

Spatial patterns of flow and their modification within and around a giant kelp forest

*Brian Gaylord*¹

Bodega Marine Laboratory and Section of Evolution and Ecology, University of California at Davis, Bodega Bay, California 94923

Johanna H. Rosman

Department of Civil and Environmental Engineering, Stanford University, Stanford, California 94305

Daniel C. Reed

Marine Science Institute, University of California at Santa Barbara, Santa Barbara, California 93106

Jeffrey R. Koseff

Department of Civil and Environmental Engineering, Stanford University, Stanford, California 94305

Jonathan Fram

Marine Science Institute, University of California at Santa Barbara, Santa Barbara, California 93106

Sally MacIntyre and Katie Arkema

Marine Science Institute and Department of Ecology Evolution and Marine Biology, University of California at Santa Barbara, Santa Barbara, California 93106

Cameron McDonald

Department of Civil and Environmental Engineering, Stanford University, Stanford, California 94305

Mark A. Brzezinski

Marine Science Institute and Department of Ecology Evolution and Marine Biology, University of California at Santa Barbara, Santa Barbara, California 93106

John L. Largier

Bodega Marine Laboratory and Department of Environmental Science and Policy, University of California at Davis, Bodega Bay, California 94923

Stephen G. Monismith

Department of Civil and Environmental Engineering, Stanford University, Stanford, California 94305

Peter T. Raimondi

Department of Biology, University of California at Santa Cruz, Santa Cruz, California 95064

Brent Mardian

Marine Science Institute, University of California at Santa Barbara, Santa Barbara, California 93106

Abstract

We present findings from two sets of measurements that quantified currents around and over the full extent of a giant kelp (*Macrocystis pyrifera*) forest located at Mohawk Reef, Santa Barbara, California. Velocities were damped inside this 200-m × 300-m forest, but not to the extent reported for larger (kilometer-scale) kelp beds, suggesting that alongshore currents may play a greater role in exchange than has often been assumed. Secondary flow features that bear on the performance of forest organisms were observed, including a region along the forest's outer boundary where velocities exceeded incident speeds by up to 200%. An offshore current on the order of 1 cm s⁻¹ developed within the kelp bed, likely due to pressure gradients established across the forest coupled with topography. Wake recirculations that might have facilitated leeward retention of waterborne subsidies were not apparent. Calculations suggest that kelp beds can interact with (and thus potentially filter) substantial

¹ Corresponding author (bpgaylord@ucdavis.edu; phone: 707-875-1940; fax: 707-875-2009).

portions of impinging waters; in our study, 40–90% of arriving waters entered the upstream end, and 20–70% reached the center of the forest. Seasonal changes in the size and density of the forest modified the levels of flow damping and filtration. The sum of these effects suggests potential influences on organisms throughout the forest community.

Giant kelp (*Macrocystis pyrifera*) forests serve as important ecosystems along many temperate coasts, including the shores of North and South America, parts of Australia and New Zealand, South Africa, and scattered islands in the Southern Ocean (Wormersley 1954; Dayton 1985). *Macrocystis* is also a foundation species (sensu Dayton 1972), providing habitat, food, and refuge for hundreds of other nearshore organisms (Foster and Schiel 1985). The vital role of giant kelp in the coastal environment is accompanied by a profound dependence on the waters in which it is immersed. For example, whereas *Macrocystis* can grow 0.5 m per day in the presence of sufficient nutrients (North 1971), it ceases to grow and may senesce if nitrate concentrations in the surrounding seawater drop below $1 \mu\text{mol L}^{-1}$ (Zimmerman and Kremer 1986). Maintenance of such concentrations typically relies on the delivery of new, nutrient-replete water via a variety of hydrodynamic mechanisms. Nearshore flows associated with currents and waves likewise dictate patterns of spore dispersal in kelp (Reed et al. 1988; Gaylord et al. 2002, 2006), with accompanying effects on population connectivity and rates of self-fertilization (Raimondi et al. 2004; Reed et al. 2004, 2006). Storm waves additionally dislodge large numbers of kelp individuals, influencing population densities and size structure within forests (Seymour et al. 1989; Dayton et al. 1992; Graham 1997).

Just as kelp forests respond to hydrodynamic processes, they in turn modify flow conditions in their interior and vicinity. Such changes may affect a wide range of forest residents. Suspension feeders rely on waterborne particles for food (Wildish and Kristmanson 1997), broadcast spawners experience differential fertilization success depending on ambient turbulence (Denny and Shibata 1989; Crimaldi and Browning 2004), and a variety of taxa produce passively dispersing larvae whose recruitment patterns are controlled by currents (Eckman 1996; Gaylord and Gaines 2000).

Kelp forests may play a more subtle but equivalently important role in altering concentrations of flow-delivered substances in nearshore areas. Along many rocky shores, terrestrial catchments are steep, such that creeks and streams flow directly into coastal waters. In such instances, freshwater runoff does not undergo the same estuary-

associated biological filtration that it might in other systems. On the other hand, runoff entering the ocean may be swept alongshore through kelp beds. This latter point raises the possibility that kelp forest ecosystems function as alternative natural filters for substances like agriculturally derived nitrate or bacterial pathogens (e.g., Gili and Coma 1998).

Such examples illustrate the importance of understanding the manner in which flow moves through and around kelp beds. Jackson and Winant (1983) and Jackson (1998) showed that alongshore flow speeds within the expansive Pt. Loma forest in Southern California were reduced to approximately a third, and they estimated that such flow reduction occurred within 100 m of the leading edge of the bed. Jackson and Winant found little variation in alongshore flow speeds across the forest perpendicular to shore. They also suggested that any flushing of the bed's interior would occur predominantly by means of cross-shore motions driven by internal waves (see also Jackson 1984).

The work of Jackson and Winant was extended recently by Rosman et al. (2007), who described currents, surface and internal waves, and turbulence in the Terrace Point kelp forest off the coast of Santa Cruz, California. As in the Jackson studies, they observed a several-fold reduction in alongshore flow speed within the forest and a lower degree of attenuation of cross-shore velocities. Their data suggest that the coverage of the kelp canopy influences the level of flow reduction. They also proposed that surface gravity waves may contribute to cross-shore transport within the forest via Stokes drift (see Monismith and Fong 2004).

These studies provide valuable insight into kelp forest hydrodynamics, but still much is unknown about broader spatial patterns of flow and their connection to the forest community. Several questions arise: (1) Do velocity patterns in smaller forests resemble those observed in larger beds? (2) Are there secondary flow features within or adjacent to kelp beds that have the potential to influence the ecology of the forest and its residents? (3) Are there regions of fluid recirculation in the wakes of kelp forests that might be important for the retention of propagules and forest subsidies? (4) What is the capacity of a kelp bed for biological filtration of nearshore waters? (5) Do flows within forests vary seasonally with changes in algal density and growth and predictable shifts in water-column stratification? We present results from two sets of flow measurements conducted in the kelp forest at Mohawk Reef, Santa Barbara, California, that provide a first examination of these issues.

Methods

Mohawk Reef is a low-lying reef that supports a *Macrocystis pyrifera* forest that extends approximately 300 m

Acknowledgments

We thank C. Nelson, S. Harrer, J. Ecker, M. Wright, M. Carter, A. Rassweiler, H. Stewart, K. Nickols, M. Reidenbach, A. Parsons-Field, B. Loose, C. Helme, and M. Foley for field and laboratory assistance. This work was funded by National Science Foundation grants OCE-024117, OCE-0523870, OCE-9982105, and DEB-0108572, and the University of California Marine Council Coastal Environmental Quality Initiative grant 04-T-CEQI-08-0048. This is contribution number 2380 from the Bodega Marine Laboratory, University of California at Davis.

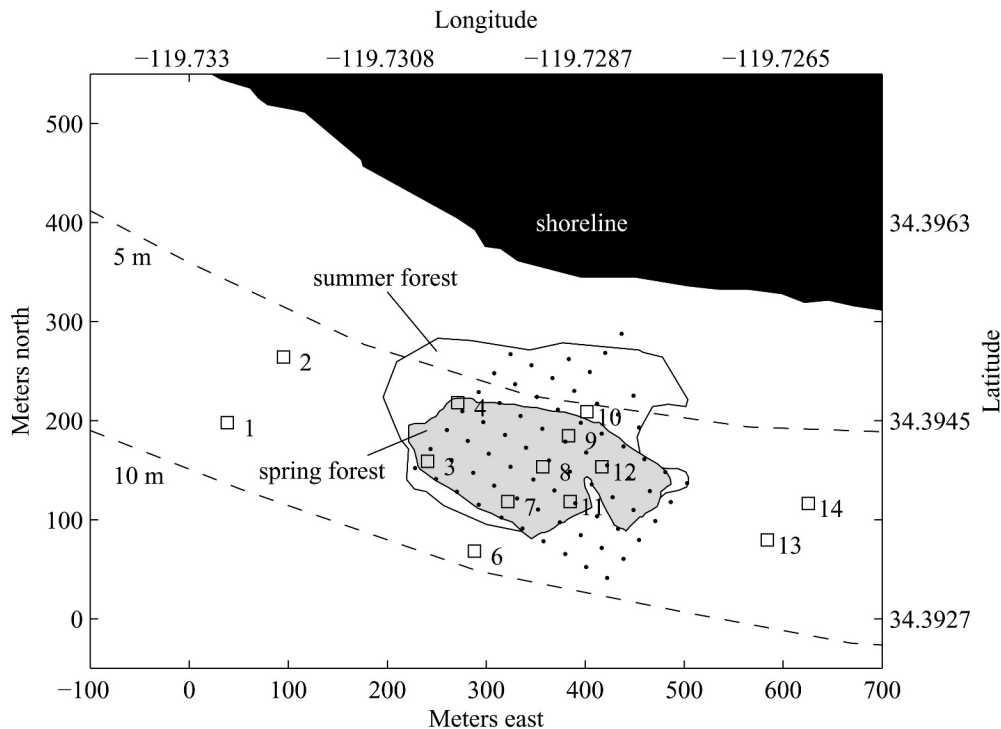


Fig. 1. Field site at Mohawk Reef. The gray and open regions depict the area of canopy coverage during the spring and summer, respectively. The grid of dots indicates locations used in the kelp density sampling. Numbered squares show the instrument stations; note that there is no sta. 5 due to an instrument malfunction. Dashed lines indicate the 5-m and 10-m depth contours.

alongshore and 120–200 m cross-shore ($34^{\circ}23'38''\text{N}$, $119^{\circ}43'45''\text{W}$; Fig. 1). Mean water depths range from 5 to 6 m at the inshore edge of the forest to 9 m at the offshore edge. In addition to giant kelp, a diverse suite of understory foliose algae, sessile invertebrates, mobile grazers and predators, and numerous fishes occur throughout the reef, as is typical of many kelp forest communities (Foster and Schiel 1985).

Intensive flow measurements were conducted at Mohawk Reef in spring (21 March to 13 April 2005) and summer (22 August to 12 September 2005). Each three-week sampling period encompassed both spring and neap tides and several weather states. Extensive arrays of velocity and temperature sensors were distributed in and around the kelp forest during each study period. Thirteen bottom-mounted, acoustic Doppler current profilers (ADCPs; 600 and 1200 kHz, RD Instruments) were deployed, with two stations up-coast of the bed, two stations down-coast, eight stations in the forest interior, and one station immediately adjacent to its offshore edge (Fig. 1).

The ADCPs measured velocity continuously at 1 Hz in 0.5-m vertical bins, extending from ~ 1.5 m above the bottom to ~ 1.5 m below the surface, and recorded time-averaged values along all three axes at one-minute intervals. The raw time series were then depth-averaged and smoothed temporally by block-averaging over 15-min segments. These smoothed time series were rotated into their principal axes, which resulted in the major principal axis at each station orienting roughly parallel to shore. The

associated dominant velocity component (u) is therefore denoted as “alongshore,” and perpendicular horizontal motions (v) are denoted as “cross-shore.”

To develop simple indices of flow differences between the upper and lower parts of the water column, alongshore and cross-shore velocities averaged over the bottom 2 m of measurements were subtracted from velocities averaged over the top 2 m of measurements. While these alongshore and cross-shore top-to-bottom velocity differences (Δu and Δv , respectively) clearly do not provide a complete description of the variation in flow with depth, they function as useful proxies appropriate for an initial examination.

Basic patterns of stratification were inferred from temperature, which was measured using thermistor chains deployed at sta. 3, 6, 7, and 8. In the spring study, the thermistors (Seabird SBE39, RBR TR-1050, and XR-420) were positioned at 1-m intervals, from 1 m above the seafloor to 2 m below mean lower low water (MLLW), and they were sampled every 30 s. In the summer study, the thermistors (RBR TR-1050 and XR-420) were positioned at 1-m intervals, from 0.6 m above the seafloor to 1 m above MLLW, and they were sampled every 10 s. Vertical profiles of conductivity were also determined (Seabird SBE 19 conductivity-temperature-depth [CTD]) to verify that salinity was not an important contributor to stratification. Such a lack of salinity stratification is common at Mohawk Reef due to an absence of consistent sources of runoff, but it does not hold universally (e.g., during heavy rainstorms). Buoyancy frequency, a common index used to describe the strength of stratification (Turner 1973), was then calculated

using temperature-density relationships, as $N = \left(\frac{-g}{\rho_{\text{avg}}} \left[\frac{\rho_{\text{top}} - \rho_{\text{bot}}}{z_{\text{top}} - z_{\text{bot}}} \right] \right)^{1/2}$, where g is the acceleration due to gravity, ρ_{avg} is the depth-averaged fluid density, ρ_{top} and ρ_{bot} are the densities at the top and bottom of the water column, respectively, and z_{top} and z_{bot} are the corresponding vertical positions.

The population density of *Macrocystis* was sampled during both the spring and summer studies across a grid that traversed the Mohawk forest (Fig. 1). Within each 25-m \times 25-m sector of the grid, divers counted the number of kelp individuals and the number of fronds longer than 1 m across two perpendicular 10-m \times 1-m transects. During the summer, when the kelp forest expanded into regions outside the sampling grid, divers supplemented the grid measurements with estimates based on the surface canopy.

Results

Kelp forest geometry—The Mohawk forest nearly doubled in area between spring and summer (Fig. 1), consistent with seasonal patterns in kelp mortality, recruitment, and growth. Concomitant with changes in the forest's size, average and maximum frond densities nearly doubled, from 2.7 and 12 fronds m^{-2} , respectively, in spring, to 5.0 and 19 fronds m^{-2} in summer (Fig. 2). The density of individuals producing these fronds increased as well, from 0.11 individuals m^{-2} in spring to 0.89 individuals m^{-2} in summer. The latter value was substantially higher than that reported for the Jackson or Rosman studies (0.14 and 0.09 individuals m^{-2} , respectively; Jackson and Winant 1983; Jackson 1998; Rosman et al. 2007).

General flow characteristics—Depth-averaged along-shore and cross-shore velocities from the spring and summer studies were dominated by tidally driven, diurnal and semidiurnal flows (Fig. 3 depicts spring patterns; analogous trends arose in summer, although instrument failures resulted in incomplete records at several stations). Similar to the recordings of Jackson (1998), peak depth-averaged alongshore velocities exceeded 30 cm s^{-1} , and maximal depth-averaged cross-shore velocities reached 5 cm s^{-1} . Such maxima were typically much larger than the mean velocities computed over the course of each study (0.1 to 5 cm s^{-1} ; Table 1). It is also clear that alongshore current speeds were faster at sites outside the forest and at locations with greater depth; this is most easily seen from the standard deviations of velocity at each station (Table 1). Such results are broadly consistent with those of the Jackson studies conducted in the Pt. Loma kelp forest, and with findings of Rosman et al. (2007) for Terrace Point. Cross-shore currents, in contrast, did not differ markedly (sta. 6 is an exception) between stations inside and outside the forest, unlike in the Jackson studies.

Spatial and seasonal patterns—The means as well as the dominant modes of variability of the depth-averaged currents can be readily discerned from “current ellipses” (Fig. 4). The major semiaxis (the longer of the two radii) of each ellipse equals the standard deviation of flow along the principal axis of flow variation, and the minor semiaxis (the

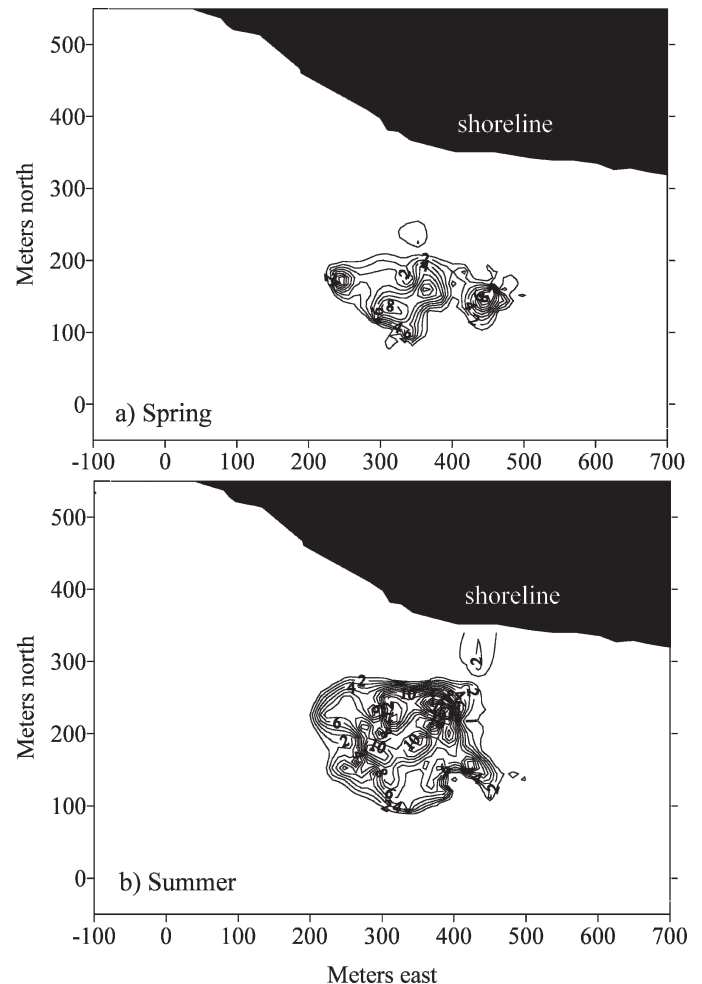


Fig. 2. Kelp densities (number of fronds m^{-2}) during (a) spring and (b) summer. Contour interpolations were computed using standard kriging methods (Surfer v. 8, Golden Software).

short radius) depicts the analogous standard deviation of flow along a perpendicular axis. Most ellipses within the kelp bed have shorter major semi-axes than those outside the bed, a reflection of the reduced alongshore flow speeds within the forest. We note that, to avoid potential biases associated with differences in record length, the ellipses in Fig. 4b were computed only over periods where data from all available stations overlapped.

An especially striking feature is the degree to which velocities at sta. 6 along the outside edge of the Mohawk forest exceeded those at other stations. This effect cannot be ascribed simply to increases in alongshore flow speed with depth. Station 6 is an outlier in a regression of velocity versus depth, and furthermore, the degree of velocity elevation at sta. 6 varied seasonally in conjunction with changes in density and size of the forest. For instance, the standard deviation of alongshore velocity at sta. 6 exceeded that at sta. 1 by 30% during spring, but this value rose to 160% in summer, when the forest was larger and denser (Table 1). Thus, a more likely explanation for the faster speeds at sta. 6 is that they resulted from spatial

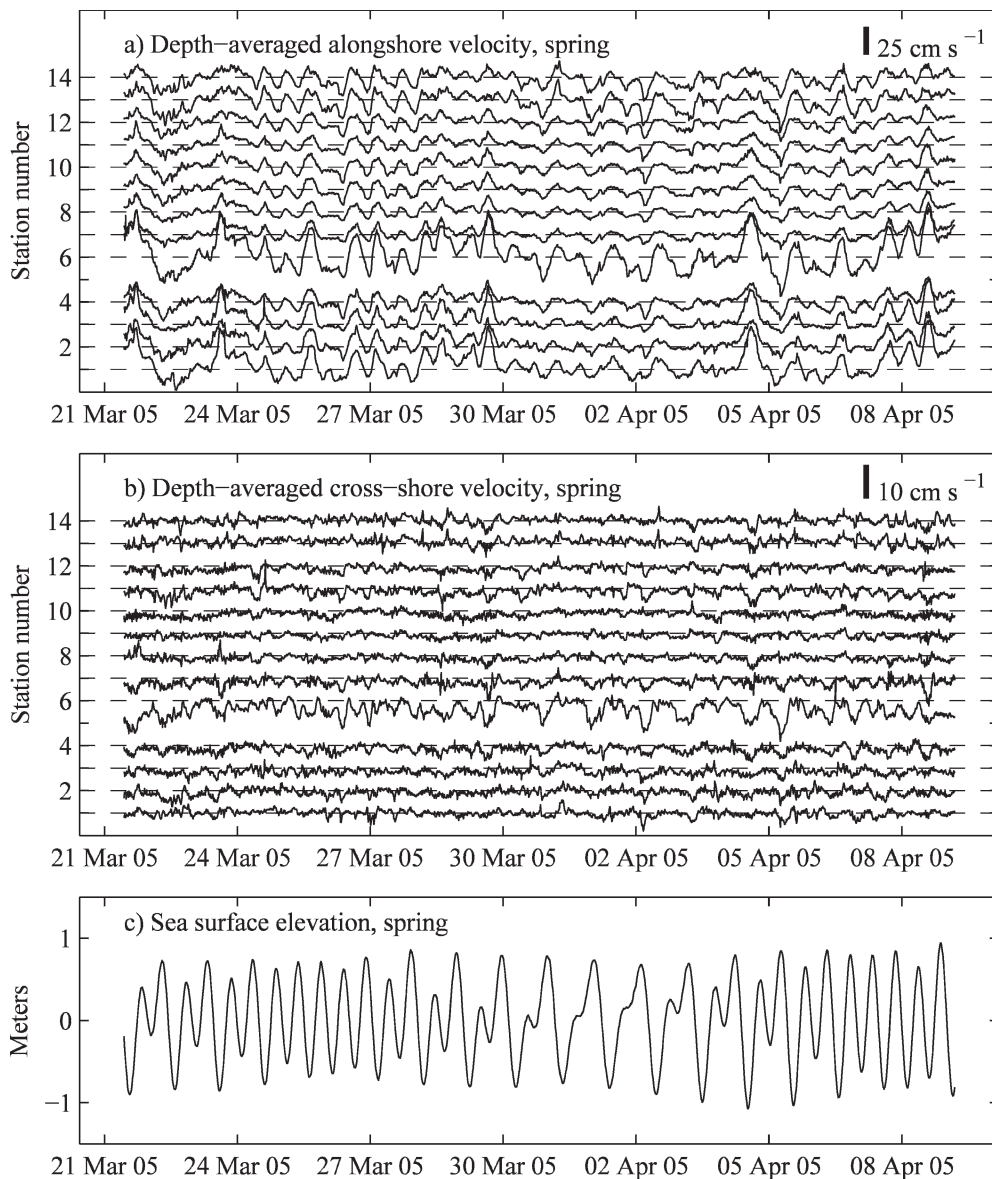


Fig. 3. General hydrodynamic patterns at Mohawk Reef. Results depicted are from the spring study, but patterns were analogous during summer. (a) Depth-averaged alongshore velocities. (b) Depth-averaged cross-shore velocities. (c) Sea-surface elevation. Note the different scale bars in panels a and b.

acceleration of water forced to pass around the periphery of the bed.

The arrows originating from the center of the ellipses in Fig. 4 depict the mean flow vectors and demonstrate two additional flow patterns occurring in and around the forest (*see also* Table 1). First, the kelp forest experienced consistent offshore transport within its midst, as evidenced by mean velocity vectors that angled away from the shore. Because the same trend is not apparent at up-coast and down-coast stations, it is probable that the offshore flow resulted at least in part from the presence of the kelp forest, although the subtle change in shoreline angle that occurs near Mohawk Reef likely played some role. Second, mean currents at either end of the forest pointed toward one

another. This characteristic likely derived from reductions in current speed behind the forest, which led to slower eastward than westward flows at sta. 13 and 14, and slower westward than eastward flows at sta. 1 and 2.

A more detailed understanding of upstream-downstream differences emerges from regression of data from each site against velocities from a reference station. Station 1 served as the reference for eastward flows, and sta. 13 served as the reference for westward flows (Fig. 5; Table 2). During eastward flows in spring, alongshore velocities in the middle of the forest (sta. 7–9) were 33–54% of those at sta. 1 upstream, while alongshore velocities downstream of the bed (sta. 13 and 14) ranged from 8% to 15% of those at sta. 1 (Table 2). Analogous patterns were apparent for

Table 1. Means and standard deviations of depth-averaged alongshore (u) and cross-shore (v) velocities recorded during spring and summer. Units are in cm s^{-1} . Entries in parentheses are values calculated only over the subset of time when data from all available stations overlapped, since instrument failures resulted in partial or complete data loss (the latter at sta. 13 and 14) at several stations in summer.

Station	Spring study				Summer study			
	Mean u	Mean v	STD u	STD v	Mean u	Mean v	STD u	STD v
1	4.31	-0.15	10.99	0.97	1.20 (2.52)	-0.36 (-0.06)	6.97 (7.92)	1.11 (1.13)
2	4.06	-0.59	7.49	1.08	1.53 (1.81)	-0.00 (0.39)	4.50 (5.20)	1.18 (1.18)
3	4.61	-1.05	8.66	0.97	2.24 (2.24)	-0.74 (-0.74)	6.03 (6.03)	1.21 (1.21)
4	1.11	-1.15	6.30	1.12	-0.56 (-0.39)	-0.12 (-0.08)	2.73 (2.86)	0.53 (0.56)
6	2.58	-2.87	14.65	2.32	-5.55 (-0.81)	-1.68 (-1.65)	11.25 (11.88)	1.60 (1.90)
7	1.16	-1.21	5.66	1.23	-0.99 (-0.27)	-0.66 (-0.53)	3.90 (4.05)	0.87 (0.82)
8	0.91	-0.73	4.96	0.87	-1.13 (-0.67)	-0.39 (-0.35)	3.56 (3.97)	0.65 (0.48)
9	0.54	-0.74	5.53	0.75	-0.90 (-0.62)	-0.08 (-0.14)	2.69 (3.09)	0.58 (0.51)
10	1.03	-1.04	5.66	0.89	-0.58 (-0.06)	-0.35 (-0.15)	2.88 (3.17)	0.66 (0.55)
11	0.18	-1.07	5.00	1.28	-1.93 (-1.29)	-0.34 (-0.31)	4.43 (4.58)	0.92 (0.74)
12	-0.23	-0.93	5.32	0.96	-1.46 (-0.93)	-0.45 (-0.41)	3.81 (4.10)	0.71 (0.56)
13	-1.43	0.44	7.61	1.07				
14	-1.11	0.06	6.17	1.08				

summer. During westward flows in spring, velocities in the middle of the bed were 36–60% of those at sta. 13, similar to the reduction for eastward currents referenced to sta. 1. Westward spring velocities at downstream locations were attenuated less than downstream currents associated with eastward flows (49–82% as compared to 8–15%).

The velocity regressions also enable an initial examination of whether stable zones of flow reversal, as might be found in regions of separation behind a solid object or cape, developed in the wake of the forest. Such features, which could act to retain waterborne materials in the lee of the bed, would be marked by oppositely directed upstream and downstream velocities. There is no evidence of such patterns, however, as is apparent from the absence of negative slopes in upstream-downstream velocity regressions (Fig. 6). Flow through the Mohawk kelp forest therefore appears to be sufficient to suppress separation in its lee.

The regression slopes of Table 2 further indicate that particular locations in the Mohawk forest experienced different levels of flow attenuation between spring and summer. This feature is not surprising given seasonal changes to the size and density of the forest (Fig. 2). However, when relative velocities (quantified by taking ratios of slopes of regressions in Table 2) are plotted against distance from the forest boundary (the location of which shifted between spring and summer), rates of decay of velocity across distance converge to a common set of curves (Fig. 7). These curves resemble the exponential decline estimated by Jackson and Winant (1983) for the Pt. Loma kelp bed. Such consistency implies that the density of kelp fronds, which differed among studies, plays a relatively subtle role in dictating rates of velocity decline from the edge of the bed. Instead, the more important pattern accompanying the higher frond densities in summer was the expansion of the forest into shallower water. This expansion likely restricted flow along the inshore edge of the bed, contributing to greater diversion of water around

the forest's offshore edge and, therefore, faster flow along its outer boundary (Fig. 7b; Table 2).

Frequencies of flow variation—Jackson (1998) observed in his study that lower-frequency flow variations within the Pt. Loma forest were damped to a greater extent than higher-frequency ones. The pattern in the Mohawk kelp forest was more complex (Fig. 8). In the case of the alongshore depth-averaged currents, variations at sta. 8 in the middle of the bed were consistently 5 to 10 times lower than at sta. 1 or 6 outside, regardless of frequency. There was also a hint that lower-frequency flow variations at sta. 1 were reduced compared to those at sta. 6, especially in summer. For cross-shore motions, velocity variations at sta. 6 were 5 to 10 times greater than those at sta. 1 or 8, particularly for frequencies close to those of the tides. The exception to this latter trend occurred during summer, when velocity variations at sta. 8 were lower than those at sta. 1 and 6 for all frequencies measured.

Top-to-bottom velocity differences—As with the depth-averaged velocities, the means of the top-to-bottom differences in flow speed were small compared with their fluctuations (Table 3). Standard deviations of alongshore and cross-shore top-to-bottom velocity differences also tended to decline toward shore and decrease from the edge of the forest to its interior, similar to the pattern for depth-averaged flows. However, the magnitudes of the fluctuations in alongshore and cross-shore top-to-bottom velocity differences, relative to the depth-averaged velocity fluctuations, were generally greater in summer as compared to spring (Fig. 9). Although this latter trend reflected at least in part the smaller standard deviations in depth-averaged velocity in summer (Table 1), increased stratification associated with warmer waters (Fig. 10) may have reduced vertical momentum transfer and contributed to greater horizontal velocity differences across depth. It is possible

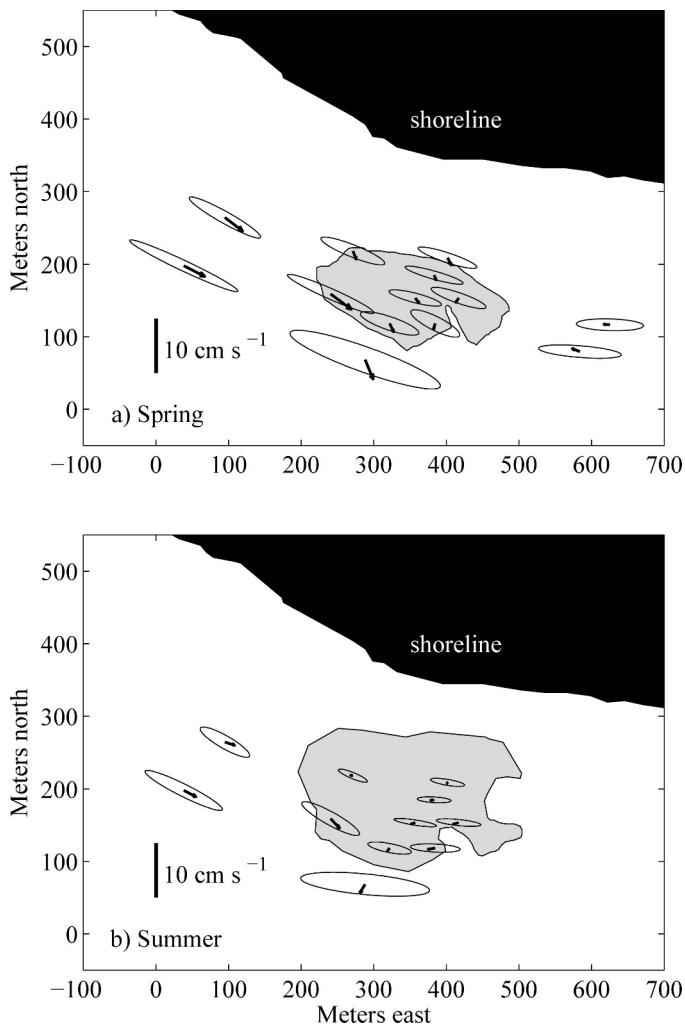


Fig. 4. Means and principal components of variability of the depth-averaged currents during (a) spring and (b) summer. The radii along the long semiaxes of the ellipses indicate standard deviations in alongshore velocity, while the radii in the perpendicular direction indicate standard deviations in cross-shore velocity. Arrows depict the mean velocities.

that the denser canopy located in the upper water column played a role as well.

Discussion

Differences among forests—The present set of studies provides insight into differences in flow characteristics among kelp beds. The Pt. Loma forest examined in the Jackson studies is one of the largest in the world, spanning 8–10 km in length and over 1 km in width (Jackson and Winant 1983; Dayton et al. 1984). By comparison, the Mohawk kelp forest is far smaller (roughly 300 m \times 200 m; Fig. 1). The smaller size of the Mohawk forest likely contributed to the fact that standard deviations in alongshore velocity within the bed were twice as large as those recorded in the Pt. Loma forest (4–5 cm s⁻¹ vs. 2 cm s⁻¹; Jackson 1998), even though exterior flows were similar (standard deviations 8–10 cm s⁻¹). Mean flows in

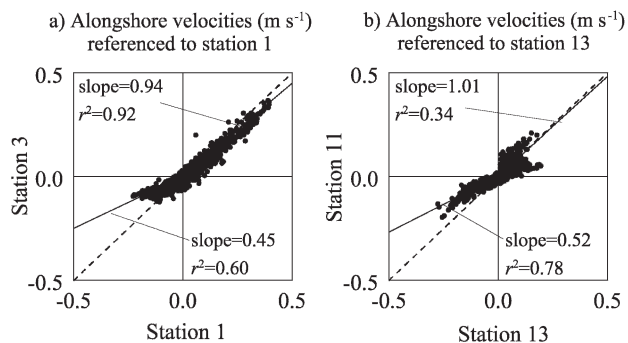


Fig. 5. Example velocity regressions, using either (a) sta. 1 as a reference, or (b) sta. 13 as a reference. Positive values are flows to the east, and negative values are flows to the west. Regression slopes indicate the relative velocity magnitudes between stations. Statistics in the upper left of the panels correspond to conditions of eastward flow at the reference station; those in the lower right correspond to conditions of westward flow at the reference station. Major-axis regression, rather than standard ordinary least-squares techniques, was used because measurement errors for the independent and dependent variables were comparable (Sokal and Rohlf 1995). Solid lines indicate the regressions, and a dashed 1:1 line is also shown to facilitate visual identification of trends. Data are from the spring study.

the interior of the Mohawk forest (0.5–1.5 cm s⁻¹ when averaged over three weeks) were more than double the within-bed values recorded by Jackson (1998), probably for the same reason. This lower level of velocity attenuation in the Mohawk forest indicates that alongshore currents may transit the full lengths of smaller beds, common in California (North et al. 1993), and may therefore play a greater role in the exchange of interior and exterior waters than is often assumed.

This latter point is important because increased rates of exchange can influence ecological processes tied to the transport of nutrients, suspended food particles, and propagules (see, e.g., Jackson 1977; Bernstein and Jung 1979; Graham 2003). In the context of growth in *Macrocystis*, faster flows and concomitant reductions in residence times may affect the availability of nitrate. Building upon data of Jackson (1977), Dayton (1985) speculated that if forests are large enough, and if flows in their interior are damped enough, then nitrate uptake by kelp becomes a local process such that rates of depletion dominate rates of resupply via flow. Under these conditions, nitrate concentrations may become sufficiently limiting that plants senesce and die within the interior of a bed. The present set of studies suggests that while such a scenario may apply in very large beds, it is less likely to occur in forests with dimensions comparable to that of the Mohawk bed. Indeed, a routine 3 cm s⁻¹ current will transport water through a 300-m forest in less than three hours.

Secondary flow features and their implications for kelp communities—The tendency for kelp forests to act as permeable flow obstructions ensures that velocities are altered differentially in various regions within and around a kelp bed. Such differences create flow microhabitats

Table 2. Regression statistics for pairwise velocity comparisons among stations. “East” and “west” indicate the rough trends in direction of the alongshore current, rather than precise compass headings. With the exception of the values denoted with asterisks, all slopes are significantly different from zero ($p < 0.05$) under the assumption of a decorrelation timescale of 12 h.

Station	Spring study								Summer study			
	Relative to station 1				Relative to station 13				Relative to station 1			
	Flow east		Flow west		Flow east		Flow west		Flow east		Flow west	
	Slope	r^2	Slope	r^2	Slope	r^2	Slope	r^2	Slope	r^2	Slope	r^2
1	1	1	1	1	6.25	0.18	0.82	0.23	1	1	1	1
2	0.65	0.83	0.72	0.53	3.42	0.21	0.49	0.31	0.83	0.46	0.57	0.28
3	0.94	0.92	0.45	0.60	4.91	0.21	0.29	0.52	1.04	0.76	0.57	0.63
4	0.46	0.76	0.94	0.51	1.71	0.75	0.75	0.65	0.24	0.43	0.51	0.50
6	1.13	0.93	1.95	0.62	6.00	0.26	1.44	0.68	2.14	0.68	2.60	0.37
7	0.54	0.86	0.48	0.57	2.16	0.21	0.39	0.75	0.44	0.54	0.69	0.47
8	0.38	0.79	0.49	0.55	1.27	0.30	0.36	0.68	0.32	0.48	0.67	0.52
9	0.33	0.69	0.79	0.52	1.13	0.29	0.60	0.65	0.24	0.44	0.46	0.51
10	0.40	0.69	0.82	0.49	1.39	0.22	0.61	0.55	0.37	0.46	0.39	0.51
11	0.33	0.74	0.64	0.51	1.01	0.34	0.52	0.78	0.32	0.38	1.05	0.47
12	0.29	0.67	0.86	0.48	0.85	0.30	0.69	0.78	0.35	0.45	0.79	0.43
13	0.08*	0.03*	1.67	0.42	1	1	1	1				
14	0.15	0.12	1.24	0.39	0.93	0.60	0.80	0.77				

within the forest (*see also* Eckman et al. 2003). Our results demonstrate that the most pronounced of these microhabitats may arise along the offshore boundary of the forest where water accelerates spatially around it. Such a region of faster-than-incident fluid movement is not surprising when viewed in the context of flow past solid bodies (e.g., Kundu 1990), but it has not been widely appreciated. Jackson and Winant (1983) and Jackson (1998) mentioned that flows tended to be faster along the edges of a forest than inside, but did not emphasize that such faster velocities reflect not only a lack of damping but an actual increase in speed relative to the incident flow.

There are strong biological consequences of such spatial differences in velocity, and rough bounds for these can be developed from simple scaling considerations. Eckman et al. (1989) and others noted that particle delivery to suspension feeders is a flux-driven process that varies not only with particle concentration but also with velocity. Although wave-driven flows often dominate in nearshore regions, a 15 versus 5 cm s⁻¹ current (representative of sta. 6 and 8; Table 1) would yield a 10% higher total velocity when combined with routine wave velocities of order 30 cm s⁻¹. Given the dominant method of particle capture (direct interception; Shimeta and Jumars 1991), propor-

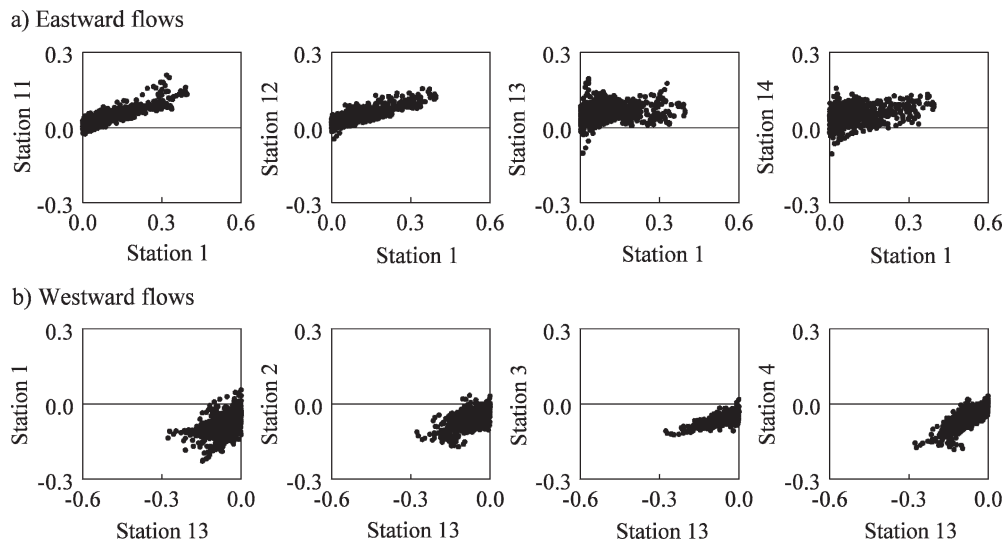


Fig. 6. Velocity regressions demonstrating that upstream velocities were always positively correlated with downstream velocities, in accordance with a lack of stable zones of recirculation in the wake of the forest. Positive values are flows to the east, and negative values are flows to the west. (a) Conditions of eastward flow in spring, using sta. 1 as an upstream reference location. (b) Conditions of westward flow in spring, using sta. 13 as an upstream reference location. Units are in m s⁻¹.

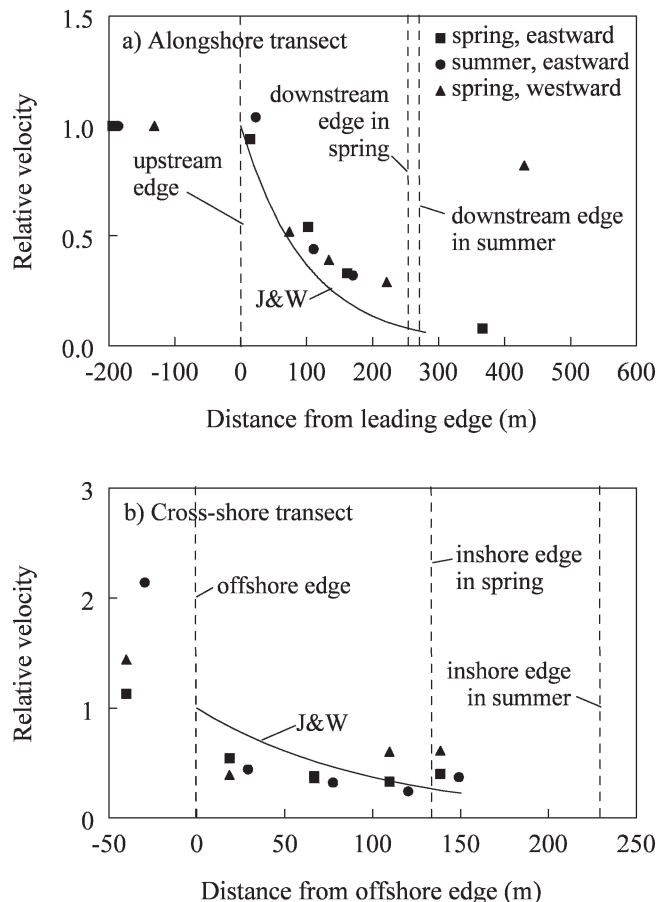


Fig. 7. (a) Alongshore and (b) cross-shore transects showing how depth-averaged alongshore velocities varied with distance from the edge of the forest. The alongshore transect encompassed sta. 1, 3, 7, 11, and 13, while the cross-shore transect encompassed sta. 6, 7, 8, 9, and 10. For flows trending eastward, velocities were expressed relative to those at sta. 1; for flows trending westward, velocities were expressed relative to those at sta. 13 (see Table 2). The vertical dashed lines indicate the boundaries of the forest where they meet the transects during spring and summer. The positions of the upstream and offshore edges of the forest were by definition set equal to zero in this graph, even though the true boundaries shifted among seasons. The simple exponential expression of Jackson and Winant (1983) is shown as a solid line.

tional increases in rates of food acquisition and growth might be anticipated. The same 5 to 15 cm s^{-1} increase in current speed could also alter intensities of turbulent mixing, which, based on trends of Denny and Shibata (1989), could decrease fertilization success in broadcast spawners by a third. In the case of macroalgae, flows less than $\sim 5 \text{ cm s}^{-1}$ may impede nutrient uptake at blade surfaces (Wheeler 1988; Hurd et al. 1997). A threefold increase in velocity at the edge of a forest could thereby result in a transition from conditions where mass transfer processes limit nutrient uptake (e.g., during times when waves are largely absent; Stevens et al. 2001) to conditions where they do not. At the population level, the sequential arrangement of *Macrocystis* forests along the shore suggests that spores may be entrained into one region of

accelerated flow after another. Relationships of Gaylord et al. (2006) indicated that a threefold increase in velocity could alter dispersal distances enough to shift the domain of connectivity among beds by a factor of two. Whether such increases in velocity might also change levels of self-fertilization in kelps has not been explored, but this issue could be relevant given the high cost of inbreeding in *Macrocystis* (Raimondi et al. 2004). Differences in current speed across the forest could additionally influence disturbance rates in this species. Depending on wave conditions, trends in Gaylord et al. (2003) suggest that a shift from a 5 to 15 cm s^{-1} current could cause a 10–20% reduction in forces applied to canopy-forming kelps, due to the ability of alongshore currents to ameliorate wave-associated drag.

Frequency-dependent damping in kelp forests (Fig. 8) also indicates that distinctions between interior and exterior flows may depend on temporal characteristics of impinging larger-scale circulation. For instance, the total velocity variance in confined waterways like Puget Sound in Washington State may be dominated to a greater extent by tidal components than are variances at open-coast sites in Southern California (Eckman et al. 2003). If different geographic locations consistently experience distinct frequency structure, then frequency-dependent flow retardation could cause more marked spatial variation in food acquisition, growth rates, fertilization success, and physical disturbance across some kelp beds than across others.

Issues of retention and exchange—The presence of within-bed mean offshore flows of order 1 cm s^{-1} (Fig. 4; Table 1) has additional bearing on retention and export. Offshore flows carrying interior waters toward the edge of the forest provide a direct connection between microhabitats in the center of the bed and the region of accelerated flow along the forest's boundary. Such flows could ensure that interior *Macrocystis* individuals, as well as those on the forest's edge, have some capacity for elevated propagule transport.

Given the ecological relevance of cross-shore exchange to retention and export, the mechanism that produces mean offshore flow within the forest warrants attention. One possibility is that the offshore flow arises as a mass balance response to shoreward transport associated with surface waves (Rosman et al. 2007). The apparent confinement of the offshore flows at the Mohawk site to regions within and just offshore of the forest, however, implies that at least some component of the seaward flow results from features associated with the forest. A second possibility is that the offshore flow results exclusively from topographic characteristics, in particular the slight shift in shoreline orientation that occurs in the vicinity of Mohawk Reef (Fig. 1). Although we cannot conclusively evaluate this latter hypothesis without developing a detailed numerical model, we consider it improbable; it appears more likely that the mean offshore flow is the result, in substantial part, of the presence of the kelp forest. This view derives from the following points.

First, as has been demonstrated in all kelp bed studies to date, water is slowed within a forest due to elevated

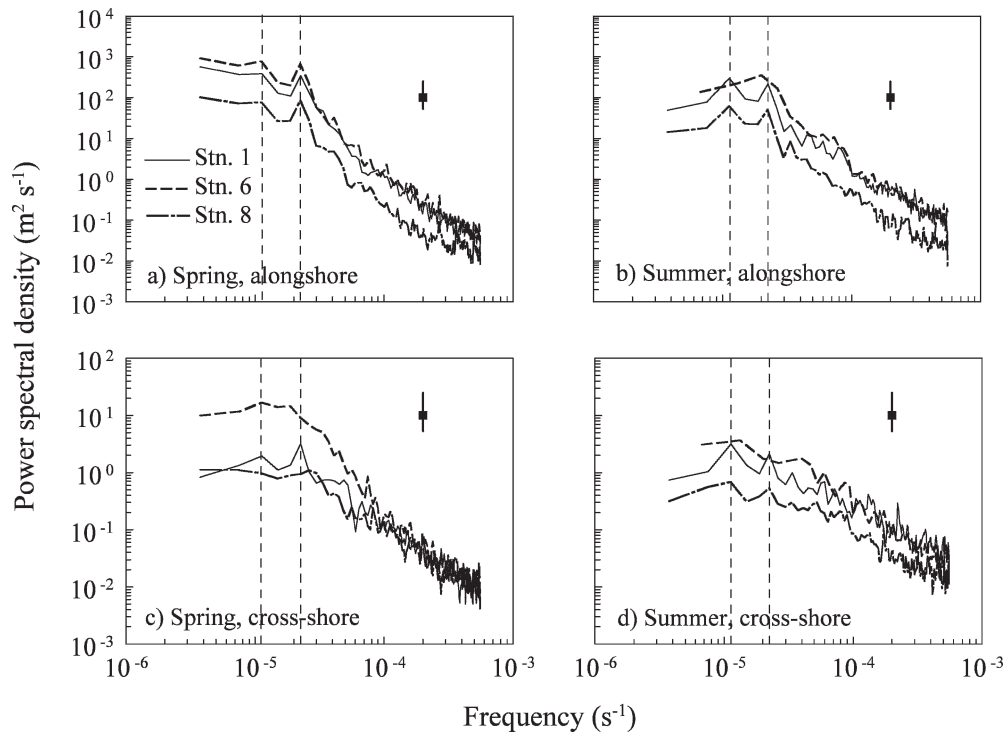


Fig. 8. Power spectra of depth-averaged (a, b) alongshore and (c, d) cross-shore velocities from sta. 1, 6, and 8 during spring and summer. Error bars indicate 95% confidence intervals, and the dashed vertical lines indicate diurnal and semidiurnal tidal frequencies. Note that the apparent absence of tidal peaks in the summer curves for sta. 6 is an artifact of their shorter record lengths compared to the others.

vegetation-induced drag. Such velocity retardation changes pressure gradients across the forest and can be expected to lead to cross-shore transport purely due to first principles (i.e., because of “continuity” or conservation of fluid mass). In simple terms, as water impinges on the bed and encounters slower flow ahead, it has to go somewhere and so gets diverted laterally. Because flow is constrained in shallow depths, greater amounts of water may be forced toward the offshore boundary of the forest as compared to

the inshore edge, setting up the residual offshore current as well as creating the accelerated flow along the offshore boundary. Second, additional 1.5-yr recordings of flow inside and outside the Mohawk forest indicate that velocity differences between sta. 6 and 8 were far smaller during winter, especially subsequent to a December 2005 storm that decimated the forest (data not shown). If topographic effects alone were responsible for the patterns observed in our study, such a seasonal pattern would not arise. Third,

Table 3. Means and standard deviations (STD) of alongshore and cross-shore top-to-bottom velocity differences (Δu and Δv , respectively) during spring and summer. Units are in cm s^{-1} .

Station	Spring study				Summer study			
	Mean Δu	Mean Δv	STD Δu	STD Δv	Mean Δu	Mean Δv	STD Δu	STD Δv
1	2.74	-0.70	6.79	3.95	1.29	-0.31	7.81	4.87
2	0.82	-0.48	2.30	1.73	-0.29	-0.36	2.47	2.01
3	2.82	0.74	4.46	2.38	0.31	-0.16	3.56	2.81
4	-0.16	-0.94	2.50	1.56	-0.13	0.12	1.20	0.85
6	1.06	-1.66	6.82	3.51	0.78	-1.36	8.47	5.31
7	1.27	-0.18	2.56	2.42	0.18	-0.08	2.46	2.03
8	0.25	0.00	1.74	1.76	-0.05	-0.02	2.05	2.10
9	-0.11	-0.64	2.40	1.46	-0.62	0.13	2.26	1.80
10	0.05	-0.74	1.80	1.28	0.11	0.16	1.09	0.80
11	-0.31	0.21	2.86	1.83	-0.47	0.14	3.43	2.70
12	-0.10	-0.33	2.65	1.34	0.38	0.21	2.51	2.24
13	0.71	-1.22	4.96	4.17				
14	1.29	-1.27	4.68	3.34				

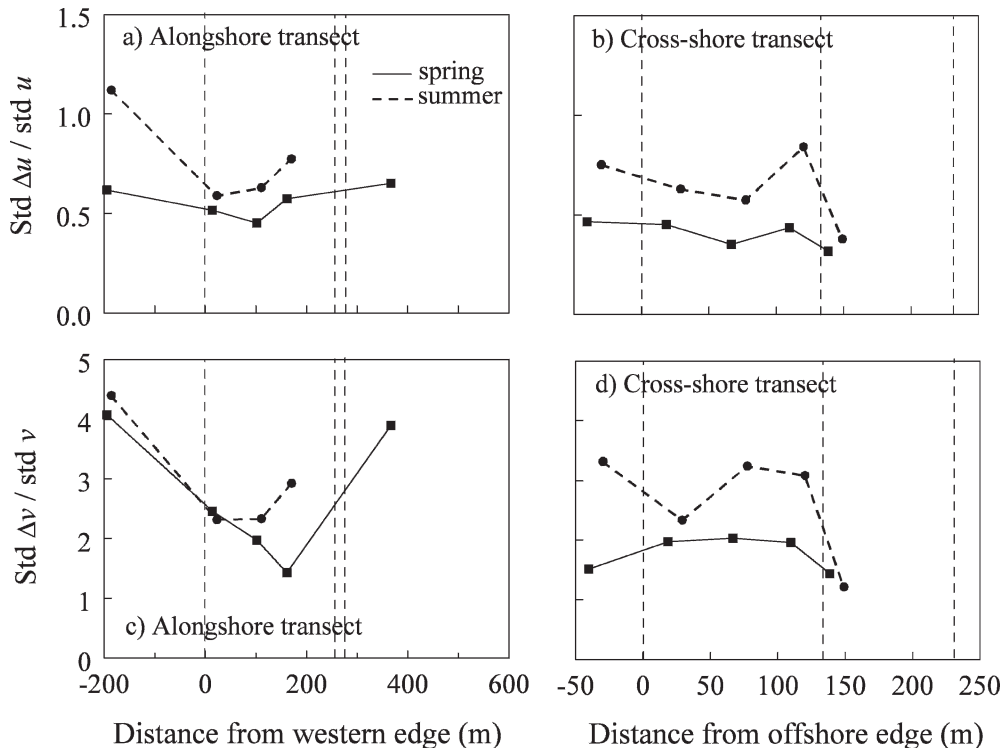


Fig. 9. Spatial patterns in normalized top-to-bottom velocity differences during spring and summer, depicted across (a, c) an alongshore transect (sta. 1, 3, 7, 11, and 13), and (b, d) a cross-shore transect (sta. 6, 7, 8, 9, 10). $\text{Std } \Delta u$ = standard deviation of alongshore top-to-bottom velocity difference; $\text{std } \Delta v$ = standard deviation of cross-shore top-to-bottom difference; $\text{std } u$ = standard deviation of depth-averaged alongshore velocity; $\text{std } v$ = standard deviation of depth-averaged cross-shore velocity. The vertical dashed lines indicate the extent of the forest as in Fig. 7.

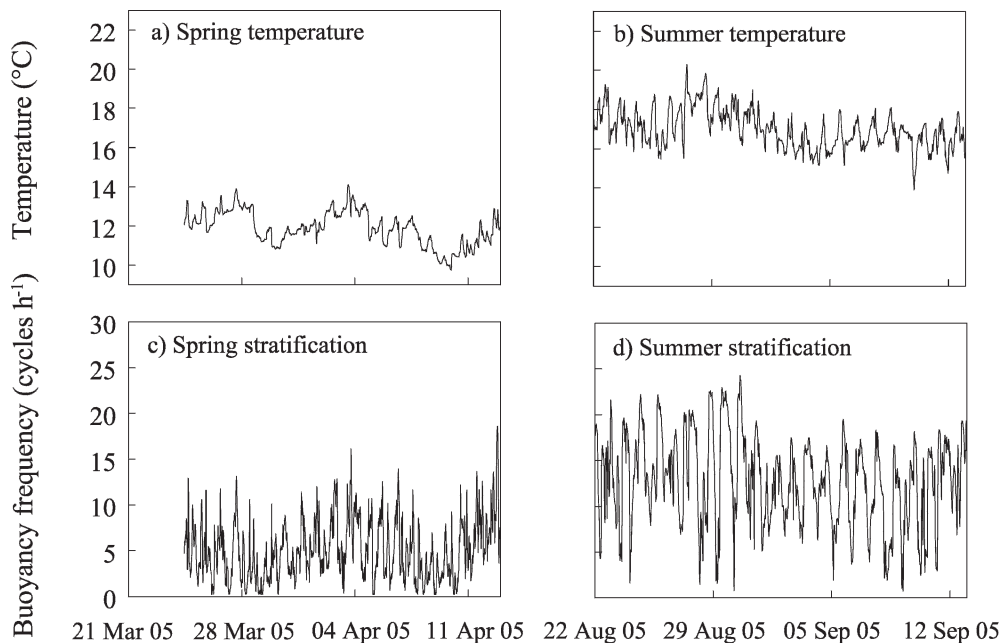


Fig. 10. (a, b) Temperature and (c, d) stratification within the forest at sta. 8 during spring and summer. Data were smoothed using 15-min block-averaging, and temperatures are depth averages.

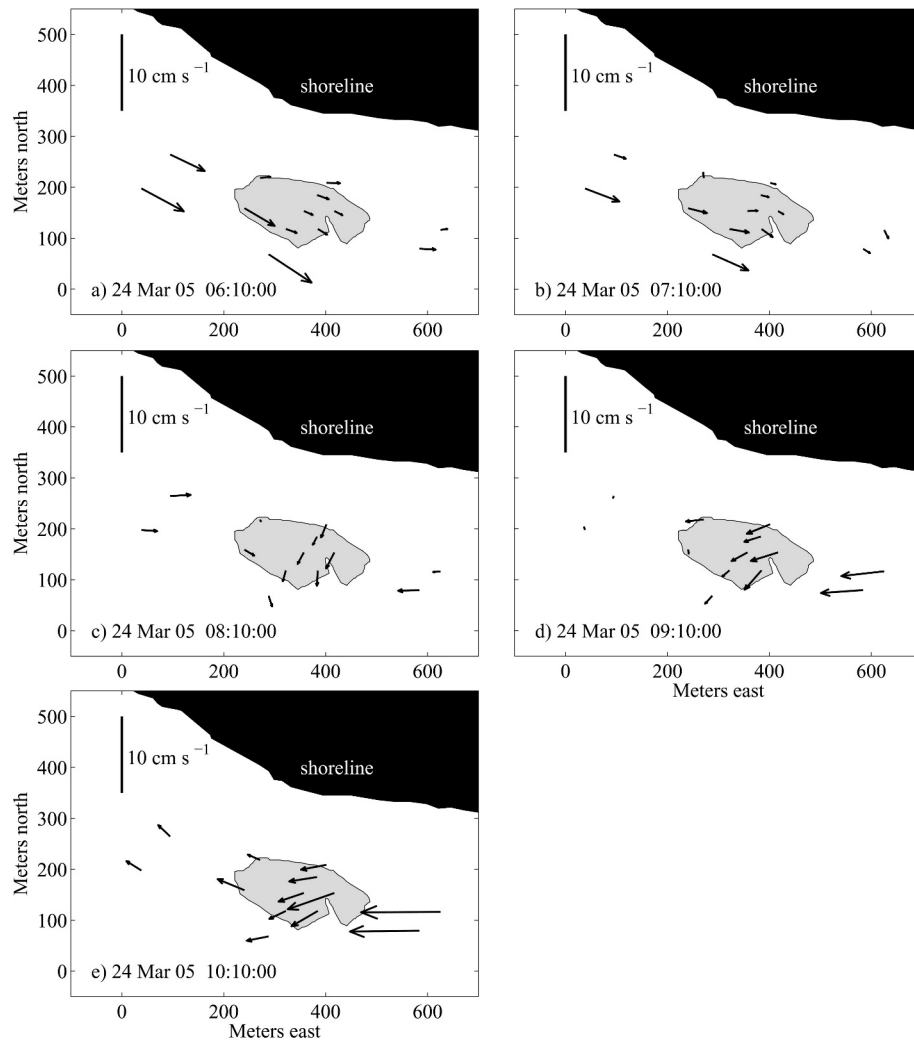


Fig. 11. Example short-term velocity patterns at Mohawk Reef, demonstrating how strong spatial gradients and relatively rapid, within-bed offshore flows often occurred during times of tidal reversals. Each panel depicts a 15-min average, with sequential panels separated in time by 1 h.

although eddies shed behind solid obstructions such as capes or headlands can produce cross-shore fluid motions, the minor shift in shoreline angle at Mohawk Reef is far subtler than the dramatic finger-like coastal protrusions that are commonly associated with eddy generation (e.g., Signell and Geyer 1991). Other kilometer-scale features that might extend beyond our immediate study area are similarly unlikely to produce the patterns observed at Mohawk forest. Such larger shoreline elements would tend to produce fluid circulations with scales considerably in excess of those that characterize the Mohawk kelp forest, where localized directional shifts (90 degree turns) occur over spatial scales similar to those of the bed itself (i.e., over ~100 m; Fig. 11).

Filtration of nearshore waters—Measurements from the spring and summer studies indicate that at least a fraction of impinging currents will penetrate the full length of beds of modest size. This finding has implications for understanding the capacity for kelp forest communities to

influence concentrations of water-column constituents. To estimate the relative magnitudes of fluid transport through the forest versus the amount that gets diverted around it (i.e., what might be termed the “filtration capacity” of the forest), we calculated the total flow through three planes oriented perpendicular to the shore: one upstream of the bed, a second spanning the leading edge of the forest, and a third extending across the center of the forest (roughly along our main cross-shore transect). We assumed no stream-wise flow acceleration associated with the relatively minor vertical relief of the reef. The volume flux (in $\text{m}^3 \text{s}^{-1}$) across each plane is then

$$Q = \int_0^L u(y)D(y)dy$$

where $u(y)$ is the depth-averaged alongshore velocity as a function of distance offshore, y , $D(y)$ is the mean water depth (also a function of distance; Table 4), and the limits

Table 4. Parameter values used in calculations of volumetric flux, Q , through several cross-shore, vertically oriented planes of length L and area A . u_1 indicates alongshore velocities measured at sta. 1, and u_{13} indicates alongshore velocities measured at sta. 13. $u(y)$ and $D(y)$ define the linear change in alongshore velocity and water depth, respectively, as a function of the distance (y) from the inshore end of each plane. The first plane is located upstream of the forest, the second spans its leading edge, and the third extends along the main instrument transect through the center of the bed. The percentage of the flow impinging on the bed that passes through each plane is given in the final column.

Spring study								
Eastward flows	$\frac{u(y)}{u_1} = by + a$		$D(y) = dy + c$		A (m ²)	L (m)	Q (m ³ s ⁻¹)	% incident flow
	a	b	c	d				
Upstream	0.61	0.0046	6.00	0.0512	870	101	$671u_1$	100
Leading edge	0.35	0.0072	6.00	0.0331	870	111	$573u_1$	85
Center of bed	0.28	0.0024	6.00	0.0208	870	120	$348u_1$	52
Westward flows	$\frac{u(y)}{u_{13}} = by + a$		$D(y) = dy + c$		A (m ²)	L (m)	Q (m ³ s ⁻¹)	% incident flow
	a	b	c	d				
Upstream	0.49	0.0050	6.00	0.0390	870	108	$603u_{13}$	100
Leading edge	0.86	-0.0043	6.00	0.0243	870	117	$572u_{13}$	95
Center of bed	0.68	-0.0042	6.00	0.0208	870	120	$414u_{13}$	69
Summer study								
Eastward flows	$\frac{u(y)}{u_1} = by + a$		$D(y) = dy + c$		A (m ²)	L (m)	Q (m ³ s ⁻¹)	% incident flow
	a	b	c	d				
Upstream	0.74	0.0022	4.33	0.0512	1283	154	$1056u_1$	100
Leading edge	-0.24	0.0109	4.33	0.0331	1283	177	$434u_1$	41
Center of bed	-0.02	0.0026	4.33	0.0208	1283	200	$202u_1$	19

of integration run from the inshore end of each vertical surface at $y = 0$ to its corresponding offshore end at $y = L$ (Table 4). In the case of eastward flows, the upstream plane passes through sta. 1 and 2, while the plane at the forest's leading edge passes through sta. 3 and 4 (Fig. 1). During westward flows, the upstream plane is located in the vicinity of sta. 13 and 14, while the leading-edge plane spans sta. 11 and 12 (Fig. 1).

Results of the flux calculations for spring reveal that ~90% of impinging flows passed through the leading edge of the Mohawk kelp forest (Table 4). Approximately 50–70% of the impinging fluid proceeded to the bed's center, thereby interacting with a substantial portion of the forest. The difference between the leading-edge percentage and centerline percentages reflects water that escaped out the lateral edges of the forest while transiting the length of the bed, which contributed to the region of flow acceleration along the forest's offshore boundary.

Analogous results for summer reveal that although a greater total amount of fluid impinged on the forest due to its broader dimensions, a smaller fraction penetrated to its center (~20%). This reduction likely ensued from the increased resistance of the kelp bed, which changed the distribution of velocity within the forest and enhanced the diversion of flow around its lateral edges (see also Ackerman and Okubo 1993; Nepf et al. 1997). Despite the reduced fractional volumetric flow rate in summer,

however, it remains clear that kelp forests have a consistent capacity to influence waterborne compounds in nearshore regions, particularly when the potential for combined effects of multiple forests in a given region is considered.

Seasonal effects in differential transport across depth—Changes in plant density and forest size between spring and summer influenced not only spatial characteristics of flow and filtration capacity but also horizontal transport at different depths in the water column. Although we did not examine vertical patterns of horizontal flow in detail, variations in the top-to-bottom velocity gradient were greater relative to variations in depth-averaged velocity during summer (Fig. 9). Future work will analyze this feature of kelp forest flows more specifically given that previous research has demonstrated the importance of vertical structure and associated internal waves in cross-shore delivery of nutrients (Jackson 1977; Zimmerman and Kremer 1984; Leichter et al. 1996). Even from our analysis, however, it is apparent that seasonal changes in depth-specific transport could impact organisms to a varying extent depending upon their position in the water column. Kelp forests provide three-dimensional habitat, and species reside both on the bottom as well as within or on the kelp canopy. Moreover, because many organisms possess seasonal life histories, where growth and/or reproduction occur during specific times of year, seasonal shifts in flow

speeds across depth have the potential to affect ecological performance of a wide range of kelp forest organisms. These effects and others discussed already have important implications for our understanding of kelp forest communities and their relationship to nearshore waters.

References

- ACKERMAN, J. D., AND A. OKUBO. 1993. Reduced mixing in a marine macrophyte canopy. *Funct. Ecol.* **7**: 305–309.
- BERNSTEIN, B. B., AND N. JUNG. 1979. Selective pressures and coevolution in a kelp canopy community in Southern California. *Ecol. Monogr.* **29**: 335–355.
- CRIMALDI, J. P., AND H. S. BROWNING. 2004. A proposed mechanism for turbulent enhancement of broadcast spawning efficiency. *J. Mar. Syst.* **49**: 3–18.
- DAYTON, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica, p. 81–96. *In* B. C. Parker [ed.], *Proceedings of the Colloquium on Conservation Problems in Antarctica (10–12 September 1971, Blacksburg, Virginia, USA)*. Allen Press.
- . 1985. Ecology of kelp communities. *Annu. Rev. Ecol. Syst.* **16**: 215–245.
- , V. CURRIE, T. GERRODETTE, B. D. KELLER, R. ROSENTHAL, AND V. VEN TRESKA. 1984. Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.* **54**: 253–289.
- , M. J. TEGNER, P. E. PARNELL, AND P. B. EDWARDS. 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* **62**: 421–445.
- DENNY, M. W., AND M. F. SHIBATA. 1989. Consequences of surf-zone turbulence for settlement and external fertilization. *Am. Nat.* **134**: 859–889.
- ECKMAN, J. E. 1996. Closing the larval loop: Linking larval ecology to the population dynamics of marine benthic invertebrates. *J. Exp. Mar. Biol. Ecol.* **200**: 207–237.
- , D. O. DUGGINS, AND A. T. SEWELL. 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.
- , ———, C. E. SIDDON. 2003. Current and wave dynamics in the shallow subtidal: Implications to the ecology of understory and surface-canopy kelps. *Mar. Ecol. Prog. Ser.* **265**: 45–56.
- FOSTER, M. S., AND D. R. SCHIEL. 1985. The ecology of giant kelp forests in California: A community profile. U.S. Fish and Wildlife Service Biol. Rep. **85** (7.2).
- GAYLORD, B., M. W. DENNY, AND M. A. R. KOEHL. 2003. Modulation of wave forces on kelp canopies by alongshore currents. *Limnol. Oceanogr.* **48**: 860–871.
- , AND S. D. GAINES. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.* **155**: 769–789.
- , D. C. REED, P. T. RAIMONDI, AND L. WASHBURN. 2006. Macroalgal spore dispersal in coastal environments: Mechanistic insights revealed by theory and experiment. *Ecol. Monogr.* **76**: 481–502.
- , ———, ———, ———, AND S. R. MCCLEAN. 2002. A physically based model of macroalgal spore dispersal in the wave and current-dominated nearshore. *Ecology* **83**: 1239–1251.
- GILI, J., AND R. COMA. 1998. Benthic suspension feeders: Their paramount role in littoral marine food webs. *Trends Ecol. Evol.* **13**: 316–322.
- 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.
- . 2003. Coupling propagule output to supply at the edge and interior of a giant kelp forest. *Ecology* **84**: 1250–1264.
- HURD, C. L., C. L. STEVENS, B. E. LAVAL, G. A. LAWRENCE, AND P. J. HARRISON. 1997. Visualization of seawater flow around morphologically distinct forms of the giant kelp *Macrocystis integrifolia* from wave-sheltered and exposed sites. *Limnol. Oceanogr.* **42**: 156–163.
- JACKSON, G. A. 1977. Nutrients and production of giant kelp, *Macrocystis pyrifera*, off Southern California. *Limnol. Oceanogr.* **22**: 979–995.
- . 1984. Internal wave attenuation by coastal kelp stands. *J. Phys. Oceanogr.* **14**: 1300–1306.
- . 1998. Currents in the high drag environment of a coastal kelp stand off California. *Cont. Shelf Res.* **15**: 1913–1928.
- , AND C. D. WINANT. 1983. Effect of a kelp forest on coastal currents. *Cont. Shelf Res.* **2**: 75–80.
- KUNDU, P. K. 1990. *Fluid mechanics*. Academic Press.
- LEICHTER, J. J., S. R. WING, S. L. MILLER, AND M. W. DENNY. 1996. Pulsed delivery of subthermocline water to Conch Reef (Florida Keys) by internal tidal bores. *Limnol. Oceanogr.* **41**: 1490–1501.
- MONISMITH, S., AND D. FONG. 2004. A note on the potential transport of scalars and organisms by surface waves. *Limnol. Oceanogr.* **29**: 1214–1217.
- NEPF, H. M., J. A. SULLIVAN, AND R. A. ZAVISTOSKI. 1997. A model for diffusion within emergent vegetation. *Limnol. Oceanogr.* **42**: 1735–1745.
- NORTH, W. J. 1971. Growth of individual fronds of the mature giant kelp, *Macrocystis*, p. 123–168. *In* W. J. North [ed.], *The biology of giant kelp beds (Macrocystis) in California*. Beihefte zur Nova Hedwigia.
- , D. E. JAMES, AND L. G. JONES. 1993. History of kelp beds (*Macrocystis*) in Orange and San Diego Counties, California. *Hydrobiologia* **260/261**: 277–283.
- RAIMONDI, P. T., D. C. REED, B. GAYLORD, AND L. WASHBURN. 2004. Effects of self-fertilization in the giant kelp, *Macrocystis pyrifera*. *Ecology* **85**: 3267–3276.
- REED, D. C., B. P. KINLAN, P. T. RAIMONDI, L. WASHBURN, B. GAYLORD, AND P. T. DRAKE. 2006. A metapopulation perspective on the patch dynamics of giant kelp in Southern California, p. 353–386. *In* J. P. Kritzer and P. F. Sale [eds.], *Marine metapopulations*. Academic Press.
- , D. R. LAUR, AND A. W. EBELING. 1988. Variation in algal dispersal and recruitment: The importance of episodic events. *Ecol. Monogr.* **58**: 321–335.
- , S. C. SCHROETER, AND P. T. RAIMONDI. 2004. Spore supply and habitat availability as sources of recruitment limitation in the giant kelp *Macrocystis pyrifera* (Phaeophyceae). *J. Phycol.* **40**: 275–284.
- ROSMAN, J. H., J. R. KOSEFF, S. G. MONISMITH, AND J. GROVER. 2007. A field investigation into the effects of a kelp forest (*Macrocystis pyrifera*) on coastal hydrodynamics and transport. *J. Geophys. Res.* **112**: C02016, doi: 10.1029/2005JC003430.
- SEYMOUR, R. J., M. J. TEGNER, P. K. DAYTON, AND P. E. PARNELL. 1989. Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in Southern California. *Estuar. Coast. Shelf Sci.* **28**: 277–292.
- SHIMETA, J., AND P. A. JUMARS. 1991. Physical mechanisms and rates of particle capture by suspension-feeders. *Oceanogr. Mar. Biol. Ann. Rev.* **29**: 191–257.

- SIGNELL, R. P., AND W. R. GEYER. 1991. Transient eddy formation around headlands. *J. Geophys. Res.* **96**: 2561–2575.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry*, 3rd ed. W. H. Freeman and Co.
- STEVENS, C. L., C. L. HURD, AND M. J. SMITH. 2001. Water motion relative to subtidal kelp fronds. *Limnol. Oceanogr.* **46**: 668–678.
- TURNER, J. S. 1973. *Buoyancy effects in fluids*. Cambridge Univ. Press.
- WHEELER, W. N. 1988. Algal productivity and hydrodynamics—a synthesis. *Prog. Phycol. Res.* **6**: 23–110.
- WILDISH, D., AND D. KRISTMANSON. 1997. *Benthic suspension feeders and flow*. Cambridge Univ. Press.
- WORMERSLEY, H. B. S. 1954. The species of *Macrocystis* with special reference to those on southern Australia coasts. *Univ. Calif. Publ. Bot.* **27**: 109–132.
- ZIMMERMAN, R. C., AND J. N. KREMER. 1984. Episodic nutrient supply to a kelp forest ecosystem in Southern California. *J. Mar. Res.* **42**: 591–604.
- , AND J. N. KREMER. 1986. In situ growth and chemical composition of the giant kelp, *Macrocystis pyrifera*: A response to temporal changes in ambient nutrient availability. *Mar. Ecol. Prog. Ser.* **27**: 277–285.

Received: 18 July 2006

Accepted: 18 April 2007

Amended: 30 April 2007