival in determining the dynamics of fish and invertebrate populations, respectively. Since the 1980s there has been an increased awareness of "supply side" ecology (Gaines and Roughgarden 1985; Lewin 1986; Young 1987; Fairweather 1991), granting larval studies a central position in the field of marine ecology. The number of articles addressing larval dispersal increased greatly during the 1990s (Fig. 1). A Web of Science search for articles using the key word "larval dispersal" shows 2003 (the last year surveyed) to be a peak year with 62 publications.

Much of the larval work conducted during the last quarter of the twentieth century focused on mechanisms of transport (for example, see reviews by Shanks 1995), rates of mortality (Rumrill 1990), larval trajectories (Levin 1984), settlement behaviors and cues (Pawlik 1992), and rates of gene flow (Burton 1983; Hedgecock 1986; Grosberg and Cunningham 2001;

Hellberg and others 2002). The primary motivation was the idea that larval supply was a key determinant of adult population dynamics.

There has been a resurgence of interest in larval dispersal, in part fueled by relatively new motivations and by new imperatives for more traditional motivations. For example, understanding the dynamics of fish and shellfish resources has long spurred interest in the dispersal of commercially valuable species such as oysters (Nelson 1924, Mazzarelli 1992). Overfishing, eutrophication, and destruction of fisheries habitats have increased the importance of understanding which populations act as sources, which populations act as sinks, and how sites are connected by larval exchange. The design of marine protected areas (MPAs) has provided major impetus for the assessment of dispersal and its role in conservation (Botsford and others 2001; Lubchenco and others 2003). As coastal ecosystems are degraded, restoration plays a more prominent role in the ecological management agenda. Recovery of restored (or disturbed) habitats may initially be controlled by the structure of the patches (Connel and
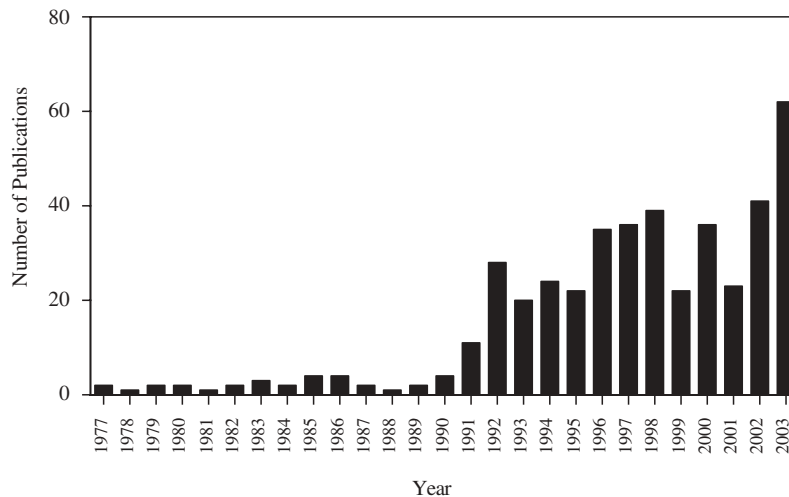
Fig. 1 The number of articles published over the last 25 years whose title or abstract contained the term larval dispersal. Based on a Web of Science survey.

Keough 1985; Sousa 1985) or the dispersal abilities of colonizing species (for example, Levin and others 1996). Thus, understanding dispersal mechanisms, rates, and distances can help scientists to determine the optimal size, configuration, and location of MPAs and restored habitats such as wetlands. Attempts to understand and control the spread of invasive species have led to a new genre of dispersal studies focusing on newly colonized, non-indigenous populations (Neubert and Caswell 2000). The growing recognition that climate change may alter species ranges on interannual (Fields and others 1993; Roy and others 2001) and much longer timescales has prompted scientists to look at the role of dispersal in this process. Finally, a general desire to maintain and sometimes maximize regional and local biodiversity has generated curiosity about the role of dispersal in this process (Stuart and others 2003).

Throughout his career, Larry McEdward's research offered invaluable insights into the evolution and consequences of invertebrate life histories. Although Larry did not directly study the dispersal of larvae, many facets of his work, from the provisioning of eggs and parental care to release times (McEdward and Janies 1997; McEdward and Morgan 2001; Reitzel and others 2004), greatly enhanced understanding of larval survival and transport.

The goal of this review is to provide an overview of how understanding of larval dispersal has changed in the past 5–10 years. I will examine the primary questions addressed, the new tools and approaches that have been developed to tackle these questions, and the insights that have emerged from these approaches. Rather than covering the multitude of articles that have

been published in an exhaustive fashion, I will focus on examples that illustrate paradigm shifts and novel methodologies. A significant number of comprehensive reviews have been published recently on different aspects of larval dispersal and its consequences. I will attempt to synthesize some of the main insights resulting from these reviews, highlighting those issues that appear to advance (or at least move) the field.

It should be emphasized that while larvae are the focus of this article, they are not the only, or always the most important, dispersive phase in animal life histories. Sperm dispersal and post-larval dispersal by drifting, rafting, dislodgement, or adult migrations can contribute to the patterns of connectivity and gene flow often attributed to larvae (Havenhand 1995).

Key questions

I maintain that the two most important questions in the study of larval dispersal are the age-old queries "Where do larvae go?" and "Where do settling larvae come from?" The first of these is the more traditional view of larval dispersal. We ask how far do larvae travel and what are the factors that influence transport? What are the roles of developmental traits, timing and location of release, nutrition, behavior, and physical processes in determining larval transport distances? In modern jargon we speak of dispersal kernels, to reflect the probability distribution of larvae as a function of their starting location (Neubert and Caswell 2000). As mentioned earlier, considerable focus in the past decades has been on determining the underlying transport mechanisms (for example, Epifanio and Garvine 2001).

The opposite side of the coin considers where settlers or recruits in a population originate. Taken in a spatial context, this is a key component in the modern concept of connectivity (Moilanen and Hanski 2001). Questions about whether populations are open or closed (Caley and others 1996; Mora and Sale 2002), the importance of retention and self-recruitment (Swearer and others 2002), the existence of sources and sinks within a metapopulation (Hanski and Gilpin 1991), and the complexity of these patterns all derive from knowing the sources (and sometimes trajectories) of settling larvae. As our ability to evaluate the origins of recruits develops, we can also begin to ask about the importance of the origin of planktonic larvae to subsequent success in the benthos.

Changing paradigms

To understand changes in the field it is necessary to view the dominant paradigms that have developed with the onset of a "supply side" mindset. The concept of "open populations," with plentiful exchange of larvae, was pervasive in the late twentieth century (Caley and others 1996). In combination, the widespread existence of planktonic larvae among invertebrates and fish, the broad distribution of larvae in the plankton, extended planktonic periods, poor swimming abilities of most larvae, and observations of gene flow among isolated patches suggest that larval exchange among subpopulations should be the rule. These observations, combined with the typical disconnection between local larval production and settlement at any one site (Dixon and others 1999), provide evidence for open populations (Swearer and others 2002). Over time exceptions have been noted (for example, Todd and others 1998) that preview shifts in the paradigm of well-mixed populations.

Recent work suggests that retention of larvae in the natal habitat is more frequent than suspected and, thus, that populations may be less open (or more closed) than originally thought. Later sections of this article demonstrate how diverse studies of dispersal utilizing physical models, genetic studies, elemental fingerprinting, and natural observations all suggest that retention is common. Taken together, these methodologies appear to be altering the "connectivity" paradigm.

That the *larval dispersal phase is advantageous* was also viewed by many as a fact during much of the past century. The key roles of dispersal in founding new populations; in habitat selection; in gene flow; and for possibly placing larvae in a safer, food-rich, predator-free setting (relative to the benthos) argued strongly for selection to promote the planktonic larval phase. However, it is now recognized that planktonic larvae offer many disadvantages and that trade-offs are clearly involved (Palmer and Strathmann 1981; Strathmann 1982; Strathmann and others 2002). Ontogenetic (life-stage) migrations provide a more balanced framework for viewing the trade-offs between transport and larval loss.

The *passive nature of larval dispersal*, particularly for marine invertebrates, is another assumption that had pervaded the study of transport and application of physical models until recently (Stobutzski 2001). The absence of information about behavior of larvae in the field (Young 1995) and of techniques to study their behavior in the field has been partly responsible for this, although Young and Chia (1987) earlier highlighted the potential importance of larval behavior in determining the distribution of larvae. Some of the most thoughtful treatment of how behavior can influence dispersal or settlement comes from studies of poecilogonous species with developmental and behavioral dimorphisms (for example, Levin and Huggett 1990; Krug and Zimmer 2004).

A fourth paradigm concerns the idea that *larval supply has key consequences for both the dynamics and genetic structure of marine populations*. Using bivalve biomass data, Thorson (1950) demonstrated that species with long-lived planktonic larvae exhibit larger abundance fluctuations than species with non-planktonic larvae. For the next 40 years the belief that dispersive larvae contribute to population variability in invertebrates was dominant. A number of treatments questioned this over the years (Josefson 1986; Levin and Huggett 1990; Olaffson and others 1994). By far the most definitive of these is a recent review by Eckert (2003) in which 570 invertebrate time series were examined for adult density variation. Species with no planktonic period were found to exhibit the greatest coefficients of variation, but taxa with short (<3 days), intermediate (3–10 days), and long (>2 weeks) planktonic periods did not differ in variability of benthic populations. Eckert (2003) argued that rather than promoting variability, the planktonic period may dampen fluctuations by spreading larvae over heterogeneous environments. Botsford and colleagues (1998) noted that dispersal allows spatially separated populations to fluctuate in phase.

Interest in the influence of dispersal on genetic structure also has a long history (Hedgecock 1986; Palumbi 2001). Planktonic dispersal was considered to play a key role in homogenizing gene frequencies, and the lack of larval exchange was thought to promote differentiation and increase genetic structure. Reviews by Palumbi (2001), Hellberg and colleagues (2002), and Palumbi (2003) look at the scales over which dispersal distance and genetic structure appear linked. These

authors conclude that the greatest influence of larval transport on genetic structure occurs at intermediate scales (~100 km). They observed little differentiation on small scales (10 m) and domination by historical influences at much larger scales (1000 km).

## The link between larval development, dispersal, and its consequences

There has been a general understanding that egg size is correlated with planktonic development time and thus to dispersal potential (Thorson 1950). Two recent compilations show a positive relationship between propagule duration in the plankton and measures of dispersal distance.

Shanks and colleagues (2003; Fig. 2) drew data from studies in which planktonic period was derived from direct observations, studies of distributions in nature, genetic and experimental studies, as well as from tracking of introduced species. Siegel and colleagues (2003; Fig. 2) examined studies for which a genetic-based average dispersal scale was estimated. Both revealed a bimodal distance distribution, comparable to observations of bimodal egg sizes (Vance 1973; Sewell and Young 1997). Few species exhibited dispersal distances between 1 and 20 km/year. Both studies also identified a number of species whose observed dispersal distances fell well below the predicted values; these were identified as possibly reflecting retention within the natal habitat.

The positive relationship between propagule duration (planktonic larval duration [PLD]) and dispersal distance was used by Grantham and colleagues (2003) to calculate habitat-specific dispersal potential. They

examined a range of ecosystems in the U.S. Pacific Northwest, collating development mode, rafting potential, and planktonic duration. From this information they inferred that assemblages in sandy intertidal habitats, which have the highest proportion of non-dispersing and non-planktonic taxa, should exhibit the most limited dispersal. Assemblages in subtidal soft-bottom habitats, which have the highest proportion of taxa with planktonic feeding and larval lifespans >30 days, should exhibit the greatest dispersal. Rocky shore assemblages in California, Oregon, and Washington were intermediate in dispersal potential.

Large eggs, the absence of feeding, and aplanktonic development or short PLDs are associated with limited dispersal potential, and thus should enhance the probability of self-recruitment (settlement at the natal site). However, comparison of larval dispersal by demersal-versus pelagic-spawning fishes revealed no inshore retention in species with non-pelagic eggs (Hickford and Schiel 2003). Two groups that rely on self-recruitment for persistence are endemic species and newly introduced species. Swearer and colleagues (2002) examined articles addressing the life histories of these groups and found no bias toward development with reduced PLDs. Pelagic larvae are well represented among endemic tropical fishes and marine mollusks, as well as among introduced Hawaiian fishes and marine invertebrates (Swearer and others 2002). Thus, retention is clearly not solely a function of life history. We must recognize, however, that endemic and introduced species are more likely to have originated from founder events associated with long distance dispersal than other species. Thus, a focus on these groups may
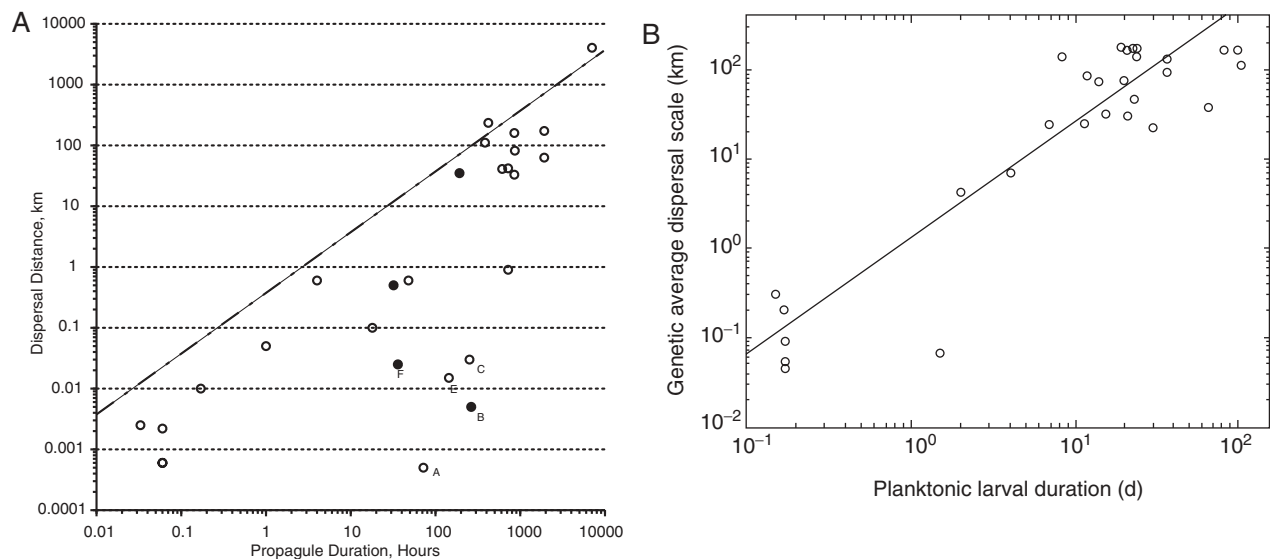
Fig. 2 The relationship between planktonic duration of propagules and dispersal distance. **A:** from Shanks and colleagues (2003), **B:** from Siegel and colleagues (2003).

bias the assessment of the link between life history and self-recruitment.

Methodological advances

While the questions about dispersal are not new, the context in which they are addressed and the methods of study are changing. A combination of thoughtful ideas, increased accessibility to computing power, advances in analytical chemistry and genetics, and even a little bit of magic have made the twenty-first century a more creative milieu for dispersal studies. Below, I focus on three methodological approaches to assess connectivity: physical modeling of larval dispersal, use of geochemical tracers, and genetic studies of isolation by distance.

Physical modeling

The past 5 years has seen an exponential increase in the application of numerical simulations to larval dispersal problems. The focus is often on the development of dispersal kernels (probability distributions of spread), estimation of self-recruitment rates, generation of site-specific data for MPA design, and the construction of null hypotheses for connectivity studies (Siegel and others 2003). Circulation models may be used to study the consequences of specific hydrographic features and are often combined with realistic estimates of mortality or behavior. Lagrangian particle tracking models and diffusion models of tracer dispersion are both used extensively. Both 2D and 3D approaches have been adopted.

A number of key insights have emerged from numerical simulations and physical models. One very prominent idea is the finding that retention (near source habitat) is more likely than expected when models incorporate mortality. This was demonstrated by Cowen and colleagues (2000) for Caribbean reef fish. Studies of the polychaete *Pectenaria koreni* in the English channel (Ellien and others 2004) and the brittle star *Ophiothris fragilis* (Lefebvre and others 2003) both reveal a greater role for mortality than hydrodynamics in determining recruitment patterns, and suggest that retention is significant.

Early modeling efforts typically assumed passive dispersal by currents, even for fish larvae (Roberts 1997). Models that incorporate vertical migration often show that vertical movements have a significant effect on transport and can lead to retention or export, which would not otherwise occur. By using a 2D TRIM (tidal residual intertidal mudflat) simulation for San Diego Bay, DiBacco and colleagues (2001) demonstrated that for larvae release in the back half of the Bay, migration to the seabed during flood tide (as occurs

for *Pachygrapsus crassipes*) will enhance transport out of the bay within 24–30 h, whereas larvae that do not migrate (such as zoeae of *Lophopanopeus* spp.) are effectively retained within the Bay. Particle simulations by Witman and colleagues (2003) mimicking crab and seastar larvae in the Gulf of Maine revealed that 15–75% are retained within the study area over 2–5 weeks. This fraction is 0 at the surface, but increases dramatically with increasing water depth. For example, 2-week retention rates were 30, 54, and 75% at 5, 10, and 15 m water depth, respectively. Paris and Cowen (2004) used CTD/ADCP (acoustic doppler current profiler)-based models to study the effect of vertical swimming by bicolor damselfish larvae. In combination with field collections, they ascertained that retention on the natal reef can be high when larvae swim downward in a directed fashion.

Another key insight is the clear role of variability in physical transport. ROMS (regional oceanic modeling system) simulations of tracer/larvae movements in a release from the mouth of San Diego Bay illustrates that larvae may move northward during periods of slope instabilities, and transport may be southward during periods when circulation is dominated by offshore eddies (E. DiLorenzo and B. Cornuelle, unpublished data). Clearly, transport is far from static, and will vary with tidal phase, season, and year as well as external forcing factors.

Physical models are often used to address how far larvae travel. Particle tracking models suggest that larvae of the shrimp *Pandalus borealis* may travel 74–122 km, with variability controlled by migration of the polar front that determines inflow of Atlantic water to the Barents Sea (Pederson and others 2003). In contrast, satellite tracking of coral larvae at Flower Garden Banks in the Gulf of Mexico suggests that larvae encounter reefs and settle in <40 m (Lugo-Fernandez and others 2001).

When used in combination with other techniques, physical models can provide powerful results. Marsh and colleagues (2001) combined physiological studies of metabolic rates, energy content, and potential larval lifespan in the vent tubeworm *Riftia pachyptila* with measurements of along-axis water movement to estimate dispersal distances of <100 km. Two-dimensional circulation models were combined with genetic studies of *Mytilus* hybrid dispersal (into pure zones) to estimate dispersal distances of 30–64 km in the United Kingdom (Gilg and Hilbish 2003).

How far do larvae go?

Scientists have been trying to answer this question since larvae were first recognized as being alternative phases

of adult forms (Wallace 1876; Young 1990). Methods for tracking marine invertebrate larvae or for estimating dispersal distances have included direct observation of larvae, laboratory rearing experiments, analysis of distributions of larvae and recruits around isolated sources, studies of the spread of newly invasive species, numerical simulations based on physical transport, genetic isolation by distance studies, and use of natural and artificial markers (see reviews in Levin 1990; Thorrold and others 2002). Dispersal distance estimates compiled by Kinlan and Gaines (2003) and by Shanks and colleagues (2003) suggest that results are highly dependent on the mode of study. Direct observations focus on larvae that disperse a few centimeters to 100 m, whereas invasion studies identify dispersal distances of 10 to >100 km, and genetic methods produce a range that spans the other two approaches.

An unexpected tool for studying dispersal distance has been the spread of newly arrived invasive species. Founder populations of exotic species typically represent an isolated source whose dispersal can be evaluated by monitoring annual changes in distribution. An isolated population of the invasive mussel *Mytilus galloprovincialis* in South Africa was found by McQuaid and Phillips (2000) to experience wind-driven dispersal distances of 12–97 km depending on direction. However, they found that 90% of recruits settled within 5 km of their release site. Natural dispersal is not always the operating transport mechanism. The gastropod species *Ocinebrellus inornatus* was found by Martel and colleagues (2004) to exhibit limited differentiation despite the lack of planktonic larvae, largely because oyster farming actively dispersed the populations and enhanced gene flow.

Recovery following catastrophic disturbance may also provide clues about dispersal distances, often with results that are counterintuitive. On local scales, *Nucella lapillus* recolonizes disturbance rapidly despite a non-planktonic larval stage (Colson and Hughes 2004). At intermediate scales, the rapid recovery of genetic diversity of manta shrimp cytochrome oxidase *c*-1 on Krakatau suggested dispersal distance of 10 to 100 km (Barber and others 2002). On very large scales, Marko (2004) found that ecology was more important than dispersal in generating the genetic structure of *Nucella* species following the first glacial maximum. Based on genetic structure, *Nucella ostrina* appears to have gone locally extinct and reinvaded, whereas *Nucella lamellosa* appears to have been retained in a Northern refuge.

Genetic isolation by distance models has proven to be a powerful tool for estimating larval dispersal distances. Isolation by distance is most evident when comparing populations separated by two to five times the mean dispersal distance (Palumbi 2003). Estimates of this mean range from 0.5 km in corals (Hellberg 1994) to 150 km in sole (Kotoulas and others 1995), with littorine gastropods (25 km, Johnson and Black 1998), Pacific urchins (50 km, Palumbi and others 1997), and vent tube worms (70 km, Vrijenhoek 1997) falling in between. However there can be a lot of scatter in the relationship between population distances and F_{st}, as shown for south Pacific urchins (Palumbi and others 1997).

Where do larvae come from?

If we knew how many larvae were produced, where all larvae dispersed to, and which ones survived to settle, it would be possible to know where larvae originated from, among any cohort of settlers. This pattern of larval exchange, and the degree to which larvae originate from outside the target population, is one definition of connectivity in a metapopulation sense (Moilanen and Hanski 2001). A large amount of self-seeding leads to low connectivity; high rates of larval exchange with other populations generate high connectivity. Interest in connectivity on land and in the sea has increased as scientists realized its importance in effective resource management (Crooks and Sanjayan 2006) and MPA design (Palumbi 2001). There has been considerable recent development of tools for examining population connectivity. Below I offer examples illustrating the application of physical modeling, natural and applied geochemical markers, and genetics to elucidate patterns of connectivity.

Connectivity matrices and physical modeling

Lagrangian particle tracking models or advection diffusion tracer models that map dispersal probability distributions for larvae originating at distinct sites can be used to create a connectivity matrix. By gathering the incoming larvae at a particular target site to determine the distribution of sources, one can establish (1) the likelihood of self-recruitment [p_{ij} where $i = j$], (2) the proportion of larvae originating outside the target site ($\sum p_{ij}$ where $i \neq j$), and (3) the diversity of sources ($\sum p_{ij} ln p_{ij}$). James and colleagues (2002) created a connectivity matrix for coral larvae using a numerical hydrodynamic model to compute the 2D depth-integrated current field for the shelf-reef complex between $14°$ and $19°$S on the Great Barrier Reef. They simulated 240 million (fish) larval trajectories in an examination of 321 reefs and dispersal over 20 years, illustrating the statistical power and expansive scale of computer methods. Behavior involving early passive and later active phases was combined with mortality estimates in an advective larval tracking model. The simulations predicted that <9% of recruits

would settle on the natal reef, and indicated that a small number of populations supplied most of the recruits. One can test computer-generated dispersal predictions against distance-based predictions and against actual data for realized dispersal (M. Neubert and H. Caswell, personal communication). This is being attempted for bivalves dispersing in New England and southern California (Levin and others 2005).

Environmental markers

To obtain information about realized connectivity patterns on ecological timescales for species whose larvae cannot be observed, it is necessary to employ a marker. Larvae may be marked artificially or natural tags may be used (Levin 1990; Thorrold and others 2002). Artificial markers are often used to label carbonate structures such as shells or otoliths, though tissues may be marked as well. Common markers include fluorescent dyes such as tetracycline and calcein, elemental tags such as $SrCl_2$ or rare earth elements, radiolabels, and even applied thermal stress marks (Levin and others 1993; Anastasia and others 1998; Thorrold and others 2002). The first direct evidence of larval retention in marine fish was provided by marking large numbers of damselfish eggs with tetracycline on Lizard Island, Australia. Jones and colleagues (1999) found that 15 of the 5000 recruiting larvae they examined were marked. Based on an estimate of the total percent of the population marked, they inferred that anywhere from 15 to 60% of juveniles may return to their natal population. This is one of the few true marking success stories. Typically dilution rates in nature are too great to yield significant numbers of marked larvae.

For this reason scientists have sought natural tags that mark all larvae exposed to a particular environment. Structural attributes, stable isotopic signatures, and trace elements can function in this mode. Gaines and Bertness (1992) used size to distinguish larvae originating in Narragansett Bay from those on the open coast. They were able to detect flushing of the larger Bay larvae to the outer coast during years of high rainfall.

Stable isotope signatures of tissues reflect consumer diets ($\delta^{13}C$, $\delta^{15}N$) or water temperature ($\delta^{18}O$). Killingley and Rex (1985) first used oxygen isotopes to document differences in developmental zones of planktotrophic and lecithotrophic larvae of deep-sea gastropods. $\delta^{18}O$ signatures of benthic planktotrophic species clearly revealed a warm-water signature in the retained larval shell but cold-water signatures in the adult shell. In contrast, lecithotrophic species with supposedly demersal development had similar adult and larval shell signatures. Surprisingly little has been done since this landmark study to use isotopes to study the water masses occupied by deep-sea larvae.

When larval habitat shifts involve a change in food sources, distinct isotope signatures should develop. Herzka and colleagues (2002) found that the red drum habitat shift from open water (as larvae) to seagrass beds (after settlement) in the Gulf of Mexico estuaries yielded a distinct increase in $\delta^{13}C$ and a decrease in $\delta^{15}N$, and that the changes stabilized within 10 days of settlement. Based on this information she was able to model the size and time of settlement of red drum larvae in a seagrass ecosystem. Similar applications should be useful in assessing larval transitions from open water to wetland ecosystems and mangrove to coral reef ecosystems.

An emerging methodology is the use of trace elemental fingerprinting to assess larval origins or trajectories. This is based on the idea that the elemental composition of larval tissues or hard parts reflects the chemistry of the water in which they were formed. If one knows the multi-elemental signatures imparted by source waters, and these are distinct among natal regions, then it should be possible to reconstruct larval origins and possibly trajectories. To apply this method it is necessary to either test the source signatures imparted while larvae are in the water or to establish that these signatures are stable over time (Gillanders 2002; Becker and others 2005). One must also know the trace elemental signatures for all possible sources.

Instrument development has played a pivotal role in making the use trace elemental fingerprinting to study larvae possible (Campana and others 1997). Different kinds of mass spectrometers and ion microprobes have been used to measure trace element concentrations in larvae. Early systems required putting the larval structures (otoliths, tissues, shells) into solution. The use of laser ablation with a highly sensitive inductively coupled plasma mass spectrometer now allows scientists to detect multiple trace elements simultaneously at ppb and ppt concentrations in individual larvae (Gunther and others 2000) or even parts of larvae at scales of 10–50 μm. From trace elements and isotope ratios of trace elements in carbonate structures it is now possible to infer much about the larval environment including salinity, temperature, proximity to land, exposure to hypoxia, pollution, upwelling, and storm events (Table 1).

To apply this technique to new recruits, the larval structure must be retained by the settled individual. This occurs in fishes which retain otoliths, in squid which retain statoliths, in gastropods which retain statoliths and prodissoconch (larval shell), and in bivalves which retain the prodissoconch at settlement.

Table 1 Use of trace elements to infer environmental characteristics from carbonate structures (mainly fish otoliths)

Factor	Elements or isotopes	References
Temperature	Sr, Mg, $^{18/16}$O, $^{88/87}$Sr	Kalish (1989)
		Fowler and colleagues (1995)
		Klein and colleagues (1996)
		Thorrold, Campana, and colleagues (1997), Thorrold, Jones, and colleagues (1997)
Salinity	Sr, Ba, U	Fowler and colleagues (1995)
		Zacherl, Paradis, and colleagues (2003)
Terrestrial influence		
Proximity to land	Sr, Mg, Pb, Mn, Ba	Swearer and colleagues (1999)
Estuarine conditions	Mg, Mn, Sr, Ba, Li	Thorrold and colleagues (1998)
Inshore/offshore	Ba, Sr	Thorrold, Campana, and colleagues (1997); Thorrold, Jones, and colleagues (1997)
Estuary/offshore	Pb, Ba	Forrester and Swearer (2002)
Pollutants	Cu, Sn, Pb	Pitts and Wallace (1994)
Hypoxia	Mn	Thorrold and Shuttleworth (2000)
Upwelling	Ba, Cd	Segovia-Zavala and colleagues (1998)
		Gillanders and Kingsford (2000, 2003)
Storm events	Cd	
DIC, diet	δ^{13}C	Herzka and colleagues (2002)

Use of otolith microchemistry to assess larval environments was pioneered among fish larvae—initially using Sr/Ca ratios by Radtke and colleagues (1990) for herring larvae. The first successful application of multiple elemental fingerprinting (to assess larval fish habitat) was accomplished by Swearer and colleagues (1999). They found that elevated concentrations of Mn, Ba, and Pb in blueheaded wrasse larvae reflected development near land (St Croix) rather than in open water. This study was among the earliest to report retention of larvae near natal sources. While some very exciting fingerprinting has been done with fish juveniles (Gillanders and Kingsford 1996; Thorrold and others 2001; Forrester and Swearer 2002), and some of these studies strongly indicate natal homing or retention, applications to fish larvae remain limited.

The first application of elemental fingerprinting to invertebrate larvae came a decade after the first work on fish larvae. DiBacco and Levin (2000) identified zoea larvae of the crab *P. crassipes* originating inside versus outside San Diego Bay, CA. Discriminant function analysis clearly identified larval source based on multiple elemental concentrations. By combining measurements of larval distributions at different times of the tide and in different depth zones in the water column, elemental fingerprinting of origins, and ADCP measurements of water transport, DiBacco and Chadwick (2001) were able to quantify the flux of larvae of different crab species into and out of San Diego Bay.

In the crab fingerprinting studies, larvae were not tracked beyond zoea stage 1, because elemental signals are lost as the larvae molt. Thus, it was not possible to determine where larvae of different origins actually settle. Elemental fingerprinting efforts now focus on species that retain a larval structure after settlement. An important precursor to the application of fingerprinting to determine settler origins is the identification of spatial variation in elemental signatures sufficient to distinguish sources. Zacherl, Manriquez, and colleagues (2003), Zacherl, Paradis, and colleagues (2003) and Zacherl (2005) document such variation for statoliths and prodissoconch in *Kelletia kelletia* and *Concholepas concholepas*, species that brood their larvae. Becker and colleagues (2005) documented distinct chemical variation in shells of newly recruited mytilid mussels in bay versus open-coast habitats and along 20-km zones of the southern California coastline. They also documented temporal stability of signatures on weekly and monthly scales. Because the shell of settled *Mytilus* is made up of calcite and the shells of larvae are of aragonite, it is desirable to obtain source signatures for larvae directly. By outplanting laboratory-spawned larvae for short periods in PVC homes on moorings placed in locations of interest, it is possible to generate the "map" of larval signatures required for determination of origins. Outplanting studies by Becker

(manuscript in preparation) documented patterns in larval shells similar to those described for recruit shell (Becker and others 2005). Mapping of the pro-dissoconch elemental signatures for settled individuals onto the outplanting signatures revealed distinct connectivity patterns for two *Mytilus* species in southern California (Becker, manuscript in preparation). Other larvae for which fingerprinting techniques are under development include soft shell clam (L. Mullineaux, personal communication), oysters (D. Zacherl, personal communication), other mytilids (C. DiBacco, personal communication), rockfish (R. Warner and S. Morgan, personal communication) and halibut (J. Fodrie, personal communication).

The potential of elemental fingerprinting for revealing patterns of larval dispersal is yet to be fully exploited. Promising applications include the detection of larval associations with hydrographic features (for example, salinity or turbidity fronts, upwelling areas, eddies, and oxygen minimum zones) and tests of larval origins for abyssal populations (Rex and others 2005). Nutritional clues, derived from isotopic or fatty acid analysis, may offer information about waters and habitats occupied by larvae. Isotopic signatures of larvae can potentially indicate utilization of symbionts (chemosynthetic or photosynthetic) as a nutritional source to prolong planktonic duration.

Gene frequencies

Genetic structure also can provide valuable information about the movements of larvae, typically integrated over multigeneration timescales that are notably longer than those for elemental fingerprinting. Valuable reviews by Palumbi (2001, 2003), and Hellberg and colleagues (2002) examine the use of genetic information to study larval dispersal distances. Short-term tracking has been done with distinct markers. Lambert and colleagues (2003) transplanted genetically distinct nudibranchs and found that they altered gene frequencies for subsequent generations of recruits, indicating that populations are not completely open. Multiyear studies of changes in barnacle (*Balanus glandula*) gene frequencies on the central California coast have illustrated the importance of regional oceanography and its variability, as well as regional history (Sotka and others 2004).

On very long timescales, historical influence (pre ice age) is shown to preclude high dispersal in structuring population genetics in the holothurian *Holothuria nobilis* (Uthicke and Benzie 2003), in the sea star *Coscinasterias muricata* (Skold and others 2003), and in *Macoma balthica* (Luttikhuizen and others 2003). Large-scale studies of vent annelids (Hurtado and others 2004) and mussels (Won and others 2003)

illustrate the importance of biogeographic filters to dispersal. Transform faults and mid-ocean ridges form clear boundaries to larval dispersal, but have different effects on different species.

Genetic structure suggests surprisingly high levels of dispersal in some species with aplanic development, for example *Abra tenuis* (Holmes and others 2004) and *Amphipholis squamata* (Sponer and Roy 2002). In contrast, unexpectedly high levels of differentiation have been observed in species with teleplanic development (Staton and Rice 1999, *Apionsoma misakianum*), in corals with broadcast spawning (Whitaker 2004), and in spider crabs (Weber and others 2000) and bryozoans (Goldson and others 2001) with broadly dispersing larvae having obligate planktonic phases lasting for weeks. From these genetic studies it is clear that intuition about dispersal based on development mode and larval PLD cannot provide the whole story.

Where are we now?

Changing paradigms are key to scientific progress. The last 5 years of published results and overviews provide growing evidence for significant amounts of retention in marine species with planktonic larvae (Warner and Cowen 2002). This evidence comes from observations of persistence of upstream populations (Gaylord and Gaines 2000), the persistence of pelagic larvae on islands (Bell and others 1995), strong stock-recruitment relationships (Swearer and others 2002), studies in which restocked species persist (Peterson and others 1996), numerical simulations based on physical measurements and behavior (Cowen and others 2000; Paris and Cowen 2004), mark recapture studies (Jones and others 1999), trace elemental fingerprinting (Swearer and others 1999), and genetic studies (reviewed in Hellberg and others 2002).

The occurrence of retention and restricted dispersal may have strong consequences for the ability of populations to adapt to local ecological habitat change (Kawecki and Ebert 2004), on rates of differentiation, and species evolution (Jablonski and Lutz 1983). The phenomenon of local adaptation in marine systems has been reported mainly for species with brooded or short-lived lecithotrophic larvae, but it also occurs in several species with longer-lived pelagic larvae (Sotka 2005). If retention is widespread then local adaptation may be more prevalent than expected (Sotka 2005). Generally, the evolutionary consequences of restricted dispersal may be significant (Jablonski and Lutz 1983). High rates of intraspecific genetic variation and population differentiation parallel the

occurrence of high species diversity on the continental margin (Etter and others 2005). Whether limited dispersal (relative to shelf or abyssal depths) contributes to these patterns remains to be determined.

Most recent articles published about dispersal emphasize retention, but tend to ignore those larvae that are not retained. If even a small fraction of these successfully recruit elsewhere, their significance for connectivity may be great. One can ask whether the pendulum has swung too far toward a new paradigm of self-recruitment as a rule. I suggest it is a matter of the cup being half full or half empty. If one is interested in the persistence of stocks within a marine reserve or the establishment of a new invader, self-recruitment may be the focus and a half-full cup of recruits may provide the needed input. However, if one is concerned with maintenance of genetic or biotic diversity, novel species invasions, or evolutionary change, those larvae that travel and recruit elsewhere (leaving a half-empty cup at home) may be of greater significance.

Another changing paradigm involves recognition of the significance of behavior to dispersal outcomes. Not long ago invertebrate larvae were thought to behave as passive plankton, moving within the water column at the direction of ocean physics. Behavior was considered important mainly as larvae approached the seabed to settle (Butman 1987). Although the potential significance of vertical migration was reviewed some time ago by Young and Chia (1987), and has been well studied in crustacean larvae (Cronin and Forward 1986), better understanding of sensory cues and responses (Kingsford and others 2002), more sophisticated field sampling (DiBacco and others 2001), and physical studies integrating behavior (Armsworth 2000; Paris and Cowen 2004; Largier 2004) have raised awareness about the roles of behavior in dispersal and recruitment (Metaxas 2001). Greater flexibility of behavior in response to hydrologic conditions and even sound (Leis and others 2003) gives larvae unexpected latitude in controlling their movements.

Finally, as our understanding of ocean physics improves, and as physicists begin to study the time and space scales relevant to larvae (Sponuaugle and others 2002), a deep appreciation for the dual importance of advection and diffusion (Largier 2003), and the significance of variability, has emerged. Along a coastline, points, jets, and retention zones cause variable transport (Richards and others 1995; Gaylord and Gaines 2000; Largier 2004). El Niño events, which transport species long distances, shift species ranges (Fields and others 1993), and alter recruitment patterns (Connoly and Roughgarden 1999; Davis 2000), have captured the most attention. However, seasonal shifts in current patterns and episodic events such as relaxation of upwelling (Largier 2004) may also have large consequences for the transport and recruitment success of larvae.

Where next?

Can we enter a new dimension in our understanding of larval dispersal with advances in fingerprinting, modeling, and genetics? I believe that an entire array of novel questions will become tractable within the coming decade. The deep sea, for example, is one realm where relatively little is known about dispersal. Geochemical techniques may be applied to address the following questions:

- What are the origins of abyssal recruits—are they vagrants from the slope or do they originate in the abyss? (Rex and others 2005).
- How much larval exchange occurs within and among reducing ecosystems such as vents, seeps, and whale falls? Analysis of short-term larval exchange among seep or hydrothermal vent ecosystems might be tractable if these impart distinct trace element signatures to larval shells.
- Can we evaluate transport from hydrographic signatures? Larval movements through upwelling zones, oxygen minima, turbidity plumes, warm or cold eddies, or salinity fronts might impart distinct elemental signatures to larval shells.
- Can isotopic signatures of individual larvae provide evidence of functional photosynthesis or chemosynthesis in larvae and a nutritional basis for long planktonic phases? While photosynthesis is known to occur via zooxanthellae in coral larvae (Weiss and others 2001), activity of chemosynthetic sulfide oxidizing or methane oxidizing bacteria has not been documented for larval symbionts in reducing ecosystems.

An integration of approaches across space and timescales (Fig. 3) offers the greatest potential for advances in understanding. Combination of numerical simulations with field measurements of physics, larval distributions, fingerprinting, behavioral studies, and genetic studies will be a challenge. Such combinations will undoubtedly provide unexpected results, raise new questions, and dispel some incorrect beliefs. This will also require more interdisciplinary interaction among scientists within and outside the field of biology.

Always inherent in our view of dispersal will be the limitations imposed by our study taxa and methodologies. For example, far more is known about echinoderm and bivalve development than for most invertebrates, and as such our theories of life histories
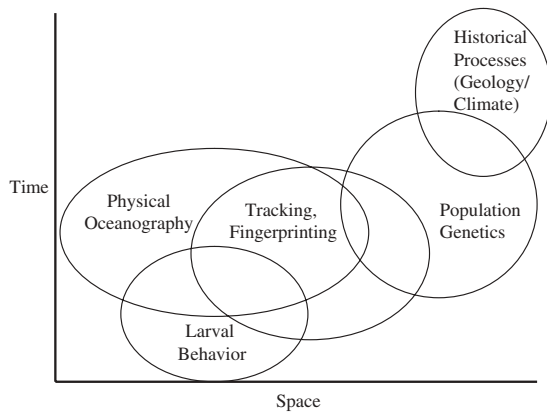
Fig. 3 Time and space scales relevant to different approaches to the study of larval dispersal. A challenge for the future is to integrate these methods.

are based on echinoderm and bivalve patterns. Much of the trace elemental fingerprinting work has focused on fish, and new results will emerge mainly for mollusks that retain larval structures. This cannot help but bias our understanding of dispersal patterns. Within these limitations we can strive to work with species having diverse life histories, but cannot get around certain developmental and morphological biases and constraints. Genetic studies do not have these limitations, but often constrain us to looking across rather than within generations. While a critical understanding of these limitations is necessary, innovative breakthroughs that surmount them should be a focus in the coming decade.

Acknowledgments

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