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CONSIDERATIONS IN ESTIMATING LARVAL DISPERSAL DISTANCES FROM OCEANOGRAPHIC DATA

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Abstract. Determination of larval dispersal distances and larval origins is a central challenge in contemporary marine ecology. In this work, the larval dispersal problem is discussed from the perspective of oceanography. Following formulation of the advection–diffusion model, the importance of scale is argued. When considering dispersion parameters at the appropriate population scales, advection is usually weaker than initially anticipated (and often used), and diffusion is stronger than typically used in model studies. Focusing attention on coastal populations, the importance of retention zones is described, and the more general existence of a coastal boundary layer is discussed. The coupling of cross-shore and alongshore dispersion results in a nonlinear relation between alongshore dispersal distance and larval planktonic period for dispersion in a sheared flow. Thus, small changes in cross-shore dispersal, whether due to environmental differences or larval behavior result in significant differences in alongshore dispersal. Finally, the interplay between advection and diffusion is explored, showing the importance of adequately representing the diffusive effects that mitigate alongshore advection. In most cases, diffusion acts to prevent ''wash-out'' of a population and allows for more flexibility in the size and spacing of effective marine reserves. Future challenges must bring oceanographers and ecologists together around specific dispersal problems if there is to be a significant improvement in the notable absence of hard data in this field of enquiry.

Key words: advection–diffusion model; coastal boundary layer; coastal oceanography; dispersal kernel; eddy diffusivity; larval dispersal; length scale; retention; shear dispersion.

INTRODUCTION

One of the central questions in marine ecology is the degree of dispersal of propagules of marine organisms and the effect of this on the persistence of spatially distributed populations. In particular, when mature organisms are fixed or exhibit limited dispersal, the dispersal of early life stages is a critical aspect of their population dynamics. Subject also to heavy exploitation by humans, many of these species are at the center of marine conservation efforts and the current drive to offer protection to them through marine reserves (or marine protected areas, MPAs). It is becoming generally accepted among specialists that MPAs are an important element of marine conservation and fisheries management in a human-dominated world (Hastings and Botsford 1999, Palumbi 2001). However, much uncertainty remains as to the optimal spatial design of MPA networks for dispersing populations. The aim of this work is to develop improved estimates of dispersal in population models and models of MPAs through encouraging careful consideration of the detail of observed water motion in coastal waters. However, the emphasis here is more on exploring critical concepts than on developing formal theory. Until better data are available and the problem is better constrained, there will be subjectivity in evaluating dispersal parameters and a well-demonstrated oceanographic insight into larval transport processes will be an important component of credible population-level studies of dispersal. In addition to providing population ecologists with an oceanographer's view of larval dispersal, this paper is intended to introduce oceanographers to this dialogue and to attract more attention to this critical question.

Present knowledge of larval dispersal is inadequate to design optimal spatial conservation strategies, which must take into account the relative length scales of larval dispersal and habitat patches (Gaines et al. 2003, Shanks et al. 2003). The design of MPAs depends critically on knowledge of larval dispersal distances and population connectivity (Botsford et al. 2001, Palumbi 2001). However, we have a reasonable idea of larval dispersal distance for very few species (Shanks et al. 2003) and most of these disperse very short distances that can be tracked visually (Olson 1985, Stoner 1992). For most species with meroplanktonic larvae, we have only vague ideas of their dispersal distance (e.g., Shanks et al. 2003). Indeed, even the very focus on ''larval dispersal distance'' is perhaps misguided as it is directed at obtaining a single statistic to capture the essence of the population dispersal problem (e.g., Roberts 1997, Shanks et al. 2003, Botsford et al., *in press*). This leads to the present binary view of dispersal (e.g., Carr et al. 2003): Is the population ''open'' or

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''closed''? Is recruitment remote or local? Is a specific location a sink or a source? Is a reserve bigger or smaller than the dispersal distance? In this paper it is argued that at least two parameters are necessary to adequately describe dispersal within a population; and that this allows for the recognition that both local and remote recruitment may be significant in the same population at the same time. Further, it should be recognized that this duplicity of strategies is a critical aspect of the persistence of the range and level of a metapopulation in an environment with a nonzero mean current. Thus, the neglect of a second parameter (e.g., Roberts 1997), or the underestimation of one of the parameters (e.g., Roughgarden et al. 1988, Possingham and Roughgarden 1990), can lead to erroneous conclusions and ineffective MPA network designs.

A complete description of larval dispersal would consist of a set of dispersal trajectories for all successful settlers in a metapopulation. For purposes of understanding population dynamics, however, this can be distilled to a connectivity matrix that reflects how many larvae from a set of origins settle successfully at a set of destinations. The connectivity matrix thus describes the spatial distribution of settlement destinations of larvae that originate from a given site. At the same time, the connectivity matrix also describes the spatial distribution of origins of larvae that settle at a given site. In metapopulation models, this is called the dispersal kernel (e.g., Botsford et al. 1994) and is more usually thought of as the probability of settlers originating from site A being delivered to site B (or probability of settlers at site B originating from site A). It is typically simplified to a simple functional form described by two or more parameters (e.g., a Gaussian distribution), partly for mathematical convenience and partly owing to a lack of knowledge of the matrix or dispersal kernel.

Information on larval dispersal can be obtained in several ways, all of them indirect and involving levels of interpretation or aggregation. In spite of the large body of literature on connectivity in marine populations (Palumbi 2001), quantitative information on connectivity is sadly inadequate. There are no direct observations, other than at very short distances (e.g., Olson 1985, Stoner 1992). Methods of estimating dispersal involve an analysis of either the dispersal process (the cause) or of the resultant population structure (the effect):

1) Population genetics can provide information on the degree of exchange between populations (Edmands et al. 1996, Burton 1998), but it is aggregated and provides poor resolution of intra- and interannual variability with no clear information on specific origin–destination links.

2) Observations of the rate of invasion of exotic species (e.g., Crisp 1958, Geller 1994, Grosholz and Ruiz 1995, 1996, Geller et al. 1997) provide an annual index of dispersal, but how this relates to the dispersal distance of larvae is confounded by postsettlement processes (including constraints due to a lack of space) and considerations of the reproductive ability of new settlers (Neubert and Caswell 2000).

3) Microchemistry of crab exoskeletons (DiBacco and Chadwick 2001), fish otoliths (Swearer et al. 1999), and mollusc shells (L. A. Levin, *unpublished manuscript*) offer unprecedented information on the source and dispersal track of successful settlers, but to date this method is limited to locations where the environment offers strong gradients in the availability of trace metals, such as is found in polluted harbor waters.

4) Inferences from correlations between settlement and oceanography (Ebert and Russell 1988, Miller and Emlet 1997, Wing et al. 1995*a, b,* 1998*a,* Morgan et al. 2000) provide valuable insights to the larval dispersal process, but results are dominated by dispersion patterns immediately prior to settling and it has proved difficult to assign sources to successful settlers.

5) Observations of meroplankton distributions provide information on relevant larval characteristics, e.g., mortality (Heath and MacLachlan 1987, McGurk 1989, Hobbs et al. 1992), vertical distribution, and vertical migration (Rothlisberg 1982, Hobbs and Botsford 1992). And these observations may also be used to infer aspects of larval dispersal (Scheltema 1986, Heath and MacLachlan 1987, McGurk 1989, Kim and Bang 1990, Wing et al. 1998*b*; Largier et al., *unpublished manuscript*). However, it is difficult to link these plankton distributions to specific origins and destinations.

6) Larval biology studies provide information on the larvae, but this information has to be coupled with information on flow structures to develop ideas on likely dispersal rates and mechanisms (Emlet et al. 1987, Katz et al. 1994). These studies are more valuable for understanding what is possible, than for obtaining connectivity estimates.

7) Numerical models of larval dispersal draw on information of water flow and simplified (deterministic) information on larval behavior to obtain predictions of dispersal (Hill 1990, Werner et al. 1993, 1996, Incze and Naimie 2000). These models are promising in that they can yield detailed connectivity matrices and also resolve dispersal trajectories. However, present models do not resolve an adequate level of detail in flow structures. Further, they rely on simplified models of larval behavior and there are inadequate observations of larval dispersal to validate model results.

Given the diversity and inadequacy of these methods, there are contradictory results in the literature. To some extent the contradictory nature of the literature on larval dispersal is owing to the inconclusive nature of the studies, but it appears that contradiction also arises from the desire of authors to obtain a singular result—

to determine whether a population is open or closed, whether a subpopulation is a sink or source, whether recruitment is local or remote, or whether a reserve is bigger or smaller than the dispersal distance. In the absence of information on dispersal pathways, or even on aggregated dispersal patterns, many studies invoke an unrealistically simple pattern of water flow and proceed to build ideas of larval exchange that are over-simplistic and misleading (e.g., Roberts 1997).

The problem of larval dispersal in marine populations is really two problems—the larval dispersal problem in which the destination of planktonic organisms is determined; and the population problem in which aggregated dispersal is used to determine population level outcomes. The large difference in time and space scales between dispersal and population dynamics makes it difficult to couple these two problems in either field studies or computer models. While dispersal may be strongly influenced by processes at time scales less than a minute (waves) and space scales less than a kilometer (shoreline morphology), population dynamics of relevance to MPA design must include time scales of many decades and space scales of thousands of kilometers. In contemporary numerical modeling one cannot expect to simultaneously resolve this wide array of scales, extending over several orders of magnitude. Further, there is little hope that high-resolution detailed observations can be sustained for decades, as is necessary to fully describe dispersal at population-relevant scales or to provide a complete model validation. In contemporary studies of populations with dispersing larvae, it is necessary to aggregate the small-scale dispersal problem and capture it in a limited number of parameters that can adequately describe connectivity in the large-scale population problem. Work on this problem has included numerical model calculations (e.g., Hill 1990, Hoffman et al. 1991) and empirical estimates (e.g., Largier et al., *unpublished manuscript*; C. N. Cudaback and J. L. Largier, *unpublished manuscript*) of the two parameters in an advection–diffusion model of larval dispersal and settlement. The results of an advection–diffusion model can then be expressed as a connectivity matrix or analytically expressed as a dispersal kernel.

Finally some notes are needed on the terminology used in this paper. Water moves with a velocity that varies in space and time. As it does so it transports water-borne material from a variety of origins to a variety of destinations. This is known as ''dispersion.'' In ecology, the changing distribution of an organism is referred to as ''dispersal.'' In the case of larvae, dispersal is effected by water-borne transport and ''larval dispersal'' is synonymous with ''larval dispersion.'' Dispersion is a combination of advection and eddy diffusion. ''Advection'' is the mean transport of a collection of particles, while (eddy) ''diffusion'' reflects the differences in transport of individual particles. Picture a cloud of dye in the water: it moves along and spreads out as it does so—advection is the mean movement and diffusion is the spreading out. Strictly, diffusion is due to turbulent eddy motions (Okubo 1971, 1980), but, in much of the literature, it has come to be used more loosely to refer to all dispersion that is not advection—i.e., the effects of flow structures that vary on time and space scales that are smaller than the scale of resolution of the problem. So, the strength of diffusion (and advection) will vary depending on whether one is interested in a single year of dispersal or whether one is interested in population changes that include many years of dispersal. This use is continued here.

For convenience, I use the words ''settle,'' ''settler,'' and ''settlement'' for all organisms (including non-benthic organisms) to refer to completion of the dispersal process which delivers a planktonic propagule/larva to acceptable habitat; the word ''recruit'' is not used as this can be understood to include a variety of processes following the planktonic dispersal process; one could also perhaps use the word ''pre-recruit,'' but this is also unclear owing to the lack of clarity in the stage at which recruitment is considered complete; ''settler'' conjures up the idea of a larva that has been adrift and has now found a home.

FORMULATING THE DISPERSION PROBLEM: ADVECTION AND DIFFUSION

As is done in parameterizing small-scale turbulence to include the primary effects of turbulence in mean flow, one can see the value in recognizing the separation of scales between dispersal dynamics and population dynamics. In most species of interest for MPAs, dispersal plays out at intra-annual time scales while population changes play out at interannual time scales. However, unlike turbulence, there is no common dynamic that controls dispersal processes and dispersal parameters cannot be developed nor evaluated through theory, but rather need to be empirically evaluated. The conventional framework for parameterizing dispersal is the advection–diffusion model that expresses a local conservation of larvae (Okubo 1994). Expressed in one dimension, one can easily see that the local change in average concentration must be accounted for by a convergence in advective or diffusive fluxes, or by a local source or sink:

$$d_t C = -d_x\,([uC] - [K d_x C]) + \lambda$$

where C is larval concentration at alongshore position x and time t, u is the mean advective velocity over a given time interval, K is the local dispersion coefficient (eddy diffusivity), and λ is the ''reaction'' term which here represents a source (or sink). ''Eddy diffusion'' is a construct developed to evaluate the effect of correlations in velocity and concentration at scales smaller than those explicitly resolved by u and C. Following semi-empirical theories of ocean diffusion (Csanady

1973, Okubo 1980), the net flux due to the cross-product of small-scale u and C fluctuations $u'C'$ can be related to the spatial gradient in concentration d_xC. The diffusive flux is then determined by the ''eddy diffusivity'' K that parameterizes the strength of small-scale motions, hence $u'C' = -(Kd_xC)$, and acts to smooth out gradients (whereas advection simply displaces them). The contribution of small-scale coherent motions to the diffusive term is much greater than that from turbulence (Okubo 1980), and the contribution from low-frequency (large scale) motions is generally more important than that from higher frequency (small scale) motions. This follows the ''mixing length'' concept of Prandtl in which K is scaled by the product of a typical velocity and a typical excursion length of the primary dispersing motion (e.g., see Arons and Stommel 1951 for a discussion of tidal waters). Thus, the diffusivity value increases with the scale of concern (Okubo 1971).

For convenience, this paper addresses a long straight coast and discusses a one-dimensional model. This scenario, reasonably represented by the west coast of the USA (and many other regions), allows development of concepts that can be used also in understanding and quantifying dispersion in more complex configurations. A similar two-dimensional model, and similar connectivity matrices, can be developed for a diversity of coastal configurations, including islands, reefs, bays, estuaries, fjords, and headlands. In this one-dimensional model, a large contribution to the nonconservative term λ is owing to offshore dispersion and ''larval wastage.''

For a pulsed source at a single origin (Fig. 1), one expects dispersion to be rapid initially, as high concentration gradients lead to strong outward ''diffusion'' from the origin. After some time, with homogeneous K and in the absence of an alongshore flow u, the distribution of particles released from a given site will be distributed symmetrically around this site—a Gaussian distribution $C(x, t) = [C_0/(4\pi Kt)]\exp(-x^2/4Kt)$. This distribution will be one line of the connectivity matrix, describing the destination of larvae released at a given site—or the distribution of origins of larvae settling at that site (as plotted in Fig. 1). This Gaussian distribution may be offset from the larval origin (or destination) by a mean flow, or it may be stretched out wider by stronger diffusion. The offset distance can be expressed as an advective length scale $L_{\mathrm{adv}} \approx uT_{\mathrm{adv}}$, and the Gaussian width can be expressed as a diffusive-length scale $L_{\mathrm{diff}} \approx (KT_{\mathrm{diff}})^{1/2}$, where T_{adv} and T_{diff} are the aggregation times in obtaining u and K values. The ratio $L_{\mathrm{adv}}/L_{\mathrm{diff}}$ then expresses the relative importance of these dispersion terms, as discussed further in *The importance of describing dispersal with two parameters* (this ratio is a form of the nondimensional Peclet number $Pe = (u \times l)/K$ where l is a length scale). The level of settlement (amplitude of curve) is influenced not only by the spatial extent of dispersal, but also by the offshore loss of larvae and by other mortality terms. The curve may be skewed by asymmetry in dispersion, which results from a nonhomogeneous flow field. In reality, advection $u(x, t)$ and diffusion $K(x, t)$ are not constant nor even necessarily smooth functions of alongshore position or time (e.g., *Oceanographic phenomena*, and discussed in *Discussion*) and neither will the final distribution of settlers be smooth.

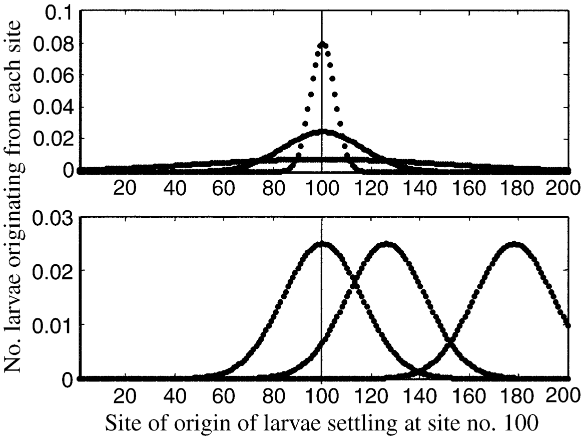

FIG. 1. Distribution of origin of larvae settling at site 100 for uniform Gaussian dispersal. In the upper panel, advection (or mean flow) $u = 0$ and $L_{\mathrm{adv}} = 0$ for all scenarios. Three scenarios are plotted, with diffusion length L_{diff} of 5, 16, and 51 sites (or diffusivity of 10, 100, and 1000 $\mathrm{m^2/s}$ for the dimensional example represented in Fig. 4). Total settlement at site 100 is 1.0 for the first two scenarios and 0.95 for the third. Local settlement is reduced as increased flow variability mixes (diffuses) local spawn away from site 100. In the lower panel, L_{diff} is 16 in all cases, and the three scenarios represent advection lengths L_{adv} of 0, 26, and 78 sites (or advection of 0, 0.01, and 0.03 m/s for the dimensional case represented in Fig. 4). Total settlement at site 100 is 1.0 for the first two scenarios and 0.92 for the third. Local settlement is reduced as local spawn is advected away in increased mean flow. For even stronger flows, spawn from all sites will be washed away, and there will be no settlement at site 100 (see Fig. 4).

Successful application of this advection–diffusion formulation rests on the selection of appropriate values to describe larval fluxes due to mean and fluctuating flows (see *Scale dependence of parameter values*). In short, values of u and K need to be evaluated in the relevant location or period, at the relevant scale, and with due regard for spatial or temporal weighting indicated by knowledge of larval distributions. Temporal considerations are determined by the species of interest for a specific generation/year, and also for many generations/years—spawning season, larval planktonic duration, and years of reproductive activity. Spatial considerations are related to extent of habitat, distribution of spawning population, offshore extent of dispersing larvae, and distribution of habitat patches (where habitat is noncontinuous, as for reef habitat or MPAs). The scales of interest depend on whether one is evaluating the dispersal problem—obtaining daily settlement at a specific site—or evaluating the population problem—obtaining population-wide annual settlement. It is worth noting that the space and time scales of only some larval dispersal and population problems overlap those of the better-studied pollutant dispersion problem, or of trophic considerations such as the dispersion of nutrients or phytoplankton, and that this means that in most cases the parameter values have to be determined rather than inherited.

SCALE DEPENDENCE OF PARAMETER VALUES

Given a lack of detailed oceanographic information to construct formal lagrangian statistics from dispersal tracks, there is subjectivity in the choice of a representative alongshore velocity u used to estimate typical dispersal distances. One tends to use a velocity that is typical of active flow in the environment of interest, whereas the appropriate value is the mean of alongshore velocity over the relevant dispersal period. In obtaining estimates of population-level settlement as done by Jackson and Strathmann (1981), Roughgarden et al. (1988), and Largier et al. (*unpublished manuscript*), one must aggregate over all propagules. So, it is not the planktonic period of a single larva, but rather the length of the planktonic season over which one must average—the period in which significant numbers of larvae are found in the plankton. Further, when interested in population sustainability, but without resolving interannual variability (e.g., Botsford et al. 1998, 2001, Gaines et al. 2003), one obtains a velocity scale by averaging over a number of spawning seasons—the reproductive lifetime of adults. This velocity scale is then consistent with the dispersal distances obtained from interpretation of population data (e.g., Geller 1994, Shanks et al. 2003).

To illustrate the importance of the averaging period, one can review the variability in almost any long-term record of coastal currents, such as the two-year record obtained by Largier et al. (1993) off northern California, and partially reproduced in Fig. 2. Based on Fig. 2A, one may represent an upwelling event by $u = 0.5$ m/s, whereas if one averages over a month in the upwelling season (planktonic period), one may obtain $u = 0.2$ m/s (Fig. 2B). However, if one were to consider the complete planktonic larval season extending over a few months, the mean alongshore flow u is of order 0.1 m/s, or smaller. Further, with an increase in the time scale of interest, and inclusion of additional variability, one can see that the standard deviation of the alongshore current should increase. These results are characteristic of the ‘‘red’’ nature of spectra of current variability and similar results are obtained for data from other locations (e.g., North Carolina coast, Lentz et al. 1999; South African south coast, Largier et al. 1992).

Spatial variability in currents is also important in the choice of a representative alongshore velocity scale. At different alongshore locations, flow statistics may be quite different (Fig. 2A; Largier et al. 1993, Gaines et al. 2003) and thus data from a single location can provide a misleading estimate of the mean alongshore velocity experienced by a dispersing larva—data should be averaged over alongshore distances comparable with dispersal distance. Further, an averaging of current meter data (eulerian mean) overestimates the mean velocity experienced by a drifting particle (lagrangian mean) because a dispersing larva will spend more time moving through a region of slow flow than a region of fast flow. For example, assuming that values of 0.5 and 0.2 m/s are representative of regions of equal size, the lagrangian mean will be 0.286 m/s—slower than the eulerian mean of 0.35 m/s.

There is also significant cross-shore shear in alongshore flow in coastal environments (Csanady 1982), often with much lower alongshore velocities inshore and/or offshore of a strong alongshore ‘‘jet’’ (e.g., Fig. 2B). The classic example of this is the wind-driven ‘‘upwelling jet’’ found during spring and summer along mid-latitude west coasts (e.g., the west coast of the USA; Smith 1968) with notably weak alongshore currents nearshore (Lentz 1994). For larvae that disperse away from the shore, one has to obtain a cross-shore mean of alongshore flow taking into account the amount of time spent by larvae at various distances from the shore. Although the nearshore region of weak flow may be narrow, most larvae are spawned there and take several days to disperse through it (see *Oceanographic phenomena*). For larvae that spend much of their planktonic phase in nearshore waters, this slow-flow boundary layer should be heavily weighted in obtaining a representative alongshore flow to describe the dispersal of successful recruits. This is explored further in *Oceanographic phenomena: The coastal boundary layer*.

As more attention is given to the spatiotemporal structure of alongshore flows and the way in which larvae are moved through these structures, attention shifts away from the more noticeable high-velocity regions and periods and invariably one obtains lower ‘‘mean’’ velocities for representing the advective part of larval dispersal. Also, as one averages over longer periods and larger areas, one combines slow and fast flow as well as important flow reversals. As a result, the mean decreases while the standard deviation increases. So, the flow energy and transport potential is not lost through aggregation, but rather appears in the diffusion term K, which represents nondirectional transport (spreading out) due to flow variability not resolved by u. As aggregation extends over larger space and time scales, larger scale motions are included in the diffusive term and K increases (Okubo 1971). This represents a loss of directionality in dispersal. In general, flow structures in the ocean are sufficiently complex that variability (and associated diffusive fluxes)

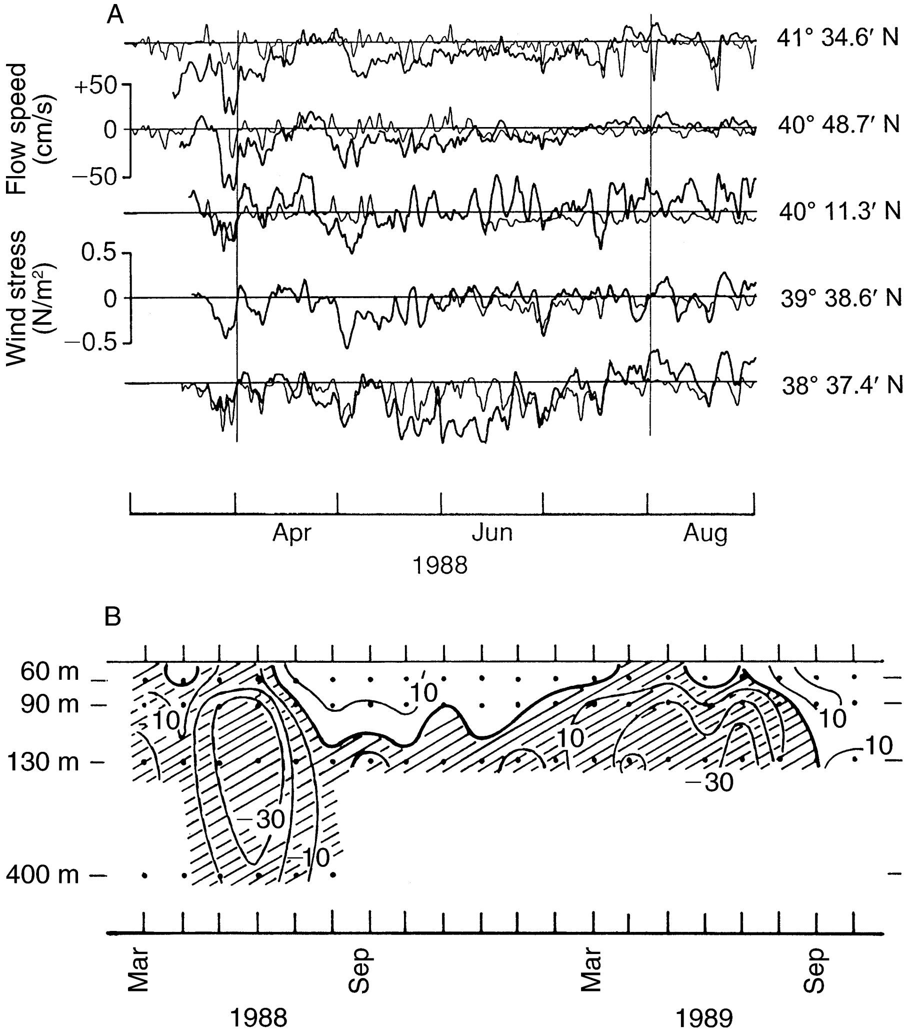

FIG. 2. (A) Near-surface alongshore flow speeds (cm/s) plotted as bold lines for five locations along the northern California coast, between San Francisco and the Oregon border (Largier et al. 1993). Positive values represent northward flow. Data are for 6 mo during spring and summer of 1988; currents were measured at 10 m below the surface in a water depth of 90 m (distance offshore varies from 5 to 20 km). Fine lines illustrate variability in wind forcing near each site (wind plotted as wind stress, N/m^2). (B) Monthly mean alongshore flow speeds (cm/s) at four locations across the northern Californian shelf at 38.6° N. Locations are labeled by water depth. All data are from 10 m below the surface, and positive values represent northward flow. Data are for 18 mo from spring 1988 to fall 1989.

is of a comparable magnitude to the mean flow (and associated advective fluxes), i.e., $L_{\mathrm{adv}}/L_{\mathrm{diff}}$ is of order unity. Indeed, for dispersal, often the mean is less important than the variability in the flow, in spite of the appearance of strong river-like coastal flow features. This comparison of the relative strengths of advective and diffusive terms is discussed further in *The importance of describing dispersal with two parameters.*

OCEANOGRAPHIC PHENOMENA

Underlying an aggregation of the dispersal problem are specific oceanographic features that are common enough to be statistically significant. In particular, the following three discussions highlight features that should not be ignored in choosing values to be used for advection and diffusion parameters.

Topographic eddies and retention zones

Coastlines are not typically straight, nor are they smooth. Where water flows along a curved or bumpy coast, it may separate from the coast and generate an eddy. There are many examples of these, including eddies in northern Monterey Bay, California (Paduan and Rosenfeld 1996, Graham and Largier 1997), southern St. Helena Bay, South Africa (Holden 1985, Penven et al. 2000), southern Mejillones Bay, Chile (N. A. Lagos et al., *unpublished manuscript*) and northern Gulf of Farallons, California (Wing et al. 1998*a*). A particularly large recirculation forms in the Santa Barbara channel downstream of Point Conception (Harms and Winant 1998), with a scale exceeding 100 km. Headland eddies also occur at smaller scales, but they are not well documented in the literature—examples are found associated with headlands along the southern coast of South Africa (J. L. Largier, *personal observation*) and south of Point Loma, California (T. Hendricks, *unpublished manuscript*). Even smaller eddies (on the order of 1 km or smaller) are observed between rocky promontories on many coasts, e.g., Sunset Bay, Oregon (A. L. Shanks, *personal communication*), Camps Bay, South Africa (J. L. Largier, *personal observation*), and El Quisco, Chile (J. L. Largier, *personal observation*), as well as in the surf zone (W. Schmidt and R. T. Guza, *unpublished manuscript*).

Water recirculates in these eddies and they can retain propagules for time scales comparable with dispersal time scales and thus may account for enhanced local recruitment at specific locations. The best studies and most striking examples come from offshore islands—perhaps because island species are compelled to select a behavior that keeps larvae in the eddy; or perhaps because the eddies form in deeper water and are more persistent and more retentive; or perhaps just because the island problem is more intriguing. Whatever the reason, based on analyses of microchemistry signals, Swearer et al. (1999) report very high levels of local recruitment (70%) of reef fish on the lee/downstream side of St. Croix, Virgin Islands, after 45 d in the plankton. The retention of larvae is consistent with the formation and persistence of an island wake due to persistent flow past the island (Wolanski et al. 1984, Pattiaratchi et al. 1987). Similar retention in the vicinity of Barbados is suggested by Cowen et al. (2000) and in earlier work (e.g., Cowen and Castro 1994). Further, Wolanski and Hamner (1988) and Wolanski et al. (1989) report high meroplankton densities in island wakes. Headland eddies can also be expected to retain propagules and Wing et al. (1998*a*) have reported high meroplankton densities in the northern Gulf of Farallons recirculation. But few notable studies have been made to date and there are no recruitment studies to compare with Swearer's work off St. Croix. Further, coastal eddies may not provide such a clear pattern as eddies will be less persistent where currents are less persistent in direction (e.g., Graham and Largier 1997) and in shallow coastal areas where bottom friction reduces the retentive ability of an eddy. It is perhaps better to call these locations ''retention zones'' as the eddy-like feature is not always that apparent. Semi-enclosed bays may be more effective at retaining water (Largier et al. 1997, Monteiro and Largier 1999) and plankton, and reducing alongshore transport, but that's a specific problem not explored further in this simplified one-dimensional open coast problem.

In addition to retaining local production, retention zones can also entrain propagules, thus potentially enhancing recruitment of non-local larvae. For example, the dense concentrations of selected meroplankton (Wing et al. 1998*a*, *b*) observed downstream of Point Reyes, California, may have originated locally but more likely originated from source populations upstream of the retention zone. This is consistent with the observation of cyclonic flow in northern Monterey Bay (Paduan and Rosenfeld 1996), where large concentrations of gelatinous zooplankton are observed (Graham et al. 1992), the shoreward entrainment of drifters south of Cape Mendocino (Barth et al. 2000), where strong urchin settlement is suggested (Ebert and Russell 1988), and the modeling of cyclonic flow downstream of Cape Columbine, South Africa (Penven et al. 2000), where high recruitment of small pelagic fish is observed (Barange and Hampton 1997). Time-series data are not yet available, but it is expected that recirculation downstream of capes dissipates following relaxation in the wind-driven alongshore flow, as has been inferred for northern Monterey Bay (Graham and Largier 1997). With a pulsing of several days, these and other coastal retention zones are not perfectly retentive and it is unlikely that settlement of long-period meroplankton is dominated by local spawn, as in the case of St. Croix Island. In fact, retention zones in upwelling areas may be remarkably effective at ''filtering'' out buoyant meroplankton from the ambient alongshore flow: cold water entrained in retention zones is warmed and forms a stratified surface lens and a buoyancy front along the separation line; this front traps buoyant or upward-swimming larvae and thus concentrates larvae in the retention zone or 'upwelling shadow' (Graham et al. 1992, Graham and Largier 1997, Wing et al. 1998*a*). In addition to Monterey Bay, upwelling shadows are found in several other bays in the California, Benguela, and Humboldt systems (J. L. Largier, *unpublished manuscript*).

Coastal retention zones may also enhance settlement in adjacent regions, as observed north of Point Reyes, California. As the retention mechanism weakens following weakening of the alongshore flow, the warm surface water can start to propagate ''upstream'' as a coastal buoyancy current, but also driven by a northward sea-level slope (Send et al. 1987). In studies north of Point Reyes, this feature may propagate 100 km to Point Arena if the wind remains weak for long enough (Wing et al. 1995*b*). As it does so, this warm, larvae-rich water leads to a strong settlement event along the 100 km of shoreline north of Point Reyes (Wing et al. 1995*a*). Results from drifters deployed downstream of Cape Columbine (Lamberth and Nelson 1987) suggest that a similar poleward propagation of bay water occurs there. Water south of Point Conception is also observed to move north during relaxation, specifically during the seasonal relaxation of southward winds during fall (Dever et al. 1998).

Eddies occur on many scales—from geostrophic scales (Point Conception) to the scale of coves on a rocky shore (Sunset Bay). The time scale of eddy persistence (retention) varies with its size, but also depends on the time scale of the ambient flow that drives the eddy. The importance of a retention zone to the population depends on the time scale of planktonic dispersal relative to that of the flow feature, and on the size of the zone to the spatial extent of the population. For species with a planktonic phase comparable with (or shorter than) the time scale of a retention zone, one can expect enhanced local recruitment. Nevertheless, any retentive feature is important to the dispersal of meroplankton as it retards the alongshore movement of larva released in or moving through the retention zone. Okubo (1994) suggests applying ideas of deterministic chaos to understand larval dispersal in the presence of organized flow systems and points out that these large persistent eddies may promote retention (as described here) or dispersal through introducing more spatial variability in the flow (as discussed in *Scale dependence of parameter values*). But, however one views it, the net effect of these spatial patterns is to lengthen the dispersal path of a specific larva relative to its alongshore displacement and thus to reduce alongshore advection (mean alongshore displacement) at the population level.

The coastal boundary layer

Flow speeds near the shore are typically slow. While alongshore flows are slowed by the drag of a shallow bottom and the roughness of the coastline, cross-shore flows are inhibited by the proximity of the solid coastal boundary. The mean of cross-shore velocities is negligible in most cases and variability in cross-shore flow occurs on short time scales. Only for vertical circulation, such as estuarine circulation (Fischer et al. 1979) and wind-driven upwelling circulation (Brink 1993), may one find a persistent cross-shore movement of near-surface waters near to the coast—but even then it is weak nearshore (order 0.01 m/s, Largier et al. 1993). Intuitively, one can picture a shore-spawned larva taking a day to get out of the swirling flow around rocks and in and out of coves, and a further few days before the larva is swept well away from the shore and into strong alongshore flows over the shelf. Even off a sandy beach, rip current studies have indicated that larvae may take a few hours to move out of a 100 m wide surf zone (Smith and Largier 1995; W. Schmidt and R. Guza, *unpublished manuscript*) and drifter studies have indicated that these larvae may be immediately re-entrained into the surf zone, or if they break free from the surf zone they may take several hours to move to a distance of 1 km offshore (George and Largier 1996). The weak currents and associated weak dispersion has prompted Wolanski (1994) to use the phrase ''sticky water'' to describe the tendency for nearshore retention of larvae (also observed by L. D. Zeidberg and W. M. Hamner, *unpublished manuscript*). To some extent, recirculation in the topographic eddies described in *Topographic eddies and retention zones* may just be considered as part of this slow, ''sticky,'' boundary layer—but the major topographic flow features are bigger, fixed, more persistent, and thus more retentive than the general eddying nature of sheared flow near the shore. The boundary layer at the coastal boundary may be observed at a variety of scales, and with a variety of strengths. It is evident as a reduced mean and reduced standard deviation in both alongshore and cross-shore flows; for example off northern California (Fig. 2; Largier et al. 1993, Wing et al. 1995*b*) and southern California (Lentz and Winant 1986).

Cross-shore dispersal near to the shore is primarily due to diffusive motions. When aggregating over time and space scales relevant to larval dispersal of a population, cross-shore advection (mean flow) is very weak and effectively zero. Just as for alongshore diffusion, cross-shore diffusion is scaled by the product of a cross-shore velocity and excursion length associated with the flow variability. Based on Prandtl's ''mixing length'' l, in a boundary layer one obtains a cross-shore diffusivity $K_y = l^2(d_y u)$, where the length scale l is proportional to the distance to the boundary y—the proximity of the shore precludes larger scale motions. Expecting the alongshore velocity shear $d_y u$ to be constant or decrease with distance from the boundary, one can approximate $K_y = ky^a$ where $1 < a < 2$ and $a = 2$ describes the case of constant shear whereas $a = 1$ describes the case where $d_y u$ decreases as $1/y$. This $K_y = ky^a$ dependence, consistent with oceanographic results of Arons and Stommel (1951) and Okubo (1971), is discussed further by Csanady (1973) and Okubo (1980). Observations in the coastal ocean off the west coast of the USA support the scale argument of increasing K_y with distance offshore (Fig. 3). Very small values of K_y are observed close to the shore and empirical relationships for specific portions of the shelf (dominated by specific forcing) yield relations of the form $K_y = ky^a$. Through analysis of drifter data over the northern California shelf, Davis (1985) obtained $K_y = 0.008y$ and through analysis of moored current meter data, Largier et al. (*unpublished manuscript*) obtained $K_y = 6.10^{-6}y^2$, with comparable values in the region of study over the shelf ($y \approx 1$–10 km). Further, a comparison of different studies indicates an exponential increase in K_y with distance from the shore (Fig. 3A): in wave-driven nearshore waters ($y \approx 0.1$ km) values on the order of 1–10 m^2/s are found (Smith and Largier 1995), whereas values on the order of 100 m^2/s are found over the wind-driven shelf ($y \approx 10$ km; Davis 1985, Largier et al. 1993), and much larger values on the order of 1000 m^2/s or greater are found in the offshore waters of the California Current ($y \approx 100$–1000 km; Swenson and Niiler 1996).

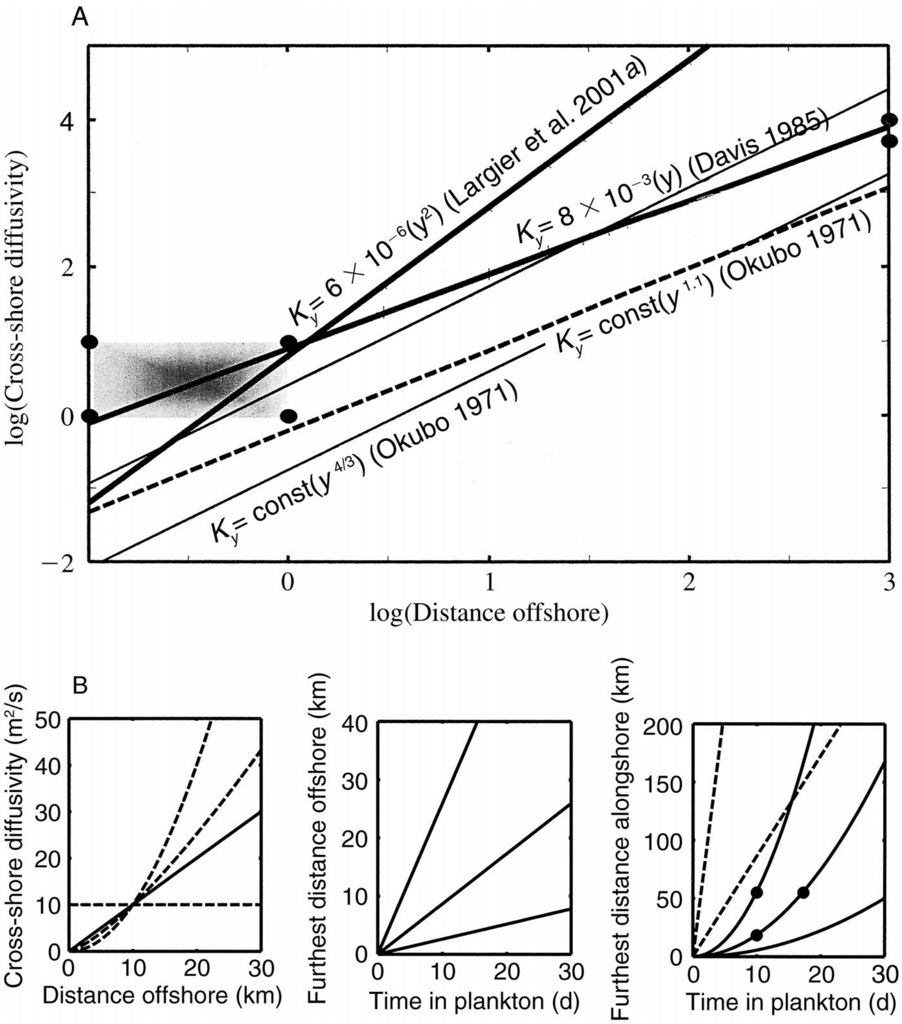

FIG. 3. (A) Empirical estimates and theoretical scaling of cross-shore diffusivity (m^2/s) as a function of distance offshore (km). The shaded rectangle represents a variety of values obtained from nearshore drifter, current meter, and tracer studies (Smith and Largier 1995, George and Largier 1996; J. L. Largier and D. Ollis, *unpublished manuscript*), and dots at large scale represent the results of drifter studies in the California Current System (Swenson and Niiler 1996). Drifters deployed over the northern California shelf by Davis (1985) and current meters deployed by Largier et al. (1993) yield empirical relationships reported by Davis (1985) and J. L. Largier, L. W. Botsford, A. M. Hastings, J. Pilliod, and C. Moloney (*unpublished manuscript*), respectively. A simple mixing length scaling, as used by Arons and Stommel (1951) for tidal waters, gives y^2 dependence over the shelf. In addition, the $y^{1.1}$ dependence obtained by Okubo (1971) is plotted as a dashed line, and the theoretically derived $y^{4/3}$ fit against dye dispersion data (Okubo 1971) is plotted as parallel fine lines. Note that all of these values represent variability on the time scale of days to months and do not include interannual variability. (B) Functional forms for cross-shore diffusivity, distance offshore for larvae, and distance alongshore for rapidly dispersing larvae released at the shoreline at time zero (numerical values are illustrative). In the left panel, cross-shore diffusivity K_y is shown as a function of distance y from the shoreline. Dependences are shown for K_y constant, $K_y \propto y$ (solid line), $K_y \propto y^{4/3}$, and $K_y \propto y^2$. In the middle and right panels, the scenario of K_y scaled linearly by y is explored for planktonic larvae. In the middle panel, the distance offshore of most rapidly dispersing larvae σ_y is given as a function of time in the plankton. The middle line represents the case where $\partial_t\sigma_y = 0.01$ m/s (rate of expansion of envelope of larval distribution), while the other lines represent $\partial_t\sigma_y$ of 0.03 and 0.003 m/s. In the right panel, σ_x the alongshore distance of these furthest offshore (rapidly dispersed) larvae is shown, assuming a cross-shore shear in the alongshore flow increasing from 0 at the shore to 0.5 m/s at a distance of 50 km offshore. (For comparison, dashed lines give alongshore dispersal distances for larvae that are immediately subject to maximum alongshore currents of 0.1 and 0.5 m/s.) A threefold increase in the 18-km alongshore dispersal after 10 d (dot on middle line), to 55 km, can be obtained either by increasing the dispersal time 1.7-fold to 17 d or by increasing K_y threefold (dot on upper line). [Note that during onshore diffusion as well as during offshore diffusion a similar dependence occurs, so that a typical rapidly dispersing larva in the plankton for 20 d would disperse offshore for 10 d and back onshore for 10 d, experiencing an alongshore movement of ∼18 km during each phase and thus achieving a total dispersal of order 36 km over 20 d.]

In Fig. 3B, the four most common forms of $K_y \propto y^a$ dependence are represented (K_y constant, $K_y \propto y$, $K_y \propto y^{4/3}$, $K_y \propto y^2$) with proportionality coefficients chosen to yield $K_y = 10$ m^2/s at $y = 10$ km in all cases. The rate at which the envelope of larval concentration will spread diffusively offshore $\partial_t\sigma_y$ (where σ_y^2 is the cross-shore variance in larval distribution) is then shown in the middle panel for linear dependence ($a = 1$), for which $\partial_t\sigma_y$ is constant over time. With reference to Csanady (1973), Okubo (1980), and the above discussion, it is expected that $a \geq 1$. In scenarios where $a > 1$, the envelope of larval concentration will diffuse offshore more rapidly (e.g., $\partial_t\sigma_y \propto t^{1/2}$ for $K_y \propto y^{4/3}$, Okubo 1980). However, even for linear $K_y(y)$ dependence, there is a nonlinear relation between alongshore dispersal and time in the plankton, due to interaction with boundary layer shear in alongshore flow (right panel of Fig. 3B; see also Csanady 1973, chapter 5). For nonlinear $K_y(y)$ dependence, the alongshore dispersal will be even more nonlinear. The further offshore the most dispersed larvae move, the stronger the alongshore currents to which they are exposed and the more rapid the alongshore spread of larvae $\partial_t\sigma_x$ (where σ_x^2 is the alongshore variance in larval distribution)—thus doubling larval period more than doubles σ_x (right panel, Fig. 3B). Thus, the coastal boundary layer affects alongshore dispersal in two ways: by the inclusion of alongshore velocities less than the characteristic velocities away from the coast; and by the heavy weighting of these slow velocities in obtaining a lagrangian mean velocity (due to the fraction of the planktonic period that larvae of nearshore populations spend in these nearshore waters).

Slow nearshore currents are thus disproportionately important in the dispersal of successful settlers, as they spend several days moving through this coastal boundary layer on their way offshore and again on their way back in to settle. For example, for a 30-d planktonic period, a typical successful larva will move offshore for 15 d and then back onshore for 15 d and even the more rapidly dispersed larvae may move no further than 10 km offshore in the scenario represented by Fig. 3B. These larvae would only briefly experience strong alongshore flows. In particular, for a high probability of settlement, larvae with planktonic periods of several days are likely to complete their planktonic life within a kilometer or two of the shore—in waters characterized by weak mean alongshore flow over the larval dispersal season (the population-relevant time scale), e.g., Fig. 2. This pattern is consistent with the results of Shanks et al. (2003), who show the alongshore ‘‘dispersal distance’’ to be <1 km for species with planktonic periods of several days or less. In contrast, Shanks et al. (2003) show that species with planktonic periods of several days or more exhibit a ‘‘dispersal distance’’ of >10 km (with a few exceptions due to active behavior), and dispersal distances on the order of 100 km for larvae in the plankton for a month or two—that is a two order of magnitude increase in L_x for a one order of magnitude increase in larval period (see Fig. 3B, right-hand panel).

The period in the plankton is thus a major determinant of alongshore dispersal within a metapopulation, with a strong nonlinear relation between alongshore dispersal distance and planktonic duration (Fig. 3B). In addition, cross-shore diffusivity K_y is also a major determinant of alongshore dispersal for nearshore populations in that it controls the time for larvae to move offshore and into strong alongshore flow. These two controls on alongshore dispersal are illustrated in the right panel of Fig. 3B. The K_y control is particularly interesting as it can be exerted either by the organism (through larval behavior—see *Vertical shear*) or by the environment (varying in both space and time). Where K_y is small, or where low K_y values extend far offshore, larvae will experience limited alongshore transport in spite of strong alongshore flow further offshore (these ‘‘sticky’’ waters offer retention to larvae released nearshore). Thus, by bringing about small changes in cross-shore dispersal, planktonic larval populations can increase or decrease alongshore dispersal.

While the above discussion focuses on the most rapidly dispersed larvae, in the interests of describing the spatial extent of larval distribution σ_x, all larvae are subject to ‘‘shear dispersion’’: cross-shore dispersal in the presence of a cross-shore shear in alongshore flow will result in an alongshore spreading of the larval concentration. Shear dispersion has been well studied (e.g., Fischer et al. 1979, Okubo 1980). Essentially, the cross-stream mixing of a patch of larvae will subject different larvae to different alongshore velocities, thus stretching out the patch alongshore. Okubo (1994) scales the alongshore diffusivity K_x due to cross-stream mixing by $(d_y u)^2 K_y t^2$, and by $u_{\max} L_y^2/K_y$ once the patch has diffused to fill the shear zone of width L_y (after time $t = L_y^2/K_y$). Larval dispersal typically occurs during times $t < L_y^2/K_y$ so that larger cross-shore diffusion K_y will subject larvae to alongshore shear sooner and the alongshore diffusion will increase earlier in the larval dispersal phase. Although not straightforward, it is clear that changes to cross-shore diffusion (whether induced by environment or larval behavior) can bring about change in alongshore diffusion as well as alongshore advection. As discussed in *The importance of describing dispersal with two parameters*, species can thus increase or decrease their alongshore connectivity by developing characteristics that alter their cross-shore diffusivity (see *Vertical shear*).

Vertical shear

Vertical shear is common in coastal waters and vertical movement of plankton has a profound effect on both cross-shore and alongshore dispersal (e.g., Hannah et al. 1998), due to interaction with vertical gradients in horizontal currents. Vertical shear results from bottom frictional drag, wind stress on the surface and/or stratification and is well represented even in long-term mean velocity structure (e.g., Fig. 2). Planktonic organisms may be moved up and down by vertical mixing (passive dispersal), or they may intentionally change their depth by migration or changes in buoyancy (active dispersal). Vertical movements are particularly important as small vertical distances separate different flow directions and speeds, different water types, and different meroplankton destinations.

Active vertical behavior is invoked in the dispersion of many species and appears to be specifically important in predictable stratified flows to/from estuaries (Boehlert and Mundy 1988) and in predictable sheared tidal flows in shallow water (Rothlisberg 1982, DiBacco and Chadwick 2001). This ''intentional'' vertical behavior—active vertical migration cued to flow structures—is extremely effective as it results in a correlation between the time-varying flow velocity and larval concentration (see *Formulating the dispersion problem: advection and diffusion*). Shanks (1995) reviews various such mechanisms for cross-shore dispersal and it rapidly becomes apparent that ''anything is possible'' unless improved information on the specific oceanography and larval biology is available to constrain one's imagination. However, other vertical migrations are motivated by predation/food and these movements may be uncorrelated with time dependence in the vertical structure of currents, as are vertical movements due to mixing. As there is so little specific information on active migration scenarios, here the focus is rather on the simpler and more general problem of passive larvae and noncorrelated vertical migrations. These uncorrelated migrations serve to average over the alongshore and cross-shore currents found at different depths.

In directional flows, the direction and speed of the flow is characterized by near-surface currents, which tend to be faster and/or in a different direction to currents at depth. This shear is particularly evident in alongshore currents and any vertical mixing of meroplankton away from the surface will tend to reduce alongshore advection. For example, in the northern California upwelling system, the annual mean depth-averaged alongshore flow is northward for a distance of 10–20 km from the shore, in spite of a mean southward wind forcing and mean southward surface currents (Largier et al. 1993). In addition to reducing mean alongshore directional transport, vertical shear increases alongshore diffusive spreading of a patch of larvae through the process of shear dispersion (described in *The coastal boundary layer* in the context of cross-shore shear in alongshore flow): Given that larvae mix quickly through the water column, alongshore diffusivity K_x is scaled by duH^2/K_z, where H is water depth and du is the velocity difference through the water column. Thus, one can see the importance of vertical mixing—as expressed by K_z (vertical eddy diffusivity)—in determining alongshore diffusion of larvae.

Cross-shore dispersion is also affected by random vertical migrations of meroplankton. We have already discussed how cross-shore advection is weak in the absence of vertical circulation—a persistent flow structure where the surface and bottom waters move in opposite directions (as in upwelling). However, in the presence of vertical circulation, vertical mixing of plankton will result in individuals experiencing both the near-surface offshore flow and near-bottom onshore flow, thus averaging out the vertical circulation. The classic example is that of copepods in the vertically sheared upwelling circulation off Oregon (Peterson et al. 1979): diel vertical migrations reduce the net advection to near zero and allow the copepod population to remain on the shelf. Again, the net effect is to reduce the mean cross-shore transport (advection), and to enhance the ''stickiness'' of the boundary. In turn, this retains the larvae of nearshore populations in the weaker alongshore flows of the coastal boundary layer, and thus reduces the net alongshore transport (as discussed in *The coastal boundary layer*). By the same interaction of alongshore and cross-shore transport, larvae that do exhibit active migrations correlated with cross-shore flows can move further offshore within a given planktonic period and thus take advantage of more time in the stronger alongshore flows found offshore. As discussed in *The coastal boundary layer*, and with reference to Fig. 3B, even a small advective transport in the right direction (offshore initially and onshore later) can yield significant increases in both alongshore advection and diffusion. Vertical migrations do not appear to be that important to enhancing cross-shore diffusivity. While vertical migration will introduce more variability in flow speeds experienced, the range and level of variability is similar to that due to temporal fluctuations. Nevertheless, even a small increase in cross-shore diffusivity may be important as it will enhance the alongshore diffusion through shear dispersion, as discussed in *The coastal boundary layer*.

THE IMPORTANCE OF DESCRIBING DISPERSAL WITH TWO PARAMETERS

From the foregoing discussions, it is clear that both advective and diffusive fluxes are important in the dispersion of larvae in the coastal ocean. Not only are they both quantitatively significant, but the interplay between the two dispersal terms leads to a variety of fundamentally different dispersal scenarios. Here the dependence of dispersal (and hence connectivity) on the relative strength of advection and diffusion is explored for the simplest case of uniform advection and diffusion over a finite spatial domain (Botsford et al. 1994, Gaines et al. 2003). Described by the advection–

diffusion equation (*Formulating the dispersion problem: advection and diffusion*), an input of larvae at one location will be mixed outward (diffusion) and transported downstream (advection), yielding a Gaussian distribution (Fig. 1). The offset L_{adv} and width L_{diff} of the Gaussian reflect advection and diffusion values, respectively, and the period of dispersal. These dispersion length scales can be compared with reserve/habitat length scales L_{res} (size of marine reserve, suitable habitat, or spawning region) and L_{gap} (distance between patches of suitable habitat, reserve spacing).

In this exercise, a unit amount of larvae is spawned at each 1-km site in the 200-km domain (Fig. 1). Outside of the domain, there is no population, no suitable habitat, and no possibility of recruitment. For zero dispersion, the same unit of larvae will settle back at each site—mortality (including offshore wastage) is poorly known and set to zero in this exploration of the effects of dispersion. For nonzero dispersion, the spawn from a given site will settle mostly at other sites and the settlement at the given site will be due to a sum of contributions from many sites. To obtain a nominal level of settlement required to sustain the population at each site, the rationale of Largier et al. (*unpublished manuscript*) is followed. If one starts with 2×10^5 larvae spawned by a highly fecund pair of benthic individuals, for example, and 1% survive the planktonic phase and 1% survive the adult phase between settlement and reproduction, then it is necessary for 10% of larvae that survive the planktonic phase to settle to maintain the population reproductive potential. For specific taxa, this settlement proportion may be larger (if fecundity less or mortality more) or smaller (if fecundity more or mortality less). In the following, critical settlement levels of 0.1 and 0.01 are considered. For the 30-d scenario presented in Fig. 4, a critical settlement of 0.01 is reasonably easily achieved at the center of a large and continuous habitat (Fig. 4B), other than for cases of strong advection ($u > 0.1$ m/s; $L_{\mathrm{adv}} > 26.0$ km) and weak diffusion ($K < 1000$ m^2/s; $L_{\mathrm{diff}} < 50$ km)—where L_{adv} significantly exceeds L_{res}. A settlement of 0.1 is found for moderate to low advection, and in many circumstances there is an excess supply of settlers in mid-domain. For low diffusion values (move along x axis), settlement remains close to unity for small advection and goes to zero rapidly as advection length scales exceed 100 km (the distance to the upstream boundary)—all larvae are washed out of the domain by strong mean flows. This is an ''advective'' flow field ($L_{\mathrm{adv}} \gg L_{\mathrm{diff}}$). For low advection values (move along y axis), settlement remains close to unity for small diffusion and decreases to zero slowly as the diffusion length scales approach and exceed the 100 km distance to the boundaries. This is a ''diffusive'' flow field ($L_{\mathrm{adv}} \ll L_{\mathrm{diff}}$). See Fig. 5 and *Discussion* for further discussion of the habitat/reserve size relative to the dispersion length scales L_{adv} and L_{diff}.

Local settlement (uniform at all sites in this uniform environment) is plotted in Fig. 4D. It is unity in the absence of advection and diffusion and only important for short advective and diffusive length scales. Local settlement is potentially self-sustaining (>0.01) for $L_{\mathrm{adv}} < 20$ km and $L_{\mathrm{diff}} < 50$ km. Diffusion mitigates the advective removal of larvae—flow variability ensures that while most larvae are carried downstream, some larvae experience zero net displacement and can settle back at their origin.

In Fig. 4A and C, settlement at sites on the edges of the suitable habitat is shown—downstream and upstream ends. In a nondiffusive scenario, settlement goes to zero for advection length scales L_{adv} of 200 km and 0 km, respectively; these being the distances to the upstream boundary L_{bndy}. For zero advection, both edge sites show the same decrease in settlement as increasing diffusion results in loss of larvae across the domain boundaries; but this decrease is weak as increasing diffusion also ensures that larvae from other sites are delivered to these edge sites. In all of these plots (Fig. 4A, B, C) where advection dominates, the contour lines have a positive slope once L_{adv} exceeds L_{bndy}, i.e., settlement increases for increasing L_{diff}—diffusion mitigates the ''wash out'' effect of advection. In this part of the contour plots, settlement depends on $L_{\mathrm{adv}}/L_{\mathrm{diff}}$. At the upstream site (Fig. 4C), a settlement of 0.1 is obtained for $L_{\mathrm{adv}}/L_{\mathrm{diff}} \approx 1.2$, and a settlement of 0.01 is obtained for $L_{\mathrm{adv}}/L_{\mathrm{diff}} \approx 2.4$. For larger values of $L_{\mathrm{adv}}/L_{\mathrm{diff}}$, the upstream edge of the domain does not receive adequate settlement to maintain the spawning population.

Clearly, it is necessary for the upstream boundary of the population to be sustained. So what happens if settlement at upstream edge is too small? The spawning population at the upstream edge must decrease and in turn the population at adjacent sites. Ultimately, a gradient region develops that is steady at population time scales. Adult population and spawning decreases towards the upstream boundary of the habitat, introducing a nonzero larval concentration gradient and an upstream diffusive flux Kd_xC that mitigates the downstream advective flux uC. This is achieved with an exponential distribution of spawning population over a distance scaled by $L_{\mathrm{diff}}^2/L_{\mathrm{adv}}$. For weak relative diffusion, the gradient region is narrow (large gradients d_xC), whereas for stronger diffusive motions the gradient is weaker and the region is broader. However, for situations where advection is too strong (diffusion relatively weak), or for situations where low population densities are not viable (e.g., broadcast spawners), this region is also not sustainable and the upstream edge slips downstream and the population is washed out (Gaines et al. 2003).

Adequately accounting for diffusive effects in larval dispersal explains why populations are not washed out in directional flows. For example, for realistic along-

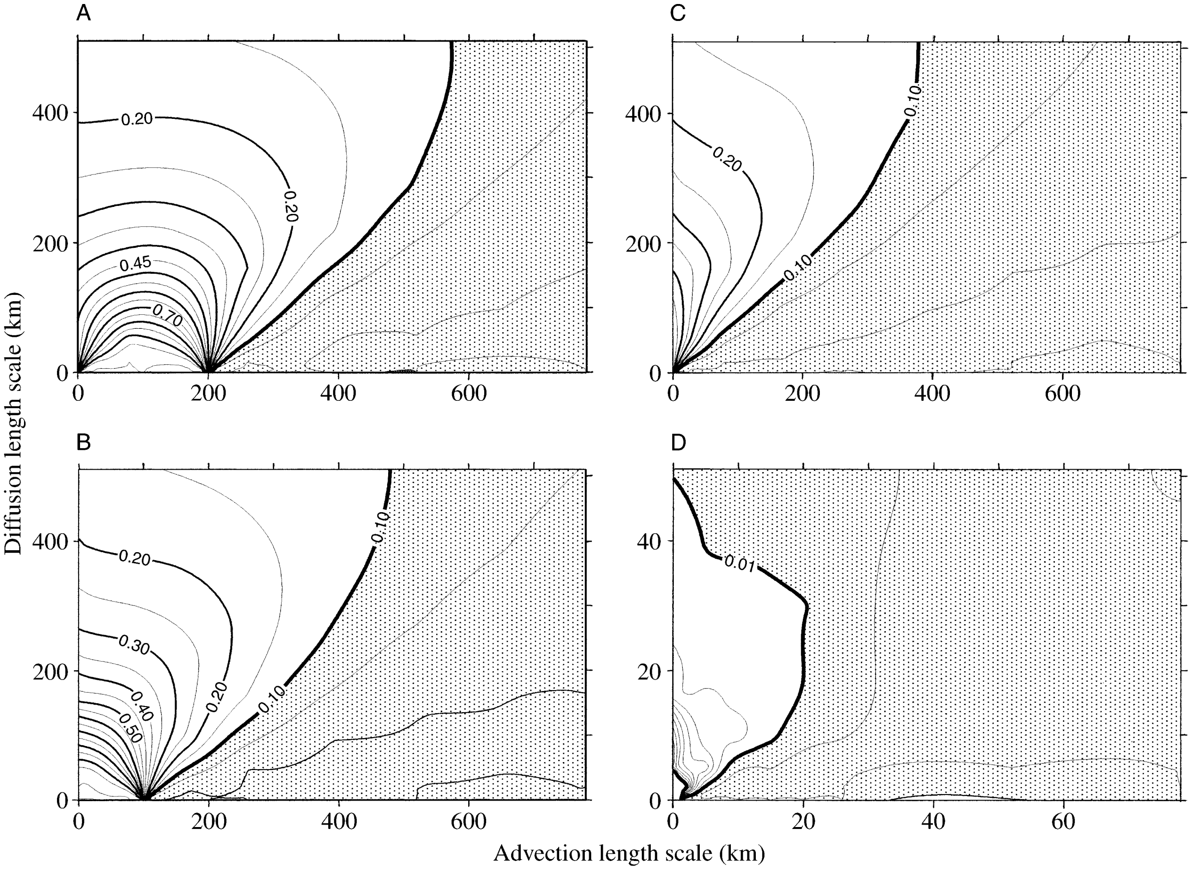

FIG. 4. Settlement levels as a function of advection and diffusion lengths L_{adv} and L_{diff}, given uniform Gaussian dispersal over the population domain (see Fig. 1). While the patterns are scale independent, these figures were developed to illustrate the case for larvae that are planktonic for a month ($T = 30$ d). The advection length L_{adv} is scaled by uT, so that 0.01 m/s corresponds to 26 km and 0.3 m/s to 780 km, and the diffusion length L_{diff} is scaled by $[K_x T]^{1/2}$, so that 10 m^2/s corresponds to 5 km and 10 000 m^2/s to 160 km. (A) Total settlement at site at downstream edge of 200-km domain. Contours are at intervals of 0.05; the critical level of 0.1 is plotted as a bold line with settlement less than 0.1 shaded. (B) Total settlement at site in middle of 200-km domain. Contours and shading are as above. (C) Total settlement at site at upstream edge of 200-km domain. Contours and shading are as above. (D) Local settlement—same at all sites. Note that axes extend only to $L_{adv} = 78$ km and $L_{diff} = 51$ km and that the contour interval is 0.01, with bold lines for settlement of 0.1 and 0.01; local settlement less than 0.01 is shaded. There is unit larval release from each 1-km site, and there is zero mortality (and no offshore larval wastage), so if larvae do not move alongshore beyond the ends of the domain, settlement should be unity everywhere. Contour plots are generated from a grid of values and small-scale features, specifically in panel (D), are an artifact of the contouring procedure.

shore diffusivity values for larvae that are planktonic for a month (e.g., 1000 m^2/s; $L_{diff} = 50$ km), the upstream site can be sustained (settlement > 0.01) in the face of advective flows up to 0.1 m/s ($L_{adv} = 260$ km), a strong flow for typical season averages (e.g., Fig. 2); see also Gaines et al. (2003). The complexity of coastal ocean flows is sampled many times as one aggregates over longer time and space scales, thus K tends to be large (*Scale-dependence of parameter values*) and L_{adv}/L_{diff} tends to be small, conditions favorable for population-sustaining settlement. Species with adults that spawn throughout an upwelling season, or that spawn for more than one year, capture more flow variability. The diffusive effect is thus larger and the upstream anchor site is more likely to be sustained. Larvae can thus increase the relative strength of alongshore diffusion (lower L_{adv}/L_{diff}) by lengthening the spawning season or by increasing the adult life expectancy, while maintaining advective distances by maintaining the planktonic period of individual larvae. By increasing larval season or number of years of reproductivity, the probability increases of spawn catching a flow event that is counter to the mean flow direction (e.g., Gaines et al. 2003). This control on dispersal pattern is an alternative to adopting larval behavior that enhances cross-shore exchange K_y (as discussed in *Oceanographic phenomena: The coastal boundary layer* and *Vertical shear*).

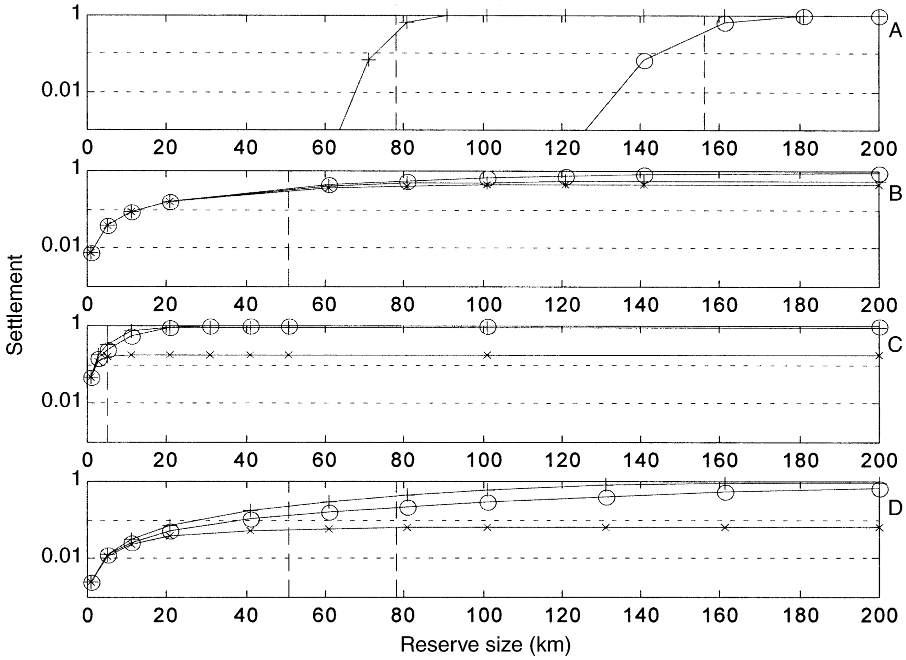

FIG. 5. Settlement at upstream (×), mid-domain (circles), and downstream (plus symbols) sites as a function of reserve size. Critical settlement levels of 0.1 and 0.01 are plotted as dotted lines. More detail is provided in *Discussion: The importance of describing dispersal with two parameters.* (A) Advective scenario (L_{adv} = 78 km, L_{diff} = 5 km). Dashed vertical lines denote L_{adv} and $2L_{\text{adv}}$. (B) Diffusive scenario (L_{adv} = 5 km, L_{diff} = 51 km). The dashed vertical line denotes L_{diff}. (C) Weak advective–diffusive scenario (L_{adv} = 5 km, L_{diff} = 5 km). The dashed vertical line denotes $L_{\text{adv}} = L_{\text{diff}}$. (D) Moderate advective–diffusive scenario (L_{adv} = 78 km, L_{diff} = 51 km). The dashed vertical lines denote L_{adv} and L_{diff}.

DISCUSSION

The interplay of advection and diffusion

The interplay of two dispersion parameters allows one to see the diversity of dispersal options open to a population with planktonic larvae. The wide spread of larval destinations or sources (Fig. 1) argues that one can simultaneously have local recruitment and recruitment at distant sites. The discussion of a single-parameter ''dispersal distance'' is not appropriate and the binary classification of dispersal (local or remote settlement, open or closed population, sink or source) precludes improved understanding of the multiple strategies offered by dispersal. Recognizing the variety of dispersal outcomes for any given population, it is not surprising that different estimates/definitions of a ''dispersal distance'' provide conflicting answers (*Introduction*)—some estimates addressing the maximum possible distance (how fast a signal can move through or a front can advance) and others addressing near-local dispersal.

One can categorize dispersal into advective or diffusive systems based on the relative strength of the terms (relative length scales). For $L_{\text{adv}}/L_{\text{diff}} \gg 1$, advection dominates, and one may think of the ''river channel'' dispersal paradigm—downstream transport of a larval cloud. For $L_{\text{adv}}/L_{\text{diff}} \ll 1$, diffusion dominates, and one may think of the ''larval pool'' dispersal paradigm—dispersion of larvae in both directions and mixing of larvae from multiple sources, yielding a uniform alongshore distribution. However, in most oceanic settings, L_{adv} and L_{diff} are comparable, and one is better served by thinking about Gaussian dispersal (Fig. 1).

Species can exert control on the effective strength of advection and diffusion and thus on the advective–diffusive balance through timing of spawning, duration of spawning, planktonic period, adult life expectancy, and larval behavior. It is generally appreciated that adults may choose spawning time to make use of desirable flows, and that the duration of the planktonic phase determines the distances over which larvae may be carried in the given flows. However, adults can also control the advection–diffusion ratio, which is critical to sustaining the upstream boundary. As discussed in *The importance of describing dispersal with two parameters*, this is achieved through the length of the spawning season and/or the number of years in which an adult spawns. Both of these strategies can increase the effective diffusivity at population-relevant time scales by increasing the probability of some larvae catching flows opposed to the mean flow. The advection length, based on mean flow and planktonic period, is independent of these selections for larval season and adult life expectancy.

In addition to options in spawning, species can exert control on advection and diffusion by larval behavior.

By vertical migrations correlated with temporal fluctuations in flow, larvae can bring about many specific dispersal outcomes, particularly in environments where flow is deterministic (e.g., estuarine tides and vertical circulation). However, in this work, vertical migrations uncorrelated with flow variability have been shown to be important in that they increase or decrease cross-shore diffusive fluxes, which in turn allow planktonic larvae to experience increased or decreased alongshore advection and diffusion (Fig. 3B; *The coastal boundary layer*). In this context, it becomes evident that even weak swimming abilities can have a significant impact on larval dispersion—not only in vertical migration, but also if swimming is horizontal and directed. A mean cross-shore movement (advection) due to swimming can make a critical difference in the time it takes a larva to get into or out of a strong alongshore flow (e.g., shoreward swimming of 0.01 m/s will move a larva 8.6 km over 10 d). Cross-shore movements have a large affect on alongshore dispersion owing to strong shear in alongshore flow. Further, even alongshore directed swimming at speeds of order 0.01 m/s can introduce an important change in alongshore advection and settlement (e.g., consider the effect in Fig. 4 of changing advective length scale by 26 km).

The importance of the size of a marine reserve

The interplay of advection and diffusion length scales becomes specifically interesting in the case of a marine reserve, or a spatially confined habitat and spawning population. Here one must consider the length scale of the unexploited adult habitat L_{res} relative to the length scales of dispersion, L_{adv} and L_{diff}. For a single reserve to be sustainable in itself, one requires the reserve L_{res} to be larger than dispersion length scales, such that sufficient dispersing larvae are contained within the reserve. In the smallest reserve (single site), settlement is only from local spawn. Local settlement is typically low (Fig. 4D), and inadequate for advective scenarios ($L_{adv} \gg L_{diff}$). In contrast, settlement in large reserves is generally high, although it may be low at the upstream edge of habitat when dispersal is primarily advective. In Fig. 5, settlement at upstream, downstream and mid-domain sites is plotted as a function of reserve size for a variety of advection–diffusion scenarios. No account is taken of subsequent recruitment and reproduction, and thus no account of population increase or decrease over time. Zero spawning is assumed outside of the reserve and within the reserve there is a uniform unit spawning. The interest is simply in how many larvae settle at selected sites under a variety of length scale combinations (L_{adv}, L_{diff}, L_{res}).

For an advective scenario (Fig. 5A), settlement depends strongly on the reserve size, with a step change at the critical L_{res}. However, the critical size of the reserve depends on whether one is interested in upstream, mid-domain, or downstream sites. The upstream site can only receive sufficient settlement if advection is zero or diffusion is significant (Fig. 5B, C, D). The critical L_{res} value for the downstream site is L_{adv} and for the mid-domain it is $2L_{adv}$. However, if there is no recruitment at the upstream site, one expects the spawning population to disappear and the spatial extent of spawning to contract—eventually the total population will be washed out. In this paper, it is argued that effective diffusivity is often stronger than assumed and thus that populations are not as readily washed out as may initially seem to be the case. The effect of larger diffusivity is shown in Fig. 5D, spreading out the sharp drop in settlement vs. reserve size.

For a diffusive scenario (Fig. 5B), there is no spatial asymmetry in the dependence, with upstream and downstream sites exhibiting similar dependence. There is no critical reserve size (not a binary classification into ‘‘big enough’’ and ‘‘not big enough’’). The mid-domain site, removed from diffusive losses over the reserve boundaries, receives full settlement when $L_{res} \gg L_{diff}$. At all sites, settlement levels are constant and high for $L_{res} > L_{diff}$, with little additional benefit in increasing reserve size beyond L_{diff}. It is only for $L_{res} \ll L_{diff}$ that settlement drops below 0.1 and settlement only drops below 0.01 for reserves small enough that $L_{res} < L_{adv} = 5$ km (Fig. 5B).

Further insight is gained from considering scenarios where advection and diffusion are comparable, where L_{adv}/L_{diff} is on the order of one (Fig. 5C, D). Comparing Fig. 5A and D, one can see the effect of increased diffusivity in decreasing the slope of dependence of settlement on reserve size. And, in comparing Fig. 5A and C, one can see the effect of decreased advection in shifting the critical reserve size to smaller lengths. The difference in critical reserve size ($L_{res} = L_{adv}$) is not as apparent in comparing Fig. 5A and B as the increased diffusivity has spread out the dependence and reduced the slope. However, one can see the effect of advection in reducing maximum settlement at the upstream site by comparing Fig. 5B and D. Fig. 5C presents a scenario of negligible dispersion of larvae (e.g., larvae in the plankton for short periods), with strong settlement for reserves larger than 5 km (L_{adv}). In Fig. 5D, both L_{adv} and L_{diff} are larger (but still moderate, see Fig. 4). Here settlement generally increases with reserve size, but at the upstream site that must anchor the population, settlement is constant once L_{res} exceeds L_{diff}. Settlement at the downstream site only asymptotes once reserve size exceeds $L_{adv} + L_{diff} = 129$ km and at the mid-reserve site as reserve size exceeds $2(L_{adv} + L_{diff})$.

Environmental variability

In this work, the flow environment has been considered to be uniform and steady at scales of the population. Variability at smaller scales has been aggregated and represented by diffusivity. In the time domain, variability is aggregated over the larval season and over the number of years for which adults are reproductive. In the space domain, variability is aggregated over dispersion length scales. However, where variability is at larger space or time scales this should be explicitly represented in space and time dependence of parameters u and K. For example, in Gaines et al. (2003), the effect of a flow reversal after 15 yr (longer than adult reproductivity) has the potential to counter an extinction trend. In particular, one would then expect a downstream slip of the upstream population edge with a sudden upstream movement of the edge after 15 yr. Observations in the region of this upstream fringe would reveal local extinction and recolonization over time.

In a similar way, future work should include alongshore variation in dispersion parameters (e.g., retention regions). This should lead to local maxima and minima in settlement and the possibility that some regions are more likely to act as an upstream anchor than are other regions. In retention zones, regions of weak or recirculating flow, the value of u is small, and one can expect enhanced local settlement (Fig. 4D) and a greater chance of enough settlement to hold an upstream boundary. If the population in this region is lost through overexploitation or natural catastrophe, one may expect the upstream population boundary to slip downstream rapidly to the next retention zone (cape/bay). Alongshore diffusivity may be locally enhanced or suppressed in the retention zone, depending on the nature of the flow. An eddy recirculation in the lee of a cape (*Topographic eddies and retention zones*) would exhibit low u and high K due to the ready alongshore exchange within the recirculating region. On the other hand, a region of slow flow (e.g., an enclosed bay) would exhibit low K in addition to u and one expects the highest levels of local settlement there. A third retention effect is offered in the absence of capes and bays, but where there is a wide zone of low cross-shore diffusivity near the coastal source of larvae, or a zone of weak alongshore currents near to the coast. Either situation results in the larvae experiencing an extended period of slow alongshore movement, as discussed in *The coastal boundary layer* and represented in Fig. 3B. So, in a nonuniform environment, the position of the upstream boundary of the population can be determined either by a change in habitat (adult success) or by a change in dispersal (larval success).

In an environment where a population is not continuous, an important aspect of dispersal is that larvae can disperse from one patch of habitat or protected reserve to another—spanning the distance but not overshooting. From the above discussion, one can see that connectivity between small patches requires $L_{\mathrm{gap}} > (L_{\mathrm{adv}} - L_{\mathrm{diff}})$ and $L_{\mathrm{gap}} < (L_{\mathrm{adv}} + L_{\mathrm{diff}})$, where L_{gap} is the interpatch length scale. The distance between patches becomes less critical as L_{diff} increases, and more critical as L_{diff} decreases and advection is more dominant. In a diffusive environment (relatively weak advection), one requires only a loose condition $L_{\mathrm{gap}} < L_{\mathrm{diff}}$, whereas in an advective environment one requires a more exact match $L_{\mathrm{gap}} = L_{\mathrm{adv}}$ for small reserves. Hence, it is easier for a population in a patchy environment to persist (or to conserve a population through marine reserves) if the species exhibits long planktonic period, larval season, or reproductive life expectancy (all leading to larger K_x). Long larval seasons and long reproductive lives provide the increased L_{diff} without obtaining large L_{adv} that may result in overshoot of available patches. The alternative to diffusive dispersal is to select for a deterministic strategy, with a single spawning event cued by optimum conditions (e.g., tidal flow), and the aim of exactly obtaining L_{gap}.

CONCLUSION

The alongshore dispersal of larvae is reasonably described by two parameters, advection and diffusion, evaluated at appropriate population scales. Oceanographic data and oceanographic insight provides an essential foundation for this work. The use of more than one parameter introduces a duplicity in dispersal and the realization that some larvae may exhibit limited dispersal even in directional flow systems. It is argued that alongshore advection is generally weaker than initially expected, and that alongshore diffusion is much stronger than some authors have assumed. This yields a broader distribution of larvae, with a smaller offset and a wider diversity of outcomes. In many cases, mean dispersal is shorter than expected, but this does not exclude simultaneous long-distance dispersal. Before comparing and expecting agreement between the variety of estimates of dispersal distances listed in *Introduction*, some better and more consistent definition of dispersal is needed.

Dispersal of coastal larvae is subject to the effects of a coastal boundary layer, which is, in effect, a retention zone along the shoreline. Low cross-shore exchange results in larvae taking some time to break free from the nearshore and one may think of nearshore waters being ‘‘sticky’’ under these circumstances. Where this boundary layer of weak flow is broad, or where it incorporates a region of slow or recirculating flow, alongshore transport is weakened and retention is enhanced. The interaction of cross-shore dispersion and alongshore shear results in a nonlinear relation between dispersal length and time in the plankton (*The coastal boundary layer*; Fig. 3B) and perhaps explains the separation of Shanks et al. (2003) data into two groups: short and long dispersal distances. In essence, larvae must go offshore to get alongshore. Thus, control on alongshore transport can be exerted through organisms controlling their vertical and cross-shore movements. This can be achieved by choices in spawning time/depth/location, by vertical behavior of the larvae, and/or by directed swimming in the vertical or cross-shore directions.

While discussions such as this paper provide insight, the understanding and quantification of larval dispersal is severely constrained by a lack of appropriate data. In addition to more dispersion data (drifters, dye, etc.) and analyses of dispersal probability, diagnostic methods need to be developed. This is a challenge, as much for oceanographers as ecologists, and it will take a collaboration of these disciplines to resolve this question. The challenge to oceanographers is to quantify the flow on appropriate scales and to do this in concert with determinations of larval concentration on the appropriate scale. Ultimately, fluctuations in flow u' and concentration C' need to be resolved to properly evaluate the diffusive term $Kd_xC = u'C'$. The statistical approach adopted in this discussion may need to give way to approaches that recognize organized flow features and larval distributions observed in the coastal ocean (e.g., Wing et al. 1998*b,* Nishimoto 2000). However, this work will lack value unless accompanied by more definite information on larval characteristics for species of interest—an equally daunting task. While it appears necessary to parameterize larval dispersal in population models, owing to the large difference in scale, this needs to be reviewed. Can it be done meaningfully, given that larval dispersal is not due to a single process or even a limited set of processes? This requires communication between oceanographer, larval/settlement ecologist, and population ecologist. We need to look at the problem in compatible ways (e.g., build a dialogue around the dispersal kernel or connectivity matrix) and be very clear about the scale of problem.

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