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PROPAGULE DISPERSAL DISTANCE AND THE SIZE AND SPACING OF MARINE RESERVES

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Abstract. This study compiled available information on the dispersal distance of the propagules of benthic marine organisms and used this information in the development of criteria for the design of marine reserves. Many benthic marine organisms release propagules that spend time in the water column before settlement. During this period, ocean currents transport or disperse the propagules. When considering the size of a marine reserve and the spacing between reserves, one must consider the distance which propagules disperse. We could find estimates of dispersal distance for 32 taxa; for 25 of these, we were also able to find data on the time the propagules spent dispersing. Dispersal distance ranged from meters to thousands of kilometers, and time in the plankton ranged from minutes to months. A significant positive correlation was found between the log-transformed duration in the plankton and the log-transformed dispersal distance ($r = 0.7776$, $r^2 = 0.60$, df = 1, 25, $P = 0.000$); the more time propagules spend in the water column the further they tend to be dispersed. The frequency distribution of the log-transformed dispersal distance is bimodal (kurtosis = -1.29, $t = -4.062$, $P < 0.001$) with a gap between 1 and 20 km. Propagules that dispersed $<$1 km spent less time in the plankton ($<$100 h), or if they remained in the plankton for a longer period, they tended to remain in the waters near the bottom. Propagules that dispersed $>$20 km spent more than 300 h in the plankton. The bimodal nature of the distribution suggests that evolutionary constraints may reduce the likelihood of evolving mid-range dispersal strategies (i.e., dispersal between 1 and 20 km) resulting in two evolutionarily stable dispersal strategies: dispersal $<$1 km or $>\sim$20 km. We suggest that reserves be designed large enough to contain the short-distance dispersing propagules and be spaced far enough apart that long-distance dispersing propagules released from one reserve can settle in adjacent reserves. A reserve 4–6 km in diameter should be large enough to contain the larvae of short-distance dispersers, and reserves spaced 10–20 km apart should be close enough to capture propagules released from adjacent reserves.

Key words: dispersal; introduced species; larvae; marine protected area; marine reserve; plankton; propagules; recruitment.

INTRODUCTION

One of the most basic aspects of reserve design is their size and distribution in space. The size and distribution of reserves are critical to the sustainability of protected populations, communities and ecosystems within reserves and can greatly influence the extent which populations protected within reserves influence unprotected populations outside reserves (Carr and Reed 1993, Roberts 1997, Allison et al. 1998, Bohnsack 1998, Hastings and Botsford 1999). To the extent that propagules (spores, eggs, and larvae) are transported away from benthic parental populations, local parental populations can influence rates and patterns of replenishment of populations elsewhere and are greatly influenced by recruitment of propagules produced elsewhere by other populations. Thus, sustainability of reserve populations and their contribution to the replenishment of unprotected populations will be influenced by the extent which populations are self-replenishing. Self-replenishment can be achieved by reserves of sufficient size to contain a substantial amount of larval dispersal, or by networked reserves at suitable distances such that propagules produced by populations in one reserve replenish populations in other reserves. An effective reserve design, i.e., reserves that sustain protected populations and enhance nonprotected populations, will benefit from our understanding of patterns of larval dispersal and how species attributes (e.g., larval behavior, developmental traits) and environmental features (e.g., hydrographic patterns, geomorphological features) influence such patterns (Roberts 1997, Jones et al. 1999, Swearer et al. 1999, Cowen et al. 2000).

Many benthic marine invertebrates and algae as well as coastal fish produce planktonic propagules. In the plankton, propagules go through a period of development after which they settle into an adult or nursery

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habitat associated with the benthos. The time propagules spend in the plankton varies from species to species. The propagules of some organisms spend as little as minutes in the water column while others can spend months as pelagic organisms. While in the plankton, propagules are carried by ocean currents from the point of their release. This movement is known as dispersal. The interaction of biotic and abiotic processes can greatly influence dispersal patterns (Shanks 1995). However, since there is a lack of detailed knowledge of such interactions for the hundreds of benthic species targeted for protection by marine reserves, simpler yet accurate estimates of dispersal potential are necessary for reserve design. The distance which propagules are dispersed should be roughly dependent on time spent in the water column. We have reviewed published and unpublished estimates of larval duration and propagule dispersal distance to determine the predictive relationship between larval duration and dispersal distance.

Before discussing the types of data that one might use to estimate the mean propagule dispersal distance, we must first more carefully define what we mean by ‘‘mean dispersal distance.’’ The dispersal of propagules affects populations by (1) maintaining genetic continuity or gene flow between separated populations and (2) by sustaining populations with new recruits.

The genetic connection between isolated populations can be maintained by a very low input of dispersing propagules into the population. For example, differentiation resulting from random genetic drift within an isolated population of moderate size can be prevented by an input of only one individual in 1000 per generation (Lewontin 1974). A much higher flux of recruits is needed to sustain a viable population of adults. Only small percentages of the propagules that settle out of the plankton survive to become adults; probably $<10\%$ of the settlers survive to reproduce (Gosselin and Qian 1997). A population that receives only enough recruitment to maintain high levels of gene flow could fall far short of sustaining numbers of an adult population. While recognizing the importance of gene flow across a metapopulation, we are concerned here with the sustainability of populations and focus our analyses on levels of dispersal sufficient to have numerical consequences to populations. We use the term ‘‘mean realized dispersal distance’’ to mean the distance that the mean propagule disperses from an adult source population. We then assume that at this distance, settlement rates are sufficient to sustain a substantive recipient adult population.

However, we should add one caveat here. There are examples of local population extinctions being reversed by rare, but highly successful, recruitment pulses (see, for example, Coe 1953, Efford 1970, Ebeling et al. 1985). In at least some of these cases, larvae dispersed from distant adult populations; the dispersal distance in these instances may be larger than our mean dispersal distance. It would be unwise, however, to design a reserve system with the expectation that uncommon large recruitment pulses from distant source populations will maintain the reserve population of that organism.

METHODS

We found four types of data sets that can be used to estimate mean realized dispersal distance. These include (1) direct observations of propagules as they dispersed, (2) observations of the spatial distribution of larvae, (3) experimental estimates of dispersal, and (4) observations of the progressive spread of an introduced species.

The observational studies of larval behavior have focused on larvae that reside only briefly in the water column. In these studies, the researcher actually followed the fate of a larva from the time it was spawned until it settled. Obviously, this is possible only with large larvae that spend short periods in the plankton. Nearly all these studies describe the behavior of the tadpole larvae of tunicates. These studies provided determinations of the mean dispersal distance and the mean time in the plankton for the tracked larvae.

Two studies describing the distribution of larvae were used to estimate larval dispersal distance. The study by Marliave (1986) looked at the very nearshore and along-shore distributions of the larvae of intertidal fish. The extremely restricted distributions of these larvae suggest that they experience limited dispersal. The other study is the work of Scheltema and Williams (1983) on the distribution of teleplanic larvae (i.e., larvae with long residence times in the plankton) of Atlantic gastropods. This research presents convincing evidence that larvae spawned off the coast of Africa can be transported across the central Atlantic and settle along the coasts of North and South America. It is difficult to determine whether the larval connection between Africa and the Americas is simply a genetic connection or whether the larvae spawned in Africa actually contribute to the maintenance of adult populations on the western side of the Atlantic. For example, Laursen (1981) points out that of 17 North American east coast prosobranch species that disperse to the eastern north Atlantic, only eight of the species are found on both sides of the Atlantic. This observation suggests that larvae found far from shore may not contribute to the maintenance of populations. The main reason for including Scheltema’s study, however, is that it seems to be the only data from which one can estimate the distance which extremely long ‘‘lived’’ propagules can be dispersed.

The experimental studies measured settlement or recruitment at increasing distances from isolated populations of adults: the presumed source of the propagules. Over time, as propagules disperse from their point of release, their concentration in the water column decreases. Because of this dilution, settlement eventually becomes undetectable at some distance from the source of the propagules. Because of this dilution effect, these studies have focused primarily on species with short planktonic periods, particularly algal propagules. In these studies, we estimated the mean 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. For example, Reed et al. (1988) found *Pterygophora* settlement out to 4 km, but settlement was infrequent and settlement rates were very low. Appreciable settlement was observed at distances within 500 m of the adult population. In the investigation of coral settlement around Helix Reef (Sammarco and Andrews 1989), settlement was found at all distances from the reef, but appreciable settlement was only observed at distances within 500 m of the reef.

Many estimates of dispersal distance come from the literature on introduced nonnative species. Most papers on new species introductions simply report the presence of the new organism; the report is of a simple range extension. There are some instances where the introduced species takes hold, the population spreads along the coast, and the spread of the introduction is followed over time. In these studies, estimates of mean realized propagule dispersal distance equal the annual extension of the spreading population. Excellent examples of these types of studies include research describing the spread of the barnacle *Elminius modestus* and the alga *Sargassum muticum* around Europe (Crisp 1958, Critchley et al. 1983). Ideally, enough locations were inspected annually that the spreading front of the introduced population was well defined. The work reported by Crisp (1958) on the spread of *E. modestus* probably best fits this ideal.

In selecting which data to include from the invasion studies, care was taken to exclude data where the spread of the introduced species could be attributed to human intervention (e.g., ballast-water transport, introduction with mariculture operations, etc.). For example, during the steady spread of *Caulerpa taxifolia* along the Mediterranean coast of France, a population suddenly appeared far from the spreading front in a harbor on an offshore island (Meinesz et al. 1993). Meinesz et al. (1993) suggest that this jump in the dispersal of *C. taxifolia* resulted from transport of plants caught on the bottom of a boat. This datum and similar data in other studies were excluded from the analysis.

All the data sets used in this study have come from species found in the intertidal zone or in shallow near-shore subtidal habitats. Further, nearly all the data have come from studies that have taken place on coastlines of continents or large islands. The dispersal of propagules released from benthic communities of the continental shelf or slope or released from populations associated with small islands may be quite different from the results presented here.

The amount of time propagules spend in the plankton prior to settling has been estimated either from direct observations in the field as in the behavioral observations on tunicate tadpole larvae or by maintaining the propagules in the laboratory until they settle. The behavioral observations on tunicate tadpole larvae provide a highly accurate measure of larval duration in a completely natural setting. These data are unique, however. The observations are only possible because of the large size of the larvae and the brief period they spend in the water column. Most data on propagule duration have come from laboratory work. Laboratory culture conditions are inherently different from those in the field. It is not at all clear how comparable propagule durations estimated from the lab are to those displayed by animals in the field.

RESULTS AND DISCUSSION

The literature search found 32 taxa for which we obtained estimates of dispersal distance; for 25 of these organisms estimates of duration in the plankton were available (Table 1). Fourteen of the studies were from experiments, six were from behavioral observations, two were from studies of larval distribution, and fifteen were studies of introduced species. For two organisms (*Sargassum muticum* and *Carcinus maenas*), we could find multiple estimates of dispersal distance resulting from their introduction on several shores. The duration in the plankton ranged from as little as <2 min to as long as 293 d, and the estimated dispersal distance ranged from as little as <1 m to as much as 4400 km.

Because of the large range in the estimated values of both propagule duration and mean realized dispersal distance, the data are presented as a log/log plot (Fig. 1). When propagule duration or mean realized dispersal distance was presented as a range of times (Table 1), the midpoint of the range was plotted in Fig. 1. Most of the data points appear to fall on a line and, in fact, there is a significant positive correlation between propagule duration and dispersal distance ($r = 0.7776$, $r^2 = 0.60$, df = 1, 25, $P < 0.000$). Propagule duration explains more than 60% of the variability in the dispersal distance.

Six points fall below the line passing through most of the data (the points labeled A through F in Fig. 1). That is, the distance which these propagules are dispersed is less than expected given their duration in the plankton. In all six cases the literature suggests that the lower than expected dispersal distance is due either to the propagules sinking (having negative buoyancy) or to behaviors that tend to direct a swimming propagule to the bottom. These propagules appear to spend their time in the plankton near the bottom. The other species presented in Fig. 1 do not tend to inhabit the near-bottom waters. For example, *Oligocottus macu-*

TABLE 1. Estimates of propagule duration and mean realized dispersal distance.

Organism (data source)	Dispersing stage	Duration	Realized dispersal distance (mean)	References
Algae				
Postelsia palmaeformis (E)	spores		3 m	11, 36
Enteromorpha (E)	spores	8 d	35 km	1, 22, 50
Macrocystis pyrifera (E)	spores	32 h	10–40 m	2, 41
Pterygophora californica (E)	spores	32 h	500 m	41
Ectocarpus siliculosus (E)	spores		≥4 km	41
Colpomenia peregrina (E)	spores		<3 m	47
Codium fragile spp. *tomentosoides* (I)	vegetative fragments, floating		12 km	6
Caulerpa taxifolia (I)	vegetative fragments, bottom		0.5 km	30
Sargassum muticum (E)	germlings	<25 d	<5 m	3, 13
Sargassum muticum (I)	vegetative fragments, floating		28 km (S. English Channel) <90 km (Atlantic coast of Europe) 10–13 km (Mediterranean coast of Europe) 43 km (Baja California)	9, 15, 25
Corals				
Balanophyllia elegans (E)	demersal planula, nonfeeding	3 d	0.1–0.5 m	16
Acroporids (E)	pelagic planula, nonfeeding	24–72 h	≤0.6 km	42
Pocilloporids (E)	brooded planula, nonfeeding	4 hr	≤0.6 km	42
Tunicates				
Didemnum molle (B)	tadpole, nonfeeding	<10 min–2 h	<50 m	33, 34
Diplosoma similis (B)	tadpole, nonfeeding	3.8 ± 2.6 min	2.2 ± 1.8 m	44, 45
Lissoclinum patella (B)	tadpole, nonfeeding	<10 min	<10 m	35
Podoclavella moluccensis (B)	tadpole, nonfeeding	<2 min	<2.5 m	10
Botrylloides sp. (B)	tadpole, nonfeeding	3.6 min	0.6 m (nonfeeding)	49
	tadpole, rafting		225 m (rafting)	
Botryllus schlosseri (E)	tadpole, nonfeeding		<1 m	17
Bryozoans				
Bugula neritina (E)	pelagic, nonfeeding	5 min–36 h	<100 m	24
Mollusks				
Cymatium parthenopeum (D)	veliger, feeding	293 d	4400 km	43
Littorina littorea (I)	veliger, feeding	30 d	42 ± 40 km	4, 5, 46, 48
Haliotis rubra (E)	veliger, nonfeeding	6 d	<15 m	38
Ensis directus (I)	veliger, feeding	16 d	111 km	23, 27
Perna perna (I)	veliger, feeding	15–20 d	235 km	21
Crustaceans				
Elminius modestus (I)	pelagic, feeding	17–34 d	41 ± 33 km	8
Alpheus immaculatus (E)	pelagic, feeding	7–14 d	30 m	26
Hemigrapsus penicillatus (I)	pelagic, feeding	16–55 d	160 km	32
Hemigrapsus sanguineus (I)	pelagic, feeding	16–55 d	33 km	14, 29
Carcinus maenas (I)	pelagic, feeding	80 d	173 ± 161 km (west coast of North America) 63 km (east coast North America)	7, 18, 19, 31
Fish				
Lutjanus kasmira (I)	pelagic, feeding	25–47 d	33–130 km	12, 39, 40
Oligocottus maculosus (B, D)	pelagic, feeding	30 d	<1 km	28, 37
Higher plants				
Zostera japonica (I)	seeds, juvenile plants		6 km	20

Notes: References are listed at the end of the table. Data sources for the dispersal-distance estimates are experimental studies (E), observations of dispersing larvae (B), observations on the distribution of larvae (D), and studies that followed the spread of introduced species (I). The data for larval duration came from either laboratory rearing experiments or observations of dispersing larvae. Larval duration has not been measured in *Hemigrapsus penicillatus*. The value used assumes that it is the same as in *Hemigrapsus sanguineus*.

References: 1, Amsler and Searles (1980); 2, Anderson and North (1966); 3, Andrew and Viejo (1998); 4, Bequaert (1943); 5, Brenchley and Carlton (1983); 6, Carlton and Scanlon (1985); 7, Chew (1998); 8, Crisp (1958); 9, Critchley et al. (1983);

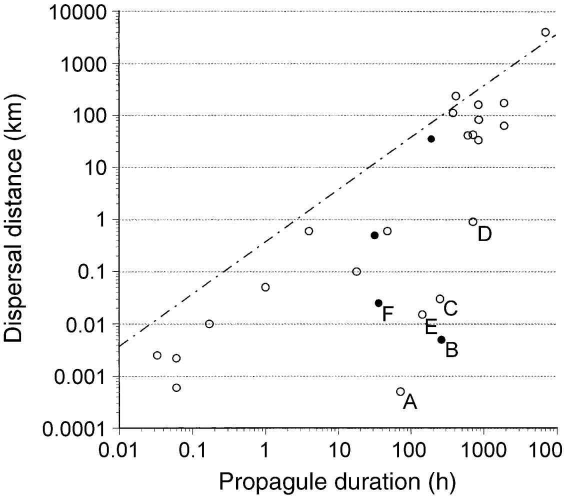

FIG. 1. A log/log plot of propagule duration (h) vs. mean realized dispersal distance (km/yr). A significant positive correlation was found between these two parameters ($r = 0.78112$, $r^2 = 0.61$, df = 1, 25, $P < 0.001$). Notice that there is a gap in the distribution of dispersal distances between ~1 and 20 km/yr. Open and filled circles represent animal and plant propagules, respectively. The points labeled A–F are species whose dispersal distance is less than expected given their propagule duration. These species include (A) the solitary coral *Balanophyllia elegans*, (B) germlings of *Sargassum muticum*, (C) the shrimp *Alpheus immaculatus*, (D) the intertidal fish *Oligocottus maculosus*, (E) the abalone *Haliotis rubra*, and (F) the giant kelp *Macrocystis pyrifera*. In each of these cases, due to their behavior or sinking, the larvae or propagules are found near the bottom where current speeds are reduced. A highly significant positive correlation was found if the analysis was run without these labeled points ($r = 0.9464$, $r^2 = 0.90$, df = 1, 18, $P < 0.001$).

losus larvae (point D, Fig. 1) aggregate near the shore (within one to several m), tend to cluster behind promontories that deflect the flow, and swim against the local current (Marliave 1986). As a second example, experiments have demonstrated that the larvae of the abalone *Haliotis rubra* (point E, Fig. 1) disperse only short distances (Prince et al. 1987). Researchers suggest that the habitat of the veligers may be immediately adjacent to the bottom and possibly under boulders (Prince et al. 1987). As a third example, the spores of *Macrocystis pyrifera* (point F, Fig. 1) are negatively phototactic and swim toward the bottom (Reed et al. 1988). If these outlying points are removed from the analysis, 94% of the variability in dispersal distance is explained by propagule duration ($r = 0.9717$, $r^2 = 0.94$, df = 1, 19, $P < 0.000$). Not surprisingly, the longer an organism is in the plankton the further it is dispersed. Propagules that, by their behavior or sinking, move down into the benthic boundary layer will experience reduced dispersal. Currents are slower within the benthic boundary layer and hence dispersal distance per unit time should be less.

Within Table 1, there are three examples of dispersal resulting from fragments of adult algae. The green alga *Caulerpa taxifolia* was introduced into the Mediterranean and is spreading along the French coast at a rate of ~0.5 km/yr. Dispersal is by vegetative fragments drifting near the bottom (Meinesz et al. 1993, Belsher and Meinesz 1995). In contrast, the introduced alga *Sargassum muticum*, which is dispersed as floating vegetative fragments (Knoepffler-Peguy et al. 1985) is also spreading along the Mediterranean coast of France, but at 10–13 km/yr. Similarly, the introduced alga *Codium fragile* spp. *tomentosoides*, which disperses as floating whole plants, is spreading along the east coast of North America at ~12 km/yr (Carlton and Scanlon 1985). Like propagules, the dispersal distance of fragments of adult algae appears to be smaller if the dispersal occurs via transport in nearbottom currents.

For two species, *Sargassum muticum* and *Carcinus maenas*, we have several determinations of mean realized dispersal distance (Table 1). Both species have been introduced to several different coasts where their spreading rates have been measured. The dispersal rate of *S. muticum* ranges from a low of 10 km/yr along the Mediterranean to a high of 90 km/yr along the Atlantic coast of Europe. The dispersal rate for *C. maenas* ranges from 63 to 173 km/yr along the east and west coasts, respectively, of North America. The dispersal rates along the different shores vary. Variation in the speed of coastal currents is probably one of the major causes for this variation in dispersal rate. Thus, the higher dispersal rate of *S. muticum* along the Atlantic coast of Europe than in the Mediterranean is probably because of faster coastal currents in the Atlantic. Dispersal rates might also be slowed by the lack of suitable adult habitat. Crisp (1958) observed this in the spread of the barnacle *Elminius modestus* and Branch (G. Branch, *personal communication* with A. L. Shanks) suggests that the spread of *C. maenas* along

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10, Davis and Butler (1989); 11, Dayton (1973); 12, E. Demartini (*personal communication*); 13, Deysher and Norton (1982); 14, Epifanio et al. (1998); 15, Espinoza (1990); 16, Gerrodette (1981); 17, Grosberg (1987); 18, Grosholz and Ruiz (1995); 19, Grosholz and Ruiz (1996); 20, Harrison and Bigley (1982); 21, Hicks and Tunnell (1995); 22, Jones and Barb (1968); 23, Kenchington et al. (1998); 24, Keough and Chernoff (1987); 25, Knoepffler-Peguy et al. (1985); 26, Knowlton and Keller (1986); 27, Luczak et al. (1993); 28, Marliave (1986); 29, McDermott (1998); 30, Meinesz et al. (1993); 31, Miller (1996); 32, Noel et al. (1997); 33, Olson (1983); 34, Olson (1985); 35, Olson and McPherson (1987); 36, Paine (1979); 37, Pfister (1997); 38, Prince et al. (1987); 39, Randall (1987); 40, Randall et al. (1993); 41, Reed et al. (1988); 42, Sammarco and Andrews (1989); 43, Scheltema (1971); 44, Stoner (1990); 45, Stoner (1992); 46, Thorson (1946); 47, Vandermeulen and DeWreede (1986); 48, Vermeij (1978); 49, Worcester (1994); 50, Zechman and Mathieson (1985).

TABLE 2. Larval duration of coastal fish species from western North America.

Species	Larval duration (d) midpoint (range)	References
Sebastes aurora	105 (90–120)	9
Sebastes carnatus	75 (60–90)	5
Sebastes flavidus	85 (60–110)	11, 17
Sebastes melanops	145 (110–180)	4
Sebastes melanostomus	105	8
Sebastes mystinus	105 (80–130)	11
Sebastes paucispinis	160 (150–170)	12
Sebastes serranoides	135 (90–180)	7
Paralabrax clathratus	30 (25–35)	1, 6
Paralabrax maculatofasciatus	22 (17–27)	14
Atractoscion nobilis	32 (29–35)	2
Medialuna californiensis	60	19, 20
Chromis punctipinnis	35 (32–38)	21
Hypsypops rubicunda	20 (18–22)	21
Halichoeres semicinctus	30 (26–34)	18
Oxyjulis californica	39 (36–43)	18
Semicossyphus pulcher	37 (34–52)	18
Heterostichus rostratus	37 (14–60)	16
Coryphopterus nicholsi	70	15
Lythripnus dalli	70	15
Paralichthys californicus	27	13
Citharichthys sordidus	271	12
Citharichthys stigmaeus	219 (113–219)	3
Eopsetta jordani	180	10

References: 1, Cordes and Allen (1997); 2, M. Franklin (*personal communication*); 3, Kendall (1992); 4, Laroche and Richardson (1980); 5, Larson (1980); 6, McClean (1999); 7, Love and Westphal (1981); 8, Moser and Ahlstrom (1978); 9, Moser et al. (1985); 10, Pearcy et al. (1977); 11, D. Woodbury [National Marine Fisheries Service–Tiburon/Santa Cruz] (*personal communication*); 12, Sakuma and Ralston (1995); 13, Sears-Hartley (1994); 14, Smith (1995); 15, M. A. Steele (*unpublished data*); 16, Stepien (1986); 17, Tagart (1991); 18, Victor (1986); 19, Waples (1987); 20, Waples and Rosenblatt (1987); 21, Wellington and Victor (1989).

the South African coast has been halted because of a lack of adult habitat.

One of the weaknesses of the data presented in Table 1 is that we could only estimate dispersal distance for two fish species. However, there has been extensive research on the duration of the larval period in fish. In Table 2, we present data on the larval duration of coastal fish species from the west coast of North America. These data are typical for coastal fish species. Larval duration ranged from a low of 20 d (480 h; *Hypsypops rubicunda*) to a high of 271 d (6504 h; *Citharichthys sordidus*). The mean for this data set is 94 d (2256 h). Unless these species have behaviors that reduce larval dispersal distances, as for *Oligocottus maculosus* as well as other larvae from intertidal fish (Marliave 1986, Kingsford and Choat 1989), the larval duration data suggest that the larvae of most west coast North American fish species have large (10s to 100s of km) mean realized dispersal distances.

The distribution of dispersal distances vs. propagule duration (Fig. 1) appears to be discontinuous and bimodal, with an apparent break between ~1 and 20 km/yr. In the data sets compiled for this paper, we found many examples of organisms that dispersed >20 km/yr or <1 km/yr, but only two organisms had a dispersal distance that fell within this gap (*Zostera japonica* and *Ectocarpus siliculosus*; Table 1). Using all the dispersal distance data, we found a significant negative kurtosis value (Fig. 2; $g_2 = -1.291$, $n = 39$, $t = -4.062$, $P < 0.001$) indicating that the distribution is significantly bimodal. The trough in the dispersal distribution is centered around dispersal distances of 1–20 km/yr.

The bimodal nature of the distribution may result from the types of studies used to create the data set. Studies of introduced species tended to find longer dispersal distances while experimental and behavioral studies found short dispersal distances. Maybe the studies in Table 1 were unable to detect dispersal between 1 and 20 km/yr. To test this hypothesis, we compared the actual dispersal distance estimated from each study to an estimate of what the study could have measured. In the case of the invasion studies, to estimate the minimum dispersal distance they could have measured we determined the mean spacing between sample collection sites. For example, the mean sample site spacing during the study of the spread of *Elminius modestus* along the coast of England was ~8 km (Crisp 1958). In the experimental and behavioral studies, we tried to estimate the maximum dispersal distance that they could have measured. In the experiments, this equals

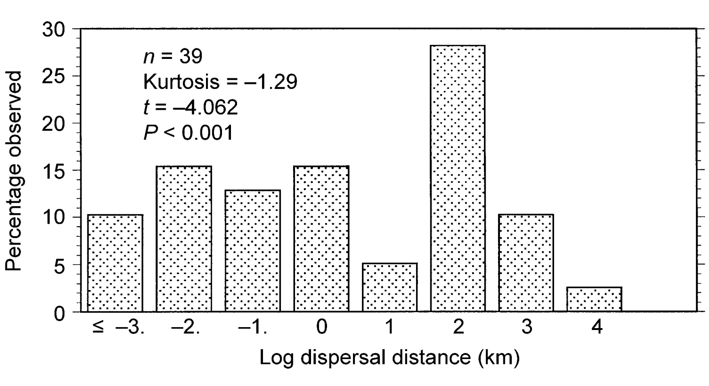

FIG. 2. Distribution of the log-transformed dispersal distance for the organisms in Table 1. The large and significant negative kurtosis value indicates that the distribution is bimodal.

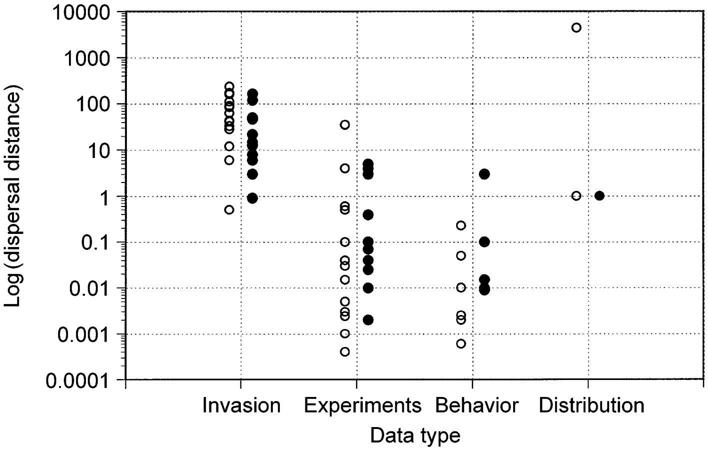

FIG. 3. Log-transformed dispersal distances plotted by data type. The open circles represent the actual dispersal distance found in the studies. The filled circles represent the dispersal distance that the different types of studies could have measured. In the case of the invasion studies, the minimum dispersal distance was set equal to the mean spacing between sample-collection sites. In the case of experimental studies, the minimum dispersal was set equal to the maximum distance that settlement plates were set from the isolated adult population. For the behavior studies, we used the maximum dispersal distance.

the maximum distance that settlement plates were set from the isolated adult population. In the Helix experiments on the Great Barrier Reef, for example, plates were sited ≤5 km from the reef but significant settlement was only seen within several hundred meters of the reef (Sammarco and Andrews 1989). For the behavior studies, we used the maximum dispersal distance. This is probably a minimum estimate of what they could have detected—one could follow a larva for hundreds of meters, but they usually settled after dispersing much shorter distances. These data are plotted by the type of data set in Fig. 3.

If the gap in the distribution of dispersal distances results from the methods used to estimate dispersal distance then we should find both few measured dispersal distances in the 1–20 km/yr range and few of the studies should have been able to measure dispersal in this range. In fact, only four studies found propagule dispersal distance in this range, but eleven of the studies could have measured dispersal distance between 1 and 20 km/yr. This suggests that if dispersal had been occurring to the distance of 1–20 km/yr that the studies should have detected it. The bimodal distribution does not appear to be a consequence of the types of studies used to estimate dispersal distance.

The bimodal distribution of dispersal distances is an exciting observation. These data suggest that there may be two evolutionarily stable dispersal strategies; propagules have evolved to disperse distances <1 km or >~20 km. Dispersing to distances between 1 and 20 km may not be an evolutionarily stable strategy. Short-distance dispersal seems to have been accomplished in two ways. First, propagules spend a short time in the plankton. For plants and animals, most of the short-distance dispersers are spores and lecithotrophic (nonfeeding) larvae, respectively (Fig. 4). Most of these propagules are competent to settle at release or shortly after. The second method of keeping dispersal distance short is by the adoption of propagule behaviors or densities that direct propagules to the bottom where slower currents are found. Longer-distance dispersal has primarily been accomplished by the evolution of propagules requiring longer periods of development in the plankton before they are competent to settle. Most of these larvae are feeding or planktotrophic larvae (Fig. 4). The two exceptions in this study have larvae that

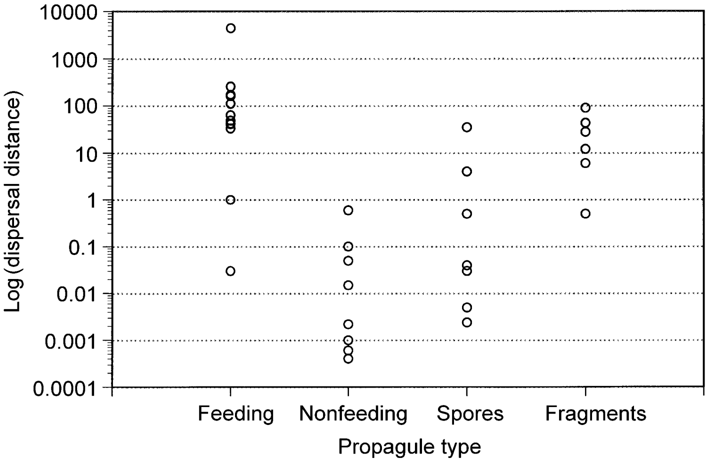

FIG. 4. Log-transformed dispersal distance plotted by propagule type.

tend to reside near the bottom (*Oligocottus maculosus* and *Alpheus immaculatus*; Table 1). What these results suggest is that possible consequences of the evolution of feeding vs. nonfeeding larvae are that the resulting larvae will tend to disperse a long or a short distance, respectively.

Why might dispersing to distances between 1 and 20 km be an unstable evolutionary strategy? The following is, obviously, speculation. The speed and direction of currents immediately adjacent to shore tend to be highly variable. This is especially true along a topographically complex shore. A propagule that remained in this environment for its entire dispersal stage would probably be carried only a short distance alongshore. To experience significant alongshore transport the propagule must migrate out of these nearshore waters and into the coastal currents; an offshore migration on the order of several hundred meters. At a coastal current speed of 10 cm/s, a propagule would be carried 5 km alongshore in only 14 h, at which time, to limit further dispersal, the organism would have to migrate back to the coast and settle. This hypothetical dispersal would take <1 d and, hence, the propagule must be essentially competent to settle at release. If propagules are competent upon release then we would expect survival to be higher if they simply settled when a suitable substrate or habitat is encountered instead of going through a potentially risky alongshore migration.

Note that local populations of organisms with larvae that disperse short distances will tend to be closed; most of the recruits are propagules from the local population. In contrast, we expect local populations whose larvae disperse longer distances (e.g., >20 km) to be more open, with a greater percentage of the recruits produced by adults outside the local population (see, however, Jones et al. 1999, Swearer et al. 1999). The more closed the population, the greater the possibility of local adaptations.

Frequently researchers make the simplifying assumption that propagules are dispersed passively by currents (see for example Roberts 1997). How reasonable is this assumption? Plotted along with the data in Fig. 1 is a dashed line that represents the distance propagules would travel if they were dispersing passively at a mean or resultant current speed of 10 cm/s (we neglect the effect of diffusion). All except two of the data points (*Perna perna* dispersing in the Gulf of Mexico and *Cymatium parthenopeum* dispersing in the Atlantic Equatorial current) fall below this line. The current speeds in the areas where these two species are dispersing are around 30 cm/s (Johnson 1939). If this faster current speed is used to estimate the passive dispersal distance then both species disperse shorter distances than they would if they were transported as passive particles. This comparison suggests that propagules are not dispersed passively by currents.

The design criterion we selected for the size of the reserve is that propagules released within the reserve settle in large enough numbers to sustain the adult population in the reserve. If we were to design a reserve around the larvae that disperse >20 km/yr then the reserve would have to be ≥40 km in diameter to contain just the propagules released from the center of the reserve. A much larger reserve would be needed if the propagules from more outlying adults were retained. This is obviously not a practical solution to the problem. A reserve 2 km in diameter, however, would contain all the larval types that disperse <1 km/yr and are released at the center of the reserve. Doubling or even tripling the size of this reserve, to ensure the maintenance of larger adult populations, still does not produce an unreasonably large reserve (e.g., 4 or 6 km in diameter or length along a coastline).

We suggest that reserves should be spaced along a coast such that larvae released from one reserve can disperse and settle into adjacent reserves. The minimum dispersal distance among the data sets from the longer range dispersing organisms was 20 km/yr (Table 1). This result suggests that a spacing of ~20 km between reserves should be close enough to allow even the ‘‘poorer’’ long-range dispersers to settle into adjacent reserves. Larvae that disperse longer distances may disperse far enough to settle into several reserves along the coast. One caveat: these estimates are based on propagule dispersal estimates and may or may not include the effects of adult movements which may be substantial for some species (especially fish species). For species with extensive adult movement, these estimates of recommended reserve size and spacing may be conservative.

Based solely upon an analysis of the distance which propagules of coastal benthic organisms are dispersed we have suggested an optimal size range for marine reserves and spacing between reserves. We suggest that marine reserves located on a continental coast or the coast of a large island be at least 4–6 km in diameter and spaced ≤~20 km apart. This size and spacing would allow larvae with short dispersal distances to settle within the reserve while larvae with longer dispersal distances would be carried to adjacent reserves.

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