



CHICAGO JOURNALS



The University of Chicago

Marine Population Connectivity: Reconciling Large-Scale Dispersal and High Self-Retention.

Author(s): Kerry J. Nickols, J. Wilson White, John L. Largier, and Brian Gaylord

Source: *The American Naturalist*, Vol. 185, No. 2 (February 2015), pp. 196-211

Published by: [The University of Chicago Press](#) for [The American Society of Naturalists](#)

Stable URL: <http://www.jstor.org/stable/10.1086/679503>

Accessed: 24/01/2015 18:05

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press, The American Society of Naturalists, The University of Chicago are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*.

<http://www.jstor.org>

Marine Population Connectivity: Reconciling Large-Scale Dispersal and High Self-Retention

Kerry J. Nickols,^{1,*} J. Wilson White,² John L. Largier,^{1,3} and Brian Gaylord^{1,4}

1. Bodega Marine Laboratory, University of California, Davis, Bodega Bay, California 94923; 2. Department of Biology and Marine Biology, University of North Carolina, Wilmington, North Carolina 28403; 3. Department of Environmental Science and Policy, University of California, Davis, California 95616; 4. Department of Evolution and Ecology, University of California, Davis, California 95616

Submitted January 21, 2014; Accepted October 3, 2014; Electronically published January 13, 2015

Online enhancement: appendixes, zip file.

ABSTRACT: Predicting connectivity patterns in systems with fluid transport requires descriptions of the spatial distribution of propagules. In contrast to research on terrestrial seed dispersal, where much attention has focused on localized physical factors affecting dispersal, studies of oceanic propagule dispersal have often emphasized the role of large-scale factors. We link these two perspectives by exploring how propagule dispersal in the ocean is influenced by the “coastal boundary layer” (CBL), a region of reduced velocities near the shoreline that might substantially modify local-scale dispersal. We used a simple simulation model to demonstrate that accounting for the CBL markedly alters transport distances, the widths of dispersal distributions, and the fraction of larvae retained near their sites of origin (self-retention). Median dispersal distances were up to 59% shorter in simulations with a CBL than in those without. Self-retention of larvae increased by up to 3 orders of magnitude in the presence of CBLs, but only minor changes arose in the long-distance tails of the distributions, resulting in asymmetric, non-Gaussian kernels analogous to those quantified for terrestrial seed dispersal. Because successfully settling larvae are commonly those that remain close to shore and interact with the CBL, ignoring this pervasive oceanographic feature will substantially alter predictions of population self-persistence, estimates of connectivity, and outcomes of metapopulation analyses.

Keywords: larval dispersal, metapopulation, marine ecology, long-distance dispersal.

Introduction

Dispersal is critical to ecological connectivity and metapopulation dynamics for populations distributed among discrete habitat patches (Levin 1974; Roughgarden and Iwasa 1986; Hanski and Gilpin 1991; Sale et al. 2006; Beck-

man and Rogers 2013), and it can have strong bearing on species' responses to habitat destruction, extraction, and climate change (Botsford et al. 2001; Ewers and Didham 2006; Harley et al. 2006; Parmesan 2006; Watson et al. 2011). For species in which adults are largely sedentary, such as plants and benthic aquatic organisms, most dispersal occurs in early life stages: seeds, spores, or larvae. The small size of these propagules and their potential to travel long distances make it difficult to quantify dispersal empirically. Therefore, much research has been directed toward developing adequate theoretical representations of dispersal to understand its effects on population dynamics (e.g., Roughgarden et al. 1988; Kot et al. 1996; Gaylord and Gaines 2000; Clark et al. 2003; Levin et al. 2003; Katul et al. 2005; Byers and Pringle 2006; Gaylord et al. 2006; White et al. 2010a; Savage et al. 2011).

Robust descriptions of dispersal are essential to our understanding of metapopulation dynamics. In terrestrial systems, a commonly used approach is to fit a dispersal kernel to empirically measured dispersal distances (e.g., Clark et al. 1999; Bullock and Clarke 2000). Dispersal kernels are probability density functions that, when integrated over a specified range of distances, describe the probability of settlement within that distance band for propagules released from a single point. Terrestrial seed dispersal kernels generally indicate a high degree of local dispersal and also a relatively long tail that extends to much greater distances (Clark 1998; Clark et al. 1999; Cain et al. 2000; Nathan et al. 2002). For coastal benthic organisms that produce planktonic offspring, empirical measures of dispersal are substantially sparser. Dispersal kernels have typically been quantified for marine systems by use of circulation models or assumption of a dispersal kernel based on simple flow statistics (e.g., Largier 2003; Siegel et al. 2003, 2008; Cowen et al. 2006; White et al. 2010a). A few studies of algal spore dispersal have estimated kernels empirically (Anderson and North 1969), in some cases for

* Corresponding author. Present address: Division of Science and Environmental Policy, California State University, Monterey Bay, Seaside, California 93955; e-mail: knickols@csumb.edu.

Am. Nat. 2015. Vol. 185, pp. 196–211. © 2015 by The University of Chicago. 0003-0147/2015/18502-5523\$15.00. All rights reserved.

DOI: 10.1086/679503

comparison to physically modeled distributions (Gaylord et al. 2006).

In contrast to wind-mediated dispersal in terrestrial systems, where most seeds are deposited near their parents, ocean currents have an intrinsic potential to disperse larvae of benthic marine species great distances from their site of origin. This capacity emerges not only from the much greater density of water than of air, which lengthens the durations that even nonmotile propagules can remain suspended, but also from the precompetency period present in many larval strategies. The precompetency period is an obligate time window during which larvae develop and are incapable of settling (Jackson and Strathmann 1981). After this window, a larva enters a competency period, during which it can continue to disperse until suitable settlement habitat is found (Jackson and Strathmann 1981). Empirical studies confirm that larvae can be transported great distances offshore, particularly during time periods when the predominant current direction is offshore (Roughgarden et al. 1988). On the other hand, growing evidence also suggests that an appreciable subset of larvae remain relatively close to their site of origin (Swearer et al. 2002; Cowen and Sponaugle 2009). A clear understanding of the mechanisms responsible for such local retention, however, remains incomplete. Some species can alter their movement relative to surrounding water masses through behaviors such as selective tidal stream transport, ontogenetic migrations, and diel vertical swimming (e.g., De Veen 1978; Tankersley and Forward 1994; Criales et al. 2007; Miller and Morgan 2013). However, unexpectedly high retention has been found across species exhibiting a diverse spectrum of behavioral strategies, suggesting that important contributions from physical processes are a common factor.

The expanding power of numerical circulation models has made it increasingly possible to approximate the dispersal distributions of marine larvae in many case studies. However, most numerical models of larval transport use relatively coarse spatial resolution (≥ 1 km), making it impossible for these models to account for small-scale (~ 0.1 -km) physical processes operating near the larval release sites of coastal benthic species (e.g., Cowen et al. 2006; Watson et al. 2010). In this respect such models are incomplete. Even when empirical field data are used to estimate dispersal distances or augment numerical models, predictions may be impaired by the historical tendency to locate oceanographic instrumentation in deeper waters, typically several kilometers offshore, rather than near the site of larval release (Largier 2003; Siegel et al. 2003; Byers and Pringle 2006).

The consequent paucity of information about nearshore flows has crucial implications for understanding marine propagule transport, because there is a nearshore ocean-

ographic feature that can strongly affect dispersal kernels: the coastal boundary layer (CBL; Nickols et al. 2012). The CBL is the region of the coastal ocean extending from just outside the surf zone to a few kilometers offshore, within which velocities (and variations in velocity) are reduced because of frictional interactions with the shore (fig. 1; Nickols et al. 2012). The ubiquity of this marked decrease in velocities near shore makes the CBL a pervasive mechanism for decreasing scales of dispersal of coastal populations (Nickols et al. 2012). Larvae of coastal benthic species start and end their pelagic duration near the shore, which requires that they twice transit the CBL, at the least, and other work suggests that larvae remain near shore for much of their larval period (Borges et al. 2007; Morgan et al. 2009; Shanks and Shearman 2009). Therefore, the CBL likely defines a substantial portion of the larval experience.

Here, we explore effects of the CBL on patterns of larval dispersal, using a simple, conceptually tractable description of nearshore flow and underlying transport processes. This approach does not capture all physical factors in the coastal zone, but it incorporates—using as few model parameters as possible—the key factors germane to the question of whether nearshore drag might meaningfully influence dispersal, connectivity, and persistence of marine populations. In particular, we investigate how accounting for the CBL affects the shapes of dispersal distributions, through its influence on median transport distance, long-distance dispersal, and self-retention. We model the CBL on the basis of recent field measurements collected unusually close to shore (Nickols et al. 2012) and use our analyses to address the following questions: (1) How does accounting for the CBL alter dispersal distance and retention? (2) Does the importance of the CBL depend on life history (e.g., pelagic larval duration [PLD])? (3) Is the importance of the CBL likely to vary among locations (e.g.,

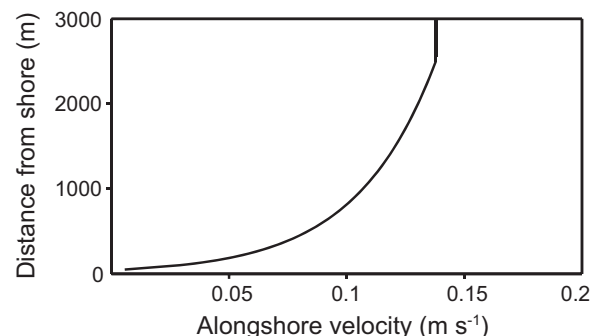


Figure 1: Schematic of a coastal boundary layer velocity gradient, with alongshore velocity plotted on the abscissa and distance from shore plotted on the ordinate.

because of the character of the velocity profile)? By addressing these questions, we reveal under what general conditions it is important to consider nearshore processes when attempting to understand patterns of larval supply and their effects on population dynamics of coastal organisms.

Methods

General Approach: Dispersal Kernels

Patterns of propagule movement are often modeled in terms of a dispersal kernel: a probability density function that when integrated over a specific range of distances describes the probability of settlement within that distance band for propagules released from a single point (fig. 2). Certain characteristics of kernels have particular significance for population dynamics: mean (or median) dispersal distance, long-distance dispersal (LDD), and self-retention (SR). The mean dispersal distance, defined here as the mean displacement of the dispersal kernel (e.g., Kaplan 2006), can be particularly important for estimating the likelihood of population persistence (Kaplan et al. 2009). For asymmetric kernels, where the mean dispersal distance is not equal to the median dispersal distance, the median is often a more informative statistic, describing the distance along the coast beyond which half of settled larvae have dispersed (fig. 2B; note that in cases with no net advection, the standard deviation of the kernel is often termed the “mean dispersal distance in either direction” [e.g., Botsford et al. 2001], but that is not the usage we follow here). Metrics of LDD, such as the ninety-fifth-percentile dispersal distance or the distances that extreme dispersers travel, are used to estimate rates of population spread (Clark 1998; Clark et al. 1999), invasion speed (Nathan 2006), and genetic connectivity (Cain et al. 2000; Kinlan and Gaines 2003). SR (also referred to as “local retention” by some authors; e.g., Botsford et al. 2009; Burgess et al. 2014) describes the proportion of larvae released at a location that settle near that same location (i.e., the area under the portion of the kernel corresponding to the natal habitat patch). The magnitude of SR within a patch relative to levels of mortality within the population determines whether that patch is self-persistent (i.e., the patch can persist in the absence of propagule input from other patches; Hastings and Botsford 2006; White et al. 2010a). These three characteristics (median dispersal distance, LDD, and SR) depend on the shape of the dispersal kernel, which may be strongly influenced by the environment.

In systems where dispersal is dominated by physical factors (e.g., wind [Greene and Johnson 1989; Vanschoenwinkel et al. 2008], rivers [Fonseca and Hart 2001; Pachep-

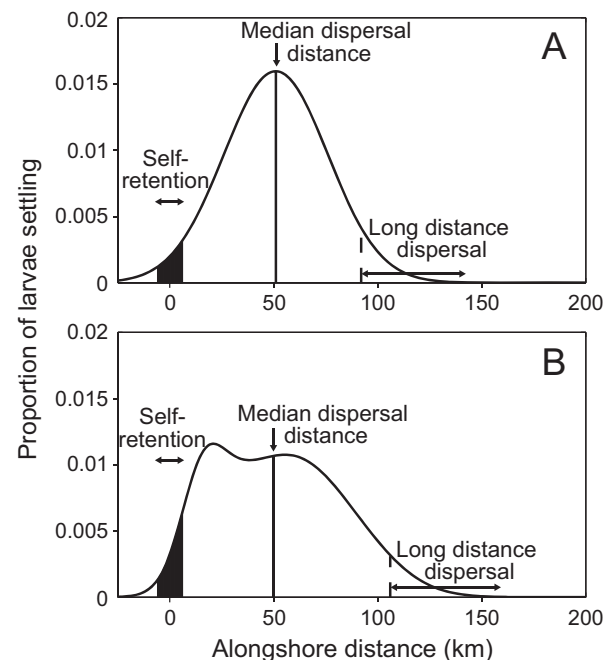


Figure 2: A, Schematic of a Gaussian larval dispersal kernel, the probability distribution function of settlement along a coast, with depictions of self-retention (defined here as the total fraction of released larvae from a site that settle within a 10-km length of coastline centered on the spawning site), median dispersal distance (equal to mean dispersal distance for Gaussian kernels), and long-distance dispersal (defined here as dispersal past the ninety-fifth-percentile dispersal distance, the distance beyond which only 5% of larvae settle, identified by the dashed vertical line). B, Schematic of a non-Gaussian larval dispersal kernel, with depictions as in A.

sky et al. 2005], and ocean currents [Scheltema 1986; Botsford et al. 1994]), the form of the dispersal kernel is dictated by fluid velocity and mixing parameters, together with attributes of the propagules (e.g., duration of the dispersal period). In marine systems, simple abstractions of ocean transport predict that, for larvae with a fixed larval duration, the kernel should follow approximately a Gaussian distribution (Okubo 1971; Largier 2003; Siegel et al. 2003), with consistent relationships among the mean (=median) and standard deviation, LDD, and SR (fig. 2A). Consequently, efforts have often focused on estimating the mean or median and standard deviation of dispersal kernels (e.g., Kinlan and Gaines 2003), and many models of marine metapopulations express dispersal in terms of the mean or median dispersal distance (e.g., Botsford et al. 2001; Gaines et al. 2003; Kaplan 2006; Kaplan et al. 2009; White et al. 2010a). However, recent evidence suggests that in many systems with fluid dispersal, kernels are asymmetric and non-Gaussian (Gaylord et al. 2002, 2006; Aiken et al. 2007; Chiswell 2012; fig. 2B). In these

Table 1: Flow parameters for each site

Site	CBL width (m)	Maximum velocity U (m s^{-1})	Maximum diffusivity K ($\text{m}^2 \text{s}^{-1}$)
Mohawk	915	.165	13.5
Pajaro	3,335	.101	18.0
Huntington Beach	5,555	.169	63.0
Hopkins	700	.0419	4.13
Terrace Point	1,595	.103	13.4

Note: For flow scenarios with a coastal boundary layer (CBL), maximum velocity and diffusivity values apply to the offshore edge of the CBL ($y = \text{CBL width}$). For the no-CBL flow scenario, these values apply to a uniform flow field (constant U and constant K).

circumstances, SR and LDD may be more difficult to predict and less closely related to the median dispersal distance than Gaussian kernels.

Estimates of dispersal kernels in coastal marine systems often use velocity measurements from current meters (e.g., Gaines et al. 2003; Largier 2003), and in many cases they include information from only one site. Because of operational constraints, current meters are rarely found inside the 30-m isobath and are unable to characterize flows within the CBL (but see Largier 2003). Therefore, we used a simple theoretical approach to explore the effects of the CBL on median dispersal distance, LDD, and SR. We analyzed dispersal kernels resulting from a two-dimensional plan-view model of the ocean along a coastline with an idealized flow field under different flow scenarios and for different bathymetric slopes. We released particles into the simulated flow fields and tracked their movement through time to generate projected dispersal kernels of settled particles.

Particle Simulation and Dispersal Kernel Calculation

We modeled dispersal of benthic species that occupy habitat in shallow waters along a linear coastline of length 750 km that is partitioned numerically into identical cells extending 1 km along shore. We released 10^4 model propagules from within a single 1-km cell (situated in the center of the coastline) at randomly selected cross-shore locations uniformly distributed between the 5- and 10-m isobaths (corresponding to 115–555 m offshore, depending on the bathymetric slope of the modeled site). Model propagules were transported through the coastal ocean during a specified “precompetency window” (Strathmann 1985), a time period after release during which larvae are developmentally incapable of settling. Once this window passed, propagules entered a “competency window,” during which they could settle if provided with suitable habitat. Although few empirical measurements of precompetency and competency windows are available, evidence suggests that the competency window is roughly equal to or greater than

the precompetency window (Jackson and Strathmann 1981). We therefore used the most straightforward representation of this life-history attribute, setting the durations of the precompetency and competency windows equal (see also Gaylord and Gaines 2000). Propagules were counted as “settled” if they moved inshore of the 10-m isobath at any point during their competency window. This rule effectively assumes that larvae close to shore either settle immediately, continue toward the coastline, or swim toward settlement habitat once inside the 10-m isobath. We simulated dispersal for several different flow scenarios, detailed below, over a range of precompetency and competency windows (incremented from 2 to 20 days in 2-day intervals). Because larvae can exit the water column at any point during their competency period, the realized PLDs of different larvae can vary within the bounds of the window duration. In presenting our results, we characterized simulations according to the midpoint of the competency window. For example, model runs with 2-day precompetency and competency windows are referred to as a 3-day PLD, and 20-day precompetency and competency windows are referred to as a 30-day PLD. To focus exclusively on the implications of spatial variation in transport associated with the CBL, we did not include larval mortality in the model.

We simulated propagule transport by using a two-dimensional Lagrangian random-walk particle-tracking model described in White et al. (2010*b*; see app. A for equations; apps. A and B available online; the model code can be found in a zip file, available online). The White et al. (2010*b*) model was modified to account for the cross-shore structure in alongshore velocity and diffusivity profiles described previously by Nickols et al. (2012) from measurements within the CBL at five sites along the coast of California (table 1). At each model time step ($\Delta t = 30$ s; see table 2 for list of symbols), particle positions in the alongshore (X) and cross-shore (Y) dimensions were updated according to advective and diffusive displacements. We note that while other model implementations are possible, many depend on greater numbers of parameters that

Table 2: List of symbols used in the article

Symbol	Definition
c	Empirically derived constant from nearshore velocity measurements
d	Empirically derived constant from nearshore velocity measurements
K	Eddy diffusivity
K_{\max}	Eddy diffusivity at the offshore edge of the coastal boundary layer (CBL)
L	Length scale
L_{CBL}	Width of the CBL
m	Empirically derived constant from nearshore velocity measurements
t	Timescale
T_{CBL}	Lower bound on average time to diffuse through CBL
T_{PLD}	Pelagic larval duration
U	Depth- and time-averaged alongshore velocity
V	Depth- and time-averaged cross-shore velocity
Δt	Model time step
x	Alongshore position
y	Cross-shore position

are often poorly resolved in very nearshore areas, making them less suitable for our goal of exploring in as general a way as possible the effects of the CBL. In particular, “random-flight” approaches (see, e.g., Siegel et al. 2003) that have seen increased attention in recent years require information about decorrelation timescales. Data appropriate for assessing these parameters are sparse in areas immediately adjacent to the shore. Although beyond the scope of our study, it can also be shown that results of random-flight models approach those of random walks when predictions are made over durations substantially in excess of the decorrelation timescale (Siegel et al. 2003); such longer-term estimates are the focus of our study.

Nickols et al. (2012) showed that mean alongshore velocity profiles within CBLs commonly adhere to a simple logarithmic form,

$$U(y) = m \ln y - d, \quad (1)$$

where U is the depth- and time-averaged alongshore velocity, y is distance from shore, and the constants m and d are empirically determined from in situ measurements (fig. 3A). We used this simple relationship to model alongshore velocities, with the condition that velocity $U(y)$ was set equal to 0 for all distances y for which $m \ln y$ was less than d (i.e., $U(y)$ would otherwise be <0). This condition describes the region immediately adjacent to the shore that is typically dominated by surf-zone processes and/or rock outcrops, where the CBL profile no longer holds (Nickols et al. 2012) and retention can be substantial (MacMahan et al. 2010). For all sites, the small regions corresponding

to $m \ln y < d$ were inshore of particle release locations and model settlement habitat.

Mean velocity in the cross-shore direction, V , was set to 0, as coastal velocity measurements were polarized in the alongshore direction and approached 0 in the cross-shore direction over periods of days to weeks (Nickols et al. 2012). The effects of flows that vary on time and space

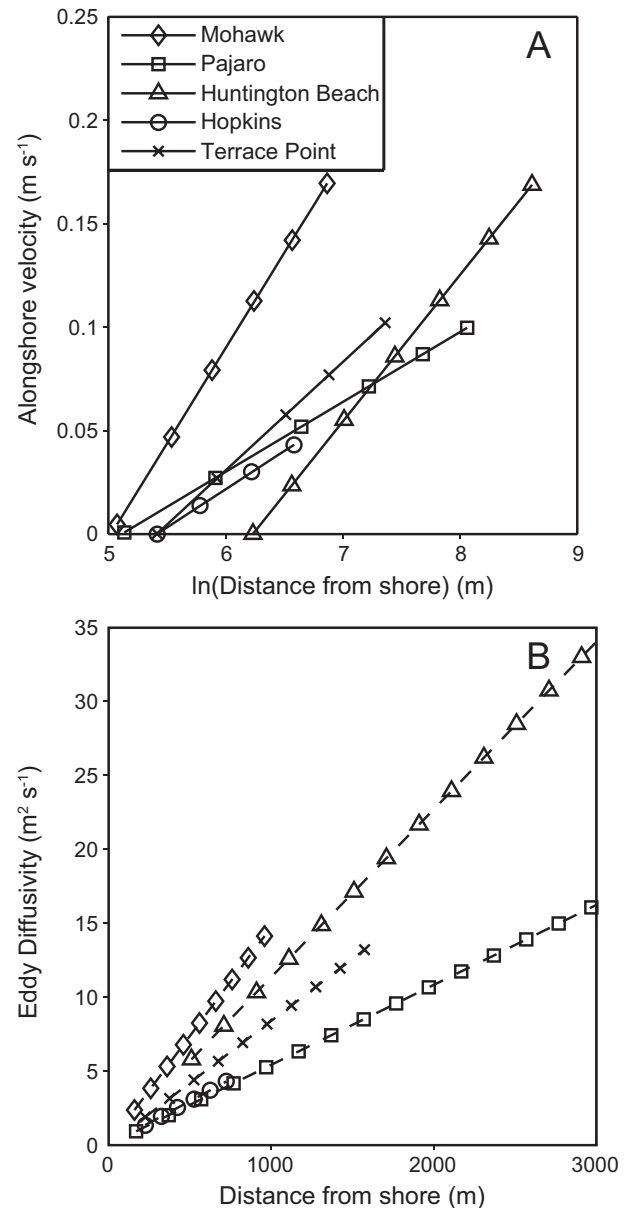


Figure 3: Alongshore velocity (A) and eddy diffusivity (B) profiles from five coastal sites. Data are from Nickols et al. (2012). Depth- and weekly averaged velocities are plotted according to the natural logarithm of distance from shore (A), and eddy diffusivity is plotted against distance on a linear scale (B).

scales smaller than the weekly averaged advective velocities U and V were approximated via the diffusive component of the model.

We modeled horizontal turbulent and tidal motions in terms of an “eddy diffusivity,” K (Taylor 1922; Okubo 1971; Largier 2003), that increased linearly with distance from shore because of the effects of the CBL (Nickols et al. 2012; fig. 3B):

$$K = cy, \quad (2)$$

where c is a constant derived from empirical measurements of velocity presented in Nickols et al. (2012). We assumed that K was equal in the cross- and alongshore directions.

Previous studies indicate that the offshore edge of the CBL is generally near the 30-m isobath (Murthy and Csanady 1981; Rao and Murthy 2001). Therefore, we extended our alongshore velocity profiles to the 30-m isobath, beyond which velocities and diffusivities were assumed to become uniform. For the five sites described by Nickols et al. (2012), the 30-m isobath corresponded to 700–5,555 m from shore, depending on the bathymetric slope of each site. The mean alongshore velocity, U , at distances just outside the CBL was between 0.0419 and 0.169 m s⁻¹, while K was between 4.13 and 63.0 m² s⁻¹ at the same positions (table 1; data from Nickols et al. 2012). These values of K are consistent with other published values of K near the 30-m isobath in coastal California, which range from 10 to 60 m² s⁻¹ (Davis 1985; List et al. 1990; Drake and Edwards 2009; Romero et al. 2013). Together, the profiles of U and K at each of the sites describe five different physical settings with which to test the effects of the CBL on dispersal.

Using the above framework, we compared the dispersal kernels estimated from simulations that included a CBL to kernels generated from simulations without a CBL (hereafter referred to as “CBL” and “no-CBL” simulations, respectively). Our null dispersal model without a CBL contained a uniform flow field parameterized by the velocity and diffusivity found at the offshore edge of the CBL, on the 30-m isobath.

Model Analysis

For each model case (characterized by PLD, bathymetry, flow strength, and CBL geometry, including the presence or absence of a CBL), we calculated the median alongshore dispersal distance (the alongshore distance from the point of origin of the larval particles to the median of the settlement distribution) and the standard deviation and skewness of the dispersal kernel. To quantify LDD, we calculated the ninety-fifth-percentile alongshore displacement (i.e., the alongshore distance beyond which only 5% of the larval particles settled). For SR, we calculated the pro-

portion of released particles that settled within a 10-km length of coastline centered on the release point (a common size for a site considered in ocean circulation models; e.g., Mitarai et al. 2009; Watson et al. 2010). For median alongshore dispersal distance, standard deviation and skewness of the dispersal kernel, and LDD, we calculated the ratio of each metric’s value in simulations that included a CBL to its value arising in the absence of a CBL, producing a dimensionless index of the effect of the CBL on dispersal predictions.

We plotted these ratios against the ratio of two time-scales: the pelagic larval duration, T_{PLD} , and the timescale of larval residence within the CBL, T_{CBL} . By definition, eddy diffusivity, K , is proportional to L^2/t , where L is a length scale and t is a timescale (Largier 2003). Thus, the timescale associated with a given diffusivity is proportional to L^2/K . This relationship provides a conservative estimate of the residence time in the CBL (erring on the side of brevity) based on the maximum value of K at the offshore edge of the CBL, K_{max} :

$$T_{\text{CBL}} = \frac{L_{\text{CBL}}^2}{K_{\text{max}}}, \quad (3)$$

where L_{CBL} is the cross-shore width of the CBL.

Given that T_{CBL} is based on K_{max} , a flow field that includes a CBL would increase the time larvae spend in the CBL as a result of lower diffusivities found closer to shore. This increase in residence within the CBL should be most important when $T_{\text{PLD}} \leq T_{\text{CBL}}$, in which case the lower velocities and diffusivities found near shore will pertain throughout the larval life span. For larvae with $T_{\text{PLD}} \gg T_{\text{CBL}}$, the time during which larvae develop within the CBL is typically a small fraction of the total time spent in the plankton, and we expected that the inclusion of a CBL in the model would likely affect only a small fraction of the dispersal trajectory.

Results

Dispersal Trajectories and Kernels

Model larvae subjected to a flow field with a CBL spent more time closer to shore than larvae dispersing in a flow field lacking a CBL. This effect was evident for all sites regardless of CBL width (fig. 4). Larvae in both flow scenarios were swept downstream from the release location; however, lower velocities near the coast with a CBL decreased rates of transport of larvae away from their release location. These larvae also experienced lower diffusivities, requiring more time for larvae to spread in either the cross- or alongshore direction than with higher diffusivities farther offshore. Therefore, it took larvae in a flow field with a CBL longer to “escape” past the 30-m isobath than larvae

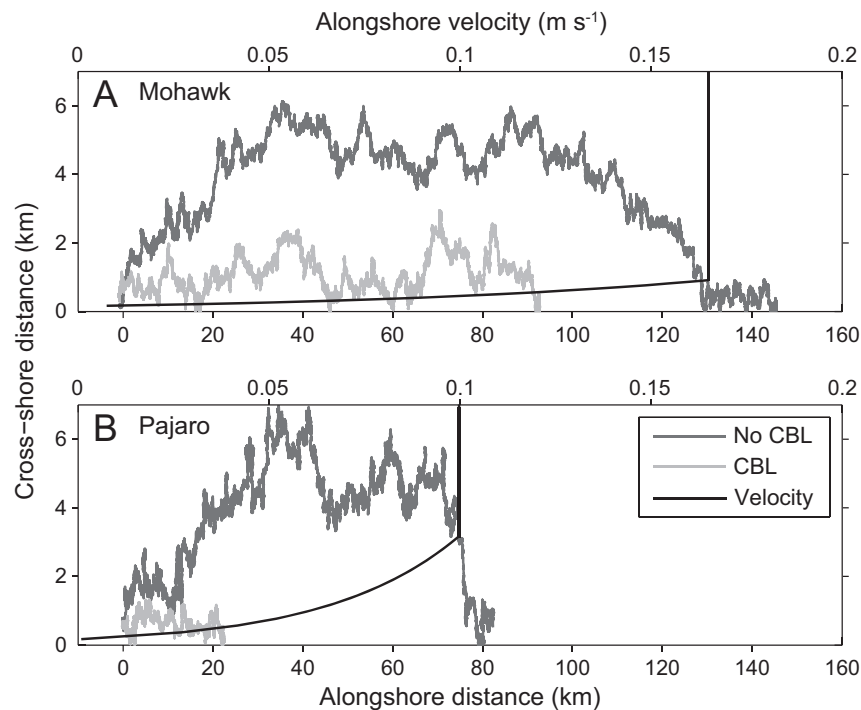


Figure 4: Sample dispersal trajectories for model larvae with and without a coastal boundary layer (CBL) for flow fields representing Mohawk (A) and Pajaro (B), with the accompanying CBL velocity profiles for these sites (black line; top axis). Depicted trajectories are for a pelagic larval duration of 15 days.

in a flow field with constant velocity and diffusivity (fig. 4).

Kernels resulting from either model scenario (i.e., with a CBL or not) were non-Gaussian (fig. 5; see Gaussian distribution with same median and standard deviation as the no-CBL kernel). The modes of the kernels largely represented the effects of the precompetency window: larvae were swept downstream until they were developmentally competent, after which all larvae near suitable habitat settled immediately. Competent larvae that had not settled continued to be carried downstream, and some were mixed into adult habitat while others were mixed offshore, resulting in lower probabilities of settlement in the rightward (downcurrent) tails of the distributions. For the subset of flow fields that included CBLs, dispersal kernels were centered closer to the release location and were broader than kernels produced by flow fields without CBLs (fig. 5). These results were consistent across sites, although the degree of reduction of median dispersal distance with a CBL varied by site according to the details of the CBL profiles enumerated in the next subsection.

Including the CBL had consequences for the predictions of the number of settlers, in addition to affecting the distributional pattern of settlement. Model runs that included the CBL resulted in 8% less settlement for all sites and

PLDs (fig. 6) because of low values of eddy diffusivity near the coast. The no-CBL case was parameterized with a uniform value of diffusivity representative of more offshore conditions, which yields greater cross-shore movements in a given time step. With a CBL, lower diffusivities close to shore produced smaller cross-shore movements, requiring a larger number of time steps to come back to shore than were required for the corresponding no-CBL scenario with a larger, constant diffusivity. Decreasing the model time step did not affect these results.

Median and Moments of the Dispersal Kernels

The CBL reduced median dispersal distance for all sites and PLDs (fig. 7A). This reduction was greatest at Huntington Beach, with ratios of CBL to no-CBL dispersal distances ranging from 0.41 to 0.81 (decreased dispersal distance of 19%–59%). The least reduction in median dispersal distance arose at Mohawk, with ratios of median dispersal distance from 0.72 to 0.93 (decreased dispersal distance of 7%–28%). Shorter PLDs led to larger deviations from the no-CBL kernels. As the PLD increased, dispersal distances with a CBL began to converge toward the median dispersal distance without a CBL, evidenced by the asymptote in figure 7A. However, the ratio of this

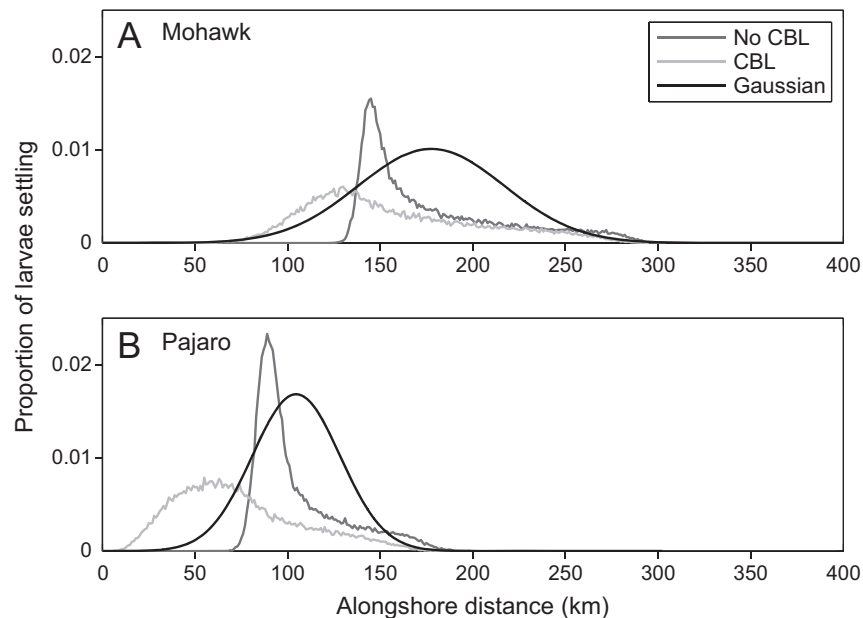


Figure 5: Larval dispersal kernels resulting from model runs with and without a coastal boundary layer (CBL) for flow fields representing Mohawk (A) and Pajaro (B) for a pelagic larval duration of 15 days. A Gaussian kernel with median and standard deviation equal to those calculated from the dispersal kernel without a CBL is shown in black for reference.

statistic never equaled 1. A ratio of T_{PLD} to T_{CBL} of 10 was required before all sites had a displacement ratio greater than 0.8. Even for the maximum timescale ratio used in the study, when T_{PLD} was more than 40 times T_{CBL} (fig. 7A, Mohawk [diamonds]), the ratio of median dispersal distance was still less than 0.95, with a reduction in median dispersal distance of 7%. When $T_{PLD} \sim T_{CBL}$, median dispersal distance was reduced by $\sim 50\%$.

The standard deviation of kernels (the square root of the second central moment of the distribution) was higher for dispersal scenarios with CBLs for all sites and PLDs: that is, the CBL/no-CBL ratios of standard deviation were always above 1 (fig. 7B). The presence of a CBL resulted in a broader range of dispersal distances, with standard deviations 9%–47% higher than those without CBLs. The standard deviation of kernels with CBLs was highest for situations where T_{PLD} was about 2 times T_{CBL} . Standard deviations with and without a CBL became more similar as T_{PLD} increased to 10 times T_{CBL} .

The increase in standard deviation with a CBL was due to the interaction of cross-shore mixing with cross-shore gradients in alongshore velocity and the larval precompetency period. Velocity gradients (“shear”) act to spread distributions of larvae in the alongshore direction, a process known as “shear dispersion” (Bowden 1965). Without a CBL, the alongshore velocity was the same for all larvae irrespective of cross-shore position, so that any differences

in their alongshore position were due solely to the random walk in the model. Thus, in the no-CBL case, at the end of the precompetency window when larvae began to settle, their initial distribution was narrow, with little spread

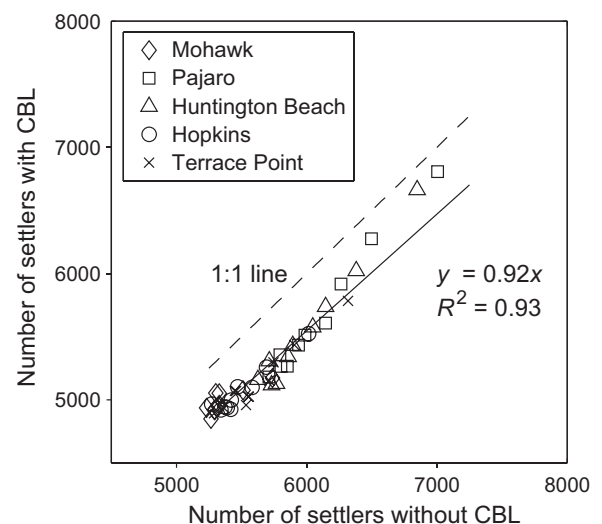


Figure 6: Total number of settling particles from model runs without a coastal boundary layer (CBL), plotted against the total number of settlers resulting from model runs with a CBL, for all sites and pelagic larval durations. A dashed 1 : 1 line is shown for reference.

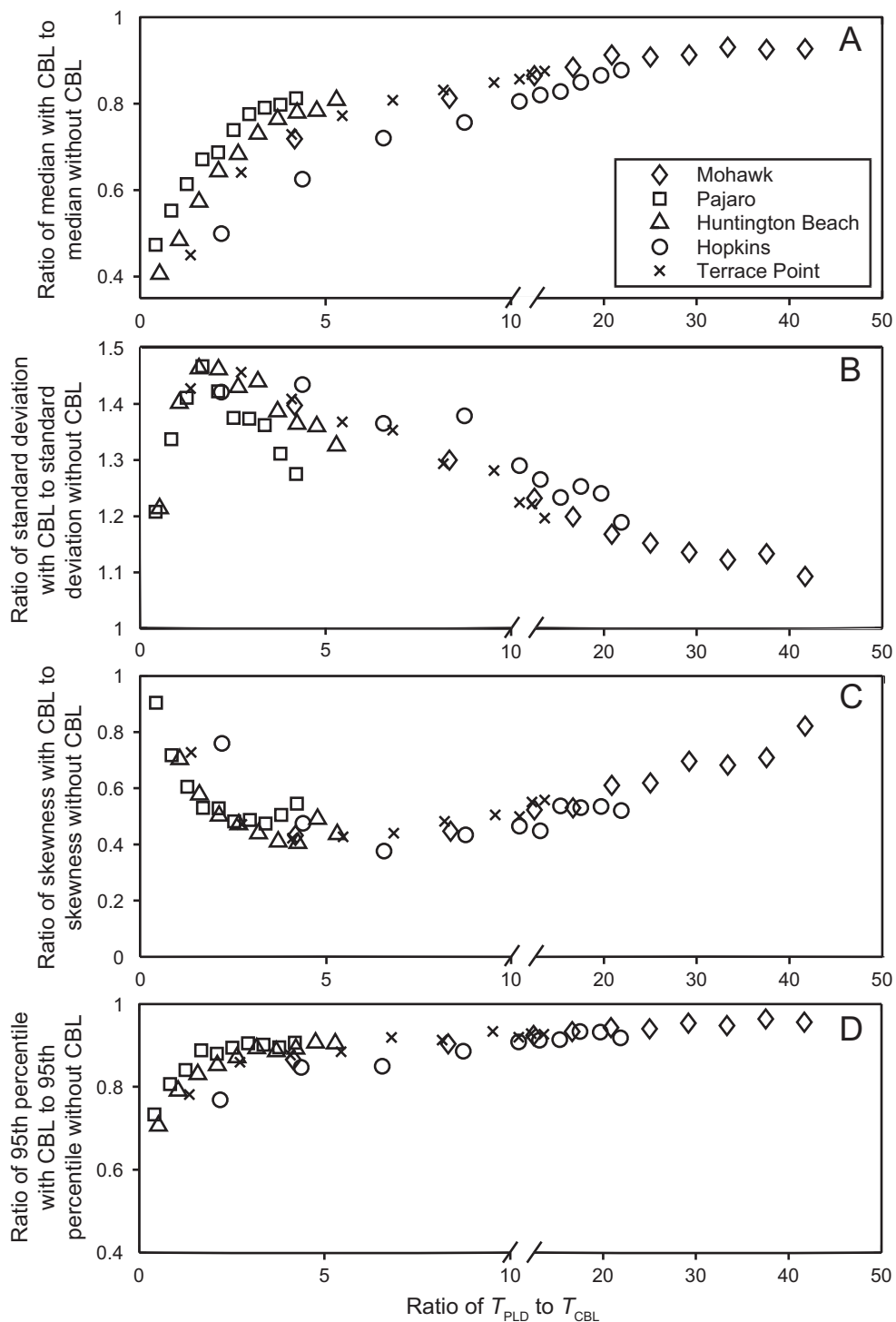


Figure 7: Ratio of pelagic larval duration time (T_{PLD}) to the timescale of the coastal boundary layer (T_{CBL}), plotted against the ratio of median dispersal distance (A), standard deviation (B), skewness (C), and long-distance dispersal (D) calculated from model runs with a CBL, relative to no-CBL values. Model runs are for all sites and PLDs. Note the break in the axis at a ratio of T_{PLD} to T_{CBL} of 10.

around the mean displacement. In contrast, with a CBL velocity gradient, larvae were advected at different rates downstream, depending on their cross-shore position—and some moved just a short distance from the release site. At the end of the precompetency window, the resultant distribution of competent larvae therefore exhibited more spread than the no-CBL case (higher standard deviation), because of shear dispersion. To determine the contribution of shear dispersion to the increased along-shore spread, we conducted additional model runs for a case in which CBL velocity gradients were combined with a constant diffusivity (as in the no-CBL case). Shear dispersion increased the standard deviation of dispersal kernels by 6%–36% above the no-CBL scenario, and adding a diffusivity gradient led to an additional increase of up to 20% of the no-CBL standard deviation (see app. B; fig. B1).

The CBL and no-CBL kernels (fig. 5) differed not just in median and standard deviation but also in skewness (the third standardized moment). Dispersal kernels from model runs without a CBL were up to 60% more skewed than kernels from model runs with a CBL (fig. 7C). The skewed nature of the no-CBL kernels indicated that dispersal was asymmetric, with the median located upcurrent of the mean (positive skewness; leftward in the figure). The lower values of skewness in the kernels with a CBL indicated a more symmetric distribution, with the mean and median displacements closer together, because the slower velocities in the CBL bolstered the upcurrent tail of the kernel, as compared to the no-CBL kernel.

Long-Distance Dispersal

Inclusion of a CBL decreased long-distance dispersal (LDD) for all sites and PLDs, although this effect was weak and much less pronounced than the decrease in median dispersal distance (fig. 7D). For low ratios of T_{PLD} to T_{CBL} , LDD was reduced by less than 30%. As T_{PLD} increased, this reduction decreased to less than 5% at Mohawk, the site where LDD was least affected (fig. 7D, diamonds). All sites exhibited a displacement ratio greater than 0.9, for a ratio of T_{PLD} to T_{CBL} of 10, corresponding to differences in LDD of less than 10%. Although reductions were still important for low ratios of T_{PLD} to T_{CBL} , the effect of the CBL on LDD showed decreased importance, compared to the effect of the CBL on median displacement.

Self-Retention

Despite a reduction in the total number of settling larvae (fig. 6), the CBL drastically increased self-retention. At least one released larva had to settle within the 10-km length of coastline centered on the release site for self-

retention to be registered in our model, resulting in a minimum self-retention probability of 10^{-4} . Without a CBL, only one site (Hopkins) reached this level of self-retention, and only for the lowest PLD (3 days; fig. 8). Including a CBL in the dispersal model increased self-retention by up to 3 orders of magnitude and led to predictions of measurable self-retention for all sites. Hopkins had the highest amount of self-retention (38% and 10% for PLDs of 3 and 6 days, respectively), with low but measurable self-retention for PLDs of up to 21 days when a CBL was represented in the model.

Discussion

The coastal boundary layer (CBL) is a prominent feature in marine systems, and by including the CBL in descriptions of dispersal for species with precompetency windows, we can understand that self-persistence is not as difficult to achieve as was previously thought. Our analysis shows that the failure to account for nearshore processes such as the CBL in dispersal models may overestimate population connectivity and underestimate self-retention and may therefore have a profound effect on predictions of population dynamics. Our results were consistent across a range of life histories (modeled by different pelagic larval durations [PLDs]) and coastal locations (represented by different sites), with the largest effects of the CBL seen for short PLDs and sites with broad CBLs. The net outcome, therefore, is one where a largely overlooked interaction between a pervasive physical mechanism (the CBL) and a pervasive life-history strategy (pelagic larval phases) substantially decouples self-retention and LDD, with tremendous increases in self-retention but minimal decreases in LDD. Although these trends are examined here in a stylized model construct, we emphasize that they should apply in computationally intensive frameworks if sufficiently fine resolution is employed (i.e., using highly nested versions of the Regional Ocean Modeling System; see e.g., Romero et al. 2013).

The Ubiquity of the CBL in Marine Systems

Dispersal trajectories shown here indicate that in the presence of a CBL, simulated larvae spent more time near shore than they do under uniform flow conditions (fig. 4). The ecological consequences of this effect depend on the relative duration of the larval period. Taking L_{CBL} (the width of the CBL) to be 2 km, an average of the CBL widths used in this study, and employing a rough estimate of eddy diffusivity, $K_{\text{max}} = 10 \text{ m}^2 \text{ s}^{-1}$, one obtains a T_{CBL} (the time scale of the CBL) of ~ 5 days. Given that a successful recruit moving out of the CBL must transit back through it to recruit to adult habitat, larvae with PLDs on

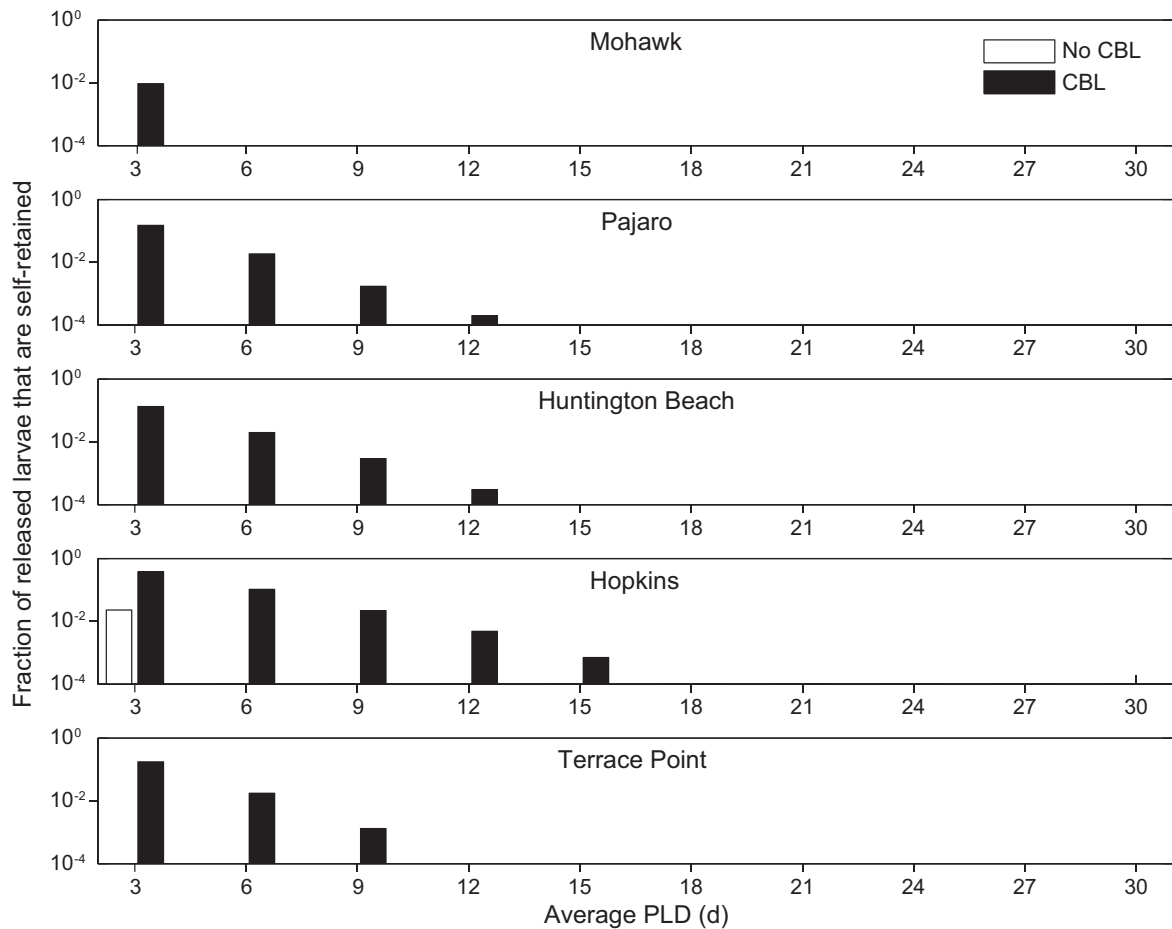


Figure 8: Fraction of released larvae that settled within a 10-km length of coastline centered on the release site (self-retention), in scenarios without a coastal boundary layer (CBL; open bars) and with a CBL (filled bars) for all sites and pelagic larval durations. The minimum self-retention measurable was 10^{-4} , as at least one settler out of 10^4 released larvae must return.

the order of 10 days are likely to spend their entire pelagic period in the CBL. Even larvae with PLDs several times longer will spend a significant time in the CBL and experience substantially reduced dispersal.

The results we predict for larvae that spend an appreciable time in the CBL are consistent with those of recent studies indicating that retention in nearshore waters is common across taxa and behavioral strategies (Morgan et al. 2009; Shanks and Shearman 2009). Because our simulations used passive particles, elaborate behavior may not be necessary to explain high nearshore retention. For those organisms that do utilize behavioral strategies, some may take advantage of the decreased velocity and diffusivity in the CBL and increase retention beyond what our model predicts. Indeed, a number of studies now suggest that larvae respond to various oceanographic and hydrodynamic signals, including some that operate at larger scales of habitat (Fuchs et al. 2010; Gaylord et al. 2013).

Including a CBL in the model affected dispersal kernels across sites with different physical characteristics (e.g., velocity gradients, bathymetry, topography), which may facilitate predictions of CBL effects for sites beyond those in this study. The velocity gradient (dU/dy) quantifies the degree of velocity attenuation over the CBL width and establishes the extent to which lower velocities dominate the inner portion of the CBL, decreasing alongshore transport. Because the width of the CBL, L_{max} , determines the denominator of the velocity gradient and its square is the numerator of the expression for T_{CBL} (eq. [3]), the velocity gradient has a nonlinear, inverse relationship with T_{CBL} (fig. 9). At sites with gentle velocity gradients (i.e., Huntington Beach and Pajaro), T_{CBL} was large, and these sites exhibited the greatest reduction in median dispersal distance for a given PLD and the greatest increase in predicted self-retention from inclusion of the CBL (figs. 7A, 8). The site with the steepest velocity gradient (Mohawk)

had a narrow CBL, with high velocities at the offshore edge and $T_{\text{CBL}} < 1$ day. This site exhibited the least reduction in median dispersal distance from inclusion of the CBL (fig. 7A) and the least amount of self-retention (fig. 8). Estimates of the steepness of velocity gradients should thus provide a rough metric for the effect of the CBL on dispersal kernels at additional sites.

Habitats with greater three-dimensional complexity may experience greater decreases in nearshore velocity, leading to yet higher retention of larvae. For example, flow is attenuated within seagrass and kelp forest habitats (Fonseca et al. 1982; Gaylord et al. 2007, 2012), and the structure associated with coral reefs can promote slower flows and decrease transport of larvae (Andutta et al. 2012). In locations with complex coastal topographic features, local geography contributes greatly to dispersal patterns (Adams et al. 2014); such areas of “sticky water” (Wolanski 1994) will tend to enhance self-retention, while the subset of larvae that are mixed out of such habitats and advected away may still experience long-distance dispersal.

Precompetency: A Challenge for Self-Persistence

Unlike terrestrial seeds and algal propagules, larvae have a precompetency period that intrinsically makes self-retention less likely. Larvae may remain near the shore initially after release, but with time larvae are diffused and advected away from shoreline habitat, and the likelihood of encountering settlement habitat declines steeply (Gaylord and Gaines 2000). As the precompetency window increases, the probability of larval settlement decreases (Siegel et al. 2003), and larvae have the potential to be transported quite far before they are competent to settle (Jackson and Strathmann 1981; Palmer and Strathmann 1981), creating a perceived challenge for self-persistence of shoreline populations.

The probability of self-persistence is greatly enhanced when larvae experience slow velocities during the precompetency window. Previous population models of marine systems have demonstrated that above certain velocities (and depending on various demographic parameters), population persistence may not be possible (Possingham and Roughgarden 1990; Hill 1991; Gaines et al. 2003; Byers and Pringle 2006). As the duration of larval precompetency lengthens, populations can persist only if experiencing relatively slow mean currents, compared with the intensity of mixing motions (Gaylord and Gaines 2000). The presence of velocity gradients within the CBL and exposure of larvae to slower velocities near shore reduce the rate of larval transport and facilitate population persistence even in high-flow environments (see also Possingham and Roughgarden 1990 for an early phenomenological exploration).

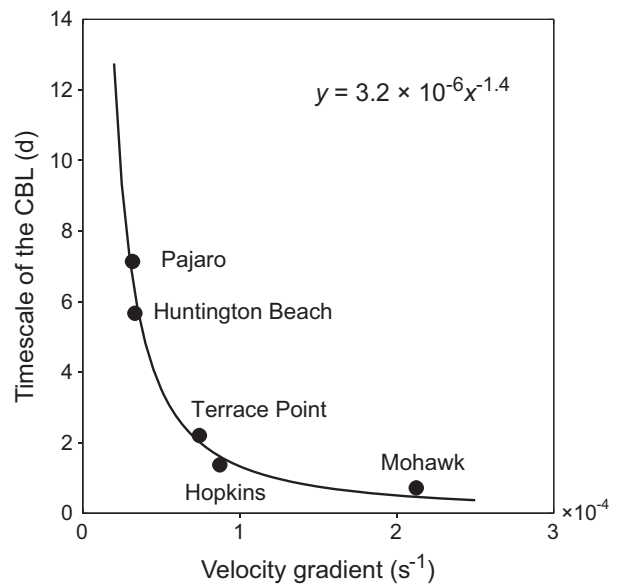


Figure 9: Velocity gradient (change in alongshore velocity over the width of the coastal boundary layer [CBL]), plotted against the timescale of the CBL (T_{CBL}) for all five sites. An increase in the velocity gradient is associated with a decrease in T_{CBL} .

While decreased transport during the precompetency window can promote self-persistence, those larvae that do escape the CBL will have difficulty returning to shore. This was apparent in our result of decreased settlement percentages under CBL conditions: with a CBL, larvae are swept offshore less frequently, but those that do move offshore are less likely to return to the nearshore environment because of weaker cross-shore mixing in the CBL. In addition, while mortality was not included in this model, as the time to return to the coast increases, there should be a concomitant increase in larval exposure to other sources of mortality (Possingham and Roughgarden 1990), which could further reduce overall settlement (although recent evidence suggests that larval mortality may also be lower than previously thought; White et al. 2014).

The CBL and Population Dynamics

For decades, ecologists have explored the evidence for and consequences of “open” versus “closed” populations and the role of the physical environment in population connectivity (Caley et al. 1996; Levin 2006). It is important to consider, however, that dispersal produces a distribution of outcomes, with both long-distance dispersal and retention; thus, populations can simultaneously self-seed and supply propagules to other habitats. The CBL is a physical mechanism within the continuum of processes that influence the degree to which populations are more open or

closed. For sites with gentle velocity gradients and broad CBLs (as in bays), we expect that larvae will be more likely to exhibit self-retention and that populations will be more likely to be self-persistent. For locations with steep velocity gradients and narrow CBLs (as at headlands), populations should retain a smaller proportion of propagules, instead largely serving as a source of propagules for other sites and relying on propagules from other populations within the network to persist (Hastings and Botsford 2006; White et al. 2010a; Burgess et al. 2014).

By not including the CBL in the estimation of dispersal kernels, we may be overestimating the spatial scale of demographic connectivity of nearshore organisms and underestimating self-persistence. The influence of variation in local demographic parameters (e.g., adult survival) on metapopulation dynamics has been shown to increase as local retention increases and habitat patches become less connected (Figueira 2009). With higher than expected self-retention, the importance of individual populations in the persistence of the overall metapopulation will increase (Hastings and Botsford 2006); metapopulations may also become more “closed” and less resilient to localized disturbances (Pinsky et al. 2012).

Asymmetric Dispersal Kernels across Systems

Missing from many previous descriptions of marine dispersal is the importance of localized processes that enhance self-retention. The CBL represents an important new step in understanding local transport processes that at least partially explain why more larvae may stay closer to their site of origin than previously thought. The CBL is a mechanism that reconciles observations that populations may have a substantial amount of self-retention yet still exhibit very long LDD, leading to asymmetric non-Gaussian kernels similar to mechanistic representations of seed and spore dispersal, whereby considerable dispersal is local yet some propagules are carried long distances (Bullock and Clarke 2000; Gaylord et al. 2002, 2006; Katul et al. 2005).

We can draw similarities between wind-mediated seed dispersal and dispersal in coastal systems. The part of the kernel adjacent to the parent is influenced by local processes: vertical movement of seeds is affected by up- and downdrafts during their horizontal advection away from a parent plant, and the cross-shore movement of larvae is affected by diffusive eddies during their transport within the CBL. In the former case, propagules that escape outside of the canopy (“seed uplift” phenomena) contribute to an asymmetric kernel with an extended tail, just as do propagules that escape the CBL within an ocean setting. In both systems, the resulting kernels simultaneously contain elements of local return and LDD. The potential for high levels of self-retention has long been recognized in ter-

restrial systems (Howe and Smallwood 1982), and recent advances in describing dispersal kernels were directed at mechanistic understanding of LDD (Clark et al. 1999; Levin et al. 2003; Katul et al. 2005; Nathan 2006). The situation has in some ways been the opposite in marine systems, where the challenge has been in reconciling the recognized, large potential for LDD with growing evidence that self-recruitment is common (e.g., Swearer et al. 2002, Hogan et al. 2011).

Clearly, there is still much work to do to rigorously quantify dispersal kernels both on land and in the sea (Zimmer et al. 2009; Hrycik et al. 2013). The field of metapopulation ecology has already benefited substantially from our growing knowledge of dispersal processes, and this trend is likely to continue. For example, inclusion of adult fish movement in addition to larval dispersal has substantially changed predictions of metapopulation dynamics and informed management decisions (Moffitt et al. 2009; White et al. 2013). Asymmetric dispersal is apparent in many contexts, from topographic dispersal barriers to directional fluid flow, and analyzing its effects has advanced our understanding of metapopulation persistence (Bode et al. 2008; Vuilleumier et al. 2010). As we continue to develop and expand these lines of inquiry in marine studies, it will be important to recognize the pervasiveness of the CBL across time and space and to account more fully for its potential for far-reaching demographic consequences.

Acknowledgments

We thank L. W. Botsford for computing resources and helpful feedback on the manuscript. Additional feedback on the manuscript resulted from a workshop at Hopkins Marine Station (led by S. R. Palumbi) and two anonymous reviewers. This work was funded by National Science Foundation grants OCE-927255, OCE-1065990, and EID-1065990 and by University of California Marine Council Coastal Environmental Quality Initiative grants 04-T-CEQI-08-0048 and 07-T-CEQI-10-0060. K.J.N. was supported by a Bodega Marine Laboratory Graduate Student Fellowship. J.W.W. was supported by a grant to J.L.L. from the Water Intake Structure Environmental Research (WISER) program.

Literature Cited

- Adams, T. P., D. Aleynik, and M. T. Burrows. 2014. Larval dispersal of intertidal organisms and the influence of coastline geography. *Ecography* 37:1–13.
- Aiken, C. M., S. A. Navarrete, M. I. Castillo, and J. C. Castilla. 2007. Along-shore larval dispersal kernels in a numerical ocean model

- of the central Chilean coast. *Marine Ecology Progress Series* 339: 13–24.
- Anderson, E. K., and W. North. 1969. In situ studies of spore production and dispersal in the giant kelp *Macrocystis pyrifera*. *Proceedings of the International Seaweed Symposium* 5:73–86.
- Andutta, F. P., M. J. Kingsford, and E. Wolanski. 2012. “Sticky water” enables the retention of larvae in a reef mosaic. *Estuarine, Coastal and Shelf Science* 101:54–63.
- Beckman, N. G., and H. S. Rogers. 2013. Consequences of seed dispersal for plant recruitment in tropical forests: interactions within the seedscape. *Biotropica* 45:666–681.
- Bode, M., K. Burrage, and H. P. Possingham. 2008. Using complex network metrics to predict the persistence of metapopulations with asymmetric connectivity patterns. *Ecological Modelling* 214:201–209.
- Borges, R., R. Ben-Hamadou, M. A. Chicharo, P. Ré, and E. J. Gonçalves. 2007. Horizontal spatial and temporal distribution patterns of nearshore larval fish assemblages at a temperate rocky shore. *Estuarine, Coastal and Shelf Science* 71:412–428.
- Botsford, L. W., A. Hastings, and S. D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecology Letters* 4:144–150.
- Botsford, L. W., C. L. Moloney, A. Hastings, J. L. Largier, T. M. Powell, K. Higgins, and J. F. Quinn. 1994. The influence of spatially and temporally varying oceanographic conditions on meroplankton metapopulations. *Deep-Sea Research II* 41:107–145.
- Botsford, L. W., J. W. White, M.-A. Coffroth, C. B. Paris, S. Planes, T. L. Shearer, S. R. Thorrold, and G. P. Jones. 2009. Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs* 28:327–337.
- Bowden, K. F. 1965. Horizontal mixing in the sea due to a shearing current. *Journal of Fluid Mechanics* 21:83–95.
- Bullock, J. M., and R. T. Clarke. 2000. Long distance seed dispersal by wind: measuring and modelling the tail of the curve. *Oecologia (Berlin)* 124:506–521.
- Burgess, S. C., K. J. Nickols, C. D. Griesemer, L. A. K. Barnett, A. G. Dedrick, E. V. Satterthwaite, L. Yamane, S. G. Morgan, J. W. White, and L. W. Botsford. 2014. Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected area design. *Ecological Applications* 24:257–270.
- Byers, J. E., and J. M. Pringle. 2006. Going against the flow: retention, range limits and invasions in advective environments. *Marine Ecology Progress Series* 313:27–41.
- Cain, M. L., B. G. Milligan, and A. E. Strand. 2000. Long-distance seed dispersal in plant populations. *American Journal of Botany* 87:1217–1227.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* 27:477–500.
- Chiswell, S. M. 2012. Non-Gaussian larval dispersal kernels in Gaussian ocean flows. *Aquatic Biology* 16:203–208.
- Clark, J. S. 1998. Why trees migrate so fast: confronting theory with dispersal biology and paleorecord. *American Naturalist* 152:204–224.
- Clark, J. S., M. Lewis, J. S. McLachlan, and J. HilleRisLambers. 2003. Estimating population spread: what can we forecast and how well? *Ecology* 84:1979–1988.
- Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80:1475–1494.
- Cowen, R. K., C. B. Paris, and A. Srinivasan. 2006. Scaling of connectivity in marine populations. *Science* 311:522–527.
- Cowen, R. K., and S. Sponaugle. 2009. Larval dispersal and marine population connectivity. *Annual Review of Marine Science* 1:443–466.
- Criales, M. M., J. A. Browder, C. N. K. Mooers, M. B. Robblee, H. Cardenas, and T. L. Jackson. 2007. Cross-shelf transport of pink shrimp larvae: interactions of tidal currents, larval vertical migrations, and internal tides. *Marine Ecology Progress Series* 345:167–184.
- Davis, R. E. 1985. Drifter observations of coastal surface currents during CODE: the statistical and dynamical views. *Journal of Geophysical Research* 90:4756–4772.
- De Veen, J. F. 1978. On selective tidal transport in the migration of North Sea plaice (*Pleuronectes platessa*) and other flatfish species. *Netherlands Journal of Sea Research* 12:115–147.
- Drake, P. T., and C. A. Edwards. 2009. A linear diffusivity model of near-surface, cross-shore particle dispersion from a numerical simulation of central California’s coastal ocean. *Journal of Marine Research* 67:385–409.
- Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81:117–142.
- Figueira, W. F. 2009. Connectivity or demography: defining sources and sinks in coral reef fish metapopulations. *Ecological Modelling* 220:1126–1137.
- Fonseca, D. M., J. S. Fisher, J. C. Zieman, and G. W. Thayer. 1982. Influence of the seagrass, *Zostera marina* L., on current flow. *Estuarine, Coastal and Shelf Science* 15:351–364.
- Fonseca, D. M., and D. D. Hart. 2001. Colonization history masks habitat preferences in local distributions of stream insects. *Ecology* 82:2897–2910.
- Fuchs, H. L., A. R. Solow, and L. S. Mullineaux. 2010. Larval responses to turbulence and temperature in a tidal inlet: habitat selection by dispersing gastropods? *Journal of Marine Research* 68: 153–188.
- Gaines, S. D., B. Gaylord, and J. L. Largier. 2003. Avoiding current oversights in marine reserve design. *Ecological Applications* 13(suppl.):32–46.
- Gaylord, B., and S. D. Gaines. 2000. Temperature or transport? range limits in marine species mediated solely by flow. *American Naturalist* 155:769–789.
- Gaylord, B., J. Hodin, and M. C. Ferner. 2013. Turbulent shear spurs settlement in larval sea urchins. *Proceedings of the National Academy of Sciences of the USA* 110:6901–6906.
- Gaylord, B., K. J. Nickols, and L. Jurgens. 2012. Roles of transport and mixing processes in kelp forest ecology. *Journal of Experimental Biology* 215:997–1007.
- Gaylord, B., D. C. Reed, P. T. Raimondi, and L. Washburn. 2006. Macroalgal spore dispersal in coastal environments: mechanistic insights revealed by theory and experiment. *Ecological Monographs* 76:481–502.
- Gaylord, B., D. C. Reed, P. T. Raimondi, L. Washburn, and S. R. McLean. 2002. A physically based model of macroalgal spore dispersal in the wave and current-dominated nearshore. *Ecology* 83: 1239–1251.
- Gaylord, B., J. H. Rosman, D. C. Reed, J. R. Koseff, J. Fram, S. MacIntyre, K. Arkema, et al. 2007. Spatial patterns of flow and

- their modification within and around a giant kelp forest. *Limnology and Oceanography* 52:1838–1852.
- Greene, D. F., and E. A. Johnson. 1989. A model of wind dispersal of winged or plumed seeds. *Ecology* 70:339–347.
- Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biological Journal of the Linnean Society* 42:3–16.
- Harley, C. D. G., A. R. Hughes, K. M. Hultgren, B. G. Miner, C. J. B. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek, and S. L. Williams. 2006. The impacts of climate change in coastal marine systems. *Ecology Letters* 9:228–241.
- Hastings, A., and L. W. Botsford. 2006. Persistence of spatial populations depends on returning home. *Proceedings of the National Academy of Sciences of the USA* 103:6067–6072.
- Hill, A. E. 1991. Advection-diffusion-mortality solutions for investigating pelagic larval dispersal. *Marine Ecology Progress Series* 70: 117–128.
- Hogan, J. D., R. J. Thiessen, P. F. Sale, and D. D. Heath. 2011. Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. *Oecologia* (Berlin) 168:61–71.
- Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13:201–228.
- Hrycik, J. M., J. Chassé, B. R. Ruddick, and C. T. Taggart. 2013. Dispersal kernel estimation: a comparison of empirical and modelled particle dispersion in a coastal marine system. *Estuarine, Coastal and Shelf Science* 133:11–22.
- Jackson, G. A., and R. R. Strathmann. 1981. Larval mortality from offshore mixing as a link between pre-competent and competent periods of development. *American Naturalist* 118:16–26.
- Kaplan, D. M. 2006. Alongshore advection and marine reserves: consequences for modeling and management. *Marine Ecology Progress Series* 309:11–24.
- Kaplan, D. M., L. W. Botsford, M. R. O'Farrell, S. D. Gaines, and S. Jorgensen. 2009. Model-based assessment of persistence in proposed marine protected area designs. *Ecological Applications* 19: 433–448.
- Katul, G. G., A. Porporato, R. Nathan, M. Siqueira, M. B. Soons, D. Poggi, H. S. Horn, and S. A. Levin. 2005. Mechanistic analytical models for long-distance seed dispersal by wind. *American Naturalist* 166:368–381.
- Kinlan, B. P., and S. D. Gaines. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–2020.
- Kot, M., M. A. Lewis, and P. van den Driessche. 1996. Dispersal data and the spread of invading organisms. *Ecology* 77:2027–2042.
- Largier, J. L. 2003. Considerations in estimating larval dispersal distances from oceanographic data. *Ecological Applications* 13(suppl.):71–89.
- Levin, L. A. 2006. Recent progress in understanding larval dispersal: new directions and digressions. *Integrative and Comparative Biology* 46:282–297.
- Levin, S. A. 1974. Dispersion and population interactions. *American Naturalist* 108:207–228.
- Levin, S. A., H. C. Muller-Landau, R. Nathan, and J. Chave. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology and Systematics* 34:575–604.
- List, E. J., G. Gartrell, and C. D. Winant. 1990. Diffusion and dispersion in coastal waters. *Journal of Hydraulic Engineering* 116: 1158–1179.
- MacMahan, J., J. Brown, J. Brown, E. Thornton, A. Reniers, T. Stanton, M. Henriquez, et al. 2010. Mean Lagrangian flow behavior on an open coast rip-channeled beach: a new perspective. *Marine Geology* 268:1–15.
- Miller, S. H., and S. G. Morgan. 2013. Interspecific differences in depth preference: regulation of larval transport in an upwelling system. *Marine Ecology Progress Series* 476:301–306.
- Mitarai, S., D. A. Siegel, J. R. Watson, C. Dong, and J. C. McWilliams. 2009. Quantifying connectivity in the coastal ocean with application to the Southern California Bight. *Journal of Geophysical Research* 114:C10026.
- Moffitt, E. A., L. W. Botsford, D. M. Kaplan, and M. R. O'Farrell. 2009. Marine reserve networks for species that move within a home range. *Ecological Applications* 19:1835–1847.
- Morgan, S. G., J. L. Fisher, S. H. Miller, S. T. McAfee, and J. L. Largier. 2009. Nearshore larval retention in a region of strong upwelling and recruitment limitation. *Ecology* 90:3489–3502.
- Murthy, C. R., and G. T. Csanady. 1981. Frictional and inertial coastal boundary layers in the Great Lakes. *Ocean Management* 6:237.
- Nathan, R. 2006. Long-distance dispersal of plants. *Science* 313:786–788.
- Nathan, R., G. G. Katul, H. S. Horn, S. M. Thomas, R. Oren, R. Avissar, S. W. Pacala, and S. A. Levin. 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418:409–413.
- Nickols, K. J., B. Gaylord, and J. L. Largier. 2012. The coastal boundary layer: predictable current structure decreases alongshore transport and alters scales of dispersal. *Marine Ecology Progress Series* 464:17–35.
- Okubo, A. 1971. Oceanic diffusion diagrams. *Deep-Sea Research* 18: 789–802.
- Pachepsky, E., F. Lutscher, R. M. Nisbet, and M. A. Lewis. 2005. Persistence, spread and the drift paradox. *Theoretical Population Biology* 67:61–73.
- Palmer, A. R., and R. R. Strathmann. 1981. Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. *Oecologia* (Berlin) 48:308–318.
- Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology and Systematics* 37: 637–669.
- Pinsky, M. L., S. R. Palumbi, S. Andréfouët, and S. J. Purkis. 2012. Open and closed seascapes: where does habitat patchiness create populations with high fractions of self-recruitment? *Ecological Applications* 22:1257–1267.
- Possingham, H. P., and J. Roughgarden. 1990. Spatial population dynamics of a marine organism with a complex life cycle. *Ecology* 71:973–985.
- Rao, Y. R., and C. R. Murthy. 2001. Coastal boundary layer characteristics during summer stratification in Lake Ontario. *Journal of Physical Oceanography* 31:1088–1104.
- Romero, L., Y. Uchiyama, J. C. Ohlmann, J. C. McWilliams, and D. A. Siegel. 2013. Simulations of nearshore particle-pair dispersion in southern California. *Journal of Physical Oceanography* 43:1862–1879.
- Roughgarden, J., S. D. Gaines, and H. P. Possingham. 1988. Recruitment dynamics in complex life-cycles. *Science* 241:1460–1466.
- Roughgarden, J., and Y. Iwasa. 1986. Dynamics of a metapopulation with space-limited subpopulations. *Theoretical Population Biology* 29:235–261.
- Sale, P., I. Hanski, and J. Kritzer. 2006. The merging of metapopulation theory and marine ecology: establishing the historical con-

- text. Pages 3–30 in J. Kritzer, and P. Sale, eds. *Marine metapopulations*. Elsevier, Burlington, MA.
- Savage, D., M. J. Barbetti, W. J. MacLeod, M. U. Salam, and M. Renton. 2011. Can mechanistically parameterised, anisotropic dispersal kernels provide a reliable estimate of wind-assisted dispersal? *Ecological Modelling* 222:1673–1682.
- Scheltema, R. S. 1986. On dispersal and planktonic larvae of benthic invertebrates: an eclectic overview and summary of problems. *Bulletin of Marine Science* 39:290–322.
- Shanks, A. L., and R. K. Shearman. 2009. Paradigm lost? cross-shelf distributions of intertidal invertebrate larvae are unaffected by upwelling or downwelling. *Marine Ecology Progress Series* 385: 189–204.
- Siegel, D. A., B. P. Kinlan, B. Gaylord, and S. D. Gaines. 2003. Lagrangian descriptions of marine larval dispersion. *Marine Ecology Progress Series* 260:83–96.
- Siegel, D. A., S. Mitarai, C. J. Costello, S. D. Gaines, B. E. Kendall, R. R. Warner, and K. B. Winters. 2008. The stochastic nature of larval connectivity among nearshore marine populations. *Proceedings of the National Academy of Sciences of the USA* 105: 8974–8979.
- Strathmann, R. R. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annual Review of Ecology and Systematics* 16:339–361.
- Swearer, S. E., J. S. Shima, M. E. Hellberg, S. R. Thorrold, G. P. Jones, D. R. Robertson, S. G. Morgan, K. A. Selkoe, G. M. Ruiz, and R. R. Warner. 2002. Evidence of self-recruitment in demersal marine populations. *Bulletin of Marine Science* 70(suppl.):251–271.
- Tankersley, R. A., and R. B. Forward Jr. 1994. Endogenous swimming rhythms in estuarine crab megalopae: implications for flood-tide transport. *Marine Biology* 118:415–423.
- Taylor, G. I. 1922. Diffusion by continuous movements. *Proceedings of the London Mathematical Society* 20:196–212.
- Vanschoenwinkel, B., S. Gielen, H. Vandewaerde, M. Seaman, and L. Brendonck. 2008. Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. *Ecography* 31:567–577.
- Vuilleumier, S., B. M. Bolker, and O. Lévêque. 2010. Effects of colonization asymmetries on metapopulation persistence. *Theoretical Population Biology* 78:225–238.
- Watson, J. R., S. Mitarai, D. A. Siegel, J. Caselle, C. Dong, and J. C. McWilliams. 2010. Realized and potential larval connectivity in the Southern California Bight. *Marine Ecology Progress Series* 401: 31–48.
- Watson, J. R., D. A. Siegel, B. E. Kendall, S. Mitarai, A. Rassweiler, and S. D. Gaines. 2011. Identifying critical regions in small-world marine metapopulations. *Proceedings of the National Academy of Sciences of the USA* 108:E907–E913.
- White, J. W., L. W. Botsford, A. Hastings, and J. L. Largier. 2010a. Population persistence in marine reserve networks: incorporating spatial heterogeneities in larval dispersal. *Marine Ecology Progress Series* 398:49–67.
- White, J. W., S. G. Morgan, and J. L. Fisher. 2014. Planktonic larval mortality rates are lower than widely expected. *Ecology* 95:3344–3353.
- White, J. W., K. J. Nickols, L. Clarke, and J. L. Largier. 2010b. Larval entrainment in cooling water intakes: spatially explicit models reveal effects on benthic metapopulations and shortcomings of traditional assessments. *Canadian Journal of Fisheries and Aquatic Science* 67:2014–2031.
- White, J. W., A. J. Scholz, A. Rassweiler, C. Steinback, L. W. Botsford, S. Kruse, C. Costello, et al. 2013. A comparison of approaches used for economic analysis in marine protected area planning in California. *Ocean and Coastal Management* 74:77–89.
- Wolanski, E. 1994. *Physical oceanographic processes of the Great Barrier Reef*. CRC, Boca Raton, FL.
- Zimmer, R. K., J. T. Fingerut, and C. A. Zimmer. 2009. Dispersal pathways, seed rains, and the dynamics of larval behavior. *Ecology* 90:1933–1947.

Associate Editor: Wolf M. Mooij
Editor: Judith L. Bronstein



Ecologists at the Bodega Marine Laboratory study marine communities while oceanographers in the boat on the horizon service an oceanographic mooring at a depth of 30 m. The area in between, from just outside the surf zone to the boat, is the coastal boundary layer (CBL), where researchers see reduced current velocities. Photograph by Kerry J. Nickols.