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Authors

Siegel, D A
Mitarai, S
Costello, C J
[et al.](#)

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The stochastic nature of larval connectivity among nearshore marine populations

D. A. Siegel*^{†‡}, S. Mitarai*, C. J. Costello*[§], S. D. Gaines*[¶], B. E. Kendall*[§], R. R. Warner*[¶], and K. B. Winters^{||}

*Institute for Computational Earth System Science, Departments of [†]Geography and [¶]Ecology, Evolution, and Marine Biology, and [§]Donald Bren School of Environmental Science and Management, University of California, Santa Barbara, CA 93106; and ^{||}Scripps Institution of Oceanography, University of California at San Diego, La Jolla, CA 92093

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Many nearshore fish and invertebrate populations are overexploited even when apparently coherent management structures are in place. One potential cause of mismanagement may be a poor understanding and accounting of stochasticity, particularly for stock recruitment. Many of the fishes and invertebrates that comprise nearshore fisheries are relatively sedentary as adults but have an obligate larval pelagic stage that is dispersed by ocean currents. Here, we demonstrate that larval connectivity is inherently an intermittent and heterogeneous process on annual time scales. This stochasticity arises from the advection of pelagic larvae by chaotic coastal circulations. This result departs from typical assumptions where larvae simply diffuse from one site to another or where complex connectivity patterns are created by transport within spatially complicated environments. We derive a statistical model for the expected variability in larval settlement patterns and demonstrate how larval connectivity varies as a function of different biological and physical processes. The stochastic nature of larval connectivity creates an unavoidable uncertainty in the assessment of fish recruitment and the resulting forecasts of sustainable yields.

coastal oceanography | fisheries | marine ecology

Nearshore ecosystems host a wide variety of marine organisms and are among the most productive environments on Earth. Yet many species harvested from these ecosystems are overfished (1–3), a problem that is especially acute for those invertebrates and fishes with a relatively sedentary adult life stage. One potential cause of overfishing is mismanagement because of a poor understanding and accounting of stochasticity in these systems (4, 5). Stochasticity caused by climate variations has long been known to influence the dynamics of ocean ecosystems and the fisheries they support (6). Climate variation affects rates of fecundity and recruitment by altering water temperature, coastal circulation patterns, or the availability of spawning grounds (7, 8); such effects can be understood and, given sufficient data, may be predictable. Here, we introduce a mechanism that generates stochasticity in spatial and temporal patterns of larval transport on annual time scales. This stochasticity is inherently unpredictable because of the chaotic nature of coastal circulations and the relatively short larval time scales.

Many harvested fish and invertebrates from nearshore ecosystems have a life cycle that includes a pelagic larval stage that can last up to months and a localized benthic adult stage (9, 10). These relatively sedentary adults release hundreds to millions of larvae that are advected and dispersed by ocean currents as they develop competency to settle (9–13). Spawning releases can occur continuously over months or in a few short events. Biotic factors, such as active swimming and vertical migration, also contribute to movement patterns (12, 14, 15). A small fraction of the larvae settle at suitable sites, and an even smaller fraction recruit to adult stages where they can reach reproductive age and contribute to fishery yields. Larval transport therefore plays a key role in the structuring and dynamics of nearshore populations. Although many larval transport models exist based on

classical advection–diffusion dynamics (9–13, 16, 17), the dynamics of larval transport on annual time scales remains poorly understood.

Conceptually, larval transport should be stochastic considering the relevant time scales. Characteristic time scales for the trajectories of surface water parcels (the Lagrangian decorrelation time) are 2–5 days in the coastal ocean (13, 17–19). Therefore, a single subpopulation continually spawning larvae over a 90-day season will have only ≈ 30 statistically independent larval releases (assuming a Lagrangian time of 3 days), of which only a small fraction will successfully return to nearshore settlement environments (13). This means that connectivity of nearshore populations, even in the absence of temporal climate fluctuations or bathymetric complexity, will be an intermittent and spatially heterogeneous process driven by the turbulent transport of larvae by coastal circulations. This process leads to spatiotemporal variability in recruitment and larval connectivity that is inherently unpredictable on the annual time scales required for fishery management. This source of uncertainty has not been considered in previous larval connectivity models of nearshore marine populations (9–12, 16).

A Bio-Physical Model of Larval Connectivity

To illustrate the stochastic nature of larval transport, we implemented a bio-physical model of larval connectivity patterned after the central California coastline (ref. 20; see *Methods*). The model domain is 256 km (along-shelf) by 288 km (cross-shelf) and is unstructured in the alongshore direction. The flow is forced by a time-varying wind field and a mean alongshore pressure gradient, both derived from observations. The bio-physical model reproduces dispersion statistics found in surface drifter observations (17–18, 20).

As a base case, we modeled larval transport for a settlement competency window between 20 and 40 days, which roughly typifies many nearshore fishes (9, 21). Larvae were released daily for 90 days from sites spaced every 2 km apart within 10 km of the coastline and were advected by the simulated currents. Biological sources of larval mortality are not included. Example trajectories [Fig. 1 and see [supporting information \(SI\) Movie S1](#)] show the advection of larvae, roughly along lines of constant sea level following the jets formed between the eddy features, and those patterns evolved rapidly. Importantly, eddies swept newly released larvae together into “packets,” which stayed together through their pelagic life stage.

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[†]To whom correspondence should be addressed. E-mail: davey@icess.ucsb.edu.

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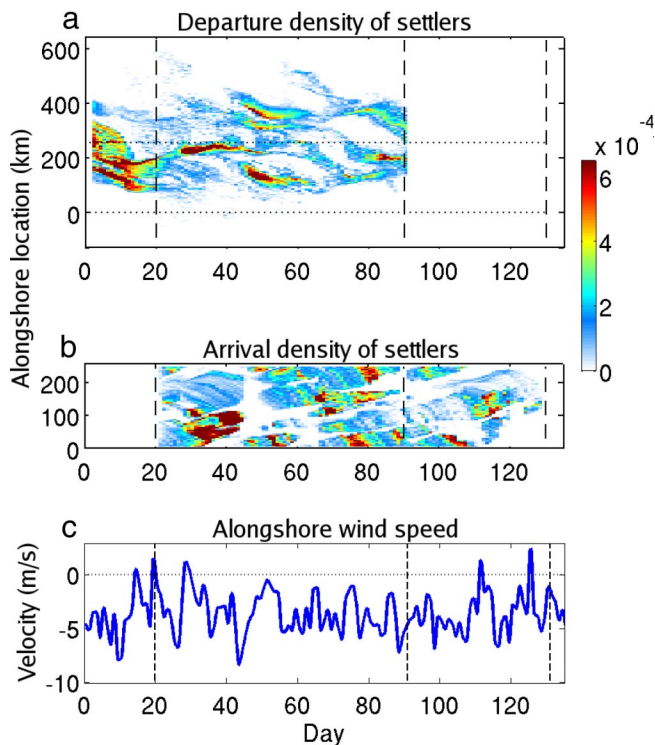


Fig. 2. Time series of the “departure density” showing the alongshore source locations (y axis), settling times (x axis), and density (color) of larvae that successfully settle anywhere within the model domain (a), the “arrival density” showing the density (color) of arrival locations for settlers (y axis) from all source locations and settling times (x axis) (b), and the alongshore wind speed for the base case simulation (negative is upwelling favorable) (c). The circulation model was first driven to a quasi-steady state, and larvae were released daily starting on day 0. Larvae could settle within their competency time window (20–40 days) if they were within suitable habitat (the inner 10 km). Larval releases stopped at day 90, and settlement was allowed to continue until day 130. The periodic interval in the alongshore direction is stretched in b to account for larval source regions that were many periodic distances upstream from their arrival locations (a feature of using periodic boundary conditions). Densities were normalized by the total number of settlers. Time and space scales for settlement were calculated by using the variogram range (39) of the arrival density with time or location held constant. Departure time and space scales (a) were 12 days and 56 km, whereas the arrival time and space scales (b) were 15 days and 44 km, respectively (which corresponds to a value of normalized arrival space scale, δ_{ev} , of 0.17; = 44 km/256 km).

Thus, larval settlement patterns will become smoother (CV_{set} decreases) as δ_{ev} , T , or f_{sv} increase, or as τ decreases.

The scaling relationship can be used to develop a packet model of larval connectivity where N_{ev} -independent, equally sized settlement packets are superimposed to model larval connectivity (see Fig. 3f for details). The packet-modeled connectivity retains the stochastic character seen in the flow simulations and provides a method for including transport stochasticity in spatial models of nearshore marine populations.

The scaling theory also provides a simple way for evaluating the role of biological parameters on connectivity. For the base case, these parameters (larval release duration, habitat extent, etc.) were chosen to allow for a high degree of successful settlement. If the spawning season (T) is shortened, values of CV_{set} increase, and a more heterogeneous connectivity matrix (fewer hot spots) is observed (Fig. 3g). Factor of two changes in the spatial scale between adjacent releases or of times between releases have only a moderate role in altering connectivity (data not shown); however, large reductions in the frequency or density of larval releases dramatically increase the stochastic

nature of connectivity (Fig. 3h), because larval releases now occur infrequently compared with eddy scales.

Reducing the larval settlement competency time window (shortening the pelagic larval duration and/or the period during which settlement can occur) makes connectivity more regular (Fig. 3i) because more larvae are found in the nearshore environment during their settlement competency window compared with the base case (thus increasing f_{sv}). Importantly, different connectivity patterns arise from the same flow field for organisms with different life histories.

Movement by individual larvae, both ontogenetic vertical migrations and late-period active swimming toward suitable habitat, also can shape connectivity patterns (12, 14, 15). Ontogenetic descents should affect larval transport by moving larvae from higher-speed surface flows to deeper, slower flows. When migrating larvae are modeled to descend from the surface to 30 m after 5 days, the resulting connectivity matrix (Fig. 3j) shows only moderate changes from the base case. Active swimming toward suitable habitat in the later stages of larval development or preferential cross-shelf transport associated with shoaling internal waves or other phenomena (24, 25) can be modeled by increasing the offshore extent of where larvae can settle. Increasing the extent of offshore habitat from 10 to 20 km only moderately reduces the stochastic nature of larval connectivity (Fig. 3k).

The base case simulated larval transport at the height of upwelling conditions, which resulted in strong, highly variable currents (Fig. 1). In the winter, upwelling-favorable winds are reduced along the California coast (23, 26). The same larval release schedule applied to a typical winter flow field (see *Methods*) still showed a stochastic pattern of connectivity, although the mean displacement of settling larvae was reduced compared with the base case (Fig. 3l) because of the reduced currents.

We have shown that alongshore larval connectivity is a stochastic process in a spatially unstructured domain. Bathymetric variability and regional variations in wind patterns may create persistent hot spots for larval export and settlement (11, 12, 27). Two realizations of connectivity for a sinuous coastline patterned after the Central California coast (see *Methods*) do not show consistent settlement patterns (Fig. 3m and n), suggesting that moderate undulations of a straight coastline will not necessarily focus settlement onto particular topographic features. It is expected that topography will have a larger role for regions dominated by concave coastlines, island chains, or enclosed seas (11, 12, 27).

A summary of the processes that help regulate the nature of connectivity is given in Table 1. Overall, we expect highly stochastic settlement patterns in organisms with long pelagic larval durations and short and periodic spawning seasons that coincide during periods of maximum upwelling, with little active larval swimming ability. Other scenarios can be developed by using the scaling model (Eq. 3 and Table 1).

Implications of Stochastic Larval Connectivity

We have shown that larval settlement is inherently a stochastic process driven by the interaction between coastal circulations and organism life histories. Thus, recruitment variability will be inherently unpredictable even in the absence of the sources of spatial and temporal variability that have been commonly studied (6–8). Connectivity among nearshore populations on annual time scales will not be well modeled by using mean field approaches such as advection/diffusion models, which will make the management of nearshore fisheries difficult (28). Fisheries scientists have long tried to explain the sources of recruitment variability so that recruitment can be predicted knowing only adult population size and environmental factors (6, 7, 12, 28, 29). Our work indicates that local rates of larval settlement will be

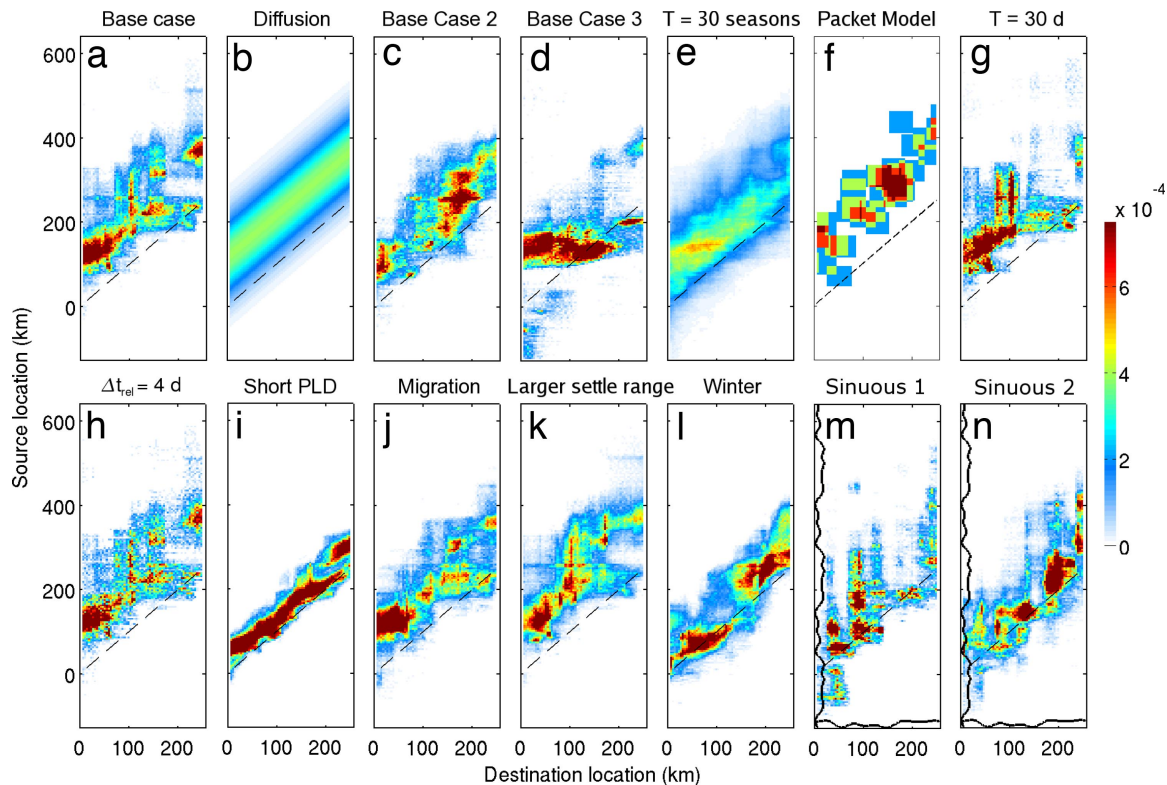


Fig. 3. Larval connectivity diagrams for various scenarios. Connectivity diagrams represent the probability density functions (color) of the relationship between source (vertical axis) and destination (horizontal axis) locations along a coastline. The connectivity matrices are normalized so that the summed probabilities equal one. The dashed slanted line represents self-settlement (where source and destination locations coincide). The broader extent of the source locations in the diagrams takes advantage of the periodic boundary conditions. (a) The base case simulation shown in Figs. 1 and 2. (b) A diffusion model assuming the same statistics of the base case simulation. (c) A second realization of base case simulation. (d) A third realization of base case simulation. (e) The average connectivity matrix summed over 30 spawning seasons. (f) An instance of the packet model. The three realizations of the base case simulation (a, c, and d) show different connectivity patterns illustrating intermittency of larval transport. The diffusion example (b) is constructed from statistics from the base case simulation (a) using a mean offset of 115 km and a spread of 64 km for a Gaussian kernel (13). The packet model (f) is implemented by calculating the number of arriving packets (N_{ev}) by using Eq. 2 (with $T = 90$ d, $\tau = 15$ d, $\delta_{ev} = 0.17$, and $f_{sv} = 1$). The value for f_{sv} is chosen because larval mortality was not considered in the base case simulation. Destination locations for the N_{ev} packets were selected randomly from within the domain, and their source locations were also determined randomly selecting from the base case Gaussian kernel model (b), which accounts for the downcoast displacement in the packet model results. (g–l) The effects of changes in biological or physical parameters on connectivity matrices for larval dispersal are shown. The base case simulation (a) was altered by reducing the larval release duration (T) from 90 to 30 days (g), increasing the time interval between larval releases (Δt_{rel}) from once a day to every 4 days (h), changing the larval settlement competency window from 20–40 days to 5–10 days (i), mimicking ontogenetic migration by making larvae swim to 30 m depth after 5 days at the surface (j), mimicking active swimming late in the larval competency window by increasing settlement range from 10 to 20 km offshore (k), simulating low upwelling conditions as is found in the winter (climatological January at CalCOFI line 70) (l). (m and n) Two realizations of larval connectivity for a sinuous coastline based on the central California Coast (see *Methods*). For the coastal configuration shown, peak to trough variations in coastline sinuosity were 20 km. With the exception of the two other realizations of the base case (c and d), the low upwelling case (l) and the two sinuous coastline cases (m and n), all of the connectivity diagrams shown were created by using the same flow field.

largely decoupled from local stocks, suggesting that stochastic larval connectivity provides an unexplored source of unresolvable noise in observed stock-recruitment relationships (28, 29). The packet model introduced here provides a way for assessing the variability in larval connectivity in stock-recruitment models.

The stochastic nature of larval connectivity will influence many ecological processes. For example, the pulsed nature of larval transport, even at long distances from a source, can act to alleviate the Allee effects that limit the success of long-distance colonization (30). Further, the occasional large, isolated pulses of larval settlement predicted here should enhance the contribution of the “storage effect” to species persistence and coexistence (31). The fact that these pulses are often the result of successful settlement of packets of larvae that have remained together throughout larval life suggests that these processes may be the mechanism leading to the “sweepstakes” patterns seen in the genetic structure of groups of arriving larvae (32). Finally, the long lives and high fecundity that are characteristic of many marine organisms have long been posited as evolutionary re-

sponses to recruitment variability (33); variability in recruitment driven by turbulent coastal circulations may provide a mechanism contributing to this variability. Although the present study identifies important features of complex nearshore systems, more work is required to understand the interactions among variable coastal circulation, organism life cycles, and the management of these important ecosystems and the fisheries they support.

Methods

Time-dependent, 3D flow fields were simulated by using the Regional Ocean Modeling System (34, 35). The flow fields were patterned after central California Current conditions and satisfied statistical stationarity and homogeneity in the alongshore direction, whereas the forcings and boundary conditions were derived from observed conditions. This model provides a numerical system capable of addressing the fundamental processes affecting larval dispersal.

The flow field was modeled after CalCOFI line 70 (offshore of Point Sur, California). The domain size was 256 km in the alongshore direction, and 288 km in the cross-shore direction. The bathymetry increased steeply in depth in

Table 1. Life history and oceanographic processes regulating the stochastic nature of larval connectivity

Forcing that will lead to stochasticity (increasing CV_{set} ; Eq. 3)	Magnitude of effect	Expected effect	Effect on conceptual model (Eq. 3)
Increase upwelling favorable winds	Moderate	Leads to decreased survivability because larvae are advected from inshore regions because of higher currents	Decreases f_{sv}
Decrease wind field variability	Small to moderate?	Provides fewer independent flow field circulations	Can decrease τ and δ_{ev}
Coastline and bathymetric variability	Moderate to large?	Adds additional length scales in the flow and allows spatial persistence in settlement to occur	May modify δ_{ev} and τ
Longer pelagic larval duration	Moderate to large	Reduces the chance that larvae are in suitable habitat during their settlement time window	Decreases f_{sv}
Reducing width of larval settlement window	Moderate to large	Reduces the time that larvae can find suitable habitat	Decreases f_{sv}
Shortening reproductive season	Moderate to large	Decreases number of independent releases	Decreases T
Decreases in the spatial scale or frequency of larval releases	Small to moderate	Makes releases more sporadic and rare	Decreases f_{sv}
Including larval mortality	Moderate?	Lowers potential for successful settlement	Decreases f_{sv}
Reduction of suitable habitat	Moderate to large	Decreases effective habitat size	Decreases f_{sv}
Reduction in the effectiveness of late larval stage swimming	Moderate to large	Decreases effective width of the nearshore habitat	Decreases f_{sv}

Question marks denote a large degree of uncertainty for some of these relationships.

the offshore direction and was constant in the alongshore direction. The minimum depth was set to 20 m at the coast, whereas the maximum depth was set to 500 m offshore. The domain was discretized by 2-km-resolution grid points horizontally; 20 vertical levels were considered with enhanced resolution near the top and bottom boundaries. The eastern boundary was set to a free-slip boundary condition, whereas an open boundary condition (36) was used on the western boundary. Northern and southern boundary conditions were periodic to enable alongshore homogeneity of the flow field. After the simulation fields reached statistically stationary conditions, passive or active particles were added to simulate the trajectories of released larvae. Here, a mean alongshore pressure gradient was imposed as an external body force, estimated by using January and July mean dynamic height differences between CalCOFI hydrographic sections off Point Arena and Point Conception (lines 60 and 80; ref. 37). Initial fields were generated by using CalCOFI Line 70 (Point Sur) hydrography for a climatological July and January (37).

Wind forcing was modeled assuming that the wind field varied on spatial scales much larger than the alongshore scale of the simulated domain while its magnitude decreased toward the shore (26, 38). Each component of the wind vector was modeled as a Markov Chain given the statistics estimated from hourly buoy wind data (National Data Buoy Center stations 46028, 46012, and 46042) and the spatial wind observations (26). Further details of model set-up and validation of the physical flow variables using CalCOFI observations can be found in ref. 20. The sinuous coastline case (Fig. 3 *m* and *n*) used the same oceanographic forcings and larval life histories as the base case but added a sinuous coastline. Coastal undulations were assessed from a Fourier analysis of central California coastline locations for spatial scales ranging from 32 to 128 km. The coastline realization was constructed by assuming random phases among the Fourier components, which ensures that the alongshore domain is periodic.

The larval release protocol was modeled after typical benthic reef fish found in California nearshore waters. For the base case simulation, nearshore habitats (where larvae were released and settled) were all waters shallower than 100 m in depth (<10 km inshore). No variations in suitable habitat were considered in the alongshore direction. The base case released larvae every day for a season (90 days) near the sea surface every 2 km in nearshore habitat. Larvae settled when they were found within the nearshore habitat for the first time during their competency time window. For most of the results presented here, the settlement competency time window is assumed to be 20–40 days, which is typical of many nearshore fishes (21). This protocol provides an extreme abundance of settling larvae from which the statistics of larval connectivity can be assessed.

Simulated larvae were modeled as Lagrangian particles and were advected by the modeled currents. The effects of subgrid scale advection processes should have had little influence on the larval connectivity patterns because of the low kinetic energy levels at the grid spatial scale (20). Larvae were modeled to stay within the upper 10 m of the domain. In the case of vertical migration, larvae remained near the surface for the first 5 days and then sank to 30 m depth after which time they remained at 30 m. Statistics for the dispersal of modeled surface trajectories (compare length and time scales and eddy diffusivities) compare well with similar statistics derived from surface drifter observations from the California Current (refs. 17–19 and see also ref. 20).

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