



Physical–biological coupling in spore dispersal of kelp forest macroalgae[☆]

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Abstract

The physical–biological linkages controlling the dispersal of spores produced by macroalgae that reside in kelp forests are complicated and laced with feedbacks. Here we discuss the fundamental elements of these interactions. Biological considerations include spore swimming and sinking speeds, their periods of viability in the plankton, and the height of spore release above the seafloor, which together determine the durations over which spores can be swept by horizontal currents before they contact the seafloor. Morphologies and material properties of canopy forming kelps may also influence the drag exerted on passing waters by the kelps, the plants' ability to persist in the face of rapid flows, and thereby the degree to which impinging currents are redirected around, or slowed within, kelp forests. Macroalgal life histories, and the size of spore sources as controlled by the dimensions of kelp forests and the density and fecundity of individuals within them, influence effective dispersal distances as well. Physical considerations encompass the mean speed, direction, and timescales of variability of currents relative to spore suspension times, the interaction of surface gravity waves with currents in producing turbulence in the benthic boundary layer, wind-driven surface mixing, water stratification, and shoreline bathymetry and substratum roughness, all of which can affect the interplay of vertical and horizontal transport of macroalgal spores. Intricate within-forest processes may induce attenuation of current speeds and consequent reductions in seabed shear, along with simultaneous production of small-scale turbulence in kelp wakes. Slower mean currents and smaller eddy scales in turn may attenuate vertical mixing within forests, thus extending spore suspension times. Further complexities likely arise due to changes in the relative rates of horizontal and vertical dispersion, modifications to the overall profiles of vertical mixing, and the creation of fine-scale secondary flows around kelp individuals and substratum features. Under conditions of more rapid currents, submergence of the surface canopy and the establishment of skimming flows at the canopy–fluid interface may introduce additional coherent flow structures that alter rates of fluid exchange to and from the forest. Many of these coupled physical–biological processes are just beginning to be examined in a rigorous fashion in kelp forests, but their potential importance is clear.

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1. Introduction

Kelp forest communities are linked inextricably to their fluid environments. Passing waters bring nutrients and food, deliver or disperse propagules, remove waste products, and ensure oxygen replenishment for respiration. In turn, flows through kelp forests are themselves influenced by the three-dimensional architecture of the plants and the reefs that support them. This coupling creates a broad spectrum of potential feedback processes. One of the stronger sets of bio–fluid interactions arises in the context of macroalgal spore dispersal within and around forests of kelps that extend throughout the water column to produce a floating canopy at the sea surface. Among the more formidable of these species are the giant kelp, *Macrocystis* spp., and the bull kelp, *Nereocystis luetkeana*, which grow to 45 m in length and provide essential habitat and food for vast numbers of nearshore marine organisms (Dayton, 1985; Schiel and Foster, 1986).

Macrocystis' dominant ecological role and its widespread distribution along much of the west coast of North and South America, Southern Australasia, and many Sub-Antarctic shores (Womersley, 1954) has ensured that it, in particular, has received considerable scientific attention in the last 30–40 years (for ecological introductions see North, 1971 or Foster and Schiel, 1985). This attention has revealed fundamental insights into stability, succession, persistence, and resilience in giant kelp forests (reviewed in Dayton, 1985; Schiel and Foster, 1986; Dayton, 1992). Still, even as kelp forest research has progressed, difficulties in quantifying dispersal characteristics of kelps and other seaweeds have limited our understanding of the processes determining the population dynamics of kelp forest macroalgae and the overall structure of kelp forest communities. Three factors have proven especially problematic: the microscopic size of macroalgal spores which makes tracking them difficult, the complexity of the flows that transport these propagules, and the effects of the plants on the fluid motions themselves. In view of the second and third of these challenges, we present here a brief conceptual discussion of a number of important but less-recognized interactions among kelps and flow that influence macroalgal spore dispersal, including connections to a disparate literature. Our focus is on biological–physical coupling in *Macrocystis* and *Nereocystis*

forests, although major conclusions may apply as well to spore dispersal in forests of other subtidal species that form surface canopies (e.g., *Alaria fistulosa*, *Ecklonia maxima*, *Egregia menzesii*, and *Pelagophycus porra*; Dayton, 1975; Abbott and Hollenberg, 1976; Estes et al., 1978; Coyer and Zauggaglund, 1982; Branch et al., 1999). These conclusions, on the other hand, are less apt to hold for intertidal species that are subjected to the complex flows resulting from wave breaking. We also target primarily just issues in spore transport, giving reduced attention to other factors (e.g., processes of spore release, attachment, movement of propagules from other life stages) that only indirectly affect dispersal or its consequences. Within these bounds, this paper provides a physically based complement to previous monographs of Santelices (1990) and Norton (1992), which were written from a more traditional phycological perspective, and functions as a targeted companion to the more far-ranging chapter of Okubo et al. (2001), which examines diffusive processes across a variety of both aquatic and terrestrial ecosystems.

2. Biological factors influencing dispersal

2.1. Spore properties

As alluded to above, spores of seaweeds are almost universally tiny (<100 μm in diameter; Clayton, 1992) and most have densities that are close to that of seawater, even though many have considerable stores of low-density lipid (Reed et al., 1999). By Stokes' Law, the sinking speed of a small particle increases in proportion to the product of the square of its radius and its excess density (Happel and Brenner, 1983). Thus, because both of these components are small in seaweed spores, these propagules sink very slowly, typically less than 1 mm/s, and for the littlest spores, two orders of magnitude slower yet (Coon et al., 1972; Okuda and Neushul, 1981; Deysher and Norton, 1982; Gaylord et al., 2002). While the spores of many macroalgae are flagellated, their absolute swimming speeds are similarly miniscule (<1 mm/s; Amstler et al., 1992, 1999; Iken et al., 2001). This means that macroalgal spores will typically be at the whim of the fluid motions to which they are subjected. Indeed, except in rather weak flows, turbulence will suffi-

ciently overwhelm sinking or swimming speeds that the time required for spores to settle to the seafloor will be controlled predominantly by the intensity of vertical mixing and the height of spore release (Norton and Fetter, 1981; Denny and Shibata, 1989; McNair et al., 1997; McNair, 2000; Gaylord et al., 2002). This will be especially the case for spores transported shoreward into the highly turbulent intertidal zone (Hoffmann and Ugarte, 1985). On the other hand, motility and behavior of macroalgal spores likely play strong roles when the propagules reach the immediate vicinity of the seabed, where chemical and tactile cues may be exploited to meet fine-scale site preferences (Harlin and Lindbergh, 1977; Amsler and Neushul, 1989a, 1990; Amsler et al., 1992; Fletcher and Callow, 1992; Greer and Amsler, 2002).

Data on the duration of spore competency are lacking for the majority of seaweeds. The traditional view has been that the spores of most taxa are able to settle immediately following release from the adult plant, and remain capable of settling for a couple of days (Santelices, 1990). However, more recent information suggests that seaweed propagules have the capacity to remain viable in the plankton for more extended periods (Reed et al., 1992; see also early clues in Kain, 1964; Hoffmann and Camus, 1989) and

that their dispersal potential is not determined by the length of their planktonic viability, but rather by the physical processes that maintain spores in suspension. Turbulent transport models predict that suspension times for spores of most seaweeds are likely to be less than 1 week, and that their dispersal in typical nearshore currents is therefore limited to distances of several kilometers (Gaylord et al., 2002). These scales are much smaller than those relevant to the larvae of most reef-associated fish and invertebrates, as will be discussed in Section 5 below.

The height of spore release is often important in dispersal (Neushul, 1972), but it becomes more so when the rates of vertical mixing are low. Under such conditions, larger release heights can lengthen substantially the time required for spores to first contact the seafloor, and thus increase the distances over which they are transported while suspended. For instance, the turbulent transport model of Gaylord et al. (2002) predicts times to first contact of nearly a day when spores are released from a few meters above the seafloor, under conditions of relatively slow currents and small waves (Fig. 1). In contrast, when mixing is intense throughout the water column, as occurs in the presence of faster currents and larger waves, spores can reach the bottom rapidly even from considerable

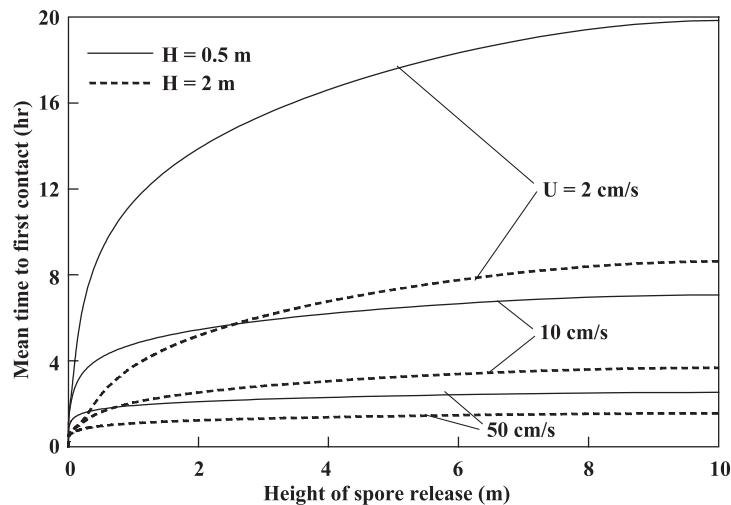


Fig. 1. Predicted mean time required for spores released from a given height to contact the seafloor for the first time, under flow conditions and patterns of vertical mixing characteristic of the sand flats that often separate kelp forests. Note, however, that because overall distributions of contact time are highly skewed, the longest contact times may exceed substantially mean values. Results are based on the turbulent transport model of Gaylord et al. (2002), which employs a random walk construct with a vertically varying eddy diffusivity that is linked explicitly to wave and current conditions. H is wave height, and U is the mean current speed.

heights (Fig. 1). Such distinctions create complex plant-flow relationships for dispersal given that different species release their spores from different vertical positions. For example, *Macrocystis* releases its spores from relatively close to the seafloor, while *Nereocystis* releases at least some fraction of its spores from near the water's surface (Amsler and Neushul, 1989b).

2.2. Kelp structural traits

Clearly, morphological traits (e.g., the height at which reproductive structures are positioned along the length of a plant) can influence spore dispersal directly by altering release heights and thereby the time it takes propagules to reach the bottom. However, what is perhaps less obvious is that the overall structural design of canopy forming kelps may also affect spore transport indirectly via differential effects on flow. For example, although *Nereocystis* and *Macrocystis* show many similarities in form, *Nereocystis* grows with a single ropelike stipe and bears all of its blades at the water's surface. *Macrocystis*, on the other hand, produces a bundle of intertwined fronds that not only terminate in a large surface canopy, but also develop blades throughout the entire water column. As a consequence, mid-water currents passing through a *Macrocystis* forest will tend to experience higher plant drag, and be slowed to a greater extent, than similar currents moving through an otherwise identical *Nereocystis* forest. Although data on the drag experienced by water masses passing through kelp plants are sparse, preliminary measurements of the drag coefficients of individuals of these two species support this concept (see, e.g., Johnson and Koehl, 1994; Stevens et al., 2001). Since current speeds can act as a primary controller of dispersal distance, this can be important.

The material properties of canopy forming kelps may also have the potential to influence dispersal, albeit secondarily. Storms cause considerable disturbance in kelp forests, and may tear fertile plants, or fragments of plants, free from their benthic sites of attachment (Ebeling et al., 1985; Seymour et al., 1989; Dayton et al., 1992; Reed et al., 1997). Dislodged individuals and reproductive fragments that avoid subsequent exportation to the beach may transit alongshore, all the while releasing spores. In this context, the strengths and stiffnesses of macroalgal tissues (e.g., Denny et al., 1989; Gaylord et al., 1994,

2001; Gaylord and Denny, 1997), and the way plants move and respond to challenging hydrodynamic conditions (Denny et al., 1997, 1998; Gaylord, 2000; Stevens et al., 2002; Gaylord et al., 2003) become relevant. Material properties of canopy forming kelps may also play a role during senescence, when water column and canopy portions of kelps fall away and change the drag a plant exerts on passing currents.

2.3. Life history considerations

It is well recognized by algal biologists that acquiring precise estimates of dispersal distance, and defining their relationship to various postulated biological or physical factors, is made more difficult by the reproductive life history strategies exhibited by some species, including canopy forming kelps (Brawley and Johnson, 1992; Reed et al., 1997). Early on, Anderson and North (1966) monitored recruitment as a function of distance from an isolated *Macrocystis* individual, and found new plants arising only out to distances of a few meters. This initial finding led many researchers to assume that dispersal is severely limited in these organisms. Such a view, however, inadequately distinguishes between effective recruitment distance and dispersal distance (Reed et al., 1988; Reed et al., 1997). Unlike the seeds of terrestrial plants, the spores of kelps must settle at relatively high densities (i.e., greater than $10/\text{mm}^2$) to ensure subsequent production of the sporophyte stage that forms the kelp canopy (Reed, 1990a). The spores themselves develop into tiny gametophytes that release eggs and sperm, which must find one another to fertilize and create the macroscopic plant; it is individuals of this macroscopic stage that are typically used as indicators of recruitment (see, e.g., Dayton, 1973). Such a life history means that increasing the number of spores in a source allows successful recruitment to occur at distances farther out into the tail of a dispersal curve even if the dispersal curve itself does not change (Reed et al., 1997). Synchronous spore release may facilitate this (Hoffmann, 1987; Amsler and Neushul, 1989b; Reed et al., 1997).

2.4. Kelp forest size

The overall dimensions of a kelp forest, as well as the density and fecundity of plants, also influence the

size of the spore source. In addition to their widely promulgated data showing restricted recruitment distances from a single individual, Anderson and North (1966) found little difference in the density of recruits out to 40 m away from the edge of a kelp forest. In accordance with the life history considerations outlined above, they proposed that this derived from a greater number and higher initial concentration of spores, which produced denser spore settlement and allowed successful recruitment to greater distances. We also noted dispersal out to at least 100 m when monitoring densities of germinated female spores (gametophytes) produced by a small, isolated experimental kelp forest off the coast of Carpinteria, Cal-

ifornia (Fig. 2). More dramatic support for the relevance of the size and population density of a kelp forest derives from observations of kilometer-scale dispersal from a dense stand of the understory kelp, *Pterygophora californica* (Reed et al., 1988), and from a large stand of *Macrocystis* (Reed et al., in press). Other workers have observed seaweed recruits or viable spores at locations hundreds to thousands of meters away from adult plants as well (e.g., Jonsson, 1972; Amsler and Searles, 1980; Ebeling et al., 1985; Zechman and Mathieson, 1985; Fredriksen et al., 1995). In many such cases, however, the alternative explanation that spores or recruits originated from floating fertile plant fragments (rather than from reproducing adults in distant established populations) cannot be eliminated. Analogous effects of source size on the distances at which dispersal can be detected have been noted in the terrestrial seed literature as well (e.g., Clarke et al., 1998). Additional consequences of the size of a kelp forest on flow (e.g., on the speed of currents and the intensity of vertical mixing within a forest) and their consequences for dispersal are examined below.

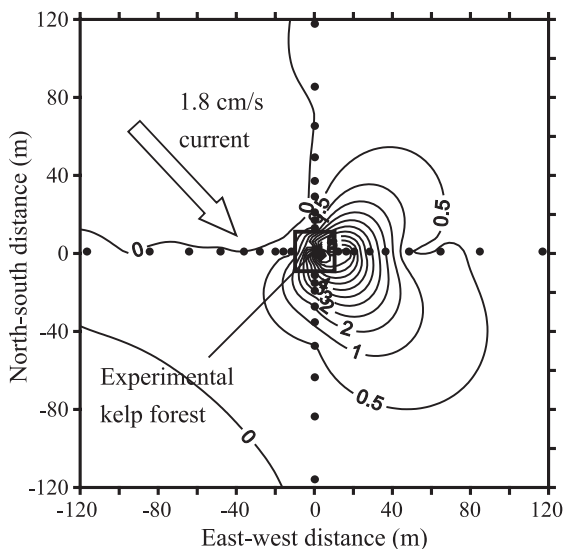


Fig. 2. Patterns of spore dispersal around a 40-plant experimental *Macrocystis pyrifera* kelp forest positioned off the coast of Carpinteria, California, during July of 1999. The square box indicates the approximate dimensions of the experimental forest. Contours are interpolated from data collected at locations indicated by the black dots, and represent the number of germinating female spores per microscope field of view (1.66 mm^2) settling on frosted glass slides deployed 10 cm above the substratum during a representative 2-day sample interval (male spores were not counted due to their exceptionally small size). Note that because spores accumulate through time over durations much longer than 2 days, spore densities can reach levels sufficient for successful recruitment ($>10/\text{mm}^2$) throughout and likely beyond the spatial array shown. Forests in nature are also typically much larger and therefore release greater numbers of spores, which similarly elevates settlement densities out to farther distances. The mean current over the 2-day sample interval was 1.8 cm/s.

3. Physical forcing

3.1. Currents

Coastal currents are a primary mechanism by which spores are transported horizontally from kelp forests, but it is of course more than just the speed of ocean flows that matters. The direction and variation in currents may also be important since these components can interact with the temporal and spatial scales of spore release, suspension in the water column, and settlement. It is worth noting, however, that many such biological–physical connections are just beginning to be explored in field experiments, so a complete picture is still unavailable.

Along many shores, diurnal and semidiurnal tides drive strong currents that are superimposed on lower frequency flow fluctuations, and winds often produce additional diurnal fluid motions near shore (Lerczak et al., 2001). As Fig. 1 indicates, estimates of the durations that seaweed spores are in the water column, indexed as the time to first contact with the seafloor, range from a few minutes to a few days in areas where

the effects of biota and significant bottom topography are minor (Gaylord et al., 2002). These durations may be reduced somewhat in areas with greater effective seabed roughness due to increased rates of vertical mixing (see Fig. 3 and discussions below). Such timescales suggest that at the shorter end of the range of spore suspension times, dominant currents may act as nearly constant, steady mean flows for dispersal. For longer suspension times, in contrast, the speed and direction of the mean flow will often change during the time a spore is suspended. This temporal variability in currents, and flow reversals in particular, may function to truncate the far tails of dispersal distributions since spores will not be transported continuously in a single direction at the peak flow speed.

Currents also vary strongly with location. For instance, typical nearshore tidal currents along the coast of Central to Southern California have maximal speeds of 20 to 40 cm/s (Winant and Olson, 1976; Washburn et al., 1999). In contrast, currents in the Strait of Juan de Fuca in Washington State can reach 1.5 m/s as flow is funneled between islands through narrow channels (Fissel and Huggett, 1976; Thomson, 1981). These differences suggest order-of-magnitude variations in gross dispersal distance simply due to regional characteristics of flow.

Cross-shore and alongshore currents influence spore dispersal in quite different manners as well. Coastal currents with characteristic frequencies below that of the tides typically move alongshore and parallel to isobaths due to the combined effects of the earth's rotation and the slope of the seafloor. Such currents tend to disperse spores along the more expansive axes of kelp forests, which typically run farther alongshore than across shore. This provides for more extensive interactions among spores, forests, and their residents. Higher frequency cross-shore fluid motions, in contrast, although typically weaker than alongshore motions, can transport spores offshore into water depths where there is insufficient light for early development or growth. This may be particularly the case in regions of steep bathymetry where overly deep waters can be located just a few tens of meters seaward of a kelp forest. In locations where upwelling favorable winds are common, the resulting offshore Ekman transport of surface waters may accomplish this (see Pond and Pickard, 1983; Strub et al., 1991 for general explanations of these processes). Such phenomena may be especially prevalent on headlands, which can accelerate along-coast winds and thus function as upwelling centers (Strub et al., 1991; Dorman et al., 1999; see also Ebert and Russell,

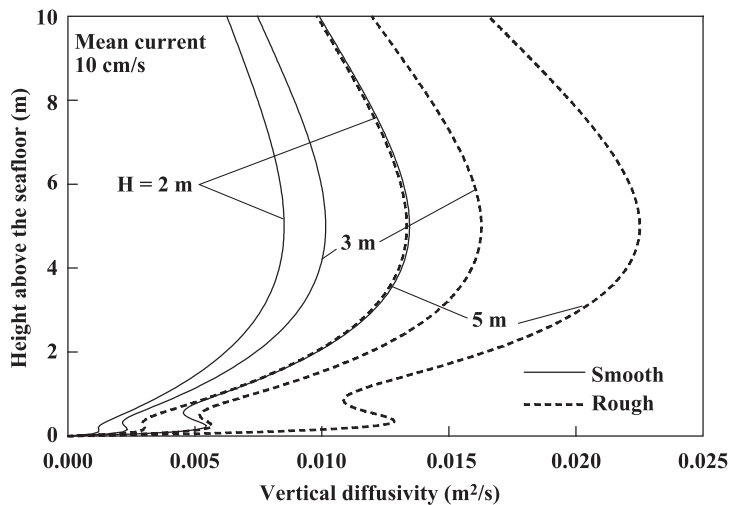


Fig. 3. Example profiles of vertical mixing in the absence of vegetation, as a function of wave height and bottom roughness. Solid lines correspond to cases where the roughness elements of the seafloor have characteristic heights of 0.008 m, typical of the sand flats that often separate reefs. Dashed lines correspond to cases where the roughness elements have characteristic heights of 0.1 m, typical of low-relief rocky reefs or cobble substrata. Results are based on the combined wave–current boundary layer model of vertical mixing developed by Grant and Madsen (1986) with modifications following Wiberg and Smith (1983). Further details can be found in Gaylord et al. (2002). H is wave height.

1988). However, there may also be simultaneous shoreward transport of spores near the seafloor during upwelling due to the movement of deeper waters upslope (Brink, 1983). This can be important since most macroalgae release their spores from relatively close to the bottom. Near-bottom offshore or onshore flow can also result from Eckman transport in the bottom boundary layer due to equatorward or poleward current flow, respectively. Alternatively, in locations where internal bore activity is prominent (e.g., Winant and Bratkovich, 1981; Breaker and Broenkow, 1994; Pineda, 1995), cross-shore transport of spores is episodically shoreward, and may carry spores to shallow depths beyond the inside edge of a forest, even into regions where wave-driven surf-zone flows dominate (e.g., Longuet-Higgins, 1970). Again, however, the precise relationships between spore movement and these potential dispersal mechanisms remain relatively unexplored.

3.2. Waves

Although the influence of surface gravity waves on dispersal may not be as fundamental as that of currents, there are a number of ways in which they too can play a role in spore transport. Perhaps most importantly, in shallow waters where wave-driven fluid motions extend to the substratum, the resulting back-and-forth surge increases bottom shear and alters the profile of vertical mixing. Typically, in the absence of a vegetation canopy and strong stratification, eddy diffusivities (a measure of the rate of diffusive flux in a flow due to mixing processes) within a depth-limited current boundary layer such as is common in the nearshore, peak at middle depths (Fig. 3; Eckman, 1990; Gaylord et al., 2002). This pattern results predominantly from the fact that the size of the dominant turbulent eddies become increasingly constrained near the seabed and the surface, but can become large in mid-water. The effect of enhanced bottom shear due to waves then functions both to increase the effective bottom roughness, which elevates the overall mixing rate within the current boundary layer, and adds a secondary peak to the diffusivity profile (Fig. 3). This near-bottom secondary peak results from the higher turbulence intensities in the relatively thin wave boundary layer, which increases rates of mixing in this region despite the

limits on eddy size (Wiberg and Smith, 1983; Grant and Madsen, 1986).

Such changes to the diffusivity profile can have strong effects on the duration that spores remain up in the water column following release (McNair et al., 1997; Gaylord et al., 2002). The associated increased bottom shear stress may also resuspend spores that have already contacted the seabed, causing them to disperse farther in a series of steps prior to final attachment. This may be particularly the case for spores that have not yet attached or have only recently settled and have not achieved full adhesive strength (Charters et al., 1972, 1973). In addition, wave-induced orbital velocities, which can reach several meters per second and are thus faster than most currents, may interact with the blades of plants to influence spore dispersal. Research indicates that the overall canopy structures of large kelps often sway with the waves such that the canopy experiences limited fluid velocities relative to itself (Koehl, 1984, 1986; Denny et al., 1997; Gaylord et al., 2003). However, the water motion relative to individual reorienting and fluttering blades produced as the direction of water motion reverses is likely to be at least sporadically faster (Gerard, 1982; see also Stevens et al., 2001). Such faster relative flows could elevate shear stresses acting on reproductive blades, thereby increasing spore release. While data are still lacking, resuspension and greater spore release by increased shear are consistent with observations of both declines in standing crop of spores and more distant dispersal during large wave events (Reed et al., 1988; Reed et al., 1997). Note that if the above mechanisms are indeed responsible for increasing spore dispersal distances, one would expect a wave period dependency to this phenomenon, with longer period waves producing greater dispersal than shorter period waves. This is due to the fact that fluid motions produced by shorter period waves do not penetrate to as great a depth as those of longer period waves (Kinsman, 1965), and because many seaweed species, like *Macrocystis*, release their spores relatively close to the seafloor.

There may also be wave period effects on the degree of damage incurred by kelp canopies during storms. Longer period swells appear to have a greater potential to tug canopies taut into configurations where entire plants can be dislodged (Seymour et

al., 1989; Denny et al., 1997). Large-scale plant loss following such wave events can have subsequent impacts on the amount of attenuation of current speed and thus on dispersal distance. Along related lines, the sudden drop in kelp densities at the inshore edges of forests is believed to be related to the depth at which the largest waves break and thereby become capable of imposing greater forces due to the accompanying faster post-breaking fluid velocities (Seymour et al., 1989; Graham, 1997; Gaylord, 1999; Denny and Gaylord, 2002).

Another potential effect of waves on spore dispersal derives from the relatively rapid (order 10 cm/s) net mass transport of fluid along the direction of wave propagation that arises under relatively steep waves (i.e., Stokes drift; Komar, 1998). Since waves typically refract to propagate perpendicular to shore, Stokes drift provides a mechanism for transporting propagules perpendicular to currents, which usually flow along isobaths as noted above. Concomitant flows near the seafloor that are thought to arise in association with Stokes drift (Longuet-Higgins, 1953) probably play a role in cross-shore velocity profiles and spore movement as well.

3.3. Winds

Winds drive currents and can therefore affect dispersal by means of a number of the processes described above. However, there may also be subtler but direct impacts from wind. For example, winds induce vertical shear and, at faster speeds, wave white-capping, thus increasing mixing at the water's surface (Agrawal et al., 1992; Anis and Moum, 1995). This process alters the upper regions of the profile of vertical mixing, and thus the duration over which a spore remains suspended after being carried into the upper reaches of the water column. Surface mixing by wind stress also breaks down stratification (Turner, 1973), with analogous and perhaps even more dramatic effects on the vertical distribution of spores in the water column, similar to what is often observed in the patterns of vertical concentrations of fine sediments (Adams and Weatherly, 1981; Middleton and Southard, 1984).

Seymour et al. (1989) further note that winds can exert shear on kelp canopies, which can orient them in asymmetrical postures with respect to their points of

attachment (this is true as long as the current has not submerged them, a topic that will be discussed further in Section 4.5). Of particular relevance are cases where the winds align with the axis of wave propagation and thereby extend kelps in the direction of the waves. This allows much larger wave forces to be imposed since a stretched-out kelp can no longer move continuously with the orbital wave-generated fluid displacements to avoid rapid relative water velocities (Seymour et al., 1989; Gaylord et al., 2003). If sufficient damage (i.e., pruning or removal) ensues, then there can ultimately be consequences for plant drag and therefore for flow within a forest.

3.4. Water stratification and related factors

As alluded to above, strong density stratification can reduce vertical mixing by constraining the largest scales of turbulent motion and by confining the vertical dispersion of spores to certain strata of the water column (Sherman et al., 1978; Weatherly and Martin, 1978). Strongly stratified waters may result from large vertical temperature gradients due to solar heating or salinity gradients due to freshwater runoff and rainfall, and can extend over the inner continental shelf where kelp forests occur (Hill, 1998; Cudaback and Largier, 2001). Density stratification offshore may also have the indirect effect of altering the propagation characteristics of internal bores, with a strong offshore thermocline enhancing propagation, and a weak or nonexistent one inhibiting it. This in turn can increase or decrease spore transport across the shelf due to internal bores (Pineda, 1995). There also may be other effects associated with temperature. Higher temperatures are often correlated with lower nitrogen availability (Zimmerman and Kremer, 1984, 1986), and this may influence the production of spores and thereby the level of spore release during subsequent dispersal events (Reed et al., 1996). More work on these topics is required.

3.5. Bathymetry and shoreline geometry

Spore dispersal can be affected by interactions of flow with the topography of the seabed and the geometry of the shoreline. Steeply sloping bathymetry tends to force horizontal currents to move tightly along-isobath, parallel to the coast (Hill, 1998). On

the other hand, steep bottom topography refracts waves strongly such that they approach more perpendicularly to a coast (Komar, 1998). Therefore, currents and waves are more apt to propagate at right angles to one another on steep shores than on coasts with shallower slopes. This suggests that steep shores will show more directional spore transport than sites with gently sloping bathymetry. In fact, sites with flat bathymetry may experience currents and waves arriving from a variety of directions, and might be expected to exhibit rather directionally isotropic spore transport resembling almost a simple diffusive pattern (see, e.g., the relatively diffuse pattern in Fig. 2, corresponding to a site with nearly flat bathymetry).

Other location-specific features such as headlands and embayments may additionally affect patterns of spore dispersal by creating flow recirculation zones that alter the ability of alongshore currents to sweep spores along dominant axes (Wolanski and Hamner, 1988). The relevance of such retention regions to spore transport, however, depends on the spatial scale of the shoreline feature. For example, bay-scale eddies with dimensions of several kilometers (e.g., Breaker and Broenkow, 1994; Nishimoto and Washburn, 2002) will appear as alongshore currents to a kelp forest within those bays, while smaller coastal features may function more as transient retention areas for spores that are otherwise propagating downstream (Denny et al., 1992).

The orientation of the coast can also be important because it can affect the intensity of upwelling as well as the vulnerability of sites to surface gravity waves. For example, in the Santa Barbara Channel off of California, the coast turns to run east–west. This reduces the speed of the alongshore component of the winds, which blow mostly meridionally at this latitude, and thus the strength of upwelling. In addition, the change in angle of the coast protects much of the Channel from the largest winter swells arriving from the North Pacific.

3.6. Bottom roughness

On a much smaller scale, substratum roughness influences the strength of bottom shear and the relative amounts of turbulence produced by it (Schlichting, 1979; Dade, 1993). Kelps typically grow on rocky reefs, which usually have far greater roughness

(individual roughness elements with characteristic dimensions from centimeters up to meters) than the sand flats that often separate reefs. Not only can this influence the gross profiles of vertical mixing (Fig. 3; Grant and Madsen, 1986), but it can also create its own secondary flows, with strong effects on fine-scale retention and the local distribution of spore settlement. Recirculation zones and turbulence within idealized cavities or over simplified substratum irregularities have been explored extensively in the engineering literature (e.g., O'Brien, 1972; Rockwell and Naudascher, 1978; Koseff and Street, 1984a,b; Nelson et al., 1993; Hudson et al., 1996). Ensuing local effects on passive deposition have been observed around worm tubes and the pits that often accompany them (Eckman and Nowell, 1984; Snelgrove et al., 1993; Yager et al., 1993), as well as around other substratum features (Harlin and Lindbergh, 1977; Norton and Fetter, 1981; Chabot and Bourget, 1988; Abelson et al., 1993; Abelson and Denny, 1997). The erosional characteristics of the substratum can conceivably be important as well, if rock friability results in the dislodgement of plants during storms (Harris et al., 1984; Dayton et al., 1989).

4. Forest-wide interactions with flow

4.1. Kelp forest effects on currents

The biological and physical factors introduced above by no means operate in isolation, and there are numerous, and sometimes complex, ways in which kelp forests and flow interact to influence dispersal. Okubo et al. (2001) discuss a number of the relevant vegetation–flow interactions, spanning multiple ecosystems. We focus here on those that apply directly to kelp forests. For example, Jackson and Winant (1983) and Jackson (1998) conducted measurements of current speeds within and outside the massive Point Loma kelp forest near San Diego, California, and found that currents inside were approximately three times slower. They also calculated that alongshore currents impinging on the upstream end of a forest would be slowed to these reduced speeds by the time they penetrated about 100 m into the forest. Analogous reductions in mean flow have been described for other aquatic (e.g., Fonseca et al.,

1982; Ackerman, 1986, 2002; Eckman, 1987; Gambi et al., 1990; Ackerman and Okubo, 1993; Leonard and Luther, 1995; Nepf et al., 1997b), and terrestrial (e.g., Shaw, 1977; Raupach and Thom, 1981; Stacey et al., 1994) plant canopies. Jackson (1984) suggests further that higher frequency cross-shore motions induced by internal waves can be damped and slowed as they propagate across kelp forests. The elevated flow resistance of a forest would also be expected to consistently divert currents around it, promoting faster flows along the lateral sides of the forest, and thus more distant dispersal from such regions. Together, each of these lines of evidence would imply that kelp forests reduce the typical distances over which spores disperse within their interiors, as compared to the distances spores disperse when in open regions between forests or along their edges. However, as is discussed below, concomitant changes to patterns of vertical mixing may make this not always the case. Such topics, as well as the issue of what happens in kelp forests that are smaller than the uniquely large Point Loma forest studied by Jackson and colleagues, remain ripe for further inquiry.

It also remains unclear how the size, distribution, and density of plants within a kelp forest affect the drag a forest exerts on a current. In flume studies, Nepf (1999) found that clusters of vertical dowels used as mimics of emergent vegetation cause about a 50% increase in drag as the density of dowels doubles, for densities resembling those found in seagrass meadows. The densities of kelps are far lower and the sizes of the plants are much larger, however, which means that they operate at very different relative spacings and Reynolds numbers (an index of the relative importance of inertial and viscous forces in a flow; Batchelor, 1967). The results of Nepf (1999) are therefore unlikely to be directly applicable. Additional drag data are available from studies of rough wall turbulent boundary layers and terrestrial plant canopies (e.g., Raupach et al., 1991), but are not entirely applicable either. This is due to the absence in such systems of an air–water interface near the level of the canopy. Kelp forests also tend to form discrete, relatively limited patches, which makes it difficult to ascertain what fraction of an impinging flow will be forced through, verses redirected around, the vegetation array. Because drag and flow rerouting offset one another in affecting within-forest mean flows, quanti-

tative estimates of the level of current reduction within forests of differing geometry and plant density are still unavailable. It is reasonable to expect that other kelp forest characteristics (e.g., the size, species of kelp forming the canopy, the depth of the water, etc.) will likely play a role as well, although this remains speculation at the present time.

4.2. Kelp forest effects on mixing processes

Dispersal distances depend not just on horizontal current speed, but also on the vertical movement of spores, which determines how long they remain aloft. This point makes the recent studies of Nepf et al. (1997b), Nepf (1999), and Nepf and Vivoni (2000) intimately relevant, in that they explore ways in which arrays of plants influence turbulence and diffusion, two processes that strongly affect net vertical motion. Okubo et al. (2001) synthesize the fundamental phenomena, and an abbreviated synopsis is given here. For vegetation that extends throughout the water column, turbulence is produced primarily at the seabed via shear and in the wakes of plants as water flows past them. The wind-induced surface mixing mentioned previously also contributes. In dense plant aggregations, the turbulence production in the wakes usually dominates over the other mechanisms, at least for plants growing on relatively smooth substrata where seabed shear is weak. In turn, there is often a resulting wake-induced increase in the amplitude of turbulent velocity fluctuations relative to those outside the plant array (Raupach et al., 1986; Nepf, 1999). Note, however, that this may not always be the case due to the nonmonotonic relationship between plant density and turbulence intensity (Nowell and Church, 1979; Eckman, 1983). A range of findings, for example, are apparent among the results of Anderson and Charters (1982), Eckman et al. (1989), Gambi et al. (1990), Koch and Gust (1999), Ackerman and Okubo (1993), Leonard and Luther (1995), Nepf et al. (1997b), and Ackerman (2002). Some of the variation in these studies may also result from differences in water depth to canopy height ratios, a topic to which we will return in Section 4.5.

If in the relatively sparse arrays of plants typical of kelp canopies the amplitude of velocity fluctuations does increase as a result of greater wake turbulence (a possibility that remains as of yet untested), this might

suggest a greater potential for vertical mixing. However, as is noted by Naot et al. (1996), Nepf (1999), and Okubo et al. (2001), the turbulent eddies generated in the wakes of plants have the same rough sizes as the plants' frontal diameters, and are therefore rather limited. Turbulence generated by flow passing through the interstices between multiple fronds of individual seaweeds exhibit even smaller length scales of mixing (Anderson and Charters, 1982). The overall plant array also tends to constrain the maximal size of eddies produced by shear at the seabed, cutting the eddy dimensions to the same order as the spacing between plant individuals (Ackerman, 2002). This contrasts with the situation in nearshore vegetation-free habitats, where the sizes of the largest eddies approach scales equal to half the water depth, at least when stratification is weak (Wiberg and Smith, 1983; Gaylord et al., 2002). Since the largest eddies typically function as the dominant agents of diffusive transport (Tennekes and Lumley, 1972; Fischer et al., 1979; Okubo et al., 2001), plant-induced reductions to their size likely overwhelm the opposing effect of greater turbulence intensity. This implies that vertical diffusion of spores within kelp forests will typically be greatly slowed relative to outside areas, although this outcome has yet to be verified experimentally in a comprehensive manner.

Such attenuation of vertical mixing can apparently be dramatic in certain circumstances. Calculations in Nepf (1999) suggest, for instance, that nearly 100-fold drops in diffusivity may arise at the exceptionally high densities characteristic of seagrass meadows (200–2000 stems/m²), both due to reduced current speed and the smaller eddies. Such extreme declines in the efficiency of mixing are probably unlikely in the sparser plant arrays that characterize kelp forests, but a full answer awaits additional measurements. Even a modest decline in mixing rate, however, raises the nonintuitive possibility alluded to above that spores could actually be carried farther downstream by slower currents while inside forests than by faster ones when outside, simply because weaker vertical mixing increases the time required for near-neutrally buoyant spores to contact the substratum.

The presence of kelp plants likely cause not only a drop in the overall gross magnitudes of turbulent diffusivity, but also modifications to the details of how vertical mixing varies with depth. As was already

noted, in the absence of a large canopy and with relatively smooth bottom topography (a common situation between the disjunct kelp forests separated by sand flats that are often observed along temperate coasts), diffusivity profiles are expected to have the basic form shown in Fig. 3. Within a dense kelp forest that extends throughout the water column, however, the vegetation likely reduces the degree of variation in diffusivity magnitude across different elevations in the water column (Seginer et al., 1976). This possibility arises because the larger eddies normally responsible for mid-water diffusivity peaks are preferentially eliminated, while the smaller eddies are retained (Nepf et al., 1997b; Ackerman, 2002). With regards to spore dispersal, the tails of dispersal distributions should expand relative to the mean dispersal distance under such conditions, since the lower mixing rates high in the water column lengthen the suspension times of the spores that reach such heights above the bottom (McNair, 2000; McNair and Newbold, 2001). Further research is required on this topic, however.

Like vertical turbulent diffusivities, horizontal diffusivities perpendicular to the mean current will tend to be relatively small in kelp forests due to constraints on length scales of mixing. However, a second process, termed “mechanical diffusion” by Nepf et al. (1997a), and discussed further by Okubo et al. (2001), may increase horizontal diffusion rates relative to vertical values. Following Nepf (1999), mechanical diffusion can be explained by means of analogy to the classic random walk of statistics (Berg, 1983). As a cloud of spores is swept downstream and impinges on a bundle of kelp fronds that extend throughout the water column, it must pass around that bundle by shifting either left or right. On the downstream end of the bundle, the presence of the wake prevents the cloud from returning to its original line of transit (i.e., it is smeared and offset laterally by an amount that scales with the diameter of the frond bundle; Nepf et al., 1997b; Nepf, 1999). At the next bundle encountered by the now-laterally displaced cloud, it again shifts left or right, and so forth. For a randomly distributed array of kelp plants, the direction shifted left or right at each obstruction is independent of previous steps, and the result for a large number of clouds and many levels of obstruction is a horizontal Gaussian distribution oriented perpendicular to the mean flow, just as would arise for traditional horizon-

tal turbulent diffusion. As is explained by Nepf (1999) and Okubo et al. (2001), the mechanical diffusion then sums with the horizontal turbulent diffusion, since the two processes are independent. During release of spores by isolated plants, this total lateral horizontal diffusion may be a strong determinant of the rate of dilution of spores released in the forest, and the probability of achieving a particular spore settlement density at a certain location downstream from a given set of source plants. A similar process may also affect the diffusion and dilution of spores along the axis of the mean current, and its interaction with the differential smearing of a spore cloud by a vertical velocity gradient (i.e., shear dispersion; Bowden, 1965; Nepf et al., 1997a).

4.3. Secondary flows around plants

In addition to processes of mixing, there may also be ordered, secondary flows associated with the presence of frond bundles of surface canopy forming kelps that can carry spores towards, or away from, the seafloor following their release. Nepf and Koch (1999) and Okubo et al. (2001) discuss such transport mechanisms in the context of seagrass stems operating in steady flows and at Reynolds numbers in the range of 10^2 – 10^3 based on stem diameter. Frond bundles of kelps, however, are much larger, operate at higher Reynolds numbers (10^3 – 10^6 ; see below), and are exposed to bi-directional wave surge, so additional evaluation is warranted. In general, a vertical cylinder protruding from the seafloor that is subjected to a steady horizontal flow in a benthic boundary layer experiences downward fluid movement on its upstream side. This follows from the tendency for faster flows higher above the seabed to impose greater pressures at higher elevations on the cylinder's surface, which in turn drives fluid towards the substratum. These downward flows roll up into a tube-like fluid structure that then loops around the base of the cylinder on either side to create a "horseshoe vortex" (Baker, 1980; Van Dyke, 1982; Pierce and Tree, 1990). Intriguingly, although most biological studies targeting these vortices have focused on flow around rather small (millimeter to centimeter scale) organisms (e.g., Eckman and Nowell, 1984; Nepf and Koch, 1999), a number of engineering studies, including some examining pier pilings of similar dimensions

to *Macrocystis* frond bundles (e.g., Breusers et al., 1977; Melville and Raudkivi, 1977; Niedoroda and Dalton, 1982; Sumer and Fredsoe, 2001a) have demonstrated that such flows can influence patterns of sedimentation and scouring even around quite large objects that protrude vertically from the substratum. Indeed, horseshoe vortices can elevate shear stresses by up to about a factor of 10 on the lateral sides of the bases of vertical cylinders, while simultaneously allowing increased sedimentation just a little further downstream (Sumer et al., 1997). Although the critical experiments have yet to be conducted, analogous processes could conceivably operate around the frond bundles of surface canopy forming kelps. This could introduce inhomogeneous, fine-scale patterns of spore deposition and resuspension. It might also be important for subsequent life stages of macroalgae if ensuing recruits are subjected to strong intra-age-class, density-dependent competition for light, for example (Reed, 1990b), and could contribute to the patchiness often observed in kelp forest macroalgae. It must be emphasized, however, that the mechanical flexibility of surface canopy forming kelps and differences in the geometry of their holdfasts makes the actual applicability of such concepts less than certain.

Frond bundles of surface canopy forming kelps may also experience upward fluid motions in their wakes for reasons that are analogous to those that cause upstream horseshoe vortices. As is outlined in Eckman and Nowell (1984), Nepf and Koch (1999), and Okubo et al. (2001), pressures behind a vertically oriented cylinder in a benthic boundary layer are negative by amounts that scale with the magnitudes of the corresponding positive pressures at the surface of the cylinder's leading face; this sets up a positively directed vertical pressure gradient in the wake that forces fluid upwards. These flows can exhibit speeds approaching 30–40% of the impinging freestream velocity (Woo et al., 1989; Nepf et al., 1997b). A number of sessile invertebrates, operating at somewhat lower Reynolds numbers than are common for kelp frond bundles (values of 10^2 – 10^3 based on organism diameter), have been shown to exploit such upward flows in feeding and respiration (Carey, 1983; Johnson, 1988, 1990). Other studies have demonstrated that upward flows in cylinder wakes occur at Reynolds numbers up to at least 10^4 (Breusers et al., 1977; Woo et al., 1989). Whether such fluid motions

arise at Reynolds numbers higher yet is less clear. There is some suggestion, for instance, that shifts in the precise pattern of vortex shedding behind a cylinder at larger Reynolds numbers may cause a switch from upward to downward wake flows, although a strong consensus appears lacking (Breusers et al., 1977). In general, depending on whether surface gravity waves are large enough to produce rapid fluid oscillations at depth or not (Kinsman, 1965), kelp frond bundles are expected to operate at peak Reynolds numbers ranging from approximately 10^3 – 10^6 .

Secondary flows in downstream wakes can also be influenced by the presence of other individuals within a plant array, and by the magnitudes of horizontal turbulent diffusivities in kelp forests. For example, complex flow patterns and interactions among multiple wakes are possible (Bearman and Wadcock, 1973; Zdravkovich, 1977; Zukauskas, 1987; Avisar et al., 2001), and the intensity of scour around the bases of grouped cylinders can be modified (Sumer and Fredsoe, 1998). Although faster mean currents typically facilitate the upward flows behind cylinders, the height to which these flows extend vertically is offset by the fluid's tendency to diffuse horizontally out of the wake via turbulence (Nepf and Koch, 1999). Such coupling once again indicates that there are strong connections between the distributions of individuals, the flows that arise in their midst, and the patterns of spore movement and deposition that lead to successive kelp generations.

4.4. Wave–plant interactions

Much of the work on flows within vegetation has been conducted in terrestrial plant canopies, in sea-grass meadows, or in salt marshes. None of these systems is subjected to the large waves that characteristically impinge on kelp forests. Indeed, there is no precise analogue in terrestrial habitats to surface gravity waves.

There are several dispersal-related complications associated with waves, however. First, as was noted above, the action of bi-directional wave surge at the seafloor increases the bottom shear and the apparent roughness of the seabed. The interaction of the waves with the current also acts in a nonlinear fashion to elevate both vertical mixing in the thin wave boundary layer, as well as mixing throughout the water

column in the much thicker current boundary layer (Fig. 3; Grant and Madsen, 1986). In combination with the substantial roughness of the reefs upon which kelps typically grow, this suggests that wave-enhanced turbulence production at the seabed may at times come to rival, or even exceed, rates of turbulence production within plant wakes. This possibility, however, must be weighed against the potential for wave-driven fluid oscillations to increase both the turbulent wake contributions of the kelps themselves, and the magnitudes of horizontal mechanical diffusion. Such questions are fundamental but remain unexplored.

Waves can also alter the nature of the secondary flows that might be produced around the holdfasts and frond bundles of kelps. The interaction of waves and currents with immersed bodies is complex and the subject of much ongoing research (e.g., Zdravkovich, 1996), but some conclusions are possible. As is detailed in Niedoroda and Dalton (1982), Sumer et al. (1997), and Sumer and Fredsoe (2001b), the periodic reversal of flow that characterizes waves can interfere with the establishment of horseshoe vortices and thereby reduce the expected intensity of scouring around vertically oriented structures. This can be especially the case in the presence of shorter period waves, since they produce orbital fluid excursions that travel only shorter distances relative to the in-line diameter of the flow obstruction (Sumer and Fredsoe, 2001a). Presumably, similar relationships would apply to the upward flows in the wakes of cylinders too, although actual studies examining this issue are lacking. Overall, this line of reasoning suggests that waves will modulate to some degree any fine-scale patterns in deposition, resuspension, and vertical movement of spores that occur close to the holdfasts and frond bundles of surface canopy forming kelps.

On the other hand, it is unlikely that the surface canopy forming kelps themselves will dramatically affect most surface gravity waves. Due to their ability to sway with oscillatory fluid motions, large canopy forming kelps commonly experience surprisingly little drag from ordinary-sized surface gravity waves (Koehl, 1984, 1986; Denny et al., 1997). As a direct consequence, they in turn damp surface gravity waves only slightly (Elwany et al., 1995; Gaylord et al., 2003). This is in marked contrast to the apparent

tendency for seagrass meadows to damp surface gravity waves (Fonseca and Cahalan, 1992), the commonly observed damping of capillary waves by kelp canopies (Seymour, 1996), and the strong capacity for kelp forests to exert feedback on currents (Jackson and Winant, 1983; Jackson, 1998).

4.5. Coherent flow structures in the canopy

Discussions above have concentrated on the situation where the canopy forming kelps extend throughout the entire water column. However, in the presence of faster currents, upper portions of *Macrocystis* or *Nereocystis* canopies can be pushed downstream until the tension in their stipes pulls them below the water's surface. Flow above the canopy then skims over it relatively unimpeded (see Fonseca et al., 1982; Shi et al., 1995; Koch and Gust, 1999; Nepf and Vivoni, 2000 for discussions of this phenomena in seagrass beds and saltmarsh systems). This situation produces a region of strong shear at the canopy–fluid interface that can induce turbulence, mixing, and the creation of coherent eddy structures of relatively large scale that can potentially invade the canopy from above (Raupach et al., 1996; Finnigan, 2000; Ghisalberti and Nepf, 2002). The existence of these eddies can often be ascertained from progressive, wave-like motions of elastic deflection of the canopy that propagate across terrestrial and aquatic plant arrays (distinguished as “honami” and “monami”, respectively, by Ackerman and Okubo, 1993). Such coherent structures are believed to be responsible for considerable mass and heat exchange, so much so that typical diffusion analogies that predict strictly down-gradient net transport of flow constituents via small, random eddies become less appropriate (Shaw, 1977; Raupach and Thom, 1981; Bache, 1986; Raupach et al., 1996). Indeed, the dominant mechanism of turbulence production under conditions of skimming flow may shift from processes involving bottom shear or flow separation in plant wakes, to the shear at the canopy–fluid interface (Finnigan, 2000; Nepf and Vivoni, 2000; Lopez and Garcia, 2001; Ghisalberti and Nepf, 2002). Under such circumstances, a substantial fraction of the total fluid exchange with external waters may occur vertically, much as it does in expansive, homogeneous terrestrial systems (like large crop fields) where horizontal advection through the vegetation is less im-

portant (Shaw et al., 1974). This suggests that under many conditions, particularly for *Macrocystis* or *Nereocystis* kelp canopies of intermediate densities where the interfacial shear is strong enough to form coherent eddies, but where the canopy is not so thick as to impede their vertical passage, it will be necessary to account for such factors when evaluating spore dispersal. This could be especially the case in kelp forests where relatively dense canopies of understory seaweed could also produce a second sheared mixing layer near the bottom at about the elevation of spore release of many macroalgae, including *Macrocystis*. The erect stipitate kelp, *P. californica*, which can reach 1–2 m in height (Abbott and Hollenberg, 1976), provides a common example. Such coherent flow structures and their influence on mixing will likely be important on the edges of kelp forests as well, due to the relatively limited widths of most forests. Such features, however, have received limited attention to date.

5. Contrasts with larval dispersal

It is clear that dispersal in macroalgae resembles that of many benthic marine invertebrates and fishes in that, in each of these groups, dispersal occurs by means of small propagules that are carried predominantly by ocean flows, while the adults themselves are relatively (if not absolutely) sessile. In other aspects, however, dispersal in macroalgae is fundamentally different. A number of these differences revolve around the more limited scales of space and time that are relevant to seaweed spores.

Unlike the spores of most macroalgae which are typically in the water column for a few to several days, the larvae of many marine animals remain in the water column for weeks to months (Strathmann, 1987). In addition, most larvae have precompetency periods during which they are physiologically and developmentally incapable of settling, even if they encounter suitable habitat. These precompetency durations vary depending on the species, but are commonly about half as long as the full planktonic larval duration (Jackson and Strathmann, 1981). Such extended planktonic durations indicate that many larvae are likely to be carried offshore at least temporarily into deep water, well beyond regions where

the inner shelf processes discussed above (such as wave effects in benthic boundary layers, forest-influenced declines in vertical mixing, and plant and topographically driven secondary flows) dominate the fluid dynamics.

This issue raises a second point as well. Because of the much longer planktonic durations of most larvae, their movements are affected by substantially larger scale processes than those that influence the transport of macroalgal spores. Such processes include meso-scale eddies (Nishimoto and Washburn, 2002), coastally trapped waves (Mysak, 1980; Battisti and Hickey, 1984; Auad and Henderschott, 1997), large-scale pressure gradients (e.g., Harms and Winant, 1998), and regional upwelling/relaxation cycles (Send et al., 1987). Thus, physical flows that would appear as simple, relatively constant forcing agents in the context of spore dispersal might actually be slowly varying components of substantially larger scale circulation features driven by other factors. Such factors may play a role in determining biogeographic patterns of abundance in widely dispersing shoreline animals (see, e.g., Gaylord and Gaines, 2000), while acting simply as event-by-event variations in steady flow over the timescales relevant to seaweeds and short-dispersing marine animals.

The larger scales of larval dispersal also tend to uncouple the local distribution of adults along a coast from the patterns of settlement of the young produced by those adults. In contrast, in kelp forest macroalgae there is a strong potential for feedbacks between local adult distributions and patterns of spore dispersal and settlement. As detailed above, kelp forests alter the flow through their interiors, which then influences where spores are transported. Due to the smaller expected spatial scales of dispersal in seaweed spores, much of this transport will be local, which in turn means that forests will influence the spatial distribution and densities of new recruits in their own vicinities. Such recruitment ultimately determines, in conjunction with other ecological factors, the density of adults in the subsequent generation, and the nature of the biological–physical coupling at that stage. The process then continues to cascade through succeeding generations. Although this line of argument by no means implies that invertebrates and fishes do not influence fine-scale settlement patterns (this capacity is well-recognized; Caley et al., 1996), the inter-

generational connection (i.e., the capacity of local settlement patterns to affect the local settlement patterns of the offspring of those individuals) is unlikely to be as strong as it is in canopy forming kelps.

6. Conclusions

Clearly, seaweeds respond to and influence fluid motion. However, to date most organismal level studies of biological–physical coupling in macroalgae have focused on three elements of the interaction: the dislodgement of these plants by waves (e.g., Koehl, 1984, 1986; Carrington, 1990; Denny et al., 1998; Gaylord et al., 1994; Gaylord, 2000; Gaylord et al., 2003), the effects of flow on nutrient and gas exchange at the surfaces of individual blades with ultimate implications for algal growth (e.g., Wheeler, 1980; Gerard, 1982; Hurd et al., 1996; Hurd, 2000; Stevens et al., 2001), and the interplay of environmental factors with the morphological plasticity of seaweeds (e.g., Norton, 1969, 1991; Mann, 1971; Gerard, 1979, 1987; Norton et al., 1981; Blanchette, 1997).

With regards to a fourth element, the physics of macroalgal spore dispersal, a mechanistic look at the overall process uncovers several themes. Emerging findings reveal that flow attenuation and vertical mixing within plant arrays likely have profound and complex effects on the distances over which spores are transported, but that these processes are just beginning to be understood in kelp forests. Forest-wide effects may also be modulated at smaller scales, as fine-level patterns in spore settlement can potentially be influenced by local secondary flows around organisms and bottom features. At times or locations where rapid currents arise, additional physical processes, such as coherent flow structures generated by mixing layers above submerged canopies, may begin to play a role in spore dispersal. Each of these factors will interface in turn with the fundamental spore properties, plant morphologies, and life history components of macroalgae themselves to determine their recruitment rates, their population dynamics, their degree of connectivity to other populations, and their relationship with the plethora of community members with whom they interact.

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References

- Abbott, I.A., Hollenberg, G.J., 1976. Marine Algae of California. Stanford Univ. Press, Stanford, CA.
- Abelson, A., Denny, M., 1997. Settlement of marine organisms in flow. *Annu. Rev. Ecol. Syst.* 28, 317–339.
- Abelson, A., Miloh, T., Loya, Y., 1993. Flow patterns induced by substrata and body morphologies of benthic organisms, and their roles in determining availability of food particles. *Limnol. Oceanogr.* 38, 1116–1124.
- Ackerman, J.D., 1986. Mechanistic implications for pollination in the marine angiosperm *Zostera marina*. *Aquat. Bot.* 24, 343–353.
- Ackerman, J.D., 2002. Diffusivity in a marine macrophyte canopy: implications for submarine pollination and dispersal. *Am. J. Bot.* 89, 1119–1127.
- Ackerman, J.D., Okubo, A., 1993. Reduced mixing in a marine macrophyte canopy. *Funct. Ecol.* 7, 305–309.
- Adams, C.E., Weatherly, G.L., 1981. Suspended-sediment transport and benthic boundary-layer dynamics. *Mar. Geol.* 42, 1–18.
- Agrawal, Y.C., Terray, E.A., Donelan, M.A., Hwang, P.A., Williams III, A.J., Drennan, W.M., Kahma, K.K., Kitaigorodskii, S.A., 1992. Enhanced dissipation of kinetic energy beneath surface waves. *Nature* 359, 219–220.
- Amsler, C.D., Searles, R.B., 1980. Vertical distribution of seaweed spores in a water column offshore of North Carolina. *J. Phycol.* 16, 617–619.
- Amsler, C.D., Neushul, M., 1989a. Chemotactic effects of nutrients on spores of the kelps *Macrocystis pyrifera* and *Pterygophora californica*. *Mar. Biol.* 102, 557–564.
- Amsler, C.D., Neushul, M., 1989b. Diel periodicity of spore release from the kelp *Nereocystis luetkeana* (Mertens) Postels et Ruprecht. *J. Exp. Mar. Biol. Ecol.* 134, 117–127.
- Amsler, C.D., Neushul, M., 1990. Nutrient stimulation of spore settlement in the kelps *Pterygophora californica* and *Macrocystis pyrifera*. *Mar. Biol.* 107, 297–304.
- Amsler, C.D., Reed, D.C., Neushul, M., 1992. The microclimate inhabited by macroalgal propagules. *Br. Phycol. J.* 27, 253–270.
- Amsler, C.D., Shelton, K.L., Britton, C.J., Spencer, N.Y., Greer, G.P., 1999. Nutrients do not influence swimming behavior or settlement rates of *Ectocarpus siliculosus* (Phaeophyceae) spores. *J. Phycol.* 35, 239–244.
- Anderson, S.M., Charters, A.C., 1982. A fluid dynamics study of seawater flow through *Gelidium nudifrons*. *Limnol. Oceanogr.* 27, 399–412.
- Anderson, E.K., North, W.J., 1966. In situ studies of spore production and dispersal in the giant kelp *Macrocystis pyrifera*. *Proc. Intl. Seaweed Symp.* 5, 73–86.
- Anis, A., Moum, J., 1995. Surface wave-turbulence interactions: scaling epison(z) near the sea surface. *J. Phys. Oceanogr.* 25, 2025–2045.
- Auad, G., Henderschott, M.C., 1997. The low-frequency transport in the Santa Barbara Channel: description and forcing. *J. Geophys. Res.* 102, 779–802.
- Avisar, B., Shemer, L., Kribus, A., 2001. Measurements of velocity fields in finite cylinder arrays with and without tip clearance. *Exp. Therm. Fluid Sci.* 24, 157–167.
- Bache, D.H., 1986. On the theory of gaseous transport to plant canopies. *Atmos. Environ.* 20, 1379–1388.
- Baker, C.J., 1980. The turbulent horseshoe vortex. *J. Wind Eng. Ind. Aero.* 6, 9–23.
- Batchelor, G.K., 1967. *An Introduction to Fluid Dynamics*. Cambridge Univ. Press, Cambridge, UK.
- Battisti, D.S., Hickey, B.M., 1984. Application of remote wind-forced coastal trapped wave theory to the Oregon and Washington coasts. *J. Phys. Oceanogr.* 14, 887–903.
- Bearman, P.W., Wadcock, A.J., 1973. The interaction between a pair of circular cylinders normal to a stream. *J. Fluid Mech.* 61, 499–511.
- Berg, H.C., 1983. *Random Walks in Biology*. Princeton Univ. Press, Princeton, NJ.
- Blanchette, C., 1997. Size and survival of intertidal plants in response to wave action: a case study with *Fucus gardneri*. *Ecology* 78, 1563–1578.
- Bowden, K.F., 1965. Horizontal mixing in the sea due to a shearing current. *J. Fluid Mech.* 21, 83–95.
- Branch, G.M., Griffiths, C.L., Branch, M.L., Beckley, L.E., 1999. *Two Oceans: A guide to the marine life of South Africa*. David Phillip Publishers, Claremont, South Africa.
- Brawley, S.H., Johnson, L.E., 1992. Gametogenesis, gametes and zygotes: an ecological perspective on sexual reproduction in the algae. *Br. Phycol. J.* 27, 233–252.
- Breaker, L.C., Broenkow, W.W., 1994. The circulation of Monterey Bay and related processes. *Oceanogr. Mar. Biol. Annu. Rev.* 32, 1–64.
- Breusers, H.N.C., Nicollet, G., Shen, H.W., 1977. Local scour around cylindrical piers. *J. Hydraul. Res.* 15, 211–252.
- Brink, K.H., 1983. The near-surface dynamics of coastal upwelling. *Prog. Oceanogr.* 12, 223–257.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. *Annu. Rev. Ecol. Syst.* 27, 477–500.
- Carey, D.A., 1983. Particle resuspension in the boundary layer induced by flow around polychaete tubes. *Can. J. Fish. Aquat. Sci.* 40 (Suppl. 1), 301–308.

- Carrington, E., 1990. Drag and dislodgement of an intertidal macroalga: consequences of morphological variation in *Mastocarpus papillatus* Kützinger. *J. Exp. Mar. Biol. Ecol.* 139, 185–200.
- Chabot, R., Bourget, E., 1988. Influence of substratum heterogeneity and settled barnacle density on the settlement of cypris larvae. *Mar. Biol.* 97, 45–56.
- Charters, A.C., Neushul, M., Coon, D.A., 1972. Effects of water motion on algal spore attachment. *Proc. Intl. Seaweed Symp.* 7, 243–247.
- Charters, A.C., Neushul, M., Coon, D., 1973. The effect of water motion on algal spore adhesion. *Limnol. Oceanogr.* 18, 884–896.
- Clarke, J.S., Macklin, E., Wood, L., 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecology* 80, 1475–1494.
- Clayton, M.N., 1992. Propagules of marine macroalgae: structure and development. *Br. Phycol. J.* 27, 219–232.
- Coon, D., Neushul, M., Charters, A.C., 1972. The settling behavior of marine algal spores. *Proc. Intl. Seaweed Symp.* 7, 237–242.
- Coyer, J.A., Zauggaglund, A.C., 1982. A demographic study of the elk kelp, *Pelagophycus porra* (Laminariales, Lessoniaceae), with notes on *Pelagophycus X macrocystis* hybrids. *Phycologia* 21, 399–407.
- Cudaback, C.N., Largier, J.L., 2001. The cross-shelf structure of wind- and buoyancy-driven circulation over the North Carolina inner shelf. *Cont. Shelf Res.* 21, 1649–1668.
- Dade, W.B., 1993. Near-bed turbulence and hydrodynamic control of diffusional mass transfer at the sea floor. *Limnol. Oceanogr.* 38, 52–69.
- Dayton, P.K., 1973. Dispersion, dispersal, and persistence of the annual intertidal alga, *Postelsia palmaeformis* Ruprecht. *Ecology* 54, 433–438.
- Dayton, P.K., 1975. Experimental studies of algal canopy interactions in a sea otter dominated kelp community at Amchitka Island, Alaska. *Fish Bull.* 73, 230–237.
- Dayton, P.K., 1985. Ecology of kelp communities. *Annu. Rev. Ecol. Syst.* 16, 215–245.
- Dayton, P.K., 1992. Community landscape: scale and stability in hard bottom marine communities. In: Giller, P.S., Hildrew, A.G., Raffaelli, D.G. (Eds.), *Aquatic Ecology: Scale, Pattern, and Process*. Blackwell Scientific, Oxford, pp. 289–332.
- Dayton, P.K., Seymour, R.J., Parnell, P.E., Tegner, M.J., 1989. Unusual marine erosion in San Diego county from a single storm. *Estuar. Coast. Shelf Sci.* 29, 151–160.
- Dayton, P.K., Tegner, M.J., Parnell, P.E., Edwards, P.B., 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* 62, 421–445.
- Denny, M.W., Shibata, M.F., 1989. Consequences of surf-zone turbulence for settlement and external fertilization. *Am. Nat.* 134, 859–889.
- Denny, M., Gaylord, B., 2002. The mechanics of wave-swept algae. *J. Exp. Biol.* 205, 1355–1362.
- Denny, M., Brown, V., Carrington, E., Kraemer, G., Miller, A., 1989. Fracture mechanics and the survival of wave-swept macroalgae. *J. Exp. Mar. Biol. Ecol.* 127, 211–228.
- Denny, M.W., Dairiki, J., Distefano, S., 1992. Biological consequences of topography on wave-swept rocky shores: I. Enhancement of external fertilization. *Biol. Bull.* 183, 220–232.
- Denny, M.W., Gaylord, B.P., Cowen, E.A., 1997. Flow and flexibility: II. The roles of size and shape in determining wave forces on the bull kelp *Nereocystis luetkeana*. *J. Exp. Biol.* 200, 3165–3183.
- Denny, M.W., Gaylord, B., Helmuth, B., Daniel, T.L., 1998. The menace of momentum: dynamic forces on flexible organisms. *Limnol. Oceanogr.* 43, 955–968.
- Deysher, L., Norton, T.A., 1982. Dispersal and colonization in *Sargassum muticum* (Yendo) Fensholt. *J. Exp. Mar. Biol. Ecol.* 56, 179–195.
- Dorman, C.E., Rogers, D.P., Nuss, W., Thompson, W.T., 1999. Adjustment of the summer marine boundary layer around Point Sur, California. *Mon. Weather Rev.* 127, 2143–2159.
- Ebeling, A.W., Laur, D.R., Rowley, R.J., 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. *Mar. Biol.* 84, 287–294.
- Ebert, T.A., Russell, M.P., 1988. Latitudinal variation in size structure of the west coast purple sea urchin: a correlation with headlands. *Limnol. Oceanogr.* 33, 286–294.
- Eckman, J.E., 1983. Hydrodynamic processes affecting benthic recruitment. *Limnol. Oceanogr.* 28, 241–257.
- Eckman, J.E., 1987. The role of hydrodynamics in recruitment, growth, and survival of *Argopecten irradians* (L.) and *Anomia simplex* (D'Orbigny) within eelgrass meadows. *J. Exp. Mar. Biol. Ecol.* 106, 165–191.
- Eckman, J.E., 1990. A model of passive settlement by planktonic larvae onto bottoms of differing roughness. *Limnol. Oceanogr.* 35, 887–901.
- Eckman, J.E., Nowell, A.R.M., 1984. Boundary skin friction and sediment transport about an animal-tube mimic. *Sedimentology* 31, 851–862.
- Eckman, J.E., Duggins, D.O., Sewell, A.T., 1989. Ecology of understory kelp environments: I. Effects of kelps on flow and particle transport near the bottom. *J. Exp. Mar. Biol. Ecol.* 129, 173–187.
- Elwany, M.H.S., O'Reilly, W.C., Guza, R.T., Flick, R.E., 1995. Effects of Southern California kelp beds on waves. *J. Waterw. Port Coast. Ocean Eng.* 121, 143–150.
- Estes, J.A., Smith, N.S., Palmisano, J.F., 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology* 59, 822–833.
- Finnigan, J., 2000. Turbulence in plant canopies. *Annu. Rev. Fluid Mech.* 32, 519–571.
- Fischer, H.B., List, E.J., Koh, R.C.Y., Imberger, J., Brooks, N.H., 1979. *Mixing in Inland and Coastal Waters*. Academic Press, San Diego, CA.
- Fissel, D.B., Huggett, W.S., 1976. Observations of currents, bottom pressures and densities through a cross-section of Juan de Fuca Strait. *Pac. Mar. Sci.*, 6–76.
- Fletcher, R.L., Callow, M.E., 1992. The settlement, attachment and establishment of marine algal spores. *Br. Phycol. J.* 27, 303–329.
- Fonseca, M.S., Cahalan, J.A., 1992. A preliminary evaluation of wave attenuation by four species of seagrass. *Estuar. Coast. Shelf Sci.* 35, 565–576.
- Fonseca, M.S., Fisher, J.S., Zieman, J.C., Thayer, G.W., 1982. Influence of the seagrass, *Zostera marina* (L.), on current flow. *Estuar. Coast. Shelf Sci.* 15, 351–364.

- Foster, M.S., Schiel, D.R., 1985. The ecology of giant kelp forests in California: a community profile. Biol. Rep. 85, U.S. Fish and Wildlife Service.
- Fredriksen, S., Sjutun, K., Lein, T. E., Ruess, J., 1995. Spore dispersal in *Laminaria hyperborea* (Laminariales, Phaeophyceae). Sarsia 80, 47–54.
- Gambi, M.C., Nowell, A.R.M., Jumars, P.S., 1990. Flume observations of flow dynamics in *Zostera marina* (eelgrass) beds. Mar. Ecol. Prog. Ser. 61, 159–169.
- Gaylord, B., 1999. Detailing agents of physical disturbance: wave-induced velocities and accelerations on a rocky shore. J. Exp. Mar. Biol. Ecol. 239, 85–124.
- Gaylord, B., 2000. Biological implications of surf-zone flow complexity. Limnol. Oceanogr. 45, 174–188.
- Gaylord, B., Denny, M.W., 1997. Flow and flexibility: I. Effects of size, shape and stiffness in determining wave forces on the stipitate kelps *Eisenia arborea* and *Pterygophora californica*. J. Exp. Biol. 200, 3141–3164.
- Gaylord, B., Gaines, S.D., 2000. Temperature or transport? Range limits in marine species mediated solely by flow. Am. Nat. 155, 769–789.
- Gaylord, B., Blanchette, C.A., Denny, M.W., 1994. Mechanical consequences of size in wave-swept algae. Ecol. Monogr. 64, 287–313.
- Gaylord, B., Hale, B.B., Denny, M.W., 2001. Consequences of transient fluid forces for compliant benthic organisms. J. Exp. Biol. 204, 1347–1360.
- Gaylord, B., Reed, D.C., Raimondi, P.T., Washburn, L., McLean, S.R., 2002. A physically based model of macroalgal spore dispersal in the wave and current-dominated nearshore. Ecology 83, 1239–1251.
- Gaylord, B., Denny, M.W., Koehl, M.A.R., 2003. Modulation of wave forces on kelp canopies by alongshore currents. Limnol. Oceanogr. 48, 860–871.
- Gerard, V.A., 1979. Growth and production of *Laminaria longicirrus* (Phaeophyta) populations exposed to different intensities of water movement. J. Phycol. 15, 33–41.
- Gerard, V.A., 1982. In situ water motion and nutrient uptake by the giant kelp *Macrocystis pyrifera*. Mar. Biol. 69, 51–54.
- Gerard, V.A., 1987. Hydrodynamic streamlining of *Laminaria saccharina* lamour in response to mechanical stress. J. Exp. Mar. Biol. Ecol. 107, 237–244.
- Ghisalberti, M., Nepf, H.M., 2002. Mixing layers and coherent structures in vegetated aquatic flows. J. Geophys. Res. 107 (C2) (Article number 3011).
- Graham, M.H., 1997. Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey peninsula, central California, USA. J. Exp. Mar. Biol. Ecol. 218, 127–149.
- Grant, W.D., Madsen, O.S., 1986. The continental-shelf bottom boundary layer. Annu. Rev. Fluid Mech. 18, 265–305.
- Greer, S.P., Amsler, C.D., 2002. Light boundaries and the coupled effects of surface hydrophobicity and light on spore settlement in the brown alga *Hinckia irregularis* (Phaeophyceae). J. Phycol. 38, 116–124.
- Happel, J., Brenner, H., 1983. Low Reynolds Number Hydrodynamics. Martinus Nijhoff Publishing, The Hague.
- Harlin, M.M., Lindbergh, J.M., 1977. Selection of substrata by seaweeds: optimal surface relief. Mar. Biol. 40, 33–40.
- Harms, S., Winant, C.D., 1998. Characteristic patterns of circulation in the Santa Barbara channel. J. Geophys. Res. 103, 3041–3065.
- Harris, L.G., Ebeling, A.W., Laur, D.R., Rowley, R.J., 1984. Community recovery after storm damage: a case of facilitation in primary succession. Science 224, 1336–1338.
- Hill, A.E., 1998. Buoyancy effects in coastal and shelf seas. In: Brink, K.H., Robinson, A.R. (Eds.), The Sea. Wiley, New York, NY, pp. 21–62.
- Hoffmann, A.J., 1987. The arrival of seaweed propagules at the shore: a review. Bot. Mar. 30, 151–165.
- Hoffmann, A.J., Camus, P., 1989. Sinking rates and viability of spores from benthic algae in central Chile. J. Exp. Mar. Biol. Ecol. 126, 281–291.
- Hoffmann, A.J., Ugarte, R., 1985. The arrival of propagules of marine macroalgae in the intertidal zone. J. Exp. Mar. Biol. Ecol. 92, 83–95.
- Hudson, J.D., Dykhn, L., Hanratty, T.J., 1996. Turbulence production in flow over a wavy wall. Exp. Fluids 20, 257–265.
- Hurd, C.L., 2000. Water motion, marine macroalgal physiology, and production. J. Phycol. 36, 453–472.
- Hurd, C.L., Harrison, P.J., Druehl, L.D., 1996. Effect of seawater velocity on inorganic nitrogen uptake by morphologically distinct forms of *Macrocystis integrifolia* from wave-sheltered and exposed sites. Mar. Biol. 126, 205–214.
- Iken, K., Amsler, C.D., Greer, S.P., McClintock, J.B., 2001. Qualitative and quantitative studies of the swimming behaviour of *Hinckia irregularis* (Phaeophyceae) spores: ecological implications and parameters for quantitative swimming assays. Phycologia 40, 359–366.
- Jackson, G.A., 1984. Internal wave attenuation by coastal kelp stands. J. Phys. Oceanogr. 14, 1300–1306.
- Jackson, G.A., 1998. Currents in the high drag environment of a coastal kelp stand off California. Cont. Shelf Res. 17, 1913–1928.
- Jackson, G.A., Strathmann, R.R., 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development. Am. Nat. 118, 16–26.
- Jackson, G.A., Winant, C.D., 1983. Effect of a kelp forest on coastal currents. Cont. Shelf Res. 20, 75–80.
- Johnson, A.S., 1988. Hydrodynamic study of the functional morphology of the benthic suspension feeder *Phoronopsis viridis* (Phoronida). Mar. Biol. 100, 117–126.
- Johnson, A.S., 1990. Flow around phoronids: consequences of a neighbor to suspension feeders. Limnol. Oceanogr. 35, 1395–1401.
- Johnson, A.S., Koehl, M.A.R., 1994. Maintenance of dynamic strain similarity and environmental stress factor in different flow habitats: thallus allometry and material properties of a giant kelp. J. Exp. Biol. 195, 381–410.
- Jonsson, S., 1972. Marine benthic algae recorded in Surtsey during the filed seasons of 1969 and 1970. Surtsey Res. Prog. Rep. 6, 75–76.
- Kain, J.M., 1964. Aspects of the biology of *Laminaria hyperborea*: III. Survival and growth of gametophytes. J. Mar. Biol. Assoc. U.K. 44, 415–433.

- Kinsman, B., 1965. Wind Waves. Dover Publications, New York, NY.
- Koch, E., Gust, G., 1999. Water flow in tide-and wave-dominated beds of the seagrass *Thalassia testudinum*. Mar. Ecol. Prog. Ser. 184, 63–72.
- Koehl, M.A.R., 1984. How do benthic organisms withstand moving water? Am. Zool. 24, 57–70.
- Koehl, M.A.R., 1986. Seaweeds in moving water: form and mechanical function. In: Givnish, T.J. (Ed.), On the Economy of Plant Form and Function. Cambridge Univ. Press, Cambridge, UK, pp. 603–634.
- Komar, P.S., 1998. Beach Processes and Sedimentation, 2nd ed. Prentice Hall, Upper Saddle River, NJ.
- Koseff, J.R., Street, R.L., 1984a. On end wall effects in a lid-driven cavity flow. J. Fluids Eng. 106, 385–389.
- Koseff, J.R., Street, R.L., 1984b. The lid-driven cavity flow: a synthesis of qualitative and quantitative observations. J. Fluids Eng. 106, 390–398.
- Leonard, L.A., Luther, M.E., 1995. Flow hydrodynamics in tidal marsh canopies. Limnol. Oceanogr. 40, 1474–1484.
- Lerczak, J.A., Henderschott, M.C., Winant, C.D., 2001. Observations and modeling of coastal internal waves driven by a diurnal sea breeze. J. Geophys. Res. 106, 19715–19729.
- Longuet-Higgins, M.S., 1953. Mass transport in water waves. Proc. R. Soc. Lond., A 245, 535–581.
- Longuet-Higgins, M.S., 1970. Longshore currents generated by obliquely incident sea waves, 1. J. Geophys. Res. 75, 6778–6801.
- Lopez, F., Garcia, M.H., 2001. Mean flow and turbulence structure of open-channel flow through non-emergent vegetation. J. Hydraul. Eng. 127, 392–402.
- Mann, K.H., 1971. Relation between stipe length, environment, and the taxonomic characters of *Laminaria*. J. Fish. Res. Board Can. 28, 778–780.
- McNair, J.N., 2000. Turbulent transport of suspended particles and dispersing benthic organisms: the hitting-time distribution for the local exchange model. J. Theor. Biol. 202, 231–246.
- McNair, J.N., Newbold, J.D., 2001. Turbulent transport of suspended particles and dispersing benthic organisms: the hitting-distance problem for the local exchange model. J. Theor. Biol. 209, 351–369.
- McNair, J.N., Newbold, J.D., Hart, D.D., 1997. Turbulent transport of suspended particles and dispersing benthic organisms: how long to hit bottom? J. Theor. Biol. 188, 29–52.
- Melville, B.W., Raudkivi, A.J., 1977. Flow characteristics in local scour at bridge piers. J. Hydraul. Res. 15, 373–380.
- Middleton, G.V., Southard, J.B., 1984. Mechanics of sediment movement, 2nd ed. Lecture notes sponsored by the Society of Economic Paleontologists and Mineralogists, Providence, RI.
- Mysak, L.A., 1980. Topographically trapped waves. Annu. Rev. Fluid Mech. 12, 45–76.
- Naot, D., Nezu, I., Nakagawa, H., 1996. Hydrodynamic behavior of partly vegetated open channels. J. Hydraul. Eng. 122, 625–633.
- Nelson, J.M., McLean, S.R., Wolfe, S.R., 1993. Mean flow and turbulence fields over two-dimensional bed forms. Water Resour. Res. 29, 3935–3953.
- Nepf, H.M., 1999. Drag, turbulence, and diffusion in flow through emergent vegetation. Water Resour. Res. 35, 479–489.
- Nepf, H.M., Koch, E.W., 1999. Vertical secondary flows in submerged plant-like arrays. Limnol. Oceanogr. 44, 1072–1080.
- Nepf, H.M., Vivoni, E.R., 2000. Flow structure in depth-limited, vegetated flow. J. Geophys. Res. 105, 28547–28557.
- Nepf, H.M., Mugnier, C.G., Zavistoski, R.A., 1997a. The effects of vegetation on longitudinal dispersion. Estuar. Coast. Shelf Sci. 44, 675–684.
- Nepf, H.M., Sullivan, J.A., Zavistoski, R.A., 1997b. A model for diffusion within emergent vegetation. Limnol. Oceanogr. 42, 1735–1745.
- Neushul, M., 1972. Functional interpretation of benthic marine algal morphology. In: Abbott, I.A., Kurogi, M. (Eds.), Contributions to the Systematics of Benthic Marine Algae of the North Pacific, Japanese Society of Phycology, Kobe, Japan, pp. 47–73.
- Niedoroda, A.W., Dalton, C., 1982. A review of the fluid mechanics of ocean scour. Ocean Eng. 9, 159–170.
- Nishimoto, M.M., Washburn, L., 2002. Patterns of coastal eddy circulation and abundance of pelagic juvenile fish in the Santa Barbara Channel, California, USA. Mar. Ecol. Prog. Ser. 241, 183–199.
- North, W.J., 1971. The biology of giant kelp beds (*Macrocystis*) in California. Nova Hedwig., Beih., p. 32.
- Norton, T.A., 1969. Growth form and environment in *Saccorhiza polyschides*. J. Mar. Biol. Assoc. U.K. 49, 1025–1045.
- Norton, T.A., 1991. Conflicting constraints on the form intertidal algae. Br. Phycol. J. 26, 203–218.
- Norton, T.A., 1992. Dispersal by macroalgae. Br. Phycol. J. 27, 293–301.
- Norton, T.A., Fetter, R., 1981. The settlement of *Sargassum muticum* propagules in stationary and flowing water. J. Mar. Biol. Assoc. U.K. 61, 929–940.
- Norton, T.A., Mathieson, A.C., Neushul, M., 1981. Morphology and environment. In: Lobban, C.S., Wynne, M.J. (Eds.), The Biology of Seaweeds. University of California Press, Berkeley, CA, pp. 421–451.
- Nowell, A.R.M., Church, M., 1979. Turbulent flow in a depth-limited boundary layer. J. Geophys. Res. 84, 4816–4824.
- O'Brien, V., 1972. Closed streamlines associated with channel flow over a cavity. Phys. Fluids 15, 2089–2097.
- Okubo, A., Ackerman, J.D., Swaney, D.P., 2001. Passive diffusion in ecosystems. In: Okubo, A., Levin, S. (Eds.), Diffusion and Ecological Problems: New Perspectives. Springer, New York, NY, pp. 31–106.
- Okuda, T., Neushul, M., 1981. Sedimentation studies of red algal spores. J. Phycol. 17, 113–118.
- Pierce, F.J., Tree, I.K., 1990. The mean flow structure on the symmetry plane of a turbulent junction vortex. J. Fluids Eng. 112, 16–22.
- Pineda, J., 1995. An internal tidal bore regime at nearshore stations along western U.S.A.: predictable upwelling within the lunar cycle. Cont. Shelf Res. 15, 1023–1041.
- Pond, S., Pickard, G.L., 1983. Introductory Dynamical Oceanography, 2nd ed. Butterworth Heinmann, Oxford, UK.
- Raupach, M.R., Thom, A.S., 1981. Turbulence in and above plant canopies. Annu. Rev. Fluid Mech. 13, 97–129.
- Raupach, M.R., Coppin, P.A., Legg, B.J., 1986. Experiments on

- scalar dispersion within a model plant canopy: Part I. The turbulence structure. *Bound.-Layer Meteorol.* 35, 21–52.
- Raupach, M.R., Antonia, R.A., Rajagopalan, S., 1991. Rough-wall turbulent boundary layers. *Appl. Mech. Rev.* 44, 1–25.
- Raupach, M.R., Finnigan, J.J., Brunet, Y., 1996. Coherent eddies and turbulence in vegetation canopies: the mixing-layer analogy. *Bound.-Layer Meteorol.* 78, 351–382.
- Reed, D.C., 1990a. The effects of variable settlement and early competition on patterns of kelp recruitment. *Ecology* 71, 776–787.
- Reed, D.C., 1990b. An experimental evaluation of density dependence in a subtidal algal population. *Ecology* 71, 2286–2296.
- Reed, D.C., Laur, D.R., Ebeling, A.W., 1988. Variation in algal dispersal and recruitment: the importance of episodic events. *Ecol. Monogr.* 58, 321–335.
- Reed, D.C., Amsler, C.D., Ebeling, A.W., 1992. Dispersal in kelps: factors affecting spore swimming and competency. *Ecology* 73, 1577–1585.
- Reed, D.C., Ebeling, A.W., Anderson, T.W., Anghera, M., 1996. Differential reproductive responses to fluctuating resources in two seaweeds with different reproductive strategies. *Ecology* 77, 300–316.
- Reed, D.C., Anderson, T.W., Ebeling, A.W., Anghera, M., 1997. The role of reproductive synchrony in the colonization potential of kelp. *Ecology* 78, 2443–2457.
- Reed, D.C., Brzezinski, M.A., Coury, D.A., Graham, W.M., Petty, R.L., 1999. Neutral lipids in macroalgal spores and their role in swimming. *Mar. Biol.* 133, 737–744.
- Reed, D.C., Schroeter, S.C., Raimondi, P.T., 2004. Spore supply and habitat availability as sources of recruitment limitation in giant kelp. *J. Phycol.* 40, in press.
- Rockwell, D., Naudascher, E., 1978. Self-sustaining oscillations of flow past cavities. *J. Fluids Eng.* 100, 152–165.
- Santelices, B., 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanogr. Mar. Biol. Annu. Rev.* 28, 177–276.
- Schiel, D.R., Foster, M.S., 1986. The structure of subtidal algal stands in temperate waters. *Oceanogr. Mar. Biol. Annu. Rev.* 24, 265–307.
- Schlichting, H., 1979. *Boundary-Layer Theory*. McGraw-Hill, New York.
- Seginer, I., Mulhearn, P.J., Bradley, E.F., Finnigan, J.J., 1976. Turbulent flow in a model plant canopy. *Bound.-Layer Meteorol.* 10, 423–453.
- Send, U., Beardsley, R.C., Winant, C.D., 1987. Relaxation from upwelling in the coastal ocean dynamics experiment. *J. Geophys. Res.* 92, 1683–1698.
- Seymour, R.J., 1996. Discussion of effects of Southern California kelp beds on waves. *J. Waterw. Port Coast. Ocean Eng.* 122, 207–208.
- Seymour, R.J., Tegner, M.J., Dayton, P.K., Parnell, P.E., 1989. Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in southern California. *Estuar. Coast. Shelf Sci.* 28, 277–292.
- Shaw, R.H., 1977. Secondary wind speed maxima inside plant canopies. *J. Appl. Meteorol.* 16, 514–521.
- Shaw, R.H., Silversides, R.H., Thurtell, G.W., 1974. Some observations of turbulence and turbulent transport within and above plant canopies. *Bound.-Layer Meteorol.* 5, 429–449.
- Sherman, F.S., Imberger, J., Corcos, G.M., 1978. Turbulence and mixing in stably stratified waters. *Annu. Rev. Fluid Mech.* 10, 267–288.
- Shi, Z., Pethick, J.S., Pye, K., 1995. Flow structure in and above the various heights of a saltmarsh canopy: a laboratory flume study. *J. Coast. Res.* 11, 1204–1209.
- Snelgrove, P.V.R., Butman, C.A., Grassle, J.P., 1993. Hydrodynamic enhancement of larval settlement in the bivalve *Mulinia lateralis* (Say) and the polychaete *Capitella* sp. I in microdepositional environments. *J. Exp. Mar. Biol. Ecol.* 168, 71–109.
- Stacey, G.R., Belcher, R.E., Wood, C.J., 1994. Wind flows and forces in a model spruce forest. *Bound.-Layer Meteorol.* 69, 311–334.
- Stevens, C.L., Hurd, C.L., Smith, M.J., 2001. Water motion relative to subtidal kelp fronds. *Limnol. Oceanogr.* 46, 668–678.
- Stevens, C.L., Hurd, C.L., Smith, M.J., 2002. Field measurements of the dynamics of the bull kelp *Durvillaea antarctica* (Chamisso) Heriot. *J. Exp. Mar. Biol. Ecol.* 269, 147–171.
- Strathmann, M.F., 1987. *Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast*. University of Washington Press, Seattle, WA.
- Strub, P.T., Kosro, P.M., Huyer, A., 1991. The nature of the cold filaments in the California current system. *J. Geophys. Res.* 96, 14743–14768.
- Sumer, B.M., Fredsoe, J., 1998. Wave scour around group of vertical piles. *J. Waterw. Port Coast. Ocean Eng.* 124, 248–256.
- Sumer, B.M., Fredsoe, J., 2001a. Wave scour around a large vertical circular cylinder. *J. Waterw. Port Coast. Ocean Eng.* 127, 125–134.
- Sumer, B.M., Fredsoe, J., 2001b. Scour around pile in combined waves and current. *J. Hydraul. Eng.* 127, 403–411.
- Sumer, B.M., Christiansen, N., Fredsoe, J., 1997. The horseshoe vortex and vortex shedding around a vertical wall-mounted cylinder exposed to waves. *J. Fluid Mech.* 332, 41–70.
- Tennekes, H., Lumley, J.L., 1972. *A First Course in Turbulence*. MIT Press, Cambridge, MA.
- Thomson, R.E., 1981. *Oceanography of the British Columbia Coast*. Dept. of Fisheries, Ottawa.
- Turner, J.S., 1973. *Buoyancy Effects in Fluids*. Cambridge Univ. Press, Cambridge, UK.
- Van Dyke, M., 1982. *An Album of Fluid Motion*. Parabolic Press, Stanford, CA.
- Washburn, L., Stone, S., MacIntyre, S., 1999. Dispersion of produced water in a coastal environment and its biological implications. *Cont. Shelf Res.* 19, 57–78.
- Weatherly, G.L., Martin, P.J., 1978. On the structure and dynamics of the oceanic bottom boundary layer. *J. Phys. Oceanogr.* 8, 557–570.
- Wheeler, W.N., 1980. Effect of boundary layer transport on the fixation of carbon by the giant kelp *Macrocystis pyrifera*. *Mar. Biol.* 56, 103–110.
- Wiberg, P., Smith, J.D., 1983. A comparison of field data and theoretical models for wave–current interactions at the bed on the continental shelf. *Cont. Shelf Res.* 2, 147–162.
- Winant, C.D., Bratkovich, A.W., 1981. Temperature and currents on the Southern California shelf: a description of the variability. *J. Phys. Oceanogr.* 11, 71–86.

- Winant, C.D., Olson, J.R., 1976. The vertical structure of coastal currents. *Deep-Sea Res.* 23, 925–936.
- Wolanski, E., Hamner, W.M., 1988. Topographically controlled fronts in the ocean and their biological influence. *Science* 241, 177–181.
- Womersley, H.B.S., 1954. The species of *Macrocystis* with special reference to those on southern Australian coasts. *Univ. Calif. Publ. Bot.* 27, 109–132.
- Woo, H.G.C., Cermak, J.E., Peterka, J.A., 1989. Secondary flows and vortex formation around a circular cylinder in constant-shear flow. *J. Fluid Mech.* 204, 523–542.
- Yager, P.L., Nowell, A.R.M., Jumars, P.A., 1993. Enhanced deposition to pits: a local food source for benthos. *J. Mar. Res.* 51, 209–236.
- Zdravkovich, M.M., 1977. Review of flow interference between two circular cylinders in various arrangements. *J. Fluids Eng.* 99, 618–633.
- Zdravkovich, M.M., 1996. Inadequacy of a conventional Keulegan–Carpenter number for wave and current combination. *J. Offshore Mech. Arct. Eng.* 118, 309–311.
- Zechman, F.W., Mathieson, A.C., 1985. The distribution of seaweed propagules in estuarine, coastal, and offshore waters of New Hampshire, U.S.A.. *Bot. Mar.* 28, 283–294.
- Zimmerman, R.C., Kremer, J.N., 1984. Episodic nutrient supply to a kelp forest ecosystem in Southern California. *J. Mar. Res.* 42, 591–604.
- Zimmerman, R.C., Kremer, J.N., 1986. In situ growth and chemical composition of the giant kelp, *Macrocystis pyrifera*: response to temporal changes in ambient nutrient availability. *Mar. Ecol. Prog. Ser.* 27, 277–285.
- Zukauskas, A., 1987. Heat transfer from tubes in crossflow. *Adv. Heat Trans.* 18, 87–159.