Observing Larval Transport Processes Affecting Population Connectivity

PROGRESS AND CHALLENGES

BY GLEN GAWARKIEWICZ, STEPHEN MONISMITH, AND JOHN LARGIER

Population connectivity is inherently bio-physical: it is determined by physical transport and dispersion, as well as biological processes such as timing of spawning, larval behavior, and mortality. Knowledge of connectivity is essential for understanding ecosystem responses to changing environmental conditions. It establishes the spatial scales over which a population is connected, and in turn the primary spatial scale of population interactions and ecosystem dynamics. Concepts in population connectivity were initially developed in terrestrial ecology, where dispersal may occur at different life stages. In the simplest form, a one-dimensional dispersal curve describes the distribution of settlers away from a source region as a function of distance. As this spatial distribution varies in time, the "dispersal kernel" defines a spatial probability density function of settlers aggregated over time (see, e.g., Okubo and Levin, 2002). This dispersal kernel may be three dimensional, but is often reduced to two dimensions (e.g., animals on a plain) or one dimension (e.g., animals living along the land-water interface).

Population connectivity in marine populations is often dominated by the dispersal of nonswimming or weakly swimming early life stages (e.g., eggs, spores, larvae, juveniles). Progress in understanding population connectivity has been limited by four important factors. First, given the large size, high fecundity, and r-selected nature of marine populations (most of the early-life-stage dispersers die), it is not possible to measure the dispersal kernel directly. We only have rough estimates deduced from population demographic studies, studies of the genetic structure of populations, and emergent techniques such as microchemical tagging that have been successful for selected populations. Much of our understanding of transport and dispersion comes from model studies, based on little or no evidence from direct field data. Second, water-borne dispersal may not even be well behaved; for example,

in flows with chaotic dispersion (Ridderinkhof and Zimmerman, 1992), *very* small differences in starting location can result in very large differences in where a larva finds itself after a short time. Third, because of the requirements of quantifying multiple parameters that describe behavior, mortality, and larval sources, in addition to transport/dispersion processes, there have not been (and may never be) comprehensive field studies that can simultaneously quantify all of the known factors affecting the time-varying spatial distribution of propagules, and thus the dispersal kernel. Finally, the initial (spawning) and final (settlement) phases of dispersal—how propagules leave and return to adult habitat—remain poorly known. These small-scale, biologically dominated processes may have a major effect on determining which propagules are successful and thus on determining the effective dispersal kernel.

The difficulty of quantifying dispersal is particularly true in the coastal ocean, where flows exhibit considerable small-scale spatial and temporal complexity. Larvae released in the coastal ocean are affected by numerous physical processes, including buoyancy-driven flows, tidal currents, wind-driven transport, internal waves and tides, surface waves, and turbulence—as well as interactions of these flows with coastal topography. The relevant physical scales range from the size of organisms (10^{-3} m) to large-scale ocean circulation patterns (10^6 m). Thus, while a substantial literature has begun to develop using circulation models to address connectivity, few studies use observations of flow to directly quantify connectivity. To date, the focus of observational studies has been on identifying, characterizing, and scaling physical processes that affect larval transport and thus the dispersal kernel.

It is straightforward to show that the flow field must be observed on spatial and temporal scales finer than the scales of its variation in order to accurately predict the path of larvae moving with the flow. Setting aside behavior and differential survival for now (i.e., assuming that larvae behave like passive particles), the principal observational challenge is to determine Lagrangian particle trajectories. These trajectories are integrals of the first-order equation:

$$\frac{d\vec{x}_p}{dt} = \vec{u}(\vec{x}_p, t), \qquad (1)$$

where $\vec{x}_p$ is the particle position, $\vec{u}$ is the velocity of the particle at that position, and t is time. Integration of Equation 1 is straightforward if velocities are available everywhere along the particle path, as in numerical models; otherwise, approximations must be made to integrate Equation 1 using limited observations. For example, for small displacements, Taylors' series expansion of the velocity field about the initial position of the particle gives

$$\vec{x}_p = \vec{x}_p(0) + \vec{\zeta} + \int_0^t \vec{\zeta} \cdot \nabla \vec{u}(\vec{x}_p(0), t) dt + O\left(\|\vec{\xi}\|^2\right), \quad (2)$$

where the displacement, $\vec{\zeta}$ is

$$\vec{\zeta} = \int_0^t \vec{u}(\vec{x}_p(0, t)) dt. \qquad (3)$$

A plot of $\vec{\zeta}$ calculated from a single-point record of current velocity is usually referred to as a "progressive vector diagram," but it is clearly of limited utility if the velocity varies spatially.

In the presence of oscillatory motions (e.g., tides, surface waves), averaging Equation 2 to eliminate those waves, which may not be resolved in either the model or in the observations, gives rise to the Stokes drift:

$$\vec{u}_s = \overline{\vec{\zeta} \cdot \nabla \vec{u}}, \qquad (4)$$

which is the difference between the mean Lagrangian velocity at a point (what is needed to follow things) and the mean Eulerian velocity at a point (something that can be measured by a current meter).

The accuracy of Equation 2 depends on the scales of current variability being larger than the displacements ("dispersal distance"); for example, it is reasonable to use Equation 2 where flow velocities are spatially uniform (or approximately so). More formally, in order that Equation 2 be accurate,

$$\left\|\vec{\zeta}\right\| << \frac{\|\vec{u}\|}{\|\nabla\vec{u}\|}. \qquad (5)$$

Thus, if we are interested in connectivity at scales larger than those over which velocity varies (i.e., the right-hand side of Equation 5), we must either have multiple velocity records across the domain of interest or we must make Lagrangian measurements using drifters that follow fluid motions (to the maximum extent possible). However, if we are interested in the dispersal of multiple particles/larvae, we must again deploy multiple instruments to characterize the variety of possible trajectories that a larva may follow.

Either way (Eulerian or Lagrangian observations), data are severely limited and we are unlikely to be able to

adequately resolve time-varying three-dimensional dispersion over large enough spatial scales—even for passive particles. And thus, we do not expect ever to be able to directly measure a dispersal kernel and rather suggest that

it is wide). This reduces the problem to a one-dimensional dispersal kernel, but it remains at least a two-dimensional transport problem as larvae are typically transported well offshore in the process of being transported alongshore

coast that reduce alongshore transport, and (2) cross-shore exchange processes that link offshore and coastal waters—describing a variety of scales. We conclude with a discussion of recent advances in technology and what these mean for quantifying connectivity.

Knowledge of connectivity is essential for understanding ecosystem responses to changing environmental conditions

observational efforts focus on better defining the problem and on determining what dispersal outcomes may be physically possible (rather than trying to determine the most probable dispersal outcome). Best estimates of connectivity will then be obtained through corroboration of dispersal suggested by biological studies (demography, genetics, microchemical tagging) with observation-based transport studies.

Most connectivity studies address coastal populations, which are typically distributed along a line (i.e., the adult population domain is much longer than

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(Largier, 2003). The problem is thus decomposed, then, into a question of alongshore transport (which determines the shape of the dispersal kernel) and a question of cross-shore transport (which determines the extent to which propagules are exposed to offshore currents, which are often stronger). Although the coastal connectivity problem is found at a variety of scales (from domains of size 10^4 m to 10^7 m), there is a commonality in this being a boundary problem, with nearshore retention as an important factor—"nearshore" being a relative term and describing waters within as little as 10 m or as much as 10^5 m of the shore (depending on the size of the domain). Similarities between problems are found based on the relative length scales of adult population extent, water circulation, and coastal topography that characterize the problems—rather than on the absolute domain size.

In this short review, we focus on two important related issues and the use of observations in addressing them: (1) defining retention zones near the

NEARSHORE RETENTION ZONES AND ALONGSHORE TRANSPORT

An important element of the broader debate about population connectivity is the issue of "open" versus "closed" systems—that is, the degree to which a population is open (exchanging propagules with distant populations) or closed (entirely dependent on propagules spawned locally). Open systems are connected over large spatial distances, with low levels of self-recruitment, while closed systems are connected over small spatial scales with high levels of self-recruitment. Where propagules are in the plankton for an appreciable period of time, higher levels of self-recruitment suggest that these propagules are retained nearshore or in bays. Largier (2003) points out that, in most coastal systems, there is likely to be a mixture of self-recruitment along with recruitment from nonlocal sources, so that the classification of regions into "open" or "closed" states may be misleading. The possibility of simultaneously strong local and distant recruitment is recognized when both advective and diffusive effects are included in the description of dispersal.

Further, one needs to recognize spatial variability in the degree to which parts of the population are "open." For example, within a given shelf region, there may

be a "closed" area near the upstream boundary where recruitment from non-local sources is weak, while an "open" area may be found near the downstream boundary where nonlocal sources are critical for recruitment success (Byers and Pringle, 2006; Pringle and Wares, 2007). In addition, spatial variations in larval production may be an important factor affecting the spatial distribution of larvae and recruits within a system.

A key factor in alongshore connectivity is the retention of larvae or propagules adjacent to the coast. Increased self-recruitment and decreased net displacement of propagules are associated with these retention zones. Typically, a retention zone is found nearshore, extending some short distance from the coastal boundary. It may be associated with topographic features such as headlands, bays, shoals, or coral reefs. This concept is common in the marine ecology literature, and there have been numerous efforts to define both cross-shore and alongshore scales over which a retention zone may be located.

Enclosed bays, lagoons, and estuaries are a special case of retention—where a larva may be removed from the open coastal flow for the period that it is within the bay. In these basins with narrow connections to the ocean (e.g., San Diego Bay), there is no throughflow, and the time scale of retention is determined by the process that governs bay-ocean exchange (e.g., tidal pumping at the mouth of San Diego Bay; Chadwick and Largier, 1999). However, in these scenarios, the deterministic nature of the flow provides many opportunities for larval behavior that can alter the direction of larval transport—with dif-

ferences at different larval stages (e.g., DiBacco and Chadwick, 2001). Bays may also be important for larvae spawned on the open coast. Where a significant fraction of the larval population is entrained into bays, their alongshore transport would be reduced. However, the longer the residence time of waters in the bay, the weaker the exchange with the ocean (residence time ~ bay volume/exchange rate) and the less likely larvae will move into or out of these semi-enclosed basins without active larval behavior. A discussion of the relative importance of different transport processes and their impacts on larval transport for Delaware Bay and East Coast estuaries appears in Epifanio and Garvine (2001).

Turning our focus to open coastal waters, there are other possibilities for retention and reduced alongshore transport. Near to the coastal boundary, flows are weaker due to bed friction and/or the form drag effect of an indented coastline. This coastal boundary layer offers opportunities for retention, specifically inshore of where the

of the proximity of the coastal boundary in limiting the horizontal scale of eddy motions, and thus limiting cross-shore dispersion. This is important because nearshore flows tend to be parallel to the coast with limited advective transport in the cross-shore direction. Because currents are generally stronger further from the shore (away from boundary-layer effects), larvae that remain close to the shore will be advected shorter distances alongshore. Small differences in cross-shelf dispersion can yield large differences in the extent to which larvae are exposed to stronger alongshore flows typically found further from the coast. The net result is a nonlinear relation between the cross-shore dispersion and the alongshore scale of connectivity—a phenomenon that appears to play out often in coastal larval dispersal patterns.

If the retention time scale is long enough (relative to the planktonic larval duration, or PLD), one can expect some locally spawned larvae to be retained in this zone, resulting in enhanced local recruitment. For larvae spawned else-

...what may be the greatest challenge of all is that of integrating biology and physics.

alongshore flow separates from the coast and recirculation may be found (e.g., northern Monterey Bay, as described by Graham and Largier, 1997; Paduan and Rosenfeld, 1996; Lipphardt et al., 2006). In addition to slower flows nearshore, Largier (2003) discusses the importance

where, however, slowing of flow (and thus weakening of the larval flux = velocity * concentration) will not in itself increase settlement of larvae in this retention zone, although it will reduce $\vec{\zeta}$—the displacement of larvae that pass through this zone. To accumulate

nonlocal larvae in this retention zone, there has to be a nonconservative "filtering" mechanism in which water flows through the zone but larvae are filtered out and retained, typically requiring some larval behavior. For example, where larval behavior (upward swimming or buoyancy) counters weak downward currents at a front (e.g., Franks, 1992; Shanks et al., 2000), one can expect accumulation of larvae. Such a front forms in northern Monterey Bay, along the boundary of the retention zone.

THE CROSS-SHORE EXCHANGE PROBLEM

Given the large cross-shore changes in circulation, with different circulation patterns (Lagrangian trajectories) separated by short distances, cross-shore transport is a key factor in determining net alongshore displacement and thus the nature of connectivity in coastal

seas. Through programs like Coastal Ocean Processes (CoOP: www.skio. peachnet.edu/coop/), significant recent observational studies have addressed this topic. A similar issue exists at different scales, including (1) the exchange of shelf waters with the deep ocean, (2) the exchange of lagoon waters with the nearshore, and (3) the exchange of nearshore waters with the shelf.

Nearshore-Shelf Exchange

While much progress has been made in observing larger-scale motions over the continental shelf, we know little about how organisms are transported the last kilometer or so inshore through nearshore kelp forests, past reefs and shoals, and/or to rocky intertidal shores. Flows in this region are complex: forcing by wind, tides, buoyancy, and waves are all important, as are flow alterations by extreme topography and kelp for-

ests (Rosman et al., 2007). For example, cross-shore temperature differences can develop due to diurnal heating and cooling over a slope (Niemann et al., 2004). This differential heating and cooling, internal tide run-up, or wind-driven internal swash can drive reversing buoyancy currents that rapidly exchange nearshore and offshore waters. Further, there is an important interplay of small-scale dispersion with larger-scale transport, as is nicely illustrated by recent drifter measurements in the outflow through a pass from a coral reef lagoon on the north shore of Moorea. Figure 1a shows a series of tracks for drifters released in the jet exiting the lagoon during a time of strong wave forcing (James Hench and Liv Walter, Stanford University, *pers. comm.*, June 2007). The wave-driven flow over the reef crest on either side of the pass entrains fluid from offshore so that drifters on the outside
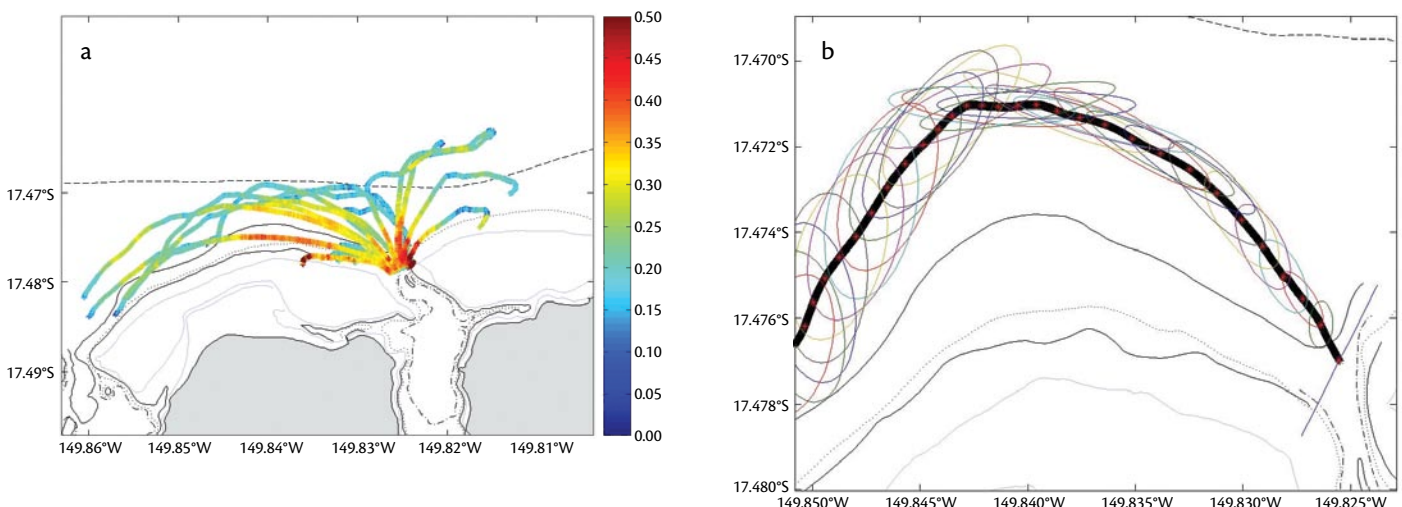

Figure 1. (a) Drifter tracks (color-coded by speed) in the jet exiting from a coral reef pass on the north shore of Moorea, French Polynesia. (b) Dispersion ellipses for a particle track similar to that seen in (a). Based on the relative dispersion of a set of 10 drifters about their center, the lengths of the major and minor axes of the ellipses show the magnitudes of the dispersion coefficients in a local coordinate system defined by the local directionally dependent dispersion. The orientation of the ellipses (i.e., the orientation of the coordinate system is chosen with the larger axis representing the direction of most rapid dispersion). *Figure courtesy of James Hench and Liv Walter*

edges of the jet re-enter the lagoon and may have a long local residence time, whereas particles that are in the center of the jet can be transported O(1 km) offshore and be entrained into the prevailing alongshore current and transported to the next reef downstream. These drifters can be used effectively to map not only transport but also, when used collectively, dispersion (Figure 1b). In general, the importance of small-scale dispersion is that it can mix particles across the streamline that defines the separation between potential retention and alongshore transport. The same proximity of retention and flow-through streamlines is seen in other comparable and larger-scale systems (e.g., Monterey Bay). Recent work by James Hench and Liv Walter (Stanford University, *pers. comm.*, June 2007) indicates that dispersion is far from scale-independent or isotropic.

Given the proximity of the shoreline boundary (through which water cannot flow), cross-shore flows are constrained in nearshore waters, reducing eddy diffusion effects. Thus, cross-shore transport is often dominated by specific vertical or lateral circulation patterns, as described above. The presence of stratification and the vertical separation of onshore and offshore flows allow shear and thus stronger cross-shore currents near to the coastal boundary. In a similar way, strong topographic influence can set up horizontal circulation patterns with localized strong offshore flow features, such as the wave-driven jet described above for a coral reef pass, rip currents exiting the surf zone (Smith and Largier, 1995; Schmidt et al., 2005), or tidal jets exiting enclosed bays or lagoons (Chadwick and Largier, 1999).

Shelfbreak Processes— Exchange Between Shelf and Offshore Waters

Connectivity can occur over large spatial scales, typically involving longer PLD and Lagrangian trajectories that cross the shelfbreak. While high-resolution velocity data and detailed information on dispersion is generally lacking for shelfbreak regions, there are a number of studies in the Middle Atlantic Bight that clarify important processes affecting large-scale Lagrangian trajectories and the connectivity matrix. Brink et al. (2002) obtained an extensive set of drifter trajectories in the Middle Atlantic Bight as part of the Global Ocean Ecosystems Dynamics

Northwest Atlantic program. When drifters were generally deployed in the Gulf of Maine, upstream of Georges Bank, the majority passed into the Middle Atlantic Bight and continued along the continental shelf in the shelfbreak frontal jet (Lozier and Gawarkiewicz, 2001). A plot of these drifter trajectories (Figure 2) confirms the general Eulerian view of a persistent southwestward flow, but shows the flow to be a meandering jet. The average advection speed for the 115 drifters drogued at 10-m depth was 14.2 km/day, with a range of 4.8 to 38.2 km/day. The average residence time shoreward of the 1000-m isobath (and thus implicitly within the shelf or shelf-
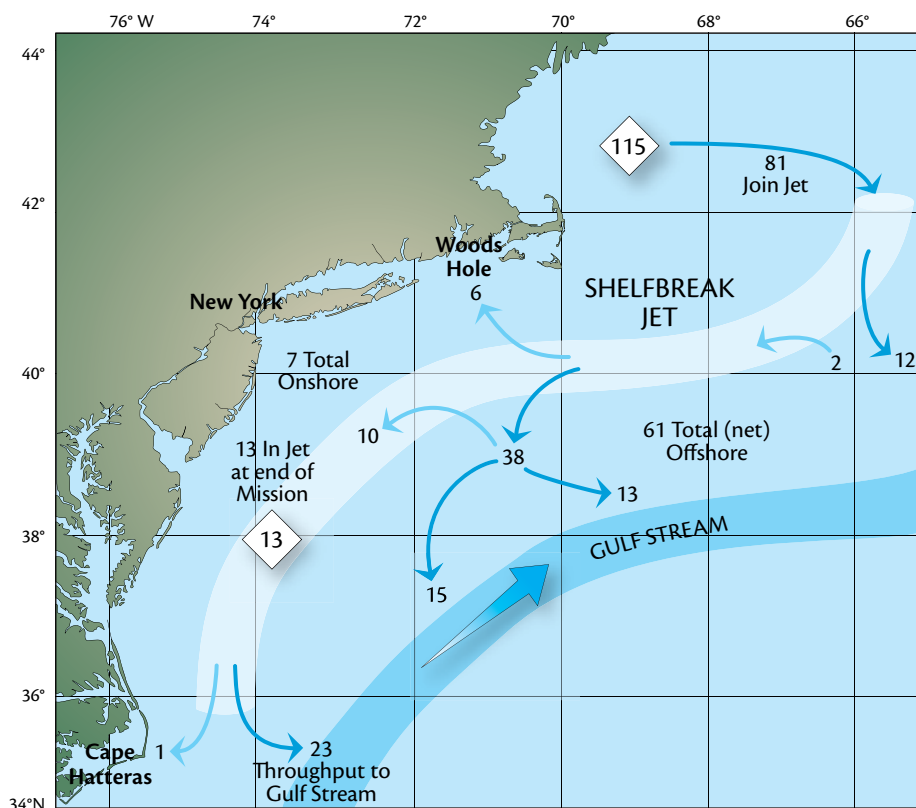

Figure 2. A cartoon indicating the distribution of near-surface drifters initially launched near Georges Bank, showing the large distances over which particles may be carried within the shelf-break frontal jet. Note that these near-surface drifters predominantly leave the jet offshore of the continental slope, and few are carried shoreward over the continental shelf (Lozier and Gawarkiewicz, 2001).

break circulation) was 28.6 days, with a standard deviation of 24.5 days. A variety of processes led to offshore transport of the drifters out of the shelfbreak jet and into the slope gyre, with the interaction of warm-core rings and slope eddies with the shelfbreak jet being the most noticeable process.

Similar results occur in a smaller set of drifter data from the shelf off the west coast of southern Africa, where Agulhas Current rings appear to play an important role in entraining shelf waters (recent work of author Largier) and in mooring data from northern California that show offshore entrainment of shelf water by mesoscale eddies in the California Current (Washburn et al., 1993; Largier et al., 1993). However, in the Benguela Current system, strong offshore flows are also associated with wind-driven transport. A major upwelling filament off Lüderitz, Namibia, accounts for offshore export of all drifters deployed in the northward shelf flow. In other eastern boundary current systems (e.g., California Current), strong offshore transport of surface waters from shelf to ocean is also associated with localized offshore flows such as upwelling filaments or deflection of the wind-driven upwelling jet.

In addition to surface circulation, larvae may be exchanged between the shelf and ocean through vertical circulation. For example, a vigorous secondary circulation is associated with the shelfbreak front in the Middle Atlantic Bight. Numerical models (Gawarkiewicz and Chapman, 1992) and dye releases (Houghton et al., 2006) show a persistent upwelling within the front that results from a convergence in the bottom boundary layer. Houghton et al., (2006) find vertical motions in the range of 5–10 m/day, consistent with a model estimate of 9 m/day (Pickart, 2000). The impact of this secondary circulation on Lagrangian flow characteristics is unclear. Barth et al. (2004) used an isopycnal float within the shelfbreak front south of Georges Bank to examine the along-isopycnal upwelling rate as well as the diapycnal diffusion of heat. Over a two-day trajectory, they found that the vertical velocity moving along the isopycnal was 17.5 m/day, while the float moved alongshelf at a speed of 0.09 m/s and was displaced offshore by 15 km. A surface drifter launched at the same point moved alongshelf at twice the speed, 0.18 m/s, and with no net offshore displacement. Thus, the trajectories of surface drifters and isopycnal floats are likely to be very different within frontal zones.

THE MULTIPLE PHASES OF DISPERSAL

We have described important features and circulation patterns that influence alongshore transport and the cross-shore exchange that allows larvae access to the different alongshore flows at different distances offshore, but it is important to consider that a planktonic larva will experience multiple features or flow systems between release from and return to adult habitat. To date, there has been inadequate recognition of the multiple phases in dispersal of larvae. Attention is usually focused on a single feature or system with the implicit assumption that this single phenomenon controls the total dispersal problem. This is not necessarily valid and, further, the dispersal outcome may not be a simple summation of transport in the different phases, as the timing of entry in time-varying circulation patterns may have a large effect on displacement.

Hare et al. (2002) address larval connectivity between the South Atlantic Bight and the continental shelf of the Middle Atlantic Bight. They concentrate on two species of fish, *Pomatomus saltatrix* (bluefish) and *Xyricthtys Novacula (*a subtropical wrasse), and suggest that there is a sequence of four processes involved in transporting larvae from the South Atlantic Bight continental shelf to the Middle Atlantic Bight continental shelf (Figure 3). The first step is entrainment from the shelf to the Gulf Stream. The second step is northeast-

> The complexity and variability of coastal and shelf flows demands intelligent use of appropriate tools...as part of strongly interdisciplinary studies of population connectivity.

ward transport within the Gulf Stream. The third step is detrainment from the Gulf Stream onto the western side of a warm-core ring, and the fourth step is onshore transport through the shelfbreak front. Hare et al. (2002) link probability density functions for the Lagrangian transport times for each of these four segments to obtain an overall expected probability density function for the age of the larval fish. They found good agreement with the directly measured age distribution of the captured larval fish. The mean observed age for *P. Saltatrix* larvae measured in June 1988 was 34.7 days versus 30.1 days in the model, with standard deviations of 4.4 and 7.8 days respectively.

While this study illustrates the importance of multiple phases, it excludes some additional phases because it does not deal with how larvae of either of these species move across the continental shelf (or alongshore) from adult habitat in estuaries of the Middle Atlantic Bight. Presumably, tidal jets and buoyancy-driven flow are important in transporting these larvae to the shelf and also alongshore (e.g., Rennie et al., 1999), but it is not obvious how the larvae are transported around Cape Hatteras to the South Atlantic Bight. Recent fieldwork (Savidge and Austin, 2007) may suggest new processes for larval transport offshore, including cross-shelf flows associated with the Hatteras Front. In their shoreward motion from the shelfbreak to the estuaries, Hare et al. (2002) invoke salinity intrusions that are commonly observed at the seasonal pycnocline as a possible transport mechanism. Recently, Lentz (2003) produced a climatology of salinity intrusions and found that they

Figure 3. A hypothesized transport pathway for two fish species carried from near Cape Hatteras to the estuaries of the Middle Atlantic Bight *(Hare et al., 2002).*

occur preferentially in summer and fall and with maximum salinity at the depth of strongest stratification. At this stage, it is not known what drives the intrusions, or their along-shelf extent or life span.

The question of multiphase dispersal, illustrated by the Hare et al. (2002) study, raises interesting points relating to our ability to measure connectivity directly. They used a very detailed hypothesis to examine a complicated chain of transport processes, for which the only point

of comparison was the integrated time scale for transport from Cape Hatteras to the shelfbreak region south of New England. The Lagrangian time scales were derived from surface drifter trajectories, and thus none of the complications of local secondary circulations in either the Gulf Stream, a warm-core ring, or the shelfbreak front were included, but the final comparison was good in terms of both the mean age as well as the standard deviation. However, while the
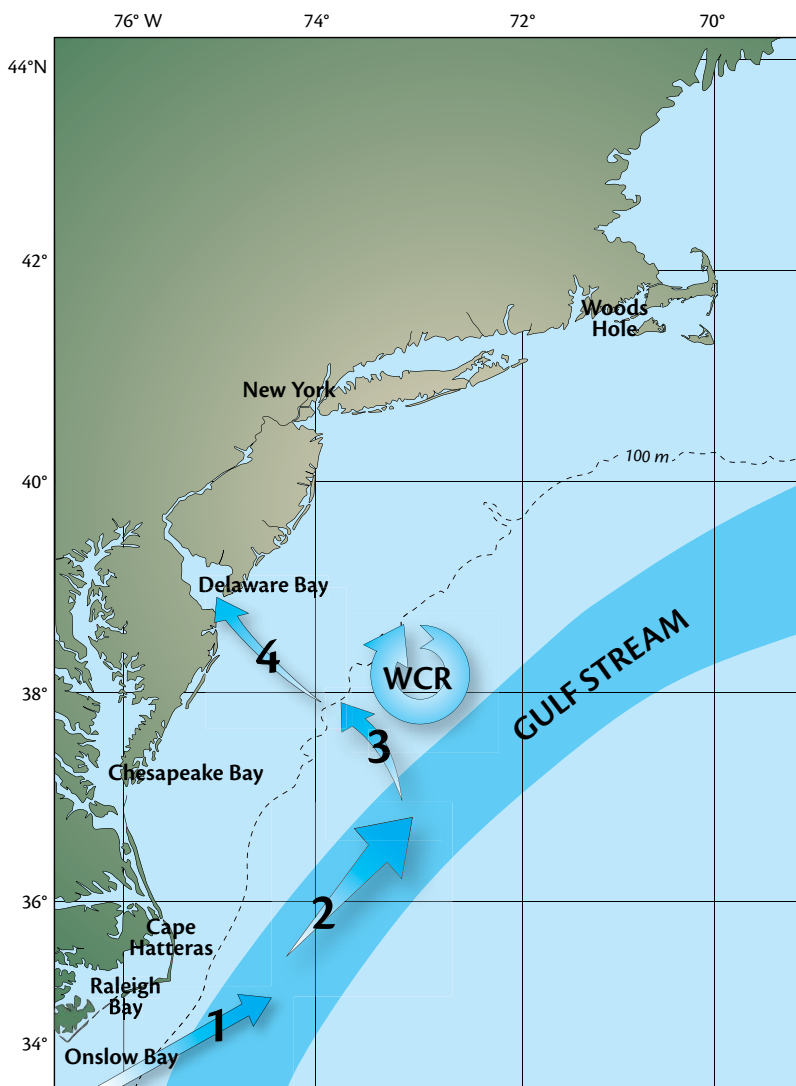
study shows that their transport hypothesis may be true (it is "possible"), there is really no way of showing that it is what happens (that it is "probable"). There are a number of other possibilities, including other source regions for the larval fish found in the Middle Atlantic Bight and other combinations of transport phases that could yield similar displacements over similar time periods. Further, when considering such large-scale coastal dispersal, it becomes clear that it will never be possible to adequately map out time-varying larval distributions concurrently with flow structures throughout the dispersal domain and for the entire dispersal period. Our research will need to be smart—to present solutions based on logical arguments for most the likely multiphase dispersal scenarios.

NEW APPROACHES

Observations of circulation pertinent to larval transport are advancing continuously and revealing a complicated and temporally varying picture of particle

water-type tracking offer other opportunities for observing water motions pertinent to larval dispersal, but we do not address these latter approaches in detail here.

The development of coastal ocean observatories provides opportunities for improved resolution and monitoring of the physical processes contributing to connectivity. Specifically, the ongoing nature of observatory data will reveal interannual variability in connectivity, as well as better define the seasons in which favorable dispersal is possible given the observed currents. Coastal ocean observatory efforts are included in the National Science Foundation Ocean Observatories Initiative, the regional associations of the Integrated Ocean Observing System, and state-funded regional programs. While these instrument arrays may not provide all the necessary data, they will make more in-depth dispersal experiments possible by providing much of the background physical oceanographic data.

Implementation of both data-assimilative models and real-time models to drive adaptive sampling is necessary.

HF-Radar Mapping of Surface Currents

High-frequency radar systems can produce maps of surface currents with sufficient spatial resolution to satisfy the condition in Equation 5. The recent availability of HF-radar systems as off-the-shelf tools for studying coastal flows allows researchers to examine both the temporal and spatial variability of quasi-Lagrangian flow characteristics in areas of complicated coastline and bathymetry (e.g., Kaplan and Largier, 2006). As such, they have become integral parts of many coastal observing systems (e.g., http://www.cencoos.org/).

New observational tools lead to new analytical approaches as well, such as the synoptic Lagrangian map (SLM) developed from HF-radar data by Lipphardt et al. (2006). They use hourly velocity maps to study the flow in Monterey Bay over a 62-day time period in 1999. The SLM technique was developed to examine the spatial and temporal distribution of two types of transport pathways: (1) particles that are exported from the bay to the ocean, and (2) particles that are delivered to the coast. The residence time within the bay as a function of space and time is also computed. The particle trajectories are integrated both forward and backwards in time to determine how long it takes before particles encounter either the coastal or offshore boundary. SLM bears some resemblance to other techniques used in dynamical systems analysis; however, dynamical systems analysis is more commonly used in either station-

There is an urgent need for more comprehensive studies that resolve oceanographic transport processes and dispersion patterns concurrently with studies of dispersal and connectivity.

paths in the coastal ocean. Two new approaches are discussed below: (1) HF-radar mapping of surface currents, and (2) innovative drifters. In addition to these, naturally occurring tracers and

We also note the coupling of observations with models is a critical need for the future. Werner et al. (this issue) discuss modeling of connectivity and issues related to model use and interpretation.

ary or periodic flows, whereas the flow in Monterey Bay is clearly nonperiodic and nonstationary. A second analytical approach is orthogonal mode analysis (OMA) being developed by Kaplan and Lekien (in press); it identifies dominant modes of circulation that can then be combined to obtain typical transport patterns, yielding results similar to those from Lipphardt et al. (2006).

The SLMs developed by Lipphardt et al. (2006) display a wealth of information on transport pathways. The pulsed nature of the bay in retaining and exporting surface waters is evident in the large variability in the percentage of particles that were exported from Monterey Bay, with almost no particles being exported on some days (as little as 17%) and almost all particles being exported on other days (as much as 92%). Figure 4 shows maps of the fate and origin of different particles within the bay over a four-week time period. There are extremely complex regions containing both long, thin filaments and circular spirals. Over the time period of the analysis, the residence time of particles varied between 4.5 and 11 days—a time scale comparable with PLDs that are from days to months for most organisms of interest (e.g., Shanks et al., 2000). In contrast, shorter residence times are observed in the 50-km radar domain over the shelf off Bodega Bay, with particles transiting this region in less than six days (average alongshore advection of order 0.1 m/s) and only 15% of particles remaining in the domain for more than six days (Kaplan and Largier, 2006; analyses based on raw data rather than SLMs).
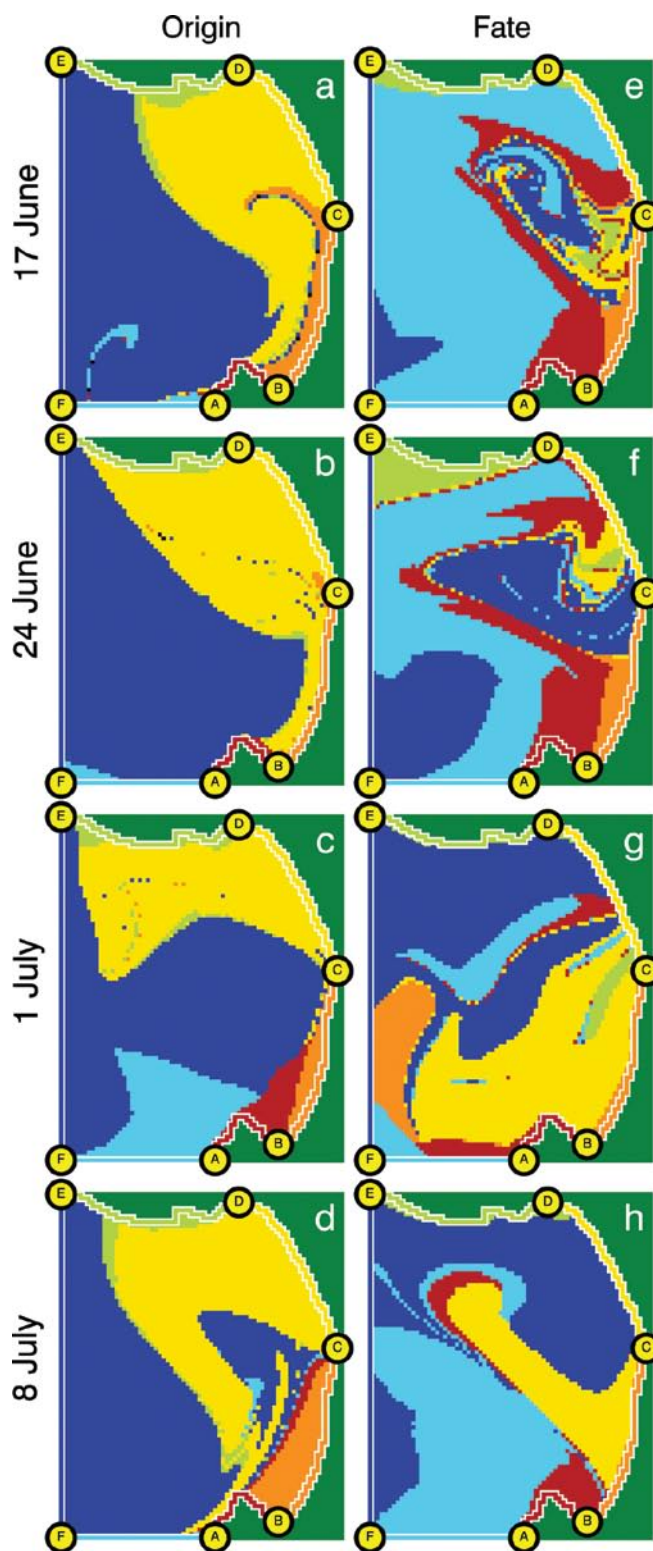
These quasi-Lagrangian flow maps

Figure 4. Synoptic Lagrangian maps of Monterey Bay representing the origin of particles that encounter open-ocean or coastal boundaries (left panels). The origins of particles are color-coded by where they hit the coastal and open boundaries with, for example, areas in red showing the initial positions of particles that end up hitting the coastline between points A and B (yellow circles). In the right panels, particles initialized on the boundary between points A and B end up in the red areas, and the areas are color-coded to reflect the boundary region from which they originate. Land areas east of Monterey Bay appear in green. *Figure from Lipphardt et al. (2006)*

show that the concept of a retention zone may be misleading because the origin of particles reaching a particular point, as well as the fate of a particle trajectory, is highly variable in both space and time. This introduces a degree of stochasticity into dispersal outcomes because some larvae may be detained for a considerable fraction of their PLD in a given region while others (entering at a different time or following a slightly different streamline) may simply move through the region in a few days, as expected from average current speeds. To determine the particle trajectories necessary for computing the probability of retention or throughflow requires a large amount of velocity data on relatively fine scales; inferring a retention zone from inadequate Eulerian data may yield incorrect answers. The real challenge of larval dispersal, however, is to determine which of these groups of larvae recruit successfully to adult habitat (those retained or those passed through)—and

ticles that are neutrally buoyant are likely to follow different trajectories. They will be transported away from the surface by buoyancy-driven secondary (vertical) circulations associated with frontal zones or internal waves, by convergence or divergence in surface flows (i.e., upwelling or downwelling), and/or by vertical mixing between surface and subsurface waters. While the technique of SLMs can be extended to three dimensions in a straightforward manner, subsurface velocity data with comparable spatio-temporal coverage is not available for shelf circulation at the present time. For smaller domains, however, it may be possible to obtain the necessary detail through deployments of arrays of acoustic Doppler current profilers (ADCPs), as was done by Gaylord et al. (2007) in quantifying flow through and around a kelp forest. However, these arrays are unlikely to resolve both the small-scale structure of the flow (see Equation 5) and the full spatial extent of the region

spatial extent of these systems is limited for a number of reasons.

Finally, it should be remembered that HF-radar data are essentially Eulerian and that the calculated trajectories are only quasi-Lagrangian. This is an issue when high-frequency or high-wave-number flows are important. Specifically, velocity maps derived from Eulerian data may not properly reflect the total Lagrangian transport in the presence of surface waves because Stokes drift, the net transport associated with waves, can be a significant fraction of the cross-shore motion (Monismith and Fong, 2004).

Innovative Drifters

Drifters (drogued floats) are the most practicable method for obtaining Lagrangian data. Analysis of multiple drifter trajectories provides transport and dispersion information that is directly relevant to estimating connectivity. Further, small-scale drifter work can be relatively inexpensive; for example, GPS drifters can now be built for about US $500 each and deployed from small boats (George and Largier, 1996). However, drifters are limited by a few characteristics: (1) they are typically surface-attached and cannot properly follow streamlines; (2) they are typically deployed in one circulation feature and have not been deployed in ways that sample the multiple phases of dispersal; and (3) they are significantly larger than planktonic larvae and do not experience small-scale shear and mixing, nor do they respond to breaking waves as do larvae. A special drifter has been developed for surf-zone studies (Schmidt et al., 2003), but with all the vertical motions

...it is essential that these studies be performed during the appropriate season and for the appropriate duration of larval dispersal.

thus to determine the dispersal kernel (i.e., the dispersion of successful recruits) rather than a general pattern of dispersion for particles in this flow system.

In spite of the immense value of HF radar, it is important to remember that these data only describe currents at the surface. While this is what one needs for particles that remain at the surface, par-

through which larvae are dispersed.

Another limitation with existing HF-radar systems is one of scale. The current generation of HF radars resolves currents on scales of 10^2 m to 10^4 m, and they are well suited for addressing larger-scale connectivity issues. While sonar systems have been used to observe small-scale flows (e.g., Smith and Largier, 1995), the
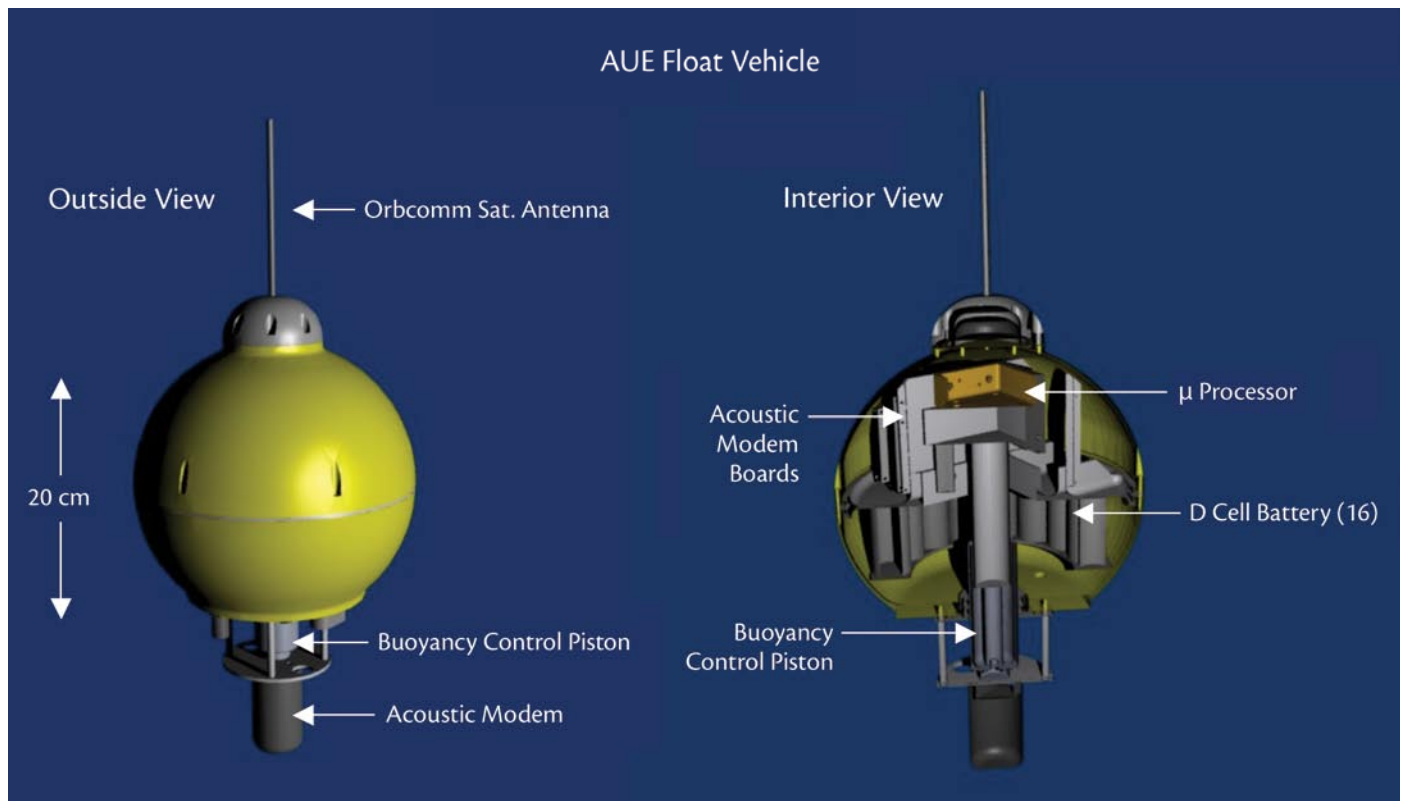
Figure 5. A smart drifter being developed by Jules Jaffe at Scripps Institution of Oceanography. The drifter is capable of vertical displacements and thus important for testing the impact of simple behaviors on connectivity.

in the surf zone, there is even more concern about how well drifters follow streamlines or whether drifters tracks represent plankton trajectories.

In response to the first limitation, a variety of neutrally buoyant drifters have been developed to follow an isopycnal (e.g., Barth et al., 2004). A simpler approach used in coastal studies is to deploy drifters drogued at a variety of depths, so that one at least has two-dimensional Lagrangian maps at a variety of depths. A third approach is to develop a smart drifter that can adjust its buoyancy to mimic larval behavior. The most recent example is a low-cost drifter being developed by Jules Jaffe at Scripps Institution of Oceanography (Figure 5). The ability to move vertically is an extremely important capability for testing hypotheses about the role of behavior in connectivity. The challenge will be to obtain enough of the resultant three-dimensional drifter tracks to yield statistically valid results that can be used to parameterize dispersion in models.

The second limitation can be overcome through smart designs for experiments, perhaps using a variety of drifter designs that integrate over the depth of mixing of near-surface larvae. Although it is difficult to design experiments that work backward from the locations of successful recruitment (the ideal experiment that one can only really do in a model or with intensive HF-radar data), it is quite feasible to work forward from locations where there are dense concentrations of spawning adults.

The third limitation may never be overcome, although some researchers have experimented with marked beads or old-fashioned drift cards or, perhaps better, marked larvae. However, without visual or electromagnetic contact, the recovery rate of these micro-drifters is very low and likely biased. Further, even when recovered, one has no data on the trajectory of the drifter, and this precludes understanding how currents control dispersal. Thorrold et al. (this issue) present a review of methods and successes in tagging larvae.

> ...studies of dispersal based on physical oceanographic observations must be continuously related and compared with results from demographic, microchemical tagging, and population genetic studies...

CONCLUSION

Our review emphasizes physical observations when, in fact, what may be the greatest challenge of all is that of integrating biology and physics. For all their complexity, the flows we have discussed are describable in terms of a few basic physical laws that have been known for 160 years. Admittedly, boundary conditions and parametrizations of unresolved processes can be difficult, yet the challenge of dealing with organisms with even simple behavior or life histories is significantly more difficult. It is important to bear in mind that even simple behaviors like selective tidal stream transport (i.e., vertical swimming phased with tidal motions, for example, Forward and Tankersley, 2001) can lead to organism trajectories that are radically different from those of neutrally buoyant particles (see, for example, Simons et al., 2007). In this regard, studies of dispersal based on physical oceanographic observations must be continuously related and compared with results from demographic, microchemical tagging, and population genetic studies (e.g., Palumbi and Sotka, 2006).

The complexity and variability of coastal and shelf flows demands intelligent use of appropriate tools, some sophisticated and very expensive and some simple and cheap, as part of strongly interdisciplinary studies of population connectivity. There is an urgent need for more comprehensive studies that resolve oceanographic transport processes and dispersion patterns concurrently with studies of dispersal and connectivity. There are very few field studies that resolve oceanographic fields with concurrent Lagrangian measurements for the duration necessary to define connectivity. Further, it is essential that these studies be performed during the appropriate season and for the appropriate duration of larval dispersal. These are the challenges for observational oceanography if it is to make significant contributions to progress in understanding population connectivity and, in turn, the impacts of climate change on marine ecosystems.

REFERENCES

Barth, J., D. Hebert, A. Dale, and D. Ullman. 2004. Direct observations of along-isopycnal upwelling and diapycnal velocity at a shelfbreak front. *Journal of Physical Oceanography* 34:543–565.

Brink, K., R. Limeburner, and R. Beardsley. 2003. Properties of flow and pressure over Georges Bank as observed with near-surface drifters. *Journal of Geophysical Research* 108: doi:10.1029/2001JC001019.

Byers, J., and J. Pringle. 2006. Going against the flow: Retention, range limits and invasions in advective environments. *Marine Ecology Progress Series* 313:27–41.

Chadwick, D.B., and J.L. Largier. 1999. Tidal exchange at the bay-ocean boundary. *Journal of Geophysical Research* 104(C12):22,901–29,919.

DiBacco, C., and D.B. Chadwick, 2001. Assessing the dispersal and exchange of brachyuran larvae between regions of San Diego Bay, California, and nearshore coastal habitats using elemental fingerprinting. *Journal of Marine Research* 59(1):53–78.

Epifanio, C., and R. Garvine. 2001. Larval transport on the Atlantic continental shelf of North America: A review. *Estuarine and Coastal Shelf Science* 52:51–77.

Forward, R.B., Jr., and R.A. Tankersley. 2001. Selective tidal stream transport of marine animals. *Oceanography and Marine Biology Annual Review* 39:305–353.

Franks, P.J.S. 1992. Sink or swim: Accumulation of biomass at fronts. *Marine Ecology Progress Series* 82:1–12.

Gaylord, B., J.H. Rosman, D. Reed, J.R. Koseff, J. Fram, S. MacIntyre, K. Arkema, C. McDonald, M.A. Brzezinski, J.L. Largier, and others. 2007. Spatial patterns of flow and their modification within and around a giant kelp forest. *Limnology and Oceanography* 52(5): 1,838–1,852.

Gawarkiewicz, G., and D. Chapman. 1992. The role of stratification in the formation and maintenance of shelfbreak fronts. *Journal of Physical Oceanography* 32:753–772.

George, R.A., and J.L. Largier. 1996. Fine-scale drifters for coastal and estuarine studies: Performance of a differential GPS tracking system. *Journal of Atmospheric and Oceanic Technology* 13(6):1,322–1,326.

Graham, W.M., and J.L. Largier. 1997. Upwelling shadows as nearshore retention sites: The example of northern Monterey Bay. *Continental Shelf Research* 17(5):509–532.

Hare, J., J. Churchill, R. Cowen, T. Berger, P. Cornillon, P. Dragos, S. Glenn, J. Govoni, and T. Lee. 2002. Routes and rates of larval fish transport from the southeast to the northeast United States continental shelf. *Limnology and Oceanography* 47:1,774–1,789.

Houghton, R., D. Hebert, and M. Prater. 2006. Circulation and mixing at the New England shelf-break front: Results of purposeful tracer experiments. *Progress in Oceanography* 70:289–312.

Kaplan, D.M., and J.L. Largier. 2006. HF-radar-derived origin and destination of surface waters off Bodega Bay, California. *Deep Sea Research II* 53(25–26):2,906–2,930.

Kaplan, D., and F. Lekien. In press. Spatial interpolation and filtering of surface current data based on open-boundary modal analysis. *Journal of Geophysical Research*.

Largier, J.L., B.A. Magnell, and C.D. Winant. 1993. Subtidal circulation over the northern California shelf. *Journal of Geophysical Research* 98(C10):18,147–18,179.

Largier, J., 2003. Considerations in estimating larval dispersal distances from oceanographic data. *Ecological Applications* 13:S71–S89.

Lentz, S., 2003. A climatology of salty intrusions over the continental shelf from Georges Bank to Cape Hatteras. *Journal of Geophysical Research* 108: doi:10.1029/2003JC001859.

Lipphardt, B., D. Small, A. Kirwan, S. Wiggins, K. Ide, C. Grosch, and J. Paduan. 2006. Synoptic Lagrangian maps: Application to surface transport in Monterey Bay. *Journal of Marine Research* 64:221–247.

Lozier, S., and G. Gawarkiewicz. 2001. Cross-frontal exchange in the Middle Atlantic Bight as evidenced by surface drifters. *Journal of Physical Oceanography* 31:2,498–2,510.

Monismith, S.G., and D.A. Fong. 2004. A note on the transport of scalars and organisms by surface waves. *Limnology and Oceanography* 49:1214–1219.

Neiman, H., C. Richter, H. Jonkers, and M.I. Badran. 2004. Red Sea gravity currents cascade near-reef phytoplankton to the twilight zone. *Marine Ecology Progress Series* 269:91–99.

Okubo, A., and S.A. Levin. 2002. *Diffusion and Ecological Problems* (2nd ed.), Springer Verlag, 488 pp.

Paduan, J.D., and L.K. Rosenfeld. 1996. Remotely sensed surface currents in Monterey Bay from shore-based HF radar (Coastal Ocean Dynamics Application Radar). *Journal of Geophysical Research* 101(C9):20,669–20,686.

Palumbi, S.R., and E.E. Sotka. 2006. The use of genetic clines to estimate dispersal distances of marine larvae. *Ecology* 87:1,094–1,103.

Pickart, R., 2000. Bottom boundary layer structure and detachment in the shelfbreak jet of the Middle Atlantic Bight. *Journal of Physical Oceanography* 30:2,668–2,686.

Pringle, J., and J. Wares. 2007. Going against the flow: Maintenance of alongshore variation in allele frequency in a coastal ocean. *Marine Ecology Progress Series* 335:69–84.

Rennie, S.E., J.L. Largier, and S.J. Lentz. 1999. Observations of a pulsed buoyancy current downstream of Chesapeake Bay. *Journal of Geophysical Research* 104(C8):18,227–18,240.

Ridderinkhof, H., and J.T.F. Zimmerman. 1992. Chaotic stirring in a tidal system. *Science* 258:1,107–1,111.

Rosman, J., J.R. Koseff, S.G. Monismith, and J. Grover. 2007. A field investigation into the effects of a kelp forest (*Macrocystis pyrifera*) on coastal hydrodynamics and transport. *Journal of Geophysical Research* 112:C02016, doi:10.1029/2005JC003430.

Savidge, D., and J. Austin. 2007. The Hatteras Front: August 2004 velocity and density structure. *Journal of Geophysical Research* 112: C07006,doi:10.1029/2006JC003933.

Schmidt, W.E., B.T. Woodward, K.S. Millikan, R.T. Guza, B. Raubenheimer, and S. Elgar. 2003. A GPS-tracked surf zone drifter. *Journal of Atmospheric and Oceanic Technology* 20:1,069–1,075.

Schmidt, W.E., R.T. Guza, and D.N. Slinn. 2005. Surf zone currents over irregular bathymetry: Drifter observations and numerical simulations. *Journal of Geophysical Research* 110:C12015, doi:10.1029/2004JC002421.

Shanks, A.L., J.L. Largier, L. Brink, J. Brubaker, and R. Hooff. 2000. Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. *Limnology and Oceanography* 45(1):230–236.

Simons, R., S. Monismith, F. Saucier, L. Johnson, and G. Winkler. 2007. Zooplankton retention in the estuarine transition zone of the St. Lawrence estuary. *Limnology and Oceanography* 51:2,621–2,631.

Smith, J.A., and J.L. Largier. 1995. Observations of nearshore circulation: Rip currents. *Journal of Geophysical Research* 100(C6):10,967–10,975.

Washburn, L., M. Swenson, J.L. Largier, M. Kosro, and S. Ramp. 1993. An anticyclonic eddy in the coastal transition zone off northern California. *Science* 261:1,560–1,564.