

A PHYSICALLY BASED MODEL OF MACROALGAL SPORE DISPERSAL IN THE WAVE AND CURRENT-DOMINATED NEARSHORE

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Abstract. Propagule dispersal in seaweeds is a process influenced by a variety of biological and physical factors, the complexity of which has hindered efforts to understand colonization, persistence, post-disturbance recovery, and dynamics of algal populations in general. In view of this limitation, we employ here modifications to an existing turbulent-transport model to explore the mechanics of nearshore macroalgal spore dispersal and its relationship to coastal hydrodynamic conditions. Our modeling efforts focus on four example species of seaweed whose reproductive propagules span a wide range in sinking speed and height of release above the sea floor: the giant kelp *Macrocystis pyrifera*, the erect furoid *Sargassum muticum*, the small filamentous brown alga *Ectocarpus siliculosus*, and the flaccid red alga *Sarcodiotheca gaudichaudii*. Results indicate that both propagule sinking speed and release height can affect dispersal distance substantially, but that the influence of these biological parameters is modulated strongly by the intensity of turbulence as dictated by waves and currents. In rapid flows with larger waves, it is primarily fluid dynamic processes, in particular current velocities, that determine dispersal distance. Additional simulations suggest that patterns of spore dispersal are highly skewed, with most propagules encountering the sea floor within a few meters to hundreds of meters of their parents, but with a sizeable fraction of spores also dispersing as far as kilometers. Such model predictions imply a much greater potential for longer range dispersal than has typically been assumed, a finding with important implications for understanding the demographics of algal populations and for predicting levels of connectivity among them.

Key words: *Ectocarpus siliculosus*; eddy diffusivity; flow; macroalgae; *Macrocystis pyrifera*; propagule; release height; *Sarcodiotheca gaudichaudii*; *Sargassum muticum*; sinking speed; turbulence; vertical mixing.

INTRODUCTION

Propagule dispersal in terrestrial and marine plants can be similar in many ways, and ecological analogies drawn between these systems have proven fruitful in a number of studies (e.g., Hoffmann and Ugarte 1985, Hoffmann 1987, Reed et al. 1988). There are, however, important differences as well. Perhaps the dominant feature distinguishing passive dispersal on land and in the sea is the mass density of the surrounding fluid (i.e., air or water). As noted by Denny (1993), air may be three orders of magnitude less dense than a typical seed, while the densities of seawater and macroalgal spores may differ by only a few percent. This relationship ensures that the vast majority of seeds in air sink faster than propagules in the ocean. As a consequence, in coastal environments it is often rates of vertical mixing due to fluid turbulence, rather than sinking

speeds per se, that control how long it takes an algal propagule to encounter the sea floor.

Dispersal in seaweeds may also depend more strongly on fluid motion for additional reasons. For instance, although animal vectors on land commonly carry seeds substantial distances (usually to locations unrelated to patterns of air movement), substantially fewer cases of vector-mediated dispersal have been described for macroalgae (reviewed in Santelices 1990; see also Norton 1992 for a more critical discussion). Instead, most of the longest distance dispersal in seaweeds is thought to occur via drifting plants or fertile plant fragments, which, much like spores, are transported according to prevailing currents (Chapman 1986, van den Hoek 1987).

In this regard, dispersal in macroalgae resembles larval dispersal of many marine invertebrates and fish (Amsler and Neushul 1989, Reed et al. 1992); both are largely controlled by advective flows and the length of time spent in the water column (Keough 1989). However, unlike algal drift or larvae of many marine animals which may spend weeks to months in offshore

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waters and can be transported vast distances in ocean currents (Scheltema 1971, Richmond 1987), most seaweed propagules are competent to settle immediately upon release and are believed to settle within a couple of days (Santelices 1990). This suggests that studies of propagule dispersal in macroalgae can ignore, at least to first order, the variability associated with many slowly evolving oceanographic processes that operate primarily at larger temporal and spatial scales, a feature we exploit in building the model discussed below.

Although a number of studies have begun to tease apart factors affecting spore dispersal in macroalgae (reviewed in Santelices 1990, Norton 1992), such efforts have nevertheless remained uncoupled from any mechanistic exploration of the physical processes that dominate nearshore flows. This limitation has resulted in a rather disjointed collection of arguments for a variety of observed or assumed patterns, including particular vertical spore distributions in the water column (Amsler and Searles 1980, Hoffmann and Ugarte 1985), greater dispersal from larger populations (Anderson and North 1966) or under certain hydrodynamic conditions (Reed et al. 1988), relationships between the height at which propagules are released or sinking speed and transport potential (Hoffmann and Camus 1989, Santelices 1990, Norton 1992, Fredriksen et al. 1995), and levels of algal population connectivity (Descombe et al. 1992). Such qualitative arguments have highlighted the need for an improved understanding of the physics of algal spore dispersal, its dependence on nearshore flow, and the resulting implications for patterns of seaweed recruitment in hydrodynamically complex coastal environments.

Many factors determine how long macroalgal propagules remain in suspension and thus their potential for dispersal. Biological characteristics such as size, shape, mass density, behavior, and the height of release above the bottom can affect the time required for propagules to settle out of the water column (reviewed in Mileikovsky 1973, Santelices 1990, Amsler et al. 1992, Norton 1992), as can physical factors such as turbulent mixing (Norton and Fetter 1981, Denny 1988, Denny and Shibata 1989). The relative importance of these parameters for determining dispersal potential, however, has proven difficult to estimate. Propagule size in macroalgae is highly variable among species, differing by as much as two orders of magnitude (Clayton 1992). Moreover, spore sinking speeds show even greater variation since terminal velocities of small particles vary with the square of diameter (Stokes' law; see, e.g., Vogel 1994). Although many algal propagules swim, they do so only slowly (Norton 1992, Amsler et al. 1999) and it has remained unclear how effectively they might control their vertical positions in the water column (much less their horizontal distributions). Furthermore, the intensity of turbulent mixing varies strongly with depth in coastal systems, and may therefore affect the vertical movement of propagules dif-

ferently at various positions in the water column. This final point indicates that there is no simple linear relationship between the height at which propagules are released and the time it takes them to reach the sea floor, a nontrivial complication modulating how far propagules can be carried by currents while suspended.

To explore in more detail the consequences for dispersal of these interacting biological and physical factors, we employ a previously developed model for vertical turbulent transport (McNair et al. 1997) that predicts hitting times (the elapsed time from release until first contact with the bottom) for propagules as a function of flow condition, their sinking speed, and the height above the bottom from which they are released. Because this model was originally developed in the context of stream ecology where mixing is induced by a steady current alone, we add turbulence components associated with waves to make it more applicable to nearshore marine environments. We then use this modified formulation to predict typical current-induced dispersal patterns in four species of macroalgae whose propagules span a wide range in sinking speed and release height. While this approach does not address fine-scale patterns ensuing from settlement behaviors (e.g., Butman et al. 1988, Raimondi and Keough 1990, Amsler and Neushul 1991, Gross et al. 1992) or effects of variable bottom roughness (e.g., Eckman 1990), it provides a general, quantitative examination of how sea state interacts with components of seaweed life history to influence vertical distributions of algal propagules in the water column and the distances over which they disperse.

STUDY SPECIES

Some of the smallest algal propagules are produced by kelps, large brown algae in the order Laminariales (Clayton 1992). Kelp spores are typically 5–7 μm in diameter, and contain unusually high levels of lipid (Reed et al. 1999), suggesting that they should sink more slowly in still water than propagules of many other macroalgae. Because of their tall stature, most kelps also release their spores relatively high in the water column. In contrast, red algae are generally shorter and release larger (up to 160 μm diameter; Santelices 1990) and denser (i.e., lipid poor; Reed et al. 1999) spores close to the bottom. Intermediate propagule characteristics can be found in some of the fucoids (brown algae in the order Fucales), which do not have spores but instead release relatively large and heavy eggs (up to 120 μm in diameter and 200 μm in length) from buoyant reproductive fronds that may extend a meter or more up into the water column. Such eggs are fertilized rapidly after release and dispersal occurs via the resulting embryos. Finally, there are a number of diminutive brown and green algae that produce small motile spores, which effectively have negative sinking rates due to their propensity to swim upward. To illustrate the consequences for dispersal of such differ-

ences in sinking speed and release height, we focus on four representative species common to central and southern California, one from each of the broad groupings above: the giant kelp *Macrocystis pyrifera*, the red alga *Sarcoditheca gaudichaudii*, the fucoid *Sargassum muticum*, and the small filamentous brown alga *Ectocarpus siliculosus*, whose spores exhibit positive phototaxis (Clayton 1992, Amsler et al. 1999).

METHODS

We use a three-step approach to examine propagule dispersal in the four species. First, we obtain information on spore sinking speeds and on the mean height above the bottom from which each species releases its spores or embryos. Second, we use the sinking speed and release height data to predict mean propagule hitting times across a range of flow conditions, employing our modified version of the McNair et al. (1997) model. Third, we estimate order of magnitude dispersal distances for each species and flow condition by multiplying hitting times by mean current speed. In this overall approach, we focus on the common situation of dispersal away from algal stands separated by relatively smooth sand flats. This avoids the related but more complicated problem of within-stand dispersal on rocky reefs, where three-dimensional, site-specific flows result from plant obstruction and any high relief topography.

Propagule sinking speeds

Data on spore or embryo sinking speeds exist for three of the four species we examine in our study. Sinking speeds of *Sarcoditheca gaudichaudii* (previously *Agardhiella tenera*) spores and *Sargassum muticum* embryos were obtained from Coon et al. (1972) and Norton and Fetter (1981), respectively. The mean swimming speed reported by Amsler et al. (1999) provided an estimate of the negative sinking speed of the positively phototactic spores of *Ectocarpus siliculosus*. Because data were not available for *Macrocystis pyrifera*, we determined the net sinking rate of its spores in the laboratory.

Macrocystis spores were obtained from fertile sporophylls collected in Monterey Bay, California, using the methods of Reed et al. (1991). Two spore suspensions were made, one with live spores and a second with spores killed with a small infusion of fresh water. These two treatments allowed us to examine the degree to which swimming behavior might influence vertical spore distributions in this species. Both suspensions were diluted with sterile filtered (0.2 μm) seawater to a density of $\sim 6.5 \times 10^5$ spores/mL and each was used to fill ten 50-mL plastic beakers to a depth of 40 mm. The beakers were stirred gently to distribute the spores evenly in suspension, a glass cover slip was centered on the bottom of each beaker, and the beakers were placed in a constant-temperature room at 15°C in the dark to minimize convective fluid motions. Every hour

for 10 h one beaker from each of the two treatments (live and dead) was removed from the constant-temperature room and its cover slip retrieved. The density of spore settlement on each cover slip was determined by counting the number of settled spores in 10 microscope fields using an inverted compound microscope. Spores adhere firmly to glass upon settling (Reed et al. 1991), thus dislodgment and loss of spores during retrieval was assumed negligible. Seven replicate trials were conducted on different dates, each using spores obtained from a different location in Monterey Bay. Spore sinking speed in *Macrocystis* was then estimated by dividing the maximum distance of spore fall (40 mm) by the mean time until spore settlement leveled off, a calculation based on the assumption that the number of settled spores on a cover slip increases over time as long as some spores remain in suspension, and that settlement stops once all spores have sunk to the bottom.

Release heights

Spores of *Macrocystis pyrifera* are produced in sporangia that occur in dense aggregations on specialized blades termed sporophylls that are clustered in a large bundle near the base of the alga. We therefore estimated the mean height of spore release in *M. pyrifera* as the mean height of the midpoint of the sporophyll bundle of 119 individuals measured in the field. Release height for embryos of *Sargassum muticum* were estimated from published measurements of the mean height of the gas-filled fronds from which they are released (Foster and Schiel 1993). Unlike *Macrocystis pyrifera* and *S. muticum*, the sporangia of the brown alga *Ectocarpus siliculosus* and the red alga *Sarcoditheca gaudichaudii* are not restricted to specialized structures but are distributed throughout the thallus. The mean release height for *E. siliculosus* was therefore estimated as one half its thallus length, using sizes reported in Abbott and Hollenberg (1976). Because length is not a good measure of height for the nonbuoyant thallus of *S. gaudichaudii* (which typically lies prostrate on the bottom), we measured the height of 53 individuals in the field and used the mean of these data to estimate mean release height for this species.

The calculation of hitting times

McNair et al. (1997) developed a model for predicting propagule hitting times that approximates turbulent transport of suspended particles as a one-dimensional stochastic diffusion process. This approach is similar to one used in the classic work of Denny and Shibata (1989), but generalizes it and corrects a subtle bias. In essence, the model tracks the time to contact the bottom for propagules taking numerous, short, randomly directed steps either up or down (i.e., a "random walk"; see Berg 1983), when released from a given height. The probability of stepping to a new vertical position is a function of the degree of mixing which

varies with elevation in the water column. Two dispersion components are present, a molecular diffusion component important only immediately adjacent to the substratum, and a turbulence component which dominates mixing throughout the rest of the water column.

For the molecular diffusion component, the probabilities of a propagule moving up or down (p_m or q_m , respectively) by a distance δ_m during a time step τ are given by

$$p_m = q_m = \frac{1}{2} \quad (1)$$

where

$$\delta_m = \sqrt{2\nu\tau} \quad (2)$$

and ν is the kinematic viscosity of seawater, 1×10^{-6} m²/s. Analogously, for the turbulence component, the probabilities of moving up or down (p_t or q_t , respectively) by a distance δ_t during time step τ are given by

$$p_t = \frac{2K + \left(\frac{dK}{dz} - s\right)\delta_t}{4K} \quad q_t = \frac{2K - \left(\frac{dK}{dz} - s\right)\delta_t}{4K} \quad (3)$$

where

$$\delta_t = \sqrt{2K\tau}. \quad (4)$$

The overall distance moved during a time step is then computed as the sum of the molecular and turbulent motions. K is the combined molecular-turbulent diffusivity (a function of height above the bottom, z) which quantifies dispersive flux in a turbulent flow (Denny 1988, Mann and Lazier 1996). The propagule sinking speed in still water is s . Eqs. 1–4 therefore allow individual propagules to be tracked, step by step, until they reach the bottom; the process is then repeated for multiple propagules until a sufficiently large number have been tracked to develop a complete hitting-time distribution. In practice, this task is accomplished via computer using Monte Carlo simulations with a standard random number generator algorithm.

McNair et al. (1997) also provide a shortcut expression that yields an explicit description of the mean hitting time, $m(z)$, for propagules released from height z :

$$K \frac{d^2 m}{dz^2} + \left(\frac{dK}{dz} - s\right) \frac{dm}{dz} = -1 \quad (5)$$

with boundary conditions $m(0) = 0$, $dm/dz(H) = 0$, where H is the depth of the water ($z = H$ at the surface). Values of m calculated from this expression equal the mean hitting times found from the random walk in the limit as the number of propagules becomes large. Although this shortcut expression provides only mean values instead of complete distributions, it allows for a more rapid examination of a wider range of hydrodynamic conditions than would be possible using the

computationally intensive Monte Carlo approach. Eq. 5 is solved numerically using standard finite difference techniques (see, e.g., Ferziger 1981).

As is apparent from Eqs. 3–5, the diffusivity profile (a proxy for mixing rate) is a critical parameter controlling hitting times. McNair et al. (1997) present a general form for K :

$$K = \frac{\nu}{2} + \sqrt{\left(\frac{\nu}{2}\right)^2 + (K_t)^2} \quad (6)$$

which applies throughout the entire water column, including the region near the seabed where molecular diffusion dominates. Unfortunately, the turbulent diffusivity component, K_t , is the subject of much current research and there are a variety of forms from which to choose (Davies et al. 1997). Here we use an expression that describes the variation of turbulent diffusivity with depth in coastal marine systems subjected to the combination of waves and currents (Wiberg and Smith 1983):

$$K_t = \kappa z \left[u_{*c}^2 \exp\left(-\frac{2z}{l_c}\right) + u_{*w}^2 \exp\left(-\frac{2z}{l_w}\right) \right]^{1/2} \quad (7)$$

where κ is the nondimensional von Karman's constant, nominally 0.4, u_{*c} is the current shear velocity, an index of the intensity of turbulence in a boundary layer associated with the steady current, and u_{*w} is the analogous shear velocity associated with the waves, l_c is the turbulent length scale for mixing due to the current, l_w is the mixing length scale of the wave motion (here taken to be $2\kappa u_{*cw}/\omega$), ω is the wave frequency, and u_{*cw} is the shear velocity associated with the maximum bottom shear stress arising from both waves and current. For shallow depths, there is often enough turbulence from the bottom boundary layer and breaking surface waves to keep the entire water column mixed so that setting l_c equal to $H/2$ is a reasonable first-order simplification (see also Eckman 1990).

The three shear velocity components of Eq. 7 are estimated from the well-known benthic boundary layer model of Grant and Madsen (1979, 1986). This method defines u_{*c} , u_{*w} , and u_{*cw} based on wave height and wave period, bottom roughness, current speed, and current direction relative to the axis of wave propagation. While the mathematics linking these quantities are somewhat involved and are not repeated here (they are outlined step by step in Grant and Madsen 1986), we provide a qualitative description of the boundary-layer physics represented by this approach in the Appendix. Using the Grant and Madsen (1979, 1986) model, we compute u_* values corresponding to a range of wave heights (0.5–3 m), wave periods (10 and 20 s), and current speeds (2–50 cm/s), in water of 10 m depth. Waves are assumed to propagate shoreward, perpendicular to alongshore currents, and bottom roughness elements are assumed to have characteristic heights of order 0.8 cm, a reasonable first-order simplification for

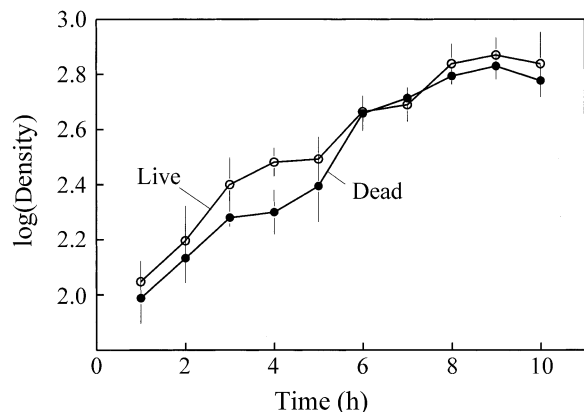


FIG. 1. Settlement rates for *Macrocyctis pyrifera* spores in still water. Density was measured in spores/mm². The figure presents means ± 1 SE; n = 7 trials.

our heuristic model where we are primarily interested in dispersal between reefs that are separated by open expanses of sandy bottom (Smith and McLean 1977, McLean et al. 1999). Although the assumption of orthogonal waves and currents can be violated under some circumstances in nature, changes in the relative angular orientation of these two flow components generally alter shear velocities by <15%.

The calculation of dispersal distances

Dispersal distances are estimated for each of the four species across the above hydrodynamic conditions (which are indexed by the *u_{*}*'s and thus *K* via Eq. 7) by multiplying current speed by the current/wave-specific hitting times obtained from model predictions. Although this procedure ignores effects of vertical variation in horizontal velocity due to a current boundary layer (i.e., we have neglected shear dispersion), we are interested in order-of-magnitude trends, which are relatively insensitive to this simplification. Flow speeds used in the calculations are based on values recorded at 10 m depth near Santa Barbara, California, USA during a continuous 18-mo study (Washburn et al. 1999). Current magnitudes at this site ranged from near zero to nearly 50 cm/s.

Vertical distributions of propagules

Details of the vertical distribution of spores in the water column can also be relevant for algae that are capable of exploiting three-dimensional habitat structure (e.g., filamentous species that grow as epiphytes on kelps high in the water column). McNair et al. (1997) show that in a horizontally uniform steady current at locations far from a source where horizontal gradients in particle concentration are small and where the majority of particles encountering the bottom do not settle, propagules are distributed vertically at steady state according to the expression

$$c(z) = \frac{\exp\left(-s \int_0^z \frac{1}{K(\zeta)} d\zeta\right)}{\int_0^H \exp\left(-s \int_0^z \frac{1}{K(\zeta)} d\zeta\right) dz} \quad (8)$$

where *c*(*z*) is the local concentration at height *z* above the bottom normalized by the depth-averaged concentration. We use this relationship to explore the influence of sinking rate on the steady state vertical distributions of macroalgal spores under different hydrodynamic conditions.

RESULTS

Sinking speeds and release heights

Settlement densities of *Macrocyctis pyrifera* spores falling through 40 mm deep laboratory suspensions leveled off after ~9 h (Fig. 1), indicating a sinking rate of ~0.0012 mm/s. Differences between sinking speeds of live and dead spores were negligible. Such sinking speeds are substantially slower than those of propagules produced by the other species examined in this study (Table 1). Together with the observed differences in species' release height (Table 1), this spectrum of sinking speeds leads to a vast range of hitting times in still water (Table 1). For example, it would take nearly 100 h for a *M. pyrifera* spore released by its parent to sink to the bottom in the absence of turbulence, whereas a *Sarcodiotheca gaudichaudii* spore would reach the sea floor in <5 min. Spores of *Ectocarpus siliculosus* would theoretically never reach the bottom in still water because they swim upward.

TABLE 1. Mean height of release above the bottom, mean sinking speed in still water, and the estimated time to sink to the bottom in still water for propagules of four species of macroalgae.

Species	Release height (cm)	Sinking speed (mm/s)	Hitting time in still water (s)
<i>Macrocyctis pyrifera</i>	42	0.0012	350,000
<i>Sargassum muticum</i>	93†	0.677‡	1,374
<i>Sarcodiotheca gaudichaudii</i>	3	0.116§	259
<i>Ectocarpus siliculosus</i>	2†	-0.051	∞

Notes: Data for *Sargassum muticum* are for embryos that lacked rhizoids. Sources: † Abbott and Hollenberg (1976); ‡ Norton and Fetter (1981); § Coon et al. (1971); || Amsler et al. (1999).

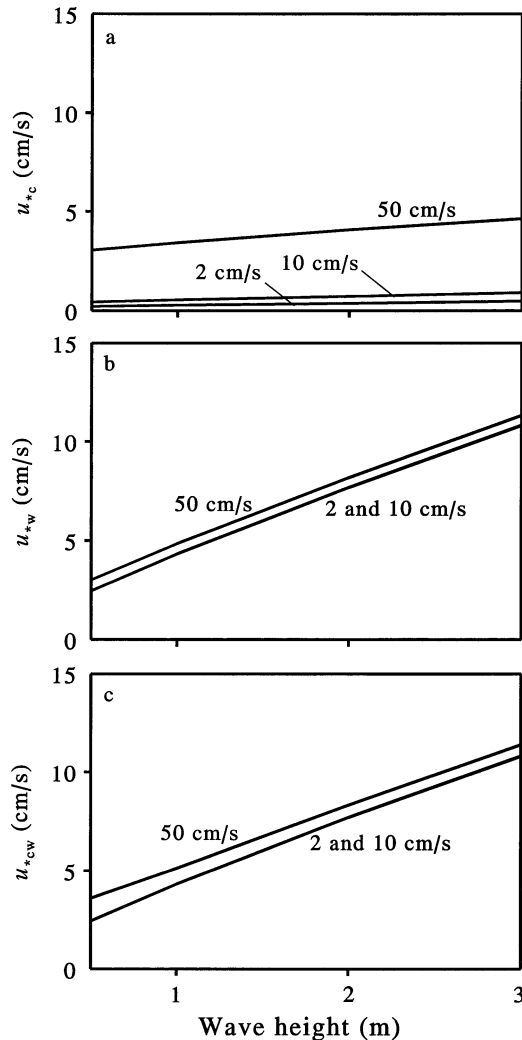


FIG. 2. (a) Current, (b) wave, and (c) current-wave shear velocities as a function of nearshore hydrodynamic conditions. Curves are based on waves with a 10-s period and a water depth of 10 m.

Mixing parameters

The three shear velocity parameters, which together dictate the profile of vertical mixing, all increase with faster currents and larger waves (Fig. 2). In general, wave and current-wave shear velocities (u_{sw} and u_{scw} respectively) are larger than current shear velocities (u_{sc}), particularly under bigger waves. The current shear velocity depends more strongly on current speed than wave height, while the opposite is true of u_{sw} and u_{scw} . It is also apparent that the magnitude of the current-wave shear velocity is largely determined by the wave shear velocity since only minor differences exist between u_{sw} and u_{scw} . (Fig. 2b, c). Note, however, that because wave and current-wave shear velocities dictate the intensity of turbulence only in a relatively thin layer near the seabed, u_{sc} plays a more dominant role in defining the profile of mixing throughout most of the

water column (see Fig. 3 for a typical diffusivity profile). Also, although Fig. 2 depicts only shear velocities for waves with a 10-s period, results are nearly indistinguishable if the wave period is doubled. We therefore present data only for 10-s waves here and throughout the remainder of this study.

Mean hitting times

Fig. 4 shows mean hitting times of the four species as a function of wave height and current speed. Several trends are apparent.

First, mean hitting times range from minutes to hours and generally decrease with increasing current speed and wave height. Mean hitting times also converge as wave heights increase and currents become more rapid. In general, *Macrocystis pyrifera* shows the longest mean hitting times of the species and flow conditions considered.

Second, *Macrocystis* spores show a greater response to changes in sea state than do propagules of the other species. This arises from the exceptionally slow sinking speeds of *M. pyrifera* spores, which cause these propagules to act almost entirely as passive particles. Thus it is the intensity of turbulence, as dictated by waves and currents, rather than sinking speed that routinely controls mean hitting time in this species. In contrast, the mean hitting times of the faster-falling (or rising) propagules of *Sargassum muticum*, *Sarcodiotheca gaudichaudii*, and *Ectocarpus siliculosus* vary less strongly with hydrodynamic conditions, at least for the release heights that characterize them.

Third, a comparison of data in Fig. 4 with the still-water sinking times of Table 1 indicates that current- and wave-induced turbulence can either increase or decrease mean hitting times, a possibility first emphasized

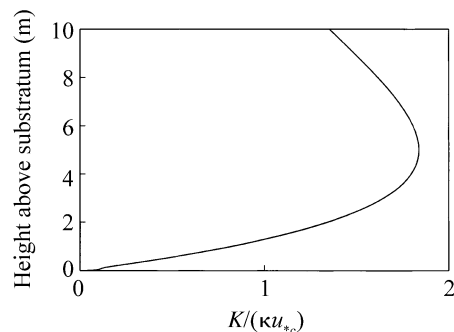


FIG. 3. Example of a normalized diffusivity profile, showing how rates of vertical mixing often vary with depth. Near the substratum, turbulent velocities can be relatively large (note in particular the inflection in the curve ~ 10 cm from the bottom due to wave boundary-layer effects), but the length scales of turbulent motion are small. Farther from the bottom, velocity scales can be small, but the length scales of turbulence are large. Analogous patterns arise with respect to the water's surface. The net result is that rates of vertical turbulent diffusion peak in midwater. The specific curve depicted is for a current speed of 10 cm/s with waves of 1 m height and 10-s period.

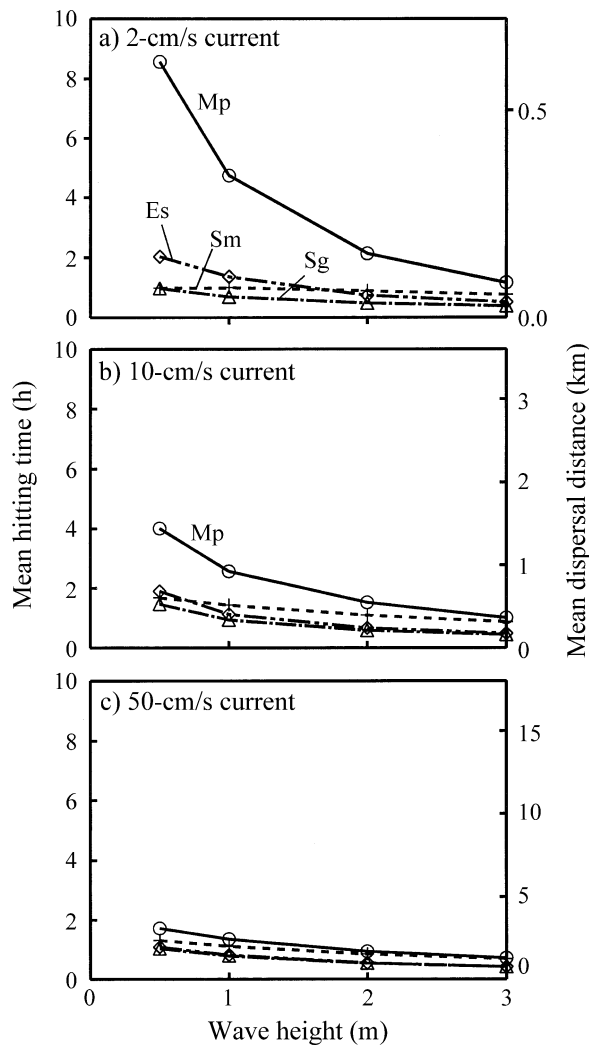


FIG. 4. Predicted mean hitting times (left axes) and mean dispersal distances (right axes) for propagules of four species as a function of wave height for three current speeds. Abbreviations: Es = *Ectocarpus siliculosus* (diamond, dashed-double-dotted line); Mp = *Macrocystis pyrifera* (circle, solid line); Sg = *Sarcodiotheca gaudichaudii* (triangle, dashed-dotted line); Sm = *Sargassum muticum* (cross, dashed line).

by McNair et al. (1997). In the case of *Macrocystis*, the mean hitting time is decreased by nearly an order of magnitude even under rather benign hydrodynamic conditions (i.e., a current speed of 2 cm/s and wave height of 0.5 m). On the other hand, the mean hitting times of *Sargassum* and *Sarcodiotheca* are actually greater in the presence of turbulence than in still water. This pattern follows from the fact that turbulence always acts to shift mean hitting times towards the mean time it takes a given fluid element (or a nonmotile neutrally buoyant propagule that moves with the fluid) to contact the bottom from a particular height. In the case of *Macrocystis* and *Ectocarpus*, spore hitting times in still water are greater than these fluid contact times,

while the opposite is true for *Sargassum* and *Sarcodiotheca*. This situation differs, of course, from that arising in nonturbulent conditions where neutrally buoyant particles would theoretically never (ignoring Brownian motion) reach the sea floor.

Fig. 4 is less useful for separating the relative effects of release height and sinking speed on mean hitting time since these dual factors are characteristic coupled traits of a particular species. Therefore, to isolate the impacts of these two parameters, we also calculate mean hitting times across a range of sea conditions with release height and sinking speed varied independently (Fig. 5). Results indicate that both release height and sinking speed are most influential under relatively quiescent hydrodynamic conditions (e.g., 2-cm/s current and 0.5-m waves). Under such benign conditions, the greatest sensitivity to release height and sinking speed occurs when propagules are released from heights above ~10 cm, outside the well-mixed wave boundary layer. As current speeds increase, wave amplitudes, release height, and sinking speed become less important and mean hitting times converge. Except when current velocities are exceptionally slow (<2 cm/s), sinking speeds play a relatively minor role in affecting mean hitting time until those speeds approach 1 mm/s. Release height remains relatively more important until hydrodynamic conditions become severe (i.e., 50-cm/s currents and 3-m waves).

Mean dispersal distances

Figs. 4 and 5 also show mean dispersal distances for each species and flow condition (see right axes). These distances range from tens of meters to over a kilometer depending on species and sea state, considerably farther than has typically been assumed. Like mean hitting times, mean dispersal distances decline with increasing wave height, but are enhanced rather than decreased by the presence of faster currents. In all other respects, patterns of mean dispersal distance mimic those of mean hitting time. Thus slower sinking speeds and higher release heights increase mean dispersal distances, particularly when currents are slow (2 cm/s), and play a lesser role in determining mean dispersal distance in the presence of more rapid currents.

Distributions of dispersal

Thus far we have considered only mean hitting times and mean dispersal distances. However, the shape of an overall hitting time or dispersal distribution may be equally if not more important than its mean, particularly if a distribution is highly skewed. The dispersal distributions predicted by our Monte Carlo simulations are indeed highly skewed, with most propagules encountering the sea floor at distances substantially shorter than their means (see also McNair 2000). Because of this extreme asymmetry, we present in Fig. 6 distributions of the log transform of dispersal distance. These data indicate a tendency for species' dispersal

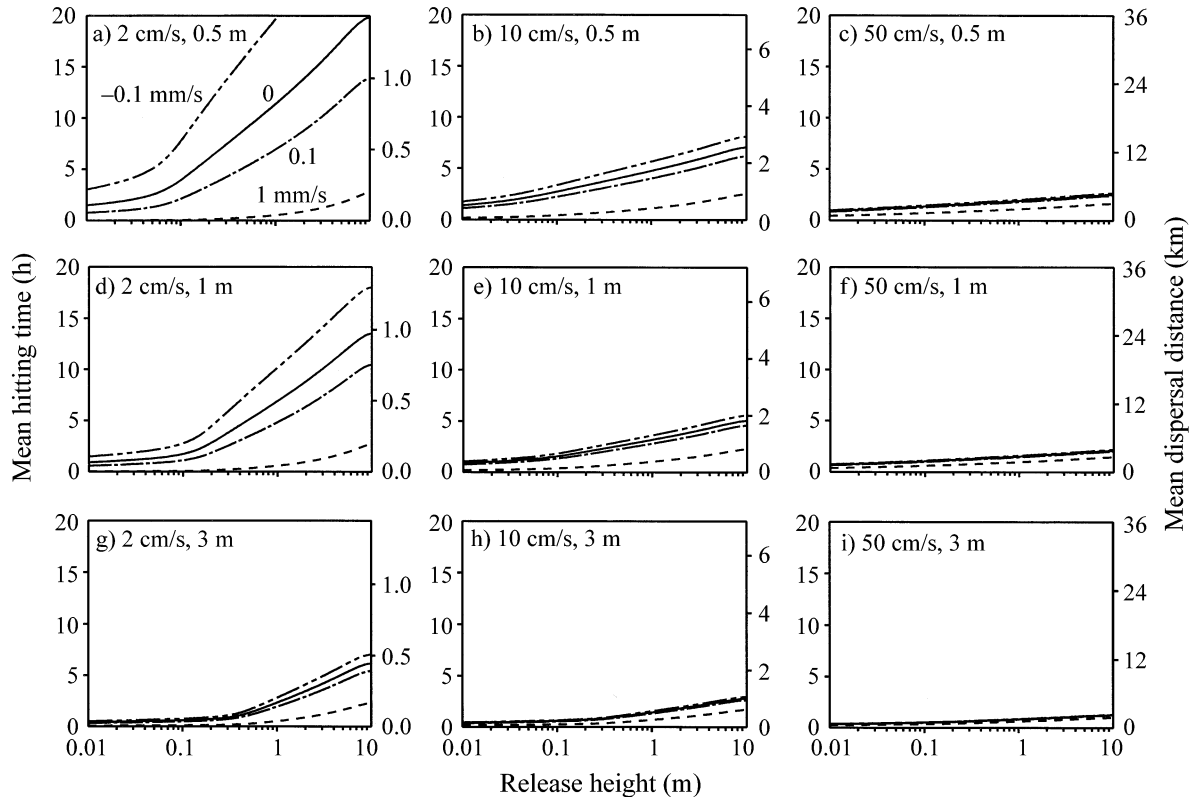


FIG. 5. Predicted mean hitting times (left axes) and mean dispersal distances (right axes) as a function of release height, for four sinking speeds, across a range of hydrodynamic conditions. Key: -0.1 -mm/s sinking speed, dashed-double-dotted line; 0 -mm/s, solid line; 0.1 -mm/s, dashed-dotted line; 1 -mm/s, dashed line. Mean current speed and wave height are noted in the upper left corner of each panel.

curves to group according to release height as wave- and current-generated turbulence increases. Thus both *Ectocarpus* and *Sarcodiotheca*, which release their spores near the sea floor, have similar log-transformed dispersal distributions, while *Sargassum* and *Macrocystis*, which release propagules from relatively higher elevations, also often have distributions that resemble one another. It is primarily only in the low-turbulence case of Fig. 6a, where the faster propagule sinking speed of *Sargassum* plays a more important role in vertical transport, that its log-transformed dispersal distribution diverges strongly from that of *Macrocystis*. Note, however, that due to the nature of log-transformed data, the relatively subtle differences in the right hand portions of the *Sargassum* and *Macrocystis* histograms of Fig. 6b reflect somewhat more noticeable differences in untransformed mean dispersal distance (Fig. 4b).

The dispersal potential of seaweeds is further clarified by the cumulative probability exceedance curves of Fig. 7. As has been observed in previous studies, many macroalgal propagules disperse to only a few meters. Consistent with this pattern, only 50% of the spores of *Ectocarpus* and *Sarcodiotheca* are predicted to disperse beyond 1 m, at least in placid hydrodynamic

conditions (Fig. 7a). Under these same calm conditions, the propagules of *Sargassum* and *Macrocystis* may travel somewhat farther, with 50% dispersing beyond ~ 50 m and ~ 100 m, respectively. We emphasize, however, that substantial fractions of propagules may disperse to much greater distances in coastal flows as well. For example, even in the presence of rather mundane 10 -cm/s currents, 10 – 20% of the propagules of *Ectocarpus*, *Sarcodiotheca*, and *Sargassum* are predicted to disperse past 1 km, while nearly 30% of *Macrocystis* spores may be transported beyond this distance (Fig. 7b). In 50 -cm/s flows, the distances corresponding to these percentages may more than double (Fig. 7c).

Vertical concentration profiles

Steady state vertical concentration profiles of propagules are also affected by flow conditions and sinking speed. Not surprisingly, sinking speed has the greatest effect on vertical distributions when nearshore conditions are benign (Fig. 8a). Propagules that sink faster become concentrated near the bottom while those that swim or float upward concentrate near the water's surface. As current speeds and wave heights increase, however, steady-state distributions approach a concentration profile that is more uniform across depth (Fig. 8b, c).

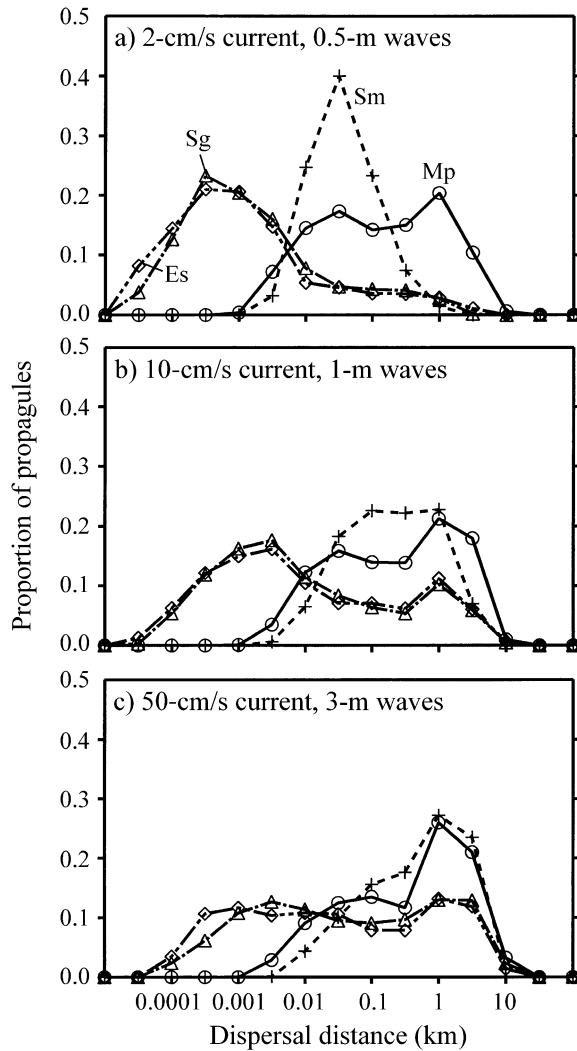


FIG. 6. Distributions of the log transform of dispersal distance for four species across a range of hydrodynamic conditions. Abbreviations: Es = *Ectocarpus siliculosus* (diamond, dashed-double-dotted line); Mp = *Macrocystis pyrifera* (circle, solid line); Sg = *Sarcodiotheca gaudichaudii* (triangle, dashed-dotted line); Sm = *Sargassum muticum* (cross, dashed line).

This is particularly the case for particles with slower sinking speeds, a finding that is consistent with laboratory experiments demonstrating that fine sediments exhibit uniform vertical distributions regardless of the shape of the diffusivity profile (Middleton and Southard 1984). Note that propagules with sinking speeds similar to that of *Sargassum muticum* (~1 mm/s) have steady-state concentrations that increase with depth even under relatively severe hydrodynamic conditions (Fig. 8c).

DISCUSSION

Dispersal potential in seaweeds

Most studies to date have concluded that spore dispersal in macroalgae is limited to a few meters (re-

viewed in Dayton 1985, Schiel and Foster 1986, Santelices 1990, Norton 1992). This view has persisted despite observations of propagules at locations multiple kilometers away from the nearest source population (Jonsson 1972, Amsler and Searles 1980, Zechman and Mathieson 1985, Reed et al. 1988). As is indicated by the data of Figs. 6 and 7, however, it appears that kilometer-scale dispersal can occur routinely even though many spores do settle within meters of their parents. In this regard, results of our model help to reconcile previous, apparently divergent, findings.

Historically, at least two coupled factors have likely contributed to the underestimation of dispersal capacities in macroalgae. First, although the percentage of

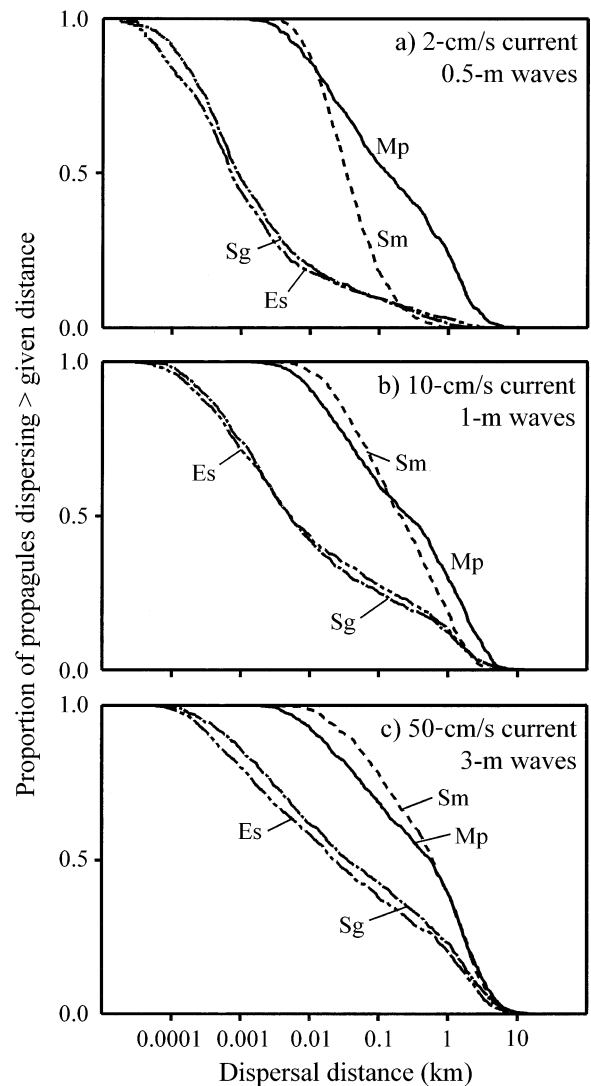


FIG. 7. Probabilities of dispersal exceeding a given distance for four species across a range of hydrodynamic conditions. Abbreviations: Es = *Ectocarpus siliculosus* (dashed-double-dotted line); Mp = *Macrocystis pyrifera* (solid line); Sg = *Sarcodiotheca gaudichaudii* (dashed-dotted line); Sm = *Sargassum muticum* (dashed line).

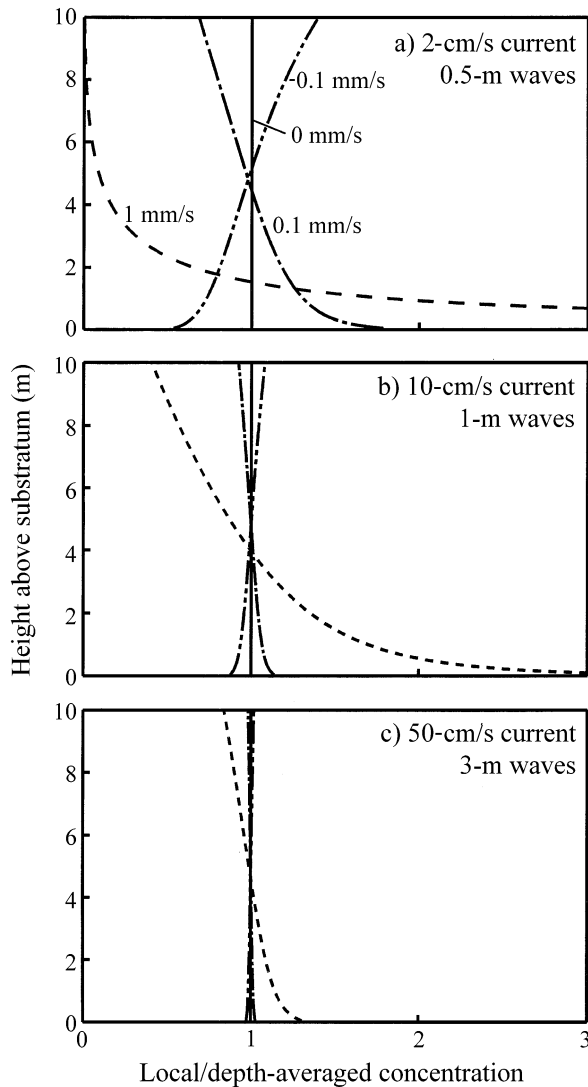


FIG. 8. Predicted vertical relative concentration profiles for propagules of different sinking speeds across a range of hydrodynamic conditions. Key: -0.1 -mm/s sinking speed, dashed-double-dotted line; 0 -mm/s, solid line; 0.1 -mm/s, dashed-dotted line; 1 -mm/s, dashed line.

propagules transported past 100 m or more may exceed 50% of all released spores (Fig. 7), such propagules ultimately get strewn across hundreds to thousands of linear meters of sea floor (witness the right-hand tails of Fig. 7). Second, the total annular area available for settlement at a given radial distance from a source increases as the distance from the source rises. This exacerbates the consequences of the tails of the dispersal curves. Together these factors ensure that densities of settling spores at larger dispersal distances are typically orders of magnitude lower than those immediately adjacent to a source plant. Because field workers traditionally evaluate dispersal potential by recording densities of propagules or recruits as a function of distance from the closest parent, rather than by measuring spa-

tially integrated patterns of abundance, instances of longer range dispersal can easily be missed during sampling.

It is also worth noting, however, that in algae with particular life history traits, colonization potential (indexed by the spatial scales over which successful colonization is possible) can differ substantially from dispersal potential (indexed by the spatial scales over which propagules disperse). For example, in seaweeds that have heteromorphic life histories where fertilization occurs in an alternate microscopic stage that arises after spore dispersal and settlement (as in kelps), successful colonization requires a minimum density of settled spores (Reed 1990). Due to the decline in density with distance, colonization potential in such a species may therefore be far lower than its dispersal potential. In this situation, increasing the abundance, per capita fecundity, and synchrony of spore release by multiple adults may advantageously increase sizes and concentrations of spore clouds, partially offsetting dilution effects (Anderson and North 1966, Reed et al. 1997). Colonization potential in species with kelp-like life histories can also be enhanced by drifting plants or plant fragments that contain sporogenous tissue (Dayton et al. 1984).

Vertical distributions and release height

Previous research (e.g., Amsler and Searles 1980) has suggested that propagules of ephemeral species are disproportionately common in upper regions of the water column. While further experiments are required to test this concept fully, results of our model indicate at least two possible factors that could contribute to such a pattern. First, if ephemeral species, as a group, have spores with strong, positive phototactic behaviors (i.e., negative sinking speeds of at least -0.1 mm/s), this could lead to uniform vertical concentration profiles under moderate to extreme hydrodynamic conditions and profiles skewed towards the surface under benign conditions. Second, it is possible that the opportunistic life histories of ephemeral species simply ensure that their spores are released from a much broader range of heights above the bottom. This could cause propagules to be found in surface waters even when they haven't been mixed to a steady state concentration profile. Indeed, this second point likely contributed to the extended dispersal observed in *Ectocarpus siliculosus* by Reed et al. (1988) since this filamentous species often grows as an epiphyte on kelps or structures that extend high into the water column, thereby increasing its release height and potential for transport.

The trends of Fig. 8 also provide some quantitative support for Norton's (1992) qualitative explanation as to why Hoffmann and Ugarte (1985) found spores of both ephemeral and nonephemeral species in surface waters of intertidal regions, while Amsler and Searles (1980; working in deeper waters offshore) found spores of nonephemeral brown algae only near the bottom. As

Norton (1992) suggests, turbulence in the surf zone is much more intense than that characterizing subtidal habitats (even when compared to conditions as extreme as those in Fig. 8c; Denny 1985, Gaylord 1999). This indicates that even rapidly sinking propagules such as those of *Sargassum* would mix rapidly to a uniform concentration.

Complicating factors

Naturally, given the complexity of nearshore processes, the model presented here includes a number of simplifications. Of these, perhaps the most important is the fact that our approach tracks propagules only until they hit the sea floor for the first time. This implies that dispersal ceases the instant a spore touches the bottom. However, it is also possible that nearbed flows resuspend spores that have already contacted the substratum, allowing them to "saltate" their way along the sea floor. Such phenomena could greatly increase total transport distances. Consistent with this notion are data from flow tank experiments in which rates of spore attachment in *Macrocystis pyrifera* declined 30-fold as bulk velocities in the flume increased from 15 to 25 cm/s (P. T. Raimondi and D. C. Reed, *unpublished data*). Reed et al. (1988) also found extended propagule dispersal in the kelp *Pterygophora californica* during a large wave event (see their Fig. 9, sample period 14), exactly the result one would expect if elevated bottom shear stresses induced by waves were interfering with spore attachment, causing the propagules to be carried (perhaps in multiple steps) farther before reaching their ultimate destination. If such resuspension effects indeed operate commonly in nature, they could offset predicted patterns of Figs. 4 and 5 where mean dispersal distances decrease under larger waves.

Other factors may also have the potential to modify predictions of our model. For example, temperate and tropical reefs where algae abound often possess complex topographies and substrata of much greater roughness than we examine in this study (Eckman 1990). Although we make no attempt to explore comprehensively the effects of irregular, high-relief, bottom features, preliminary model runs indicate that even roughness elements as high as 10 cm may decrease mean dispersal distances by as much as half an order of magnitude relative to transport distances across sand. This suggests a strong tendency for more limited dispersal on rocky reefs. Furthermore, assemblages of reef-dwelling organisms, some of which are flexible and reconfigure in flow (see, e.g., Gaylord and Denny 1997), can introduce additional, nontrivial, fluid-boundary complications (Eckman et al. 1989, Ackerman and Okubo 1993). Together such factors indicate that the results presented above should not be applied ad hoc to questions of dispersal within kelp forests growing on rough substrata. However, for studies of longer distance dispersal between reefs, where topographic variation is minimal and more easily quantified,

and where extensive algal stands are absent, our approach may provide quite reasonable insight.

Several other complicating factors (e.g., aspects of spore behavior, hour-by-hour variation in tidal currents or wave conditions, or the influence of water column stratification on profiles of turbulent mixing) can also modify details of our report, but appear unlikely to alter major conclusions. Thus, in spite of such simplifications, we believe that the model presented here captures the basic elements of macroalgal propagule dispersal in many nearshore marine environments. As such, it places quantitative, order-of-magnitude bounds on the effects of several dominant factors affecting the movement of algal propagules through the water column, provides estimates of how far spores may often disperse, and helps clarify our understanding of the mechanisms that underlie colonization and persistence of seaweeds in their flow-dominated environments.

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APPENDIX

A description of the current-wave boundary layer is available online in ESA's Electronic Data Archive: *Ecological Archives* E083-019-A1.