

# Pelagic Larval Duration and Dispersal Distance Revisited

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**Abstract.** I present dispersal distances for 44 species with data on propagule duration (PD) for 40 of these. Data were combined with those in Shanks *et al.* (2003; *Ecol. Appl.* **13**: S159–S169), providing information on 67 species. PD and dispersal distance are correlated, but with many exceptions. The distribution of dispersal distances was bimodal. Many species with PDs longer than 1 day dispersed less than 1 km, while others dispersed tens to hundreds of kilometers. Organisms with short dispersal distances were pelagic briefly or remained close to the bottom while pelagic. Null models of passively dispersing propagules adequately predict dispersal distance for organisms with short PDs (<1 day), but overestimate dispersal distances for those with longer PDs. These models predict that propagules are transported tens of kilometers offshore; however, many types remain within the coastal boundary layer where currents are slower and more variable, leading to lower than predicted dispersal. At short PDs, dispersal distances estimated from genetic data are similar to observed. At long PDs, genetic data generally overestimate dispersal distance. This discrepancy is probably due to the effect of rare individuals that disperse long distances, thus smoothing genetic differences between populations. Larval behavior and species' life-history traits can play a critical role in determining dispersal distance.

## Introduction

In 2003, I co-authored a paper (Shanks *et al.*, 2003a) that presented a data set of observed larval dispersal distances coupled with the pelagic propagule duration (PD) for these larvae and plant propagules. We found that both dispersal distances and PDs ranged over orders of magnitude (*e.g.*, meters to hundreds of kilometers and seconds to months,

respectively). We reported a significant correlation between PD and dispersal distance, but given the huge range of PDs, we suggested that this was not surprising. We also observed that the distribution of dispersal distances was bimodal; many types of larvae with PDs longer than 1 day (8 out of 19 species with PDs > 1 day) had dispersal distances less than 1 km. The dispersal distances of these organisms were as short as those for organisms with PDs shorter than 1 h. The surprisingly short dispersal distances for these organisms was due to the fact that, during their pelagic phase, they occupied the very near-bottom waters where transport would be much slower; larval behavior profoundly affected their dispersal. Lastly, we compared the distance to which these larvae would disperse if they behaved passively in a 10 cm/s steady current and found that nearly all the dispersal distances were much shorter than predicted by an admittedly very simplistic passive dispersal model. That observation also suggests that behavior, either the behavior of the larvae or the spawning behavior of the adults, can greatly decrease dispersal distance. The major weakness in that paper was the small size of the data set; we had only 27 data pairs.

That paper has been heavily cited, but surprisingly, mostly used to support the argument that dispersal distance is proportional to PD. Our observations of the importance of behavior in determining dispersal distance have largely been ignored. Since Shanks *et al.* (2003a) was published, a number of papers have presented models of larval dispersal that have attempted to estimate dispersal distance using PD coupled with oceanographic models with various degrees of sophistication (Siegel *et al.*, 2003, 2008; Kinlan *et al.*, 2005; Edwards *et al.*, 2007). Many of these models have assumed that larvae are passive; they present the null hypothesis of passive dispersal. One of the purposes of my revisiting and expanding this data set was to test this null hypothesis. With enough PDs and coupled observed dispersal distances, it

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Abbreviations: LDD, long-distance dispersal; PD, propagule duration.

should be possible to test the hypothesis that larval dispersal is passive.

In the ensuing years, researchers have used genetics data as an indirect estimator of dispersal distance, and these data are significantly correlated with PD (Kinlan and Gaines, 2003; Siegel *et al.*, 2003). There is far more data on the genetic structure of marine populations than actual observations of dispersal distance, and these data are far easier to obtain than observations of dispersal distance. If dispersal distances estimated from genetic data are similar to observed dispersal distances, then the available data on dispersal distance would be hugely expanded. With a larger set of observed dispersal distances and PDs, one should be able to determine the accuracy of genetic estimates of dispersal distance.

I found the most intriguing feature of the original study to be the fact that the distribution of dispersal distances was bimodal. This suggested that there are two general strategies for dispersal—disperse a short distance only ( $< 1$  km) or disperse tens of kilometers. Further, the data suggested that short-distance dispersal was due to behavior; larvae remaining briefly in the plankton or very close to the bottom would disperse short distances. A larger data set would more rigorously test whether the distribution of dispersal distances is bimodal.

### Materials and Methods

I found four types of data sets that can be used to determine dispersal distance. These are (1) direct observations of propagules as they dispersed, (2) experimental estimates of dispersal, (3) observations by year of the progressive spread of introduced species, and (4) the dispersal of “tagged” larvae. Shanks *et al.* (2003a) described in fair detail the types of studies used for data sets 1–3. I will describe these types of data sets briefly here and the type 4 data set in more detail. In the terminology used by Kinlan and Gaines (2003), data types 1, 2, and 4 would be considered direct data, while type 3 would be considered invasive data.

In many of the observational studies, researchers followed the fate of a larva from the time it was spawned until it settled. Most of these studies describe the behavior of the tadpole larvae of tunicates and provide average dispersal distance and propagule duration (PD) for the tracked larvae. In other observational studies, researchers described the behavior of propagules and then inferred dispersal distance given larval behavior and the distribution of settlers. These latter studies were all on organisms with very short PDs—propagules that immediately settle to the bottom and either metamorphose where they land or crawl before metamorphosing. The experimental studies measured settlement or recruitment at increasing distances from isolated populations of adults. In these studies, I estimated the dispersal

distance as the distance from the source population to the settlement plate at which settlement was deemed high enough to sustain an adult population. Many estimates of dispersal distance come from descriptions of the spread of introduced non-native species. In these studies, estimates of realized dispersal distance equal the annual extension of the spreading population.

A number of studies exploited some natural or man-made “tag” to estimate dispersal distances. Natural tags included genetic markers, otolith microchemistry, and larval or recruit sizes. The man-made tags have, thus far, been used only on fishes, and in all cases the otoliths of larval fish were tagged and the researchers sampled the settlers and looked for their tag.

The time that propagules are pelagic prior to settling has been determined from direct observations in the field, as in the behavioral observations on tunicate tadpole larvae; estimated from propagules maintained in the laboratory; or determined from analyses of fish otoliths. Behavioral observations and fish otoliths provide highly accurate measures of larval duration in a completely natural setting, but these data are available only for tunicate tadpole larvae and fish. Most data on PD have come from laboratory work. Laboratory culture conditions are inherently different from nature, and it is not clear how PDs from the field compare to those estimated from the laboratory.

Plotted on the scatter graph of pelagic duration *versus* dispersal distance was the relationship between pelagic duration and dispersal distance from the Lagrangian passive larval dispersal model of Siegel *et al.* (2003) and the regression line relating pelagic duration to dispersal distance calculated from genetic data. Comparisons between the modeled and observed relationships were used to test whether the Lagrangian model and genetic dispersal distances were realistic representations of dispersal distance.

In Shanks *et al.* (2003a), the distribution of dispersal distances appeared bimodal, and we statistically tested if the distribution was bimodal by calculating kurtosis and, using a Chi-squared test, comparing the distribution to a normal distribution. That analysis was repeated with the data from Shanks *et al.* and the new data presented in this paper combined. In addition, because organisms with short PDs can disperse only short distances, the analysis was repeated without organisms with PD shorter than 10 h.

Dispersal distance appeared to be bimodal. Could this be an artifact of the data set? Given that PD explains close to 50% of the variation in dispersal distance, if PDs of intermediate duration (half a day to a week)—the time needed for a passively dispersing larva to travel 1 to 10 km—were under-represented in the data set, then the dispersal distance distribution would be bimodal and an artifact of the sample set. To test this hypothesis, I compared the distribution of PDs in Shanks *et al.* (2003a) plus those reported here to an independent data set of PDs constructed from Strathmann

(1987), a comprehensive data set on the reproduction and development of marine invertebrates from the northeastern Pacific Ocean. I chose this source because it represents a rare compilation of data on larvae from a geographic area that has been very well studied and has a very diverse invertebrate fauna. For the analysis, I excluded PDs for tunicate tadpole larvae. Field observations of these larvae indicate that they settle very soon after release (minutes; Table 1 and Shanks *et al.*, 2003a). In contrast, laboratory studies (the data reported in Strathmann, 1987) find PDs to be hours. I also excluded from this analysis the PDs for plants presented here and in Shanks *et al.* (2003a).

## Results

In the original paper (Shanks *et al.*, 2003a), we presented data on the dispersal distance of 35 species, and pelagic larval or propagule duration (PD) for 27 of those species. In this paper, data are presented on the dispersal distance of 44 additional species, with PD data for 40 of these species (Table 1). For the current study, I have used a new estimate of dispersal distance for the alga *Macrocystis pyrifera* (Table 1 and Shanks *et al.*, 2003a). The data on teleplanic larvae used in Shanks *et al.* (2003a) have been excluded because, while such long-distance dispersal would clearly affect population connectivity, the low number of larvae successfully dispersing such long distances would have little impact on the maintenance of populations. In the combined data sets (Shanks *et al.*, 2003a, and this paper), the distances of 24 species were determined experimentally, 29 were from invasions, 15 from direct observations of dispersal, and 7 from “tagging” studies.

In the combined data sets, we have data on dispersal distance for 75 species and dispersal distance paired with PD for 67 species. This data set, far larger than the original, should allow a more robust investigation of the relationship between PD and dispersal distance; specifically, it should allow a test of the hypothesis that PD is proportional to dispersal distance, or stated another way, that PD is an indicator of dispersal potential. In Figure 1, PD is plotted against dispersal distance in a log/log plot. PD varies from a couple of minutes to several months, and dispersal distance varies from less than 1 meter to hundreds of kilometers. Variation in PD accounts for almost 50% of the variation in dispersal distance. With this large a range in PD it is not surprising that PD and dispersal distance are correlated; organisms that are only briefly free in the water column can be carried only a short distance by ocean currents, while organisms that are pelagic for weeks or months can be carried much farther.

Does this relationship mean that dispersal tends to be passive and that dispersal distance is a function of PD multiplied by ocean current speed? Plotted in the figure (shaded zone) is the distance to which a passively dispersing

organism would be transported in a steady long-shore current at speeds of 10 to 30 cm/s. All data points but one fall below these lines; realized dispersal distance is shorter than dispersal by passive particles in a steady current. A steady current is a poor representation of true ocean currents (Largier, 2003). Siegel *et al.* (2003) developed a model to describe the dispersal of passive larvae in a more realistic Lagrangian flow field. The fine dashed line in Figure 1 is the relationship between PD and dispersal distance calculated from this model. Five data points are either on or above this line. Organisms with very short to short PDs (<1 to 10 h), tend to disperse distances 10 to 100 times shorter than predicted if they were transported as passive particles. Organisms with PDs from days to months break into two groups. One group, organisms with dispersal distances longer than 10 km, have dispersal distances about a factor of 10 or less than predicted for a passive particle. Organisms with similar PDs but much shorter realized dispersal distances (<1 km) have dispersal distances 1 to 5 orders of magnitude less than predicted. Note that a number of species with PDs on the order of days to weeks have dispersal distances similar to those of organisms with PDs shorter than 1 h. Clearly, these organisms are not transported as passive particles; they experience much slower transport than passive particles, and the deviation from passive dispersal is species-dependent. Both models, passive larval drift in a steady current or in a more realistic Lagrangian model, predict longer dispersal distances than observed.

As in the original paper (Shanks *et al.* 2003a), I found no organism with realized dispersal distances from 1 to about 20 km (Fig. 1); the data appear to be bimodal. Using all dispersal distance data (Table 1 and that in Shanks *et al.* 2003a), I found a significant negative kurtosis (Fig. 2A) supporting this impression. However, organisms with short PDs can disperse only short distances; perhaps their inclusion unduly biases the analysis. Inspection of Figure 1 suggests that the distribution is, however, bimodal for organisms with PDs longer than 10 h. When I limited the analysis to organisms with such PDs (>10 h), I still found a significant negative kurtosis, indicating that the distribution is indeed bimodal (Fig. 2B).

A Kolmogorov-Smirnov test found that the two distributions of PDs, those reported here and in Shanks *et al.* (2003a) and a compilation made from Strathmann (1987), were significantly different (Fig. 3); compared to the distribution of PDs from Strathmann, the data set used here had a greater percentage of organisms with intermediate PDs (hours to days) and a lower percentage of organisms with long PDs (>1000 h).

## Discussion

In a recent review, Bradbury *et al.* (2008) asserted that dispersal studies have historically focused on “low-dispersal/low-latitude” species, and they suggested that these stud-

Table 1

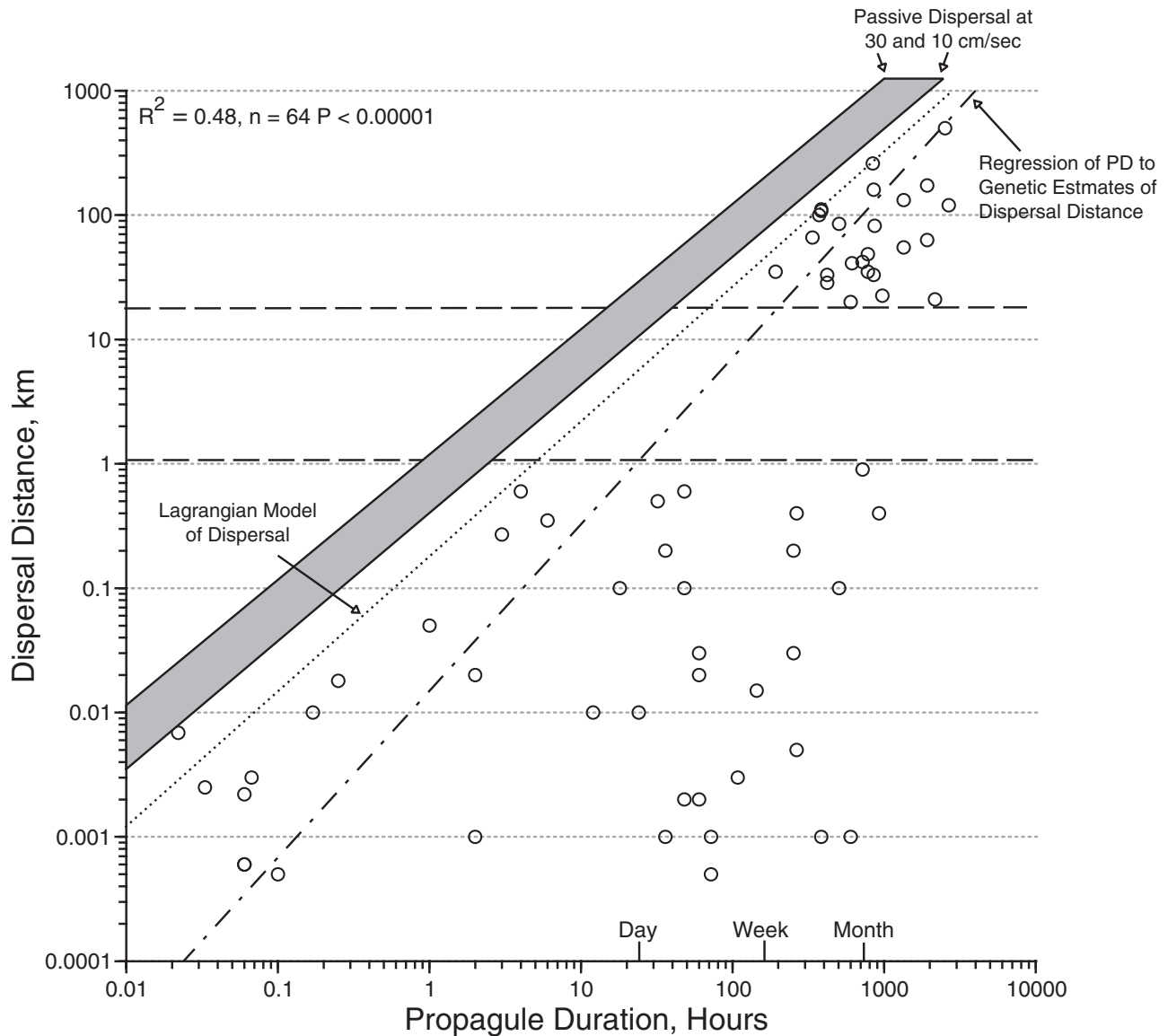
Estimates of propagule duration and dispersal distance

Organism (data source)	Dispersing stage	Propagule duration	Dispersal distance	References
<b>Algae</b>				
<i>Sargassum</i> spp. (E)	spores	25 days	1 m	Deysher and Norton (1982); Kendrick and Walker (1995)
<i>Grateloupia doryphora</i> (I)	spores		10 km	Villalard-Bohnsack and Harlin (2001)
<i>Sarcothalia crispate</i> (E)	spores		900 m	Opazo and Otaiza (2007)
Crustose corallines (E)	spores		900 m	Opazo and Otaiza (2007)
<i>Fucus serratus</i> (I)	spores		4 m	Arrontes (2002)
<i>Macrocystis pyrifera</i> (E)	spores	32 h	200 m	Reed <i>et al.</i> (2006)
<b>Cnidaria</b>				
<i>Allopora californica</i> (E)	demersal planulae	minutes	0.5 m	Fritchman (1974); Ostarello (1976)
<i>Athenaria actinia</i> (O)	egg	minutes	1 m	Nyholm (1940)
<i>Alcyonium siderium</i> (E)	demersal planulae	4.5 days	3 m	Sebens (1983)
<i>Favia fragum</i> (E)	planulae	4 min	3 m	Carlson and Olson (1993)
<i>Heliopora coerulea</i> (E)	planulae	6 h	350 m	Harri <i>et al.</i> (2002); Harri and Kayanne (2003)
<i>Tubularia larynx</i> (O)	actinula	<5 min pelagic, crawling 1 day	centimeters to meters	Pyefinch and Downing (1949)
<b>Sponges</b>				
<i>Scopalina lophyropoda</i> (E)	larvae	5–10 min	0.5–2 m	Uriz <i>et al.</i> (1998)
<i>Halichondria moorei</i> (O)	larvae	60 h	2 m	Bergquist and Sinclair (1968)
<i>Stylopsus</i> spp. (O)	crawling larvae	1–4 days	meters	Ayling (1980)
<i>Chondropsis</i> spp. (O)	crawling larvae	1–4 days	meters	Ayling (1980)
<b>Tunicates</b>				
<i>Molgula pacifica</i> (O)	adhesive benthic egg	36 h	<1 m	Young <i>et al.</i> (1988)
<i>Trididemnum solidum</i> (O)	tadpole larvae	15 min	<200 m <sup>1</sup>	van Duyl <i>et al.</i> (1981)
<i>Ecteinascidia turbinate</i> (O)	tadpole larvae	81.5 s	6.87 m	Bingham and Young (1991)
<b>Bryozoans</b>				
<i>Crisia denticulate</i> (T)	larvae	<2 h <sup>2</sup>	10–20 m	Pemberton <i>et al.</i> (2007)
<i>Tubulipora tuba</i> (E)	larvae	<2 h <sup>2</sup>	1 m	Knowlton and Jackson (1993)
<b>Molluscs</b>				
<i>Crepidula fornicata</i> (I)	larvae	2–3 weeks	28.5 km	Coe (1949); Dommasnes and Scham (1973)
<i>Rapana venos</i> (I)	larvae	14–17 days	100 km	Zolotarev (1996); Harding and Roger (1999)
<i>Philine</i> spp. (I)	larvae	30–40 days	260 km	Hansen and Ockelmann (1991); Cadien and Ranasinghe (2003)
<i>Dendropoma corallinaceum</i> (O)	crawling larvae	1–5 days	<1 m	Hughes (1978)
<i>Venerupis philippinarum</i> (I)	larvae	3–4 weeks	20 km	Bourne (1982); Quayle (1964); Strathmann (1987)
<i>Musculista senhousia</i> (I)	larvae	16 days	116 km	Willan (1987); Semenikhina <i>et al.</i> (2008)
<i>Perna viridis</i> (I)	larvae	2–3 weeks	33 km	Benson <i>et al.</i> (2001); Fajans and Baker (2005)
<i>Mya arenaria</i> (I)	larvae	10–35 days	35 km	Strathmann (1987); Zolotarev (1996)
<i>Drupella cornus</i> (T)	larvae	3 weeks	<100 m	Johnson <i>et al.</i> (1993)
<i>Adalaria proxima</i> (E)	larvae	1–3 days	100 m	Lambert <i>et al.</i> (2003)
<b>Polychaetes</b>				
<i>Spirorbis spirillum</i> (E)	larvae	15 min	<500 m	Dirnberger (1993)
<i>Terebrasabella heterouncinata</i> (I)	crawling larvae	12 h	15 m	Kuris and Culver (1999); Culver and Kuris (2000)
<i>Marenzelleria viridis</i> (I)	larvae	8 weeks	55–64 km	Boudouresque (1994); Bochet (1997)
<b>Crustaceans</b>				
<i>Paralithodes camtschaticus</i> (I)	larvae	90 days	32 km	Kuzmin <i>et al.</i> (1996); Epelbaum <i>et al.</i> (2006)
<i>Balanus glandula</i> (I)	larvae	2–4 weeks	85 km	Schwindt (2007)
<i>Cancer magister</i> (T)	larvae	3–4 months	500 km	Shanks (unpubl. data)
<b>Echinoderms</b>				
<i>Asterias amurensis</i> (I)	larvae	40–50 days	22.5 km	Buttermore <i>et al.</i> (1994); Nozais <i>et al.</i> (1997)
<i>Acanthaster planci</i> (I)	larvae	14 days	49–81 km	Moran <i>et al.</i> (1992)
<b>Fishes</b>				
<i>Pterois volitans</i> (I)	larvae	25–40 days	48.5 km	Ruiz-Carus <i>et al.</i> (2006)
<i>Sebastes melanops</i> (T)	larvae	83–174 days	<120 km	Miller and Shanks (2004)
<i>Amphiprion percula</i> (T)	larvae	10–13 days	100–500 m	Almany <i>et al.</i> (2007)
<i>Chaetodon vagabundus</i> (T)	larvae	29–48 days	100–500 m	Almany <i>et al.</i> (2007)
<i>Pomacentrus amboinensis</i> (T)	larvae	9–12 days	100–200 m	Jones <i>et al.</i> (1999)

The data presented in this table are new. The data analysis and figures presented in this paper were based on these new data and the data presented in Shanks *et al.* (2003a). Dispersal distances are from experimental data (E), the spread of invasive species (I), observations of dispersing larvae (O), and the displacement of “tagged” larvae (T). Propagule duration values are from either laboratory rearing experiments or field observations of dispersing larvae.

<sup>1</sup>Distance estimated assuming 15 min in the plankton and a current of 20 cm/s.

<sup>2</sup>Estimated from Keough and Chernoff (1987).



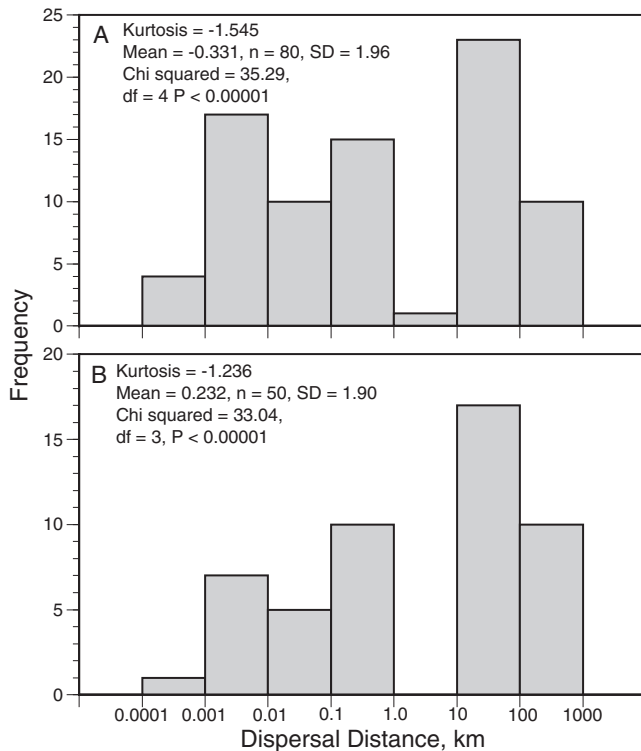
**Figure 1.** Log/log plot of propagule duration (PD) in hours and dispersal distance in kilometers. Data are from Shanks *et al.* (2003a) and Table 1 in this paper. Plotted with the data points are (1) the distance propagules would be dispersed if they behaved as passive particles in a steady flow of 10 and 30 cm/s (gray shaded zone), (2) the distance passively drifting larvae would disperse as calculated using a Lagrangian model of dispersal (dotted line) (Siegel *et al.*, 2003), and (3) dispersal distance estimated from a regression relating PD to dispersal distance calculated from genetic data (dot and dash line) (Siegel *et al.*, 2003). Statistical results are from a correlation of the log/log data.

ies are not generally applicable or representative of global patterns. In both Shanks *et al.* (2003a) and this study, most of the data are from temperate species (72%). Of the species with dispersal distances longer than 1 km, 27 were temperate species and 6 were from low latitudes. For species with short dispersal distances (<1 km), 26 were temperate and 15 were tropical. Studies of short-distance dispersers make up a somewhat larger percentage of tropical studies (15 of 21), while temperate studies are distributed evenly between species with dispersal distances shorter and longer than 1

km (26 and 27, respectively). Dispersal studies do not actually appear to have focused on “low-dispersal/low-latitude” species.

**Is PD an indicator of dispersal potential? Crudely, the answer is yes.** Organisms that spend only a brief time as larvae have dispersal distances shorter than those of larvae that are pelagic for longer periods of time. Note, however, that the distribution of data points is not well suited to a correlation analysis. The distribution is composed of two clouds of points: a relatively tight cloud represented by





**Figure 2.** Frequency distributions of dispersal distances for all data (A) and for propagules with propagule durations (PD) > 10 h (B). Data are from Shanks *et al.* (2003a) and Table 1 this paper. The Chi-squared test compared the observed distributions to a normal distribution.

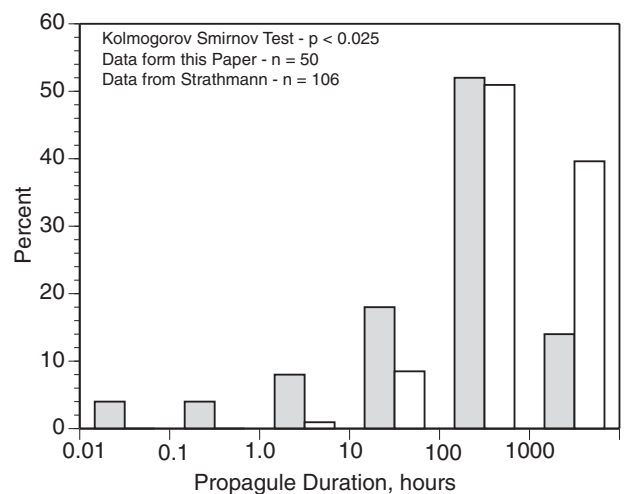
organisms with long PDs and dispersal distances, and a more diffuse cloud of organisms characterized by short dispersal distances and a range of PDs. This type of data distribution leads to a problematic correlation analysis and, perhaps, even makes a correlation inappropriate (Anscomb, 1973). If one focuses on this correlation, one will miss a great deal of fascinating and important biology.

Dispersal is far shorter than one would expect if dispersal were by passive larvae in a steady current; nearly all the data points in the scatter graph fall below the passive dispersal curves (Fig. 1). Siegel *et al.* (2003) present as a null hypothesis a much more detailed model of the dispersal of a passive larva in a coastal current regime. Their modeled dispersal distance is slightly better than the predicted larval dispersal in a steady current, but more than 90% of the data points still fall below the modeled relationship. Larvae are behaving, and larval behavior slows dispersal, resulting in dispersal distances up to 100,000 times smaller than that expected for a passive particle in a steady or fluctuating (Siegel *et al.*, 2003) current. Many larval types that are pelagic for days to weeks have dispersal distances as short as those of larvae that are only pelagic for minutes to hours: there are 48 species with PDs of 1 day or more, and 23 (48%) of these have dispersal distances less than 1 km.

Larval behavior can, obviously, profoundly affect dispersal distance.

This is clearly true for larvae that have longer PDs but disperse short distances, but perhaps PD can be used as an indicator of dispersal potential for organisms that disperse long distances (*i.e.*, >20 km). A correlation between log PD and log dispersal distance for organisms that dispersed more than 20 km was not significant ( $R^2 = 0.055$ ,  $n = 25$ ,  $P > 0.10$ ); for these organisms as well, PD is a poor predictor of dispersal potential. The dispersal distances of these organisms is also less than one would expect if they were transported as passive particles in an ocean current; behavior appears to be slowing their dispersal as well.

Behaviorally an organism could achieve a short dispersal distance by simply staying in the plankton briefly; an organism that dispersed like a passive particle for 1 h in a 10 cm/s current would travel only 360 m. A short PD will contribute to a short dispersal distance, but the realized dispersal distances were far shorter than that which would be achieved by a passive particle dispersing over a similar period. Larvae that disperse short distances nearly universally do so by remaining close to the bottom where currents are much reduced. Immediately upon release, many fall or swim to the sea floor and then crawl across the bottom searching for a settlement site. Others remain pelagic but stay very near the bottom and, in some cases, swim against the current (Marliave, 1986; Kingsford and Choat, 1989). There is evidence that some larval types with short PDs may be released during periods of lower flow (Pyefinch and Downing, 1949). The recent work on self-recruitment in several tropic fish populations suggests that active migration by late-stage larvae or early juveniles may also be playing a



**Figure 3.** Frequency distribution of propagule durations (PDs) from Shanks *et al.* (2003a) and Table 1 this paper (gray bars) compared to PDs for invertebrate larvae in Strathmann (1987) (open bars). For the Kolmogorov-Smirnov Test the whole data sets were compared, not the binned percent data presented in the figure.

role in dispersal for at least some more mobile organisms (Leis, 2006; Montgomery *et al.*, 2006).

Organisms that disperse longer distances appear to be using a different set of behaviors, which may contribute to slowing their dispersal. Larvae of a variety of coastal invertebrates tend to avoid the surface layer (upper 5 to 10 m) where currents tend to be faster, and instead, reside deeper in the water column (Shanks and Brink, 2005; Shanks and Eckert, 2005; Morgan *et al.*, 2009a, b; Shanks and Shearman, 2009); residing in slower deeper currents will retard transport. Some types of larvae vertically migrate in and out of the surface layers, which also can slow dispersal because deeper currents are generally slower and not infrequently flowing in a different direction than surface currents (Largier, 2003). Larvae whose offshore dispersal is limited to the coastal boundary layer (Csanady, 1974) will experience the back-and-forth alongshore flow generated by wind reversals producing alterations in the coastal flow. These generally take the form of wind-driven upwelling and downwelling—a phenomenon that has been most actively studied in eastern boundary currents, but which also occurs along most shores though to a lesser extent (see, for example, Shanks and Brink, 2005). Wind-driven oscillations in alongshore flow will tend to limit the net alongshore transport of larvae (Largier, 2003). The timing of spawning in nearshore fishes and benthic crustaceans in the California Current may have evolved to exploit exactly this type of oscillatory flow, perhaps to limit alongshore transport of their larvae (Shanks and Eckert, 2005).

In Shanks *et al.* (2003a), as in this larger data set, there is a gap in the distribution of dispersal distances between 1 and 20 km. The gap in the data, I suspect, is a consequence of the way in which dispersal distances were determined and the fact that the data are bimodal; the gap itself (the complete absence of data points between 1 and 20 km) may be an artifact; the bimodal distribution is not. Most of the dispersal distances longer than 1 km are from invasions. In these studies, dispersal distance was the annual distance the species spread, but obviously, individuals disperse to distances less than the distance to the annual spreading front. This can be clearly seen in Crisp's data on the spread of *Elminius modestus* (Crisp, 1958). The spread of the species was about 25 km per year, but large numbers of recruits were present from the previous year's spreading front out to 25 km; in other words, settlement adequate to sustain the population was observed from 0 to 25 km from the spreading front. By using as the dispersal distance just the one value—the average annual distance the species spread—we focus not on a maximal dispersal distance, but on one that is well away from the center of the dispersal kernel curve. This, I think, may have caused the gap in the distribution of dispersal distances.

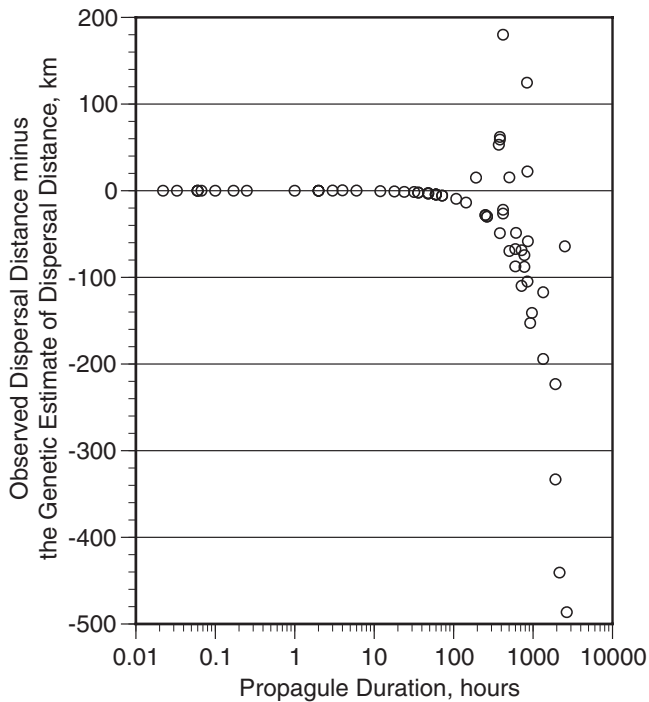
The bimodal distribution of dispersal distances may be due to an under-representation of PDs that are hours to days

long (the time needed for a passively drifting organism to travel 1 to 10 km; Fig. 1). To test this hypothesis, I compared the distribution of PDs from Shanks *et al.* (2003a) and this study to an independent data set of PDs. The distributions were significantly different, but the difference was due to an over- and under-representation of PDs of hours to days and more than 1000 h (41 days), respectively, in my data relative to the independent data set of PDs. If dispersal is fairly passive, simply a function of PD and flow, then the observed distribution of PDs is an unlikely cause of the bimodal distribution of dispersal distances.

An indirect estimate of dispersal distance can be calculated from genetic data (Palumbi, 1995). Kinlan and Gaines (2003) surveyed the available literature and presented a compilation of species for which they could find both a PD and enough genetic data to calculate dispersal distance. The observed distribution of dispersal distances presented here is strongly bimodal (Figs. 1 and 2), but the distribution of estimated dispersal distances in Kinlan and Gaines (2003) is not. Siegel *et al.* (2003) present the regression relating these two variables, and I have included this regression line in Figure 1. At PDs below about 10 h, dispersal distances estimated from genetic data are similar to observed dispersal distances. The estimated distances are smaller than the observed, but both estimated and observed dispersal distances are short (<1 m to <1 km). Between PDs of about a day and a week, the estimated dispersal distances range from longer than 1 to longer than 10 km, but all observed dispersal distances are shorter than 1 km. At PDs longer than a week, the genetic estimates of dispersal distances are generally larger than the observed distances, and in many cases the estimate is much larger (>100 kilometers larger) than observed (Fig. 4). At PDs shorter than 10 h, dispersal distances estimated from genetic data are similar to observed dispersal distances, but at longer PDs the regression relating PD to genetic estimates of dispersal distance is a poor predictor of observed dispersal distances.

The bimodal distribution of observed dispersal distances suggests that there are at least two general dispersal strategies: disperse less than 1 km or disperse tens of kilometers. Looking more closely at the data, I hypothesize, however, that dispersal strategies might be broken down into four functional groups.

1. *Organisms with PDs < half a day.* Organisms with short PDs have correspondingly short observed dispersal distances as well as short dispersal distances estimated from genetic data. Both types of dispersal distances are shorter than that predicted from the Lagrangian dispersal model of Siegel *et al.* (2003), but the differences are not large (meters to tens of meters). The basic larval strategy is simple: either stay out of the water column as much as possible by moving immediately to the bottom and crawling, or



**Figure 4.** Propagule duration (PD) plotted with the difference between the observed dispersal distances minus dispersal distances calculated using the observed PDs and a regression equation relating PDs to dispersal distances calculated from genetic data (Siegel *et al.*, 2003).

have a pelagic phase that is brief. For species that use this pattern of dispersal, currents will minimally impact dispersal, dispersal distances will be small, and populations will self-recruit on scales around tens to hundreds of meters. Long-distance dispersal (LDD) will be due to rare events such as rafting of adults or storm events transporting propagules or attached adults long distances. Many clonal species have short PDs (Jackson, 1986); many of their larvae are non-feeding, and nonfeeding larvae tend to have shorter dispersal distances than feeding larvae (Shanks *et al.*, 2003); and clonal species make up most of this functional group.

2. *Organisms with PDs  $\geq$  half a day (range 12 h to > 30 days), but with dispersal distances < 1 km.* Larvae of these species disperse much shorter distances, orders of magnitude shorter, than either hydrodynamic models or genetic data suggest. As adults, species in this cluster appear to be inhabitants of shallow coastal environments; their larvae appear to minimize their dispersal, despite their long PDs, by staying close to the bottom where currents are much slower and, in the case of the more active larval types, even by swimming against the current. Under favorable hydrodynamic conditions (average currents), dispersal distances are short (meters to hun-

dreds of meters) and self-recruitment may be on the scale of hundreds of meters—that is, a scale of self-recruitment similar to that observed in recent studies on several coral reef fish species (Jones *et al.*, 1999; Almany *et al.*, 2007).

Because the larvae in this functional group are pelagic for longer periods, the possibility of adverse hydrodynamic events (*e.g.*, storms) affecting their dispersal is greater than in group #1. During a storm, the stronger flow may overwhelm the swimming ability of larvae and carry them away from the bottom and out to sea. Most of these displaced larvae are probably lost as larval wastage. A few may succeed in settling into a suitable habitat, but they have likely been displaced some distance from their origin (*i.e.*, LDD) and may recruit into a new local population. *Oligocottus maculosus*, an eastern Pacific tidepool fish, appears to fit this scenario. Its larvae tend to remain very close to shore during development (Marliave, 1986), and the annual abundance of new recruits is negatively correlated with large wave events; new recruits are most abundant in years with few large wave events during the seasonal larval period (Shanks and Pfister, 2009). The longer PDs allows more opportunity for extreme events to cause LDD, and these vagrant larvae would strongly contribute to the spatial distribution of genotypes in the species. Because the genetics of local populations would be more similar to each other, dispersal distances calculated using genetics will be significantly larger than “normal” (*i.e.*, non-LDD) dispersal.

I suspect that the clusters of species with long PDs and long dispersal distances is actually composed of two functional groups: species that as adults live very close to shore (<30 m depth) and those that live over the continental shelf. This division is speculative, as we have many examples of species that live in shallow nearshore habitats, but very few species from the deeper waters of the continental shelf. This division is based on the data presented in this paper and insights from Shanks and Eckert (2005).

3. *Species with long PDs (>1 week), long dispersal distances (>20 km), and adults that inhabit shallow coastal waters.* The adult habitat of species in this functional group is similar to that of the species in group #2 (*i.e.*, shallow coastal waters), but larval behavior is apparently different. These larvae do not remain close to the benthos, and as a consequence, they are carried offshore into the coastal ocean. Siegel *et al.* (2003) suggest that larvae that have similar PDs and are released at the shore will be carried tens to hundreds of kilometers offshore during their development. The actual cross-shelf distributions of coastal and intertidal invertebrate larvae appear,



however, to be confined to waters very close to shore. Shanks and co-authors (Shanks *et al.*, 2002, 2003b; Shanks and Brink, 2005) working on the east coast of North America found that the larvae of a variety of benthic invertebrates remained within 5 km of shore despite upwelling, downwelling, and the complete exchange of the waters in the coastal boundary layer. In the upwelling system off Oregon and California, the larvae of intertidal barnacles (all species and stages) as well as the larvae of a variety of other intertidal invertebrates remained within 4 km of shore during upwelling and downwelling (Shanks and Shearman, 2009; Morgan *et al.*, 2009a, b). The modeled and observed distribution of these larvae is not similar; larvae remain far closer to shore than the model suggests they should. By remaining close to shore, within the coastal boundary layer, larvae would be subjected to alongshore currents with reduced velocities and, with changes in the wind direction, alternating directions (Largier, 2003). Wind direction along a coast typically changes every 4 to 15 days, and changes in wind direction often lead to changes in coastal current direction. During a one-month PD, pelagic larvae may experience several current reversals, and the back-and-forth transport by these current reversals may limit net alongshore transport of the larvae. Shanks and Eckert (2005) suggest that a variety of life-history traits (*e.g.*, timing of reproduction, types of propagules, PD, larval behavior) of coastal (adult habitat < 30 m) fishes and benthic crustaceans in the California Current may have evolved, at least in part, to capture this back-and-forth movement of the water in the coastal boundary layer and limit the net alongshore transport of their larvae. The observed dispersal distances of many of the larval types in this functional group are about an order of magnitude smaller than the estimated dispersal distances from the Lagrangian dispersal model of Siegel *et al.* (2003). The difference between this null model and the observed dispersal distances may be because larvae remain in the coastal boundary layer where currents are both slower and more highly variable than offshore (Largier, 2003), leading to smaller realized dispersal distances.

For this group, dispersal distances estimated from genetic data are generally longer, tens to hundreds of kilometers longer, than observed dispersal distances (Fig. 4). Larvae in this functional group are spending days to weeks in the coastal waters. I am hypothesizing that under “normal” conditions their net alongshore transport is smaller than predicted because they are capturing the slower and more variable flow in the coastal boundary layer, but dispersing in this fashion exposes these larvae to a greater chance of

transport over long distances due to episodic extreme flow events. These vagrant individuals, if they successfully return to shore and recruit, would contribute to a smoothing of the genetic differences between local populations, which in turn would lead to a higher estimate of dispersal distance from the genetic data.

4. *Species with long PDs (>1 month), long dispersal distances (>20 km), and adults that inhabit the waters over the continental shelf.* Of the four functional dispersal groups, this is the most speculative; we have very little data on dispersal distances from species that as adults inhabit the deeper waters over the continental shelf. In the data sets (Shanks *et al.*, 2003a, and Table 1), the only shelf /slope species are *Cancer magister* (PD = 3 to 4 months, dispersal distance = 500 km), *Sebastes melanops* (PD = 83 to 174 days, dispersal distance < 120 km), and *Paralithodes camtschaticus* (PD = 90 days, dispersal distance = 32 km). Dispersal distances for *C. magister* and *S. melanops* are from populations on a topographically simple continental shelf (*i.e.*, the shelf off Washington and Oregon). The data for *P. camtschaticus* are from a population that was transplanted to waters off northwest Russia and has spread to northern Norway; this invasion has occurred in a topographically complex environment, which may contribute to the smaller dispersal distance.

Species inhabiting the deeper waters over the continental shelf release larvae directly into the more energetic and less variable flow over the continental shelf and seaward of the coastal boundary layer (Largier, 2003). Larvae released into a mean current will drift downstream from their release site, most will settle downstream of their parents, and if this process goes unchecked, the species will go extinct from the upstream edge of its distribution to the downstream (Gaines *et al.*, 2003; Shanks and Eckert, 2005; Byers and Pringle, 2006). This is known as the “drift paradox” (Müller, 1982) and is a problem for all species with pelagic larvae; however, given the stronger flow in offshore waters, it may be particularly severe for species living away from shore on the continental shelf. Modeling by Byers and Pringle (2006) suggested that spreading spawning over several seasons, short PD, and prodigious larval production might mitigate larval washout. Contranant spawning migrations have also probably evolved to “solve” this problem (Cushing, 1975). Shanks and Eckert (2005) investigated this question by looking at the life-history characteristics of shelf and slope species of fishes and benthic crustaceans in the California Current and attempted to relate the life-history traits to the flow field experienced by their larvae. These

species were, on average, characterized by having very long lives, high fecundity, winter spawning, long PDs (average 136 days), and larvae that are pelagic during the winter when flow over the shelf is predominately to the north and into the spring/summer when flow is on average to the south. They hypothesized that, for these species in this habitat, the drift paradox was “solved” by the dispersal of their larvae capturing both the north and south flow of the seasonally changing current regime; larval dispersal is limited by capturing a major diffusive component of the current regime (the north/south seasonal change in flow) to mitigate the effect of alongshore advection (Largier, 2003).

Sinclair (1988) hypothesized that populations form in geographic settings where enough larvae return to maintain a viable population. For species with pelagic larval development, larval return (closure of the reproductive cycle) is dependent on their life-history characteristics (*e.g.*, timing of spawning, type of larvae, larval behaviors, PD) coupled with the local hydrodynamics. The four dispersal strategies hypothesized above may be due to selection toward closure of the reproductive cycle in different topographic/hydrodynamic settings. How closure occurs should depend on at least the following conditions:

1. *The topographic setting in which spawning occurs.* Propagules released in shallow waters adjacent to the shore will experience a very different flow regime than ones released in the waters over the continental shelf; flow in shallow waters next to shore should generally be more variable and often slower than flow over the continental shelf.
2. *The distribution and prevalence of suitable settlement habitat.* In some species, the habitat is quite restricted (*e.g.*, tidepool sculpins require high intertidal tidepools on a rocky shore); the target habitat is small and scattered along a coastline. For other species the target habitat is extensive; *Cancer magister* megalopae settle on the benthos almost anywhere along the coast in waters less than 80 m deep, and intertidal barnacles settle on any hard surface in the intertidal zone. Ensuring closure to the larval period when the target settlement habitat is restricted and rare likely requires a different interplay between life-history traits and hydrodynamics than when the target settlement habitat is widely distributed and common.
3. *The hydrographic setting in which dispersal occurs.* The above discussion of the four functional dispersal groups stressed the interplay between geography, hydrodynamics, and dispersal strategies. Dispersal is

not simple; modeling dispersal as PD multiplied by currents, no matter how sophisticated the oceanographic model, will provide, at best, a very crude description of dispersal. Each species has a unique set of constraints or selective pressures on its dispersal (*e.g.*, what is the topographic and hydrographic setting, what is the target settlement habitat, what are the species' phylogenetic constraints), and evolution has sculpted life-history traits to these constraints.

## Conclusions

1. Propagule duration (PD) was significantly correlated with dispersal distance, but there were many exceptions.
2. The distribution of dispersal distances was bimodal. About a third of the organisms with long PDs (>1 day to a month) dispersed distances as short (<1 km) as organisms with short PDs (*e.g.*, <1 h), while many other organisms with long PDs dispersed tens to hundreds of kilometers.
3. Organisms with short dispersal distances either were pelagic only briefly or, if their PD was long, tended to remain very close to the bottom while pelagic. These results clearly demonstrate that larval behavior can play a crucial role in determining dispersal distance.
4. Null models of passively dispersing larvae do a good job of predicting dispersal distance for larvae with short PDs (<10 h), but at longer PDs the models are poor predictors. These null models, because they do not include larval behavior, vastly overestimate the dispersal distances for species with long PDs and short observed dispersal distances.
5. Passive null models also overestimate the dispersal distance of larvae with long PDs and long dispersal distances (>10 km). Passive null models predict that larvae will be dispersed tens of kilometers offshore where they will experience currents faster than those near the coast. Throughout their development, many types of larvae are, however, able to remain within the coastal boundary layer where they would experience slower and more variable currents. This difference in the modeled *versus* the actual pelagic habitat of the larvae may account for the overestimations of dispersal distance by the passive models and again indicates the importance of behavior in determining dispersal.
6. At short PDs, estimates of dispersal distances from genetic data are similar to observed dispersal distances, but at long PDs the genetic data frequently overestimates dispersal distance. The error is particularly large for the organisms with long PDs and

short dispersal distances. The discrepancy between the estimated and observed dispersal distances is probably due to the effect of rare individuals that disperse long distances, smoothing the genetic differences between local geographic populations, which would contribute to overestimation of dispersal distances (Palumbi, 1995).

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