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DISPERSAL POTENTIAL OF MARINE INVERTEBRATES IN DIVERSE HABITATS

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Abstract. Life-history parameters were used to estimate the dispersal potential of 1021 marine macroinvertebrates recorded in species lists from 91 sites comprising rocky intertidal, subtidal, kelp forest, sandy beach, and soft-bottom habitats in Washington, Oregon, and California. Mean species richness was significantly greater in the California rocky subtidal habitat. Data on development mode, planktonic larval duration, rafting potential, and adult mobility were compiled, and summaries of the dispersal potentials of taxa within each habitat type were generated and compared. In summary, development mode was known or estimated for 76% of species; larval planktonic duration for 49%; adult mobility for 76%; and rafting potential for 46%. In comparisons of species' life-history traits among habitats, sand-dominated habitats were distinct from rocky habitats. In rocky habitats, ~42% of species had planktonic feeding larvae, 43% had planktonic nonfeeding larvae, and 15% had nonplanktonic larvae. Sandy intertidal habitats had higher proportions of taxa with nondispersing, nonplanktonic larvae and lower proportions of planktonic feeding and nonfeeding larvae than all other sites. Soft-bottom subtidal communities had the highest proportion of taxa with planktonic feeding development and larvae with planktonic lifespans >30 d. Species in soft-bottom subtidal sites, therefore, have the greatest potential for extensive larval dispersal, whereas species in soft-bottom intertidal sites have the least potential for larval dispersal. In these sites with limited larval dispersal potential, there is greater potential for adult dispersal through adult movement and rafting. These differences in the dispersal potential of larvae and adults suggest that the effect of environmental changes and the effectiveness of reserves may differ between habitats. Conservation methods, including the use of marine reserves, must therefore be tailored to the habitat of interest if effective protection of community resources is to be achieved.

Key words: *dispersal; larvae; life history; marine invertebrates; marine protected area; marine reserve.*

INTRODUCTION

Marine communities are comprised of taxa with widely varying reproductive patterns, ranging from species with directly developing juveniles to those with larvae that spend months in the plankton (Thorson 1950, Strathmann 1987, Pechenik 1999). These life-history differences influence each species' larval dispersal potential, resulting in communities whose species occupy varying positions on the continuum between populations that are demographically open or closed (Todd 1998, Swearer et al. 1999). Consequently, marine communities consist of groups of populations that may be regulated at different spatial scales. Effective management of marine communities, therefore, depends on our ability to understand the scale at which these populations are regulated, particularly under conditions of change.

Understanding patterns of larval dispersal is critical to addressing questions of population persistence and community dynamics. Unfortunately, larval dispersal distances are known for only a few species with limited dispersal (reviewed in Shanks et al. 2003). Although new genetic (Palumbi 2003), otolith microchemistry (Swearer et al. 1999), and marking (Jones et al. 1999) methods show great promise for providing direct or indirect measures of larval dispersal distance, their widespread implementation is still far off. In the absence of empirical measurements, one alternative is to infer larval dispersal distances from known life-history parameters. This method has a long history in larval ecology (Todd and Doyle 1981, Scheltema 1986, Todd 1998, Bohanek 1999) and remains the only way of examining larval dispersal potentials for many species.

In this study, we used life-history parameters to summarize the dispersal potentials of invertebrates from different marine habitats in Washington, Oregon, and California, USA. Comparisons among these profiles showed habitat-specific differences in dispersal patterns. We discuss the implications of these results for the maintenance of marine communities, with particular emphasis on the design of marine reserves.

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TABLE 1. Species richness and location information for the seven habitat types.

Habitat	Code	Location	Species list source	No. sites	No. species Mean	No. species 1 SE
CA Sandy Intertidal	CA-S-I	Channel Islands	Straughan (1982), Dugan et al. (1993)	11	13.5$^{\mathrm{d}}$	1.9
CA Sandy Subtidal	CA-S-S	Channel Islands	Channel Islands Research Program, *unpublished data*	22	54.8$^{\mathrm{c}}$	6.1
CA Rocky Subtidal	CA-R-S	Channel Islands	Richards et al. (1992, 1993, 1997), Richards and Kushner (1994), Kushner et al. (1995, 1997*a*, 1997*b*, 1998, 1999)	16	311.3$^{\mathrm{a}}$	15.8
CA Rocky Intertidal	CA-R-I	Channel Islands	Seapy and Littler (1993)	15	89.6$^{\mathrm{b}}$	5.5
OR Rocky Intertidal	OR-R-I	Central OR	Goddard (1997)	12	60.3$^{\mathrm{bc}}$	4.8
WA Rocky Intertidal	WA-R-I	San Juan Island	M. Dethier, *unpublished data*	10	51.5$^{\mathrm{bcd}}$	4.1
WA Sandy Intertidal	WA-S-I	Central WA, San Juan Island	M. Dethier, *unpublished data*	5	21.8$^{\mathrm{cd}}$	7.8

Notes: The number of species was compared among habitat types using ANOVA. Significant differences ($P < 0.05$) in Tukey post-hoc comparisons are indicated by different superscript letters. The mean number of species across all habitat and location combinations is 86.1. State abbreviations are: CA, California; OR, Oregon; and WA, Washington.

METHODS

Ninety-one species lists of macroinvertebrates from intertidal and subtidal, rock and sand habitats in Washington (WA), Oregon (OR), and California (CA), USA were obtained from a variety of sources (Table 1). Species richness (number of species in each site) was compared among habitats with single-factor ANOVA. All statistical analyses were conducted using SAS version 6.11 (SAS Institute 1996). The taxa in these habitats have been extensively studied and thus provide some of the most complete life-history information available for marine species. For each species on these lists, larval development mode and planktonic larval duration characteristics were obtained from Morris et al. (1980), Strathmann (1987), Eckert (1999), and the primary literature (Appendix). Larval development mode was categorized as either nonplanktonic, planktonic with feeding larvae, or planktonic with nonfeeding larvae (Thorson 1950, Strathmann 1987). Estimates of planktonic duration were primarily based on laboratory studies. Because of the uncertain relationship between laboratory and field observations, data were collapsed into the following categories: 0 h (no time spent in plankton), >0–<24 h, 24–<168 h (7 d), 168 to <720 h (30 d), and >720 h (30 d). In order to determine if these categories had any effect on the analysis, alternative categories with equal bins were also used. These categories were 0 h, >0–<240 h (10 d), 240–<480 h (20 d), 480–<720 h (30 d), and >720 h (>30 d).

Information on rafting potential and adult mobility was obtained from the same sources as development mode and planktonic larval durations; however, we estimated these parameters for many species (Appendix). Rafting potential, the ability of adult organisms to disperse while attached to mobile substrata, was classified as unlikely, likely, or very likely based on rafting reports or observations for similar taxa. Mobility of adults was classified as sessile (attached or with movements on the order of meters or less per year) or mobile. Only characteristics that could be inferred with confidence were included in the analyses; where uncertainty existed these parameters were coded as unknown. Data was obtained for a large proportion of species at a site within all habitats (Table 2). In summary, development mode was known or estimated for 76% of species, larval planktonic duration for 49%, adult mobility for 76%, and rafting potential for 46%.

TABLE 2. Mean ± 1 SE proportion of species within each habitat with life history data.

	Proportion of species with data			
Habitat	Development mode	Planktonic larval duration	Mobility	Rafting
CA-S-I	0.78 ± 0.03	0.58 ± 0.03	0.67 ± 0.03	0.60 ± 0.05
CA-S-S	0.68 ± 0.01	0.30 ± 0.01	0.75 ± 0.01	0.24 ± 0.02
CA-R-S	0.59 ± 0.00	0.27 ± 0.00	0.82 ± 0.00	0.21 ± 0.00
CA-R-I	0.66 ± 0.01	0.46 ± 0.01	0.87 ± 0.01	0.43 ± 0.01
OR-R-I	0.92 ± 0.01	0.69 ± 0.01	0.93 ± 0.01	0.76 ± 0.02
WA-R-I	0.91 ± 0.01	0.75 ± 0.03	0.90 ± 0.01	0.77 ± 0.03
WA-S-I	0.77 ± 0.01	0.37 ± 0.11	0.37 ± 0.14	0.22 ± 0.09
Mean	0.76	0.49	0.76	0.46

Note: Habitat codes are as in Table 1.

The frequency of species in each life-history category (development mode, larval planktonic duration, adult mobility, and rafting potential) was calculated for each species list and contingency table analyses were used to make comparisons. First, the frequency of species in each life-history category was compared among sites within a habitat type. Every habitat showed no significant association of site and life-history category within habitat type, except the Washington sandy intertidal habitat for development mode, therefore sites are pooled within habitat type. The proportion of species in each life history category was calculated for a site and then averaged by habitat for graphical comparison. For statistical analysis, the frequency of species in each life-history category was compared among habitats. Dispersal profiles for the habitats were then prepared by plotting the cumulative mean proportion of taxa within each planktonic duration category.

The data sets used here have several limitations. The species lists vary in collection methods, effort, and spatiotemporal coverage, factors that can influence the number of taxa observed. Cryptic or very small species are likely to be undersampled in each habitat. However, in such a broad and synthetic study, biases resulting from these limitations cannot be eliminated. We also do not know the life histories and movement potential for all species in each species list (Table 2). In fact, more information is available for species in certain habitats (i.e., rocky intertidal) than others (i.e., sandy habitats). For these limitations, we make the assumption that the characteristics that we know from the species reported from each site are representative of the habitat. Third, we have compared planktonic duration using categories. To evaluate the effect of the categories chosen, alternative categories have also been used (with no difference in the result detected).

RESULTS

A total of 1021 taxa were recorded in species lists from 91 sites examined in seven habitats. The overall mean (±1 SE) number of taxa per habitat was 86.1 (±38.7; Table 1). Mean species richness was significantly greater in the California rocky subtidal habitat (311.3 ± 15.8 species) than in all other habitats and lowest in the sandy intertidal habitats from Washington and California (21.8 ± 7.8 and 13.5 ± 1.9 species, respectively; Table 1; single-factor ANOVA, df = 6, 90, $F = 142.78$, $P > 0.0001$). In general, the rocky subtidal habitat in California had a greater number of species than all rocky intertidal habitats in California, Oregon, and Washington. Rocky intertidal habitats were generally more diverse than sandy subtidal and sandy intertidal habitats. The life-history data were most complete for species found in rocky intertidal habitats from Washington and Oregon, where development mode was known for 91% and 92% of the species in a site, planktonic larval duration for 75% and 69%, adult mobility for 90% and 93%, and rafting potential for 77% and 76% of the species in a site, respectively (Table 2).

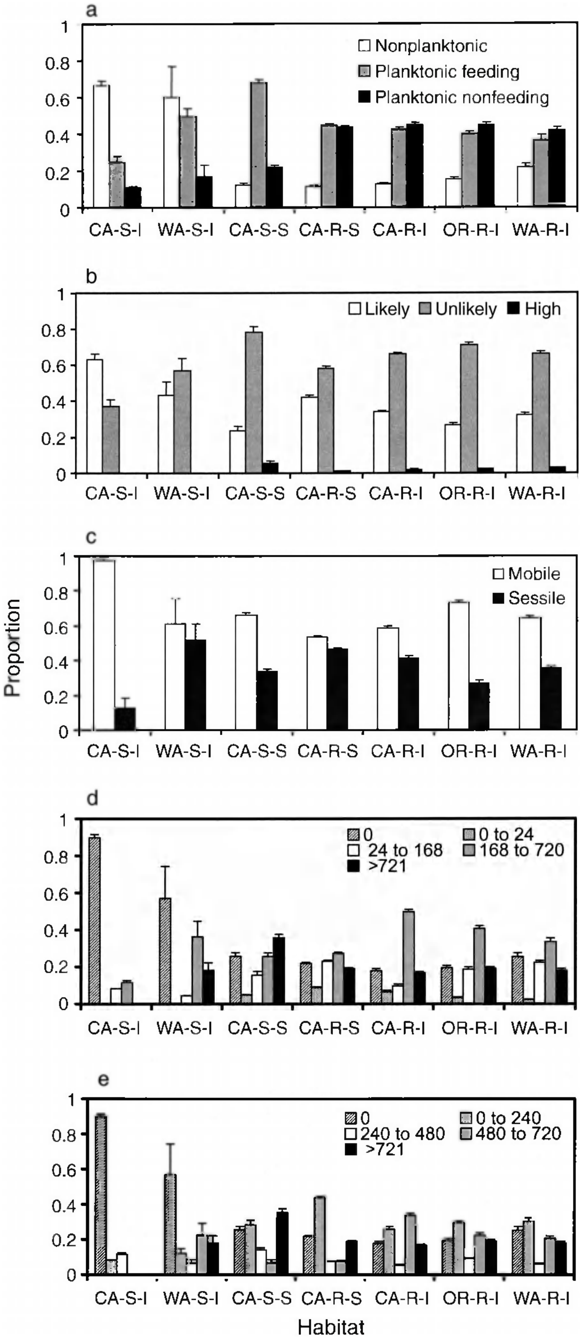

FIG. 1. Proportions (mean + 1 SE) of (a) development mode, (b) rafting potential, (c) adult mobility, and (d, e) larval planktonic duration (using two sets of categories) among seven habitats from Washington (WA), Oregon (OR), and California (CA). Habitat codes are described in Table 1. See *Methods* for a description of development mode categories.

Significant associations were found between each life-history characteristic and habitat type. The pattern

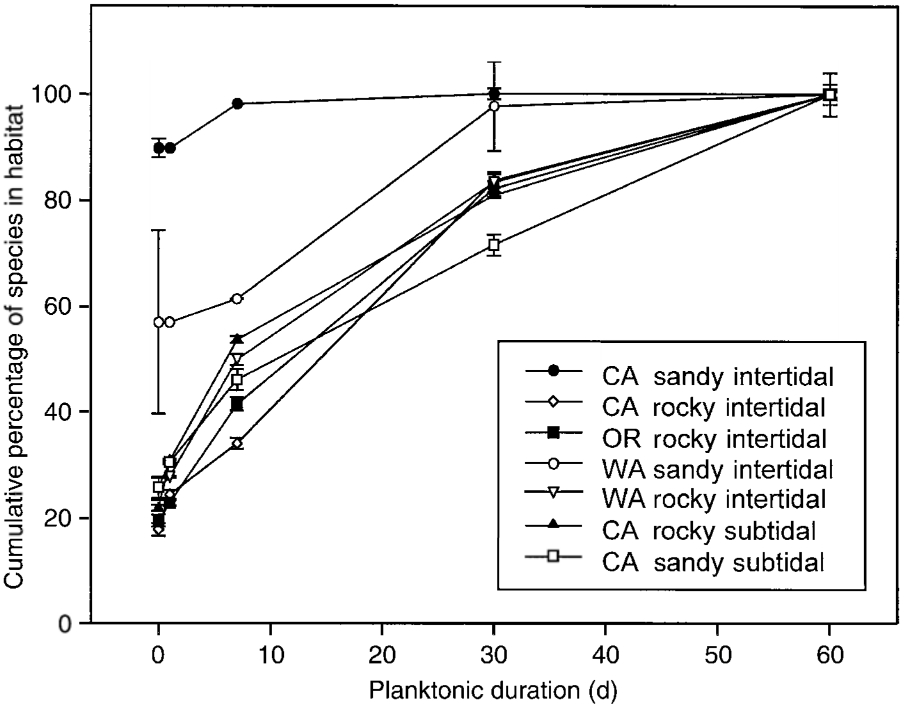

FIG. 2. Dispersal profiles of marine invertebrates for sites along the U.S. West Coast. Plots show how the cumulative mean percentage of each assemblage's species changes with increasing time in the plankton. For illustration purposes, the >30 d dispersal category is plotted as 60 d.

is striking in the development-mode analysis (Fig. 1a; df = 12, $\chi^2 = 542.5$, $P = 0.001$) where species from sandy sites show a different distribution of development modes than rocky sites. The sandy intertidal habitats in California and Washington had higher mean proportions of nonplanktonic development (66% ± 0.03% and 60% ± 0.17%, respectively) than all other habitats (all other habitats < 22%; Fig. 1a). The sandy subtidal habitat was unique in having high proportions of species with planktonic feeding larvae (68% ± 0.02%). The proportion of species likely to disperse by rafting varied among habitats (Fig. 1b; df = 12, $\chi^2 =$ 100.1, $P = 0.001$) and was noticeably low in the sandy subtidal habitat. Adult mobility varied across habitats (Fig. 1c; df = 6, $\chi^2 = 175.1$, $P = 0.001$) and was high in the California sandy intertidal habitat. Planktonic larval duration was also associated with habitat and the result was similar with different bins (Fig. 1d; df = 24, $\chi^2 = 464.8$, $P = 0.001$; and Fig. 1e; df = 24, $\chi^2 = 587.7$, $P = 0.001$). As was found in the development mode analysis, there was a strikingly high proportion of species with planktonic larval durations of 0 d in the sandy intertidal habitats. The different bins resulted in the same general pattern, with the data more evenly distributed when the categories were more evenly distributed.

The dispersal profiles (Fig. 2), show several types of curves. The first type represents the sandy intertidal habitats, with large proportions of nonplanktonic larvae; the second represents the rocky intertidal and subtidal habitats; and the third represents sandy subtidal habitats that have low proportions of species with larval durations of 7–30 d and high proportions with durations >30 d. Rebinning of the larval duration data into alternative time blocks did not alter the qualitative differences in dispersal profiles.

DISCUSSION

In a study of the larvae of the Øresund, Thorson (1946) observed that 63% of species had long-lived planktotrophic larvae, 6% had short-lived (<1 wk) planktonic larvae, and 31% had nonplanktonic larvae. In our study, we observed great variation in the distribution of development modes at a site, ranging from 10% to 80% of species with long-lived planktotrophic larvae, 5% to 51% with short-lived planktonic larvae, and 5% to 100% of species with nonplanktonic larvae. The distribution was related to habitat type with a consistent pattern found in almost half of the sites (n = 43) from this study: ~42% of species had long-lived planktotrophic larvae, 43% short-lived planktonic larvae, and 15% nonplanktonic larvae (Fig. 1a). This pattern represents a much more general result than Thorson's (1946), but is limited to habitats with rocky substrate. Habitats with sandy substrate had much different patterns of distribution, with sandy intertidal sites being dominated by species with nonplanktonic development and sandy subtidal sites being dominated by species with long-lived planktotrophic larvae (Fig. 1a). A similar pattern was found using estimates of planktonic larval duration instead of larval development mode.

The habitats examined here showed significant among-habitat differences in the relative representation of development modes and larval durations. The high incidence of nonplanktonic development observed in the sand-dominated habitats suggests that larval exchange with nearby sites is likely to be very low. In the other habitats, the high proportions of species with planktonic feeding larvae and longer larval durations are expected to result in increased larval export and a greater dependence on outside populations for recruitment. Likewise, the differences in aggregate dispersal characteristics seen in this study translate into habitats that differ in the spatial scale at which their populations are regulated. As a result these populations may be decoupled during periods of environmental change, producing substantial changes in community structure.

Less clear were site-specific differences in rafting potential and adult mobility. Transport by rafting appears to be common among sessile species like barnacles, snails, amphipods, and ascidians, but the contribution of rafting to dispersal in these species is unknown (Highsmith 1985, Martel and Chia 1991, Worcester 1994). Rafting events may ensure gene flow and occasionally allow establishment of new, outlying populations (Johannesson 1988), but its importance in population maintenance remains an open question. Adult mobility may also be an important factor affecting a species' distribution, but reliable information is available for very few species. Other methods of transport, such as dispersal by sperm and eggs, may also be important in determining dispersal patterns (Grosberg 1991, Havenhand 1995, Palumbi 1995, Pechenik 1999) but even less is known about these processes.

Habitat-specific differences in the life-history characteristics of species assemblages have been observed in other studies. Todd (1998) found higher numbers of planktotrophic larvae in epifaunal assemblages than in intertidal communities, leading him to suggest that short-distance dispersal in intertidal species was ''almost obligatory.'' Similarly, Levin (1984) found that many species inhabiting back-bay habitats in the Kendall-Frost mudflat (Mission Bay, California) had life histories consistent with low dispersal. Species assemblages from southern California mudflats and salt marshes separated by long stretches of sandy, high-energy coastline also had high proportions of taxa with reduced dispersal potential (Levin 1984, Levin and Bridges 1995). Talley et al. (2000) found differences in the proportion of direct and planktonic developing polychaetes among sites within a single habitat type—tidal flats in Baja, California and Mission Bay, California. However, a high prevalence of brooding species (nonplanktonic development) was present in each these assemblages, a pattern which is consistent with our observation of greater proportions of nonplanktonic development in sandy intertidal sites.

Although many processes could produce among-habitat differences in life histories, the interaction between substrate characteristics and frequency of disturbance is thought to be a particularly powerful selective force on the evolution of dispersal in marine organisms. It is well known that substrate characteristics affect the species diversity and composition of sessile invertebrate communities (Talley et al. 2000). High disturbance rates, particularly in patchy environments where larvae leaving a patch are unlikely to encounter another patch, should favor the evolution of nonplanktonic or short-lived planktonic larvae (Pechenik 1999). In contrast, large-scale disturbances should favor the evolution of long-distance dispersal (Levin 1984). Levin (1984) and Levin and Huggett (1990) found that the life histories and dispersal characteristics of species and species assemblages determined patterns of recovery following disturbance. Over evolutionary time longer dispersal minimizes the likelihood of extinction (Jablonski and Lutz 1983), but makes species less adaptable to local conditions (Bertness 1989). Trade-offs between these two processes should have important impacts on the evolution of dispersal patterns. However, there is always an advantage to retaining some dispersal ability as long as local extinctions occur, since only dispersing individuals can recolonize empty space and thereby avoid extinction (Palmer and Strathmann 1981). This may be why species with life histories consistent with low dispersal potential often seem to include postsettlement stages capable of dispersing (Levin 1984). Our observations that sandy sites generally had higher proportions of species with high adult mobility or rafting potential are consistent with this observation. A more thorough discussion of the habitat-specific mechanisms that could drive the evolution of alternate life histories is beyond the scope of this paper. Readers are instead referred to the recent review paper (and references cited therein) of Pechenik (1999).

Gaps in our knowledge of basic life histories continue to hinder our understanding of marine communities. Even on the west coast of the United States, arguably among the most intensively studied of coastal communities worldwide, we lack a basic knowledge of the life histories of many marine species. Although we were able to estimate development mode for, on average, 76% of the species from a site, larval duration could be estimated for only 49% of the species from a site, and estimates of rafting potential were even lower. The proportion of species for which adult mobility was estimated was relatively high, but these values represent our confidence in estimating adult mobility only within very coarse categories. Little information

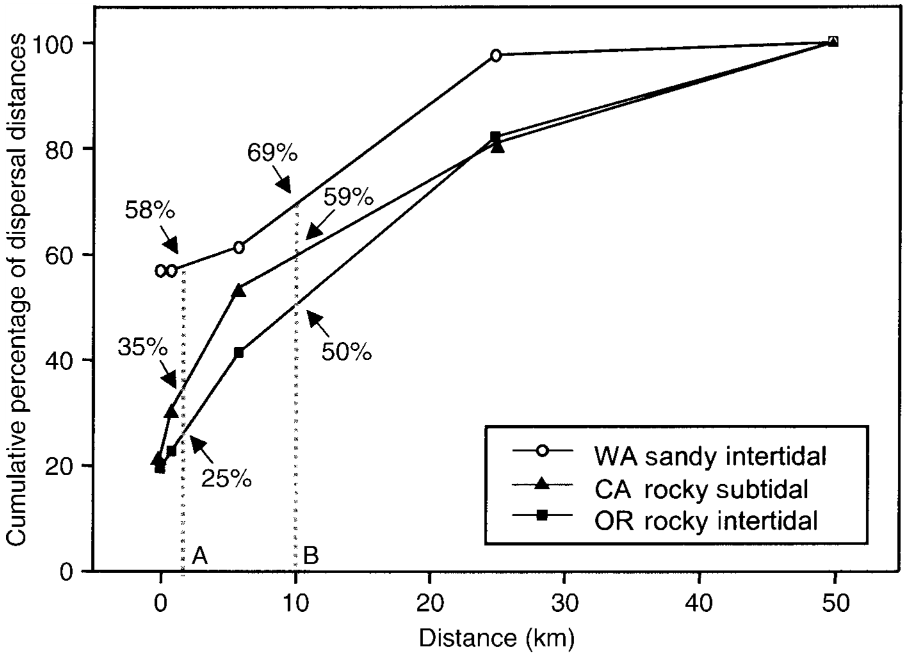

FIG. 3. Hypothetical example showing how the percentage of dispersal distances encompassed by increasing reserve sizes differs among three habitat types. Curves represent the cumulative percentage of each habitat's planktonic larval durations as shown in Fig. 1d. Reserve size A (2 km) exceeds or equals the dispersal distances of 58% of the taxa in the WA sandy intertidal assemblages, 35% in the CA rocky subtidal assemblages, and only 25% in the OR rocky intertidal assemblages. Increasing reserve size to B (10 km) raises these proportions to 69%, 59%, and 50%, respectively.

is available on adult dispersal for most marine invertebrates, so the use of narrower categories was impossible. Despite having incomplete data, genetic studies, showing that gene flow is typically higher in species with life histories indicative of long-distance dispersal than in those without (Palumbi 1995, Bohanek 1999), suggest that using life histories to characterize the dispersal properties of species assemblages is reasonable.

IMPLICATIONS FOR MARINE RESERVE DESIGN

There is increasing agreement that marine reserves are important management tools (Allison et al. 1998, Bohnsack 1998, Guénette et al. 1998, Hall 1998, Lauck et al. 1998, Ruckelshaus and Hays 1998, Sumaila 1998, Murray et al. 1999, and others), but basic questions such as how many reserves are needed, how large they should be and where they should be located remain unanswered. In the absence of outside sources of replenishment, reserves or reserve systems must be sufficiently large to encompass sustainable populations. The variation in life-history characteristics observed here suggests that these marine habitats will respond differentially to changes in reserve size and therefore reserve design must be tailored to the community of interest. The dispersal profiles generated in this study can help to address these issues.

An obvious next step in this analysis is to relate dispersal profiles to absolute dispersal distances, but insufficient information on dispersal distances is available to accurately do this. Nonetheless, relating these results to a rough estimate of maximum dispersal distance is instructive. Until recently the dispersal distances of most planktonic larvae have been assumed to be quite high. However, recent evidence from plankton distributions (Grantham 1997), studies of larval fish retention around oceanic islands (Jones et al. 1999, Swearer et al. 1999), direct observations of dispersal (Grosholz 1996, Shanks et al. 2003), and genetic isolation by distance methods (Palumbi 2003) suggests that dispersal distances may be much shorter than previously expected. As an example, we have applied a maximum dispersal distance of 50 km to the species with the longest planktonic period to generate dispersal profiles for three of the habitat types from our study (Fig. 3). A small reserve protects a greater proportion of the taxa in a sandy habitat than in the others. These results support the assertion that small reserves can protect assemblages of taxa with limited dispersal (Roberts and Hawkins 1997, Shanks et al. 2003) but stress the importance of reserve systems for the effective protection of whole habitats. Our reasoning is based on the assumption that networks of reserves and larger reserves established to protect species with widely dispersing larvae will benefit those with shorter dispersal distances as well. Under this scenario marine reserves may benefit from the use of umbrella, focal, or keystone species (Simberloff 1998). Commercially important marine invertebrates may work well as focal

TABLE 3. Planktonic larval durations of some common marine invertebrates taken by commercial and sport fishermen in Washington, Oregon, and California.

Common name	Scientific name	Larval duration
Sea urchins	*Strongylocentrotus purpuratus*	48–74
	S. droebachiensis	35
	S. franciscanus	66
	Allocentrotus spp.	>30†
Sea cucumbers	*Parastichopus californicus*	96
Dungeness crabs	*Cancer magister*	80
Red rock crabs	*Cancer antennarius*	>60†
Red crabs	*Cancer products*	68–150
Turban snails	*Tegula funebralis*	6
Abalone	*Haliotis* spp.	7–12
Butter clams	*Saxidomus giganteus*	28
Littleneck clams	*Tapes philippinarus*	28
Softshell clams	*Mya arenaria*	23
Geoducks	*Panope abrupta*	18
Mussels	*Mytilus edulis*	32
	Mytilus californianus	9
Shrimp	*Pandalus* spp.	>30†
Mud/ghost shrimp	*Callianassa* spp.	>30†
Barnacles	*Pollicipes polymerus*	21
Sand crabs	*Emerita analoga*	>30†

Note: List compiled from Washington, Oregon, and California 1999 Sport Fisheries Regulations.

† Estimated minimum larval duration.

species because their planktonic larval durations tend to be a month or more (Table 3).

Considerable effort has been directed at modeling the size and spacing criteria for single-species reserves (Polacheck 1990, Botsford et al. 1993, DeMartini 1993, Quinn et al. 1993, Mann et al. 1995, Sladek Nowlis and Roberts 1997, Guénette and Pitcher 1999, Hastings and Botsford 1999, Hastings and Botsford 2003), but there have been few efforts to model multispecies reserves. Single-species models have been important in demonstrating how dispersal distance and the shape of the dispersal curve (Botsford et al. 2001), as well as adult mobility (Polacheck 1990, DeMartini 1993, Guénette and Pitcher 1999) influence reserve success, that reserve networks can provide better protection than isolated reserves (Quinn et al. 1993, Mann et al. 1995), and that reserves can be as effective as traditional techniques in fisheries management (Hastings and Botsford 1999). However, multispecies models are necessary if the ecosystem-oriented approaches espoused by many scientists and formally adopted in the United States Magnusen-Stevens Act are to be fruitful. We anticipate that the dispersal profiles generated in this study can be used as starting points for models examining how habitats comprised of species with widely varying dispersal distances will respond to alternative reserve size and spacing scenarios.

CONCLUSIONS

Understanding the complexities of larval dispersal is critical if ecosystem-oriented approaches to marine conservation are to be successful. This study is among the first to characterize the dispersal profiles of marine invertebrates and to show that dispersal patterns differ sufficiently between habitat types. These differences can have important consequences for the conservation of marine communities and particularly for the design and development of marine reserves. The results presented here provide an empirical starting point for incorporating diverse dispersal characteristics into the reserve design process.

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APPENDIX

A table showing life-history characteristics of marine invertebrates found in species lists at the 91 sites analyzed for this study is available in ESA's Electronic Data Archive: *Ecological Archives* A013-001-A1.