

Connectivity of Marine Populations: Open or Closed?

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Most marine populations are thought to be well connected via long-distance dispersal of larval stages. Eulerian and Lagrangian flow models, coupled with linear mortality estimates, were used to examine this assumption. The findings show that when simple advection models are used, larval exchange rates may be overestimated; such simplistic models fail to account for a decrease of up to nine orders of magnitude in larval concentrations resulting from diffusion and mortality. The alternative process of larval retention near local populations is shown to exist and may be of great importance in the maintenance of marine population structure and management of coastal marine resources.

Most marine species have life histories that include at least one potentially widely dispersive stage. For nonbrooding, benthic species, this dispersive stage is typically the pelagic larval stage wherein the larvae may be subjected to transport by ocean currents. Given the spatial and temporal scales of ocean currents, the implications have been that larval dispersal may be extensive (1) and that marine populations are "open" over ecological time scales (2). Genetic studies have suggested that many populations of marine species are homogeneous over large spatial scales (3); coupled with models of passive larval drift (4), they support the contention that larvae are transported regularly between local and distant populations.

Knowledge of larval exchange among populations of marine organisms is vital to the study of marine population dynamics, management of fishery stocks, and the design of marine reserves. Decisions predicated on the assumption that larvae are widely dispersed may lead to erroneous actions if the assumption is wrong (5). However, lack of evidence to the contrary has generally resulted in the acceptance of the concept of well-mixed populations on both ecological and evolutionary scales. This, in turn, has been interpreted to infer that ocean current trajectories (usually mean trajectories) and larval duration may predict exchange between populations (4). Larvae, however, are not simply passive particles. Vertical migration behaviors by larvae may couple with vertically stratified flows to retain larvae nearshore (6, 7). Some studies have indicated that mesoscale and sub-mesoscale circulations may minimize long-distance dispersal by retaining

larvae for a portion of or throughout their pelagic stage (7, 8). The existence of endemic species around isolated oceanic islands (9) also suggests successful retention. Hence, the paradigm of marine populations as open systems needs to be reevaluated.

As a starting point, we use a two-dimensional (2D) Eulerian advection-diffusion model with constant mortality to consider the basic factors involved in determining the lev-

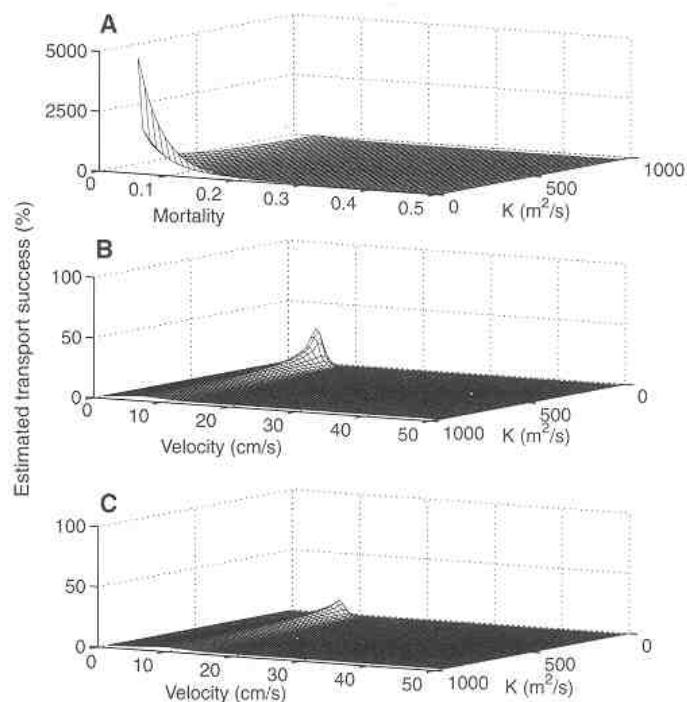
el of larval exchange. The conclusions from this model are then tested in a Lagrangian model using a mesoscale-resolving ocean general circulation model (OGCM). Although the simulations are concentrated on the eastern Caribbean island of Barbados and its neighbors, the scales are applicable to other tropical archipelagoes and coastlines.

The 2D Advection-Diffusion-Mortality model (10) examines how many individuals actually reach downstream sites under different conditions of each of three processes (advection measured as constant current speed, turbulent horizontal diffusion, and larval mortality).

$$\frac{\partial N}{\partial t} = -u \frac{\partial N}{\partial x} - v \frac{\partial N}{\partial y} + K \left(\frac{\partial^2 N}{\partial x^2} + \frac{\partial^2 N}{\partial y^2} \right) - \mu N \quad (1)$$

where N is the concentration of larvae at any point in space and time, u and v are current speed in the x and y direction, respectively, K is horizontal diffusivity (assume $K_x = K_y = \text{constant}$), and μ is the mortality coefficient. This model differs from simple trajectory models by including the effect of diffusion and larval mortality in the transport process, both of which act

Fig. 1. Results of 2D Advection-Diffusion-Mortality model. (A) Effect of mortality and diffusion on estimated transport success from Barbados; (B) estimated transport success to the closest island (St. Lucia – 140 km) for varying current speeds and diffusion constants; (C) estimated transport success to Martinique (200 km) for varying current speeds and diffusion constants. Near-surface current speeds in this area are typically 0.35 m s^{-1} based on estimates from both shipboard and 18-month moored Acoustic Doppler Current Profilers (ADCP), so we modeled over a range from 0 to 0.5 m s^{-1} . Diffusivity constant, K , was taken from Okubo (27); for this study we modeled a full range from 0 to $1000 \text{ m}^2 \text{ s}^{-1}$ with $K = 100 \text{ m}^2 \text{ s}^{-1}$ taken as the typical value for the spatial scale covered here. Published estimates of larval mortality rates range from a μ of 0.03 to 0.62 (~ 3 to 46% mortality day^{-1} ; $n = 42$ species) (28). Because these are field-derived estimates, some bias may be added via loss of larvae due to physical transport (25), therefore we modeled over a range of 0 to 0.5, and at the mode of 0.20. Realistic reproductive effort and settlement rates are critical inputs for this model. We estimated these values from an 18-month time series of daily reproduction ($n = 75$ fish per day) and settlement rates for a species of benthic, egg-laying coral reef fish (*Stegastes partitus*, Pomacentridae) (26). Mean reproductive effort was $43.9 \text{ eggs m}^{-2} \text{ day}^{-1}$, and mean settlement rate was $0.00646 \text{ fish m}^{-2} \text{ day}^{-1}$. Reef area was taken as total area from shore to 20 m isobath around each island modeled. Finally, we used measurements of the typical larval duration of *S. partitus* of 28 days (29) for this model iteration.



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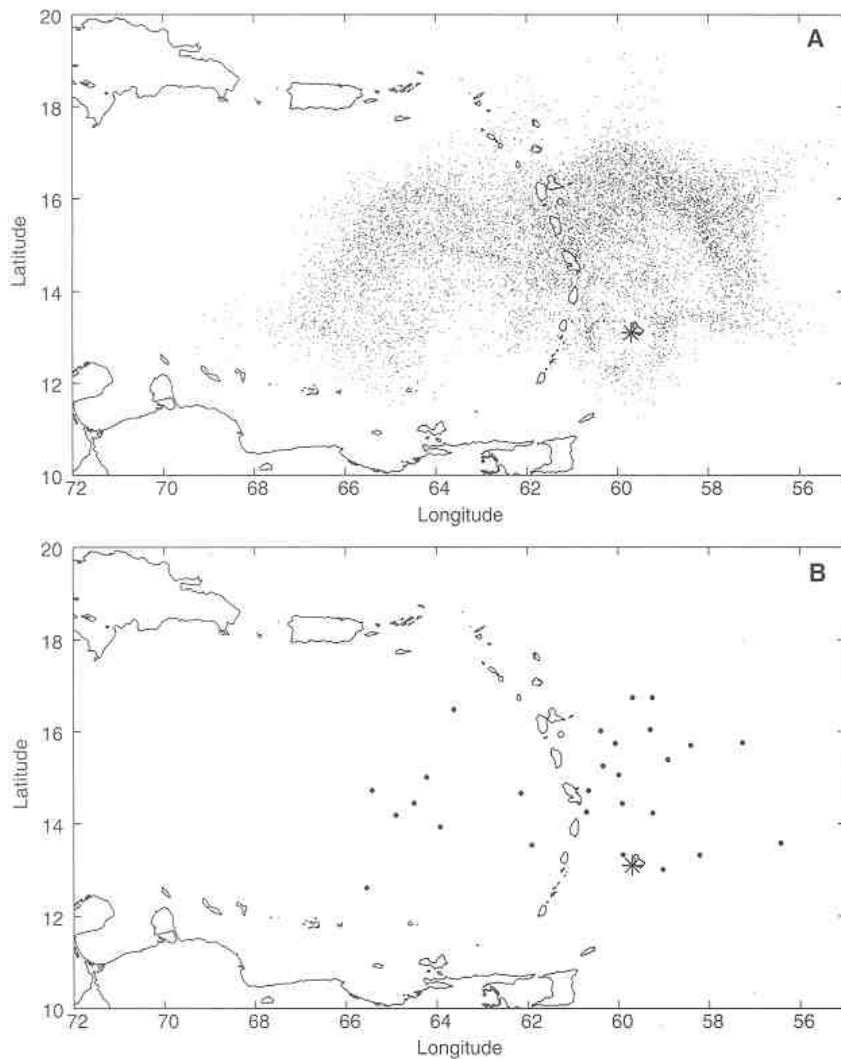


Fig. 2. Transport endpoints of 10,000 virtual larvae released from a 1-km² area off Barbados (*) using mixed layer flow model. **(A)** Model results of the dispersion of larvae after 30 days; **(B)** same model run as in **(A)**, but with effect of larval mortality at a typical rate of 18% day⁻¹ ($\mu = 0.2$). We used the Miami Isopycnic Coordinate Ocean Model (MICOM) (23) to model the circulation for a 30-day period. Subgrid turbulent motion of each virtual larva was modeled using a random flight model (24) with $K = 10 \text{ m}^2 \text{ s}^{-1}$. The MICOM model resolves mesoscale turbulence, thereby providing more realistic estimates of diffusive motion than that incorporated in the 2D model above.

to reduce significantly the concentration of larvae as they are advected toward the next island. Though large numbers of larvae (in our model, 10^9 larvae day⁻¹) may be released from a given source population, significant numbers reaching downstream locations only 140 km away quickly diminish to near zero level when realistic levels of diffusion ($K = 100 \text{ m}^2 \text{ s}^{-1}$) and/or larval mortality ($\mu = 0.2$) are included (Fig. 1A).

Model simulations indicate that larval exchange, even between closely located islands, is simply not sufficient to sustain downstream populations over ecological time scales (Fig. 1B). In all scenarios of typical current speeds (30 to 50 cm s⁻¹), the estimated transport success (11) is effectively zero, even where diffusion is zero. Measurable transport success occurs only when current speeds are too low for this region ($\sim 8 \text{ cm s}^{-1}$) and diffusion remains unrealistically low or nonexistent.

The very steep nature of the “successful” set of conditions indicates the rarity with which such conditions are likely to occur. As expected, estimated transport success decreases when distance from the source increases, indicating the additional diluting (or dispersion) of larvae over an ever increasing area (Fig. 1, B and C). Thus, while current trajectories might indicate the potential outcome of larval transport (4), they fail to account for the probability of successful downstream transport because larval concentrations are reduced by at least five (and potentially greater than nine) orders of magnitude by diffusion and mortality of larvae.

The 2D model used above is restricted in its ability to resolve adequately the mesoscale variability in the ocean. Mesoscale flows may serve to concentrate larvae along frontal features thereby increasing their speed of transport and/or altering the transport trajectories of larvae.

To this end, we used a high-resolution (6 km) general circulation model (12) to simulate larval dispersal under realistic, mixed layer flow conditions in the eastern Caribbean. The capacity for dispersal is clearly demonstrated in the model results (Fig. 2A). Within 30 days, virtual larvae released from a 1 km² location near Barbados spread over $\sim 10^6 \text{ km}^2$, which represents a dilution of the original concentration of larvae by six orders of magnitude. When the diluting effect of mortality is added, the outcome is obvious (Fig. 2B). There simply are not enough larvae occurring within any coastal region to sustain downstream populations from a source population such as Barbados, even when all larvae produced at the source leave the source area. To understand the sensitivity of the results to variations within the simulations, dispersion runs were made for 10 different periods in the North Atlantic model. The results show variations of the size of the dispersed patch of approximately a factor of two with the main difference occurring between times when North Brazil rings (13) are present and when they are not. The conclusion is that the order of magnitude of the dispersal is robust.

Absent from these models of long-distance dispersal is the effect of retention of locally spawned larvae. However, if downstream recruitment is unlikely, it follows that mechanisms should exist to maximize retention of larvae near the source population. Mesoscale features may act to concentrate larvae locally near their source locations. Also, the upper water column (100 m) is vertically stratified (due to changes in temperature and salinity with depth), which enables vertically layered flows. This condition is well demonstrated in a depth profile of the residual east-west flow averaged over a 30-day period off the western coast of Barbados (Fig. 3A) and has been identified as a common feature of this (7, 14) and other coastal locations (15). Surface flows along the western side of the island tend to flow offshore due to prevailing winds from the northeast, resulting in a consistent upwelling and onshore flow between 20 to 50 m evident in both the residual record and in Lagrangian drifters (Fig. 3B). Relatively early in their development (~ 6 to 9 days after hatching), postflexion-stage fish larvae (the developmental stage associated with formation of the caudal fin and capability for some directional swimming) descend in the water column (from near surface as preflexion larvae) to a mean depth of $\sim 35 \text{ m}$ (Fig. 3C). By avoiding the surface layer, postflexion larvae are in water with a mean onshore flow, thereby enhancing local retention and countering the outward advection of the surface currents. Besides enhancing local replenishment of the source population, such retention further reduces the number of larvae available for downstream transport.

These results, combined with accumulating evidence of local retention (16), suggest that

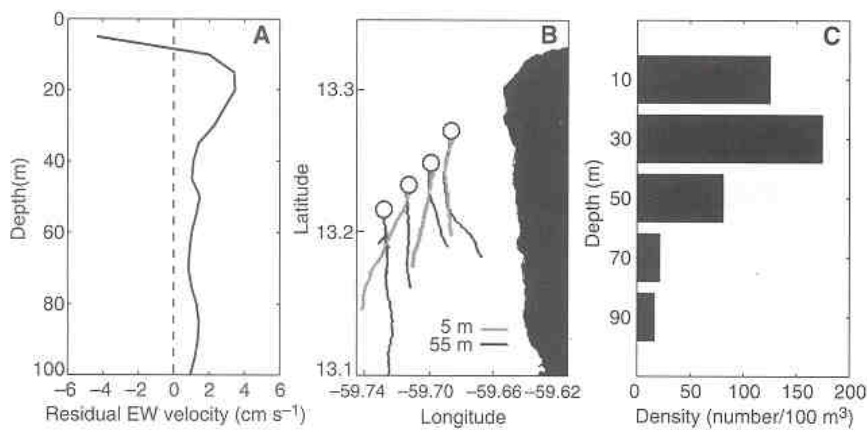


Fig. 3. Vertical structure of flow and larval fish distributions along the west coast of Barbados. (A) Onshore/offshore (east-west, indicated by E-W) component of residual flow at depths between 0 and 100 m; (B) GPS drifter tracks during one 12-hour experiment of Lagrangian flow along the west coast of Barbados; (C) Vertical distribution of postflexion larvae of the family Pomacentridae in each of five, 20 m depth bins to a maximum depth of 100 m. Residual flow was determined from ship-mounted, bottom-tracked 150-kHz ADCP during a 30-day cruise in May 1996. All current estimates were from a sampling domain extending 10 km offshore and 20 km along the western shore; we averaged by depth for the full 30-day period. Drifter tracks were determined from satellite-tracked, GPS drifters drogued with 1×10 m holeysock drogues centered at 5 and 55 m. Each track represents approximately 8 to 12 hours of drift time. Point of deployment is denoted by open circle (○). Vertical distribution of larvae was determined from vertically discrete ichthyoplankton collections ($n = 176$ stations) using a 1-m^2 MOCNESS, fitted with $333\text{-}\mu\text{m}$ mesh nets towed at 5 discrete depths: 0 to 20, 20 to 40, 40 to 60, 60 to 80, and 80 to 100 m.

coastal marine populations may not be as open as previously thought. Populations may in fact have a large degree of coupling between local production and recruitment (17). Lack of strong empirical evidence supporting this contention, however, is probably due to losses in the plankton rather than coupling with some distant, upstream source (18). The issue is largely one of scale. Though explicit levels of exchange required to sustain a downstream population are not defined, even a 10% level is many orders of magnitude higher than required for retaining genetic homogeneity.

Several physical/behavioral linkages may modify some of the details of the picture derived here. Behaviorally modified advection of larvae within fronts associated with the edges of eddies can increase concentrations on time/space scales of 30 days and 100 km (19). There is also the potential for long-range dispersal to occur due to short-term climatic variations (20). However, such events may be relatively rare and/or detrimental to larval survival (for example, hurricanes). Toward the end of their larval period, fish also have significant swimming capabilities (21) which may allow a larger radius of settlement on islands (depending on the radius of relevant taxis cues). Clearly, the level of exchange in a given system will fall along a continuum from isolated islands to continental coastlines. Yet, even for the latter, mesoscale circulation features (such as coastal currents and eddies), coupled with vertical and horizontal larval swimming behaviors, might lead to ecologically scaled retention of larvae relatively close to source populations (22).

In regions such as the Caribbean, the question of whether populations of fishery

resources are regularly transported among islands or along long stretches of coastline is an international issue. One country's fisheries have the potential to impact the resources of another. However, our results suggest that management decisions based on open population models might overestimate the level of population exchange. Such overestimates might lead to a false sense of security among managers of "downstream" resources (5). If local retention is more the rule, then local management initiatives predicated on the appropriate population models (limited exchange) have a greater chance of producing local results.

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- Model output value of "estimated transport success" was based on the density of larvae at day 28 that were within 2 km of the target island, standardized to mean daily settlement density observed at the source island of Barbados. Here, we assume that the settlement rates measured at Barbados are a reasonable indicator (order of magnitude) of typical rates elsewhere. Thus, to sustain a downstream population at the same population density as the source and assuming no self-replenishment from the downstream population, the estimated transport success must equal 100%. Assuming partial self-replenishment (say, 70%), then the estimated transport success must be ~30%. Finer resolution is not reasonable for the simplified assumptions of this model. Assuming some accumulation of larvae prior to day 28 will increase the estimated transport success, for example, accumulating over the last 10 days of the larval period will potentially increase transport success by a factor of 10.
- The numerical model is a version of the Miami Isopycnic Coordinate Ocean Model (MICOM) (23), configured to simulate the North Atlantic circulation. The Lagrangian particle simulations have a stochastic turbulent diffusion to the flow to account for the subgrid scale variance in velocity that is not simulated by the numerical model. This assures that the amount of variability matches that found in drifters in this region of the ocean (24).
- North Brazil Rings are mesoscale, anticyclonic eddies shed from the North Brazil Current retroflection, which translate northward to the Lesser Antilles island chain [W. E. Johns, T. N. Lee, F. A. Schott, R. J. Zantopp, R. H. Evans, *J. Geophys. Res.* **95**, 22103 (1990); P. L. Richardson, G. E. Hufford, R. Limeburner, W. S. Brown, *J. Geophys. Res.* **99**, 5081 (1994)].
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