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Authors

Seymour, R J
Tegner, M J
Dayton, P K
et al.

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Storm Wave Induced Mortality of Giant Kelp, *Macrocystis pyrifera*, in Southern California

R. J. Seymour, M. J. Tegner, P. K. Dayton and P. E. Parnell

Scripps Institution of Oceanography, University of California, San Diego, La Jolla, CA 92093, U.S.A.

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The storm-related mortality rates of adult *Macrocystis pyrifera* in a Southern California giant kelp forest were determined over several winter storm seasons and compared with the hydrodynamic attributes of the most energetic storms. The data include stormy and relatively benign years and an exceptional storm which resulted in almost total destruction of a major *Macrocystis* forest. High orbital velocities (associated with large, high frequency waves), the presence of breaking waves, and entanglement by drifters were found to increase mortality through stipe breakage or holdfast failure. Longshore variability in wave intensity was found to affect kelp mortality rates. The data suggest that wave breaking may be an important factor in determining the inner boundary of the kelp bed.

Introduction

The interaction between hydrodynamic flows in the ocean and the structure of large marine plants has been studied in some of its aspects. Jackson and Winant (1983) considered the drag of *Macrocystis pyrifera* forests on slowly-oscillating shore-parallel currents, such as tides, and found that these currents are substantially diminished within large kelp beds. By making reasonable estimates of the drag coefficient and the cross-sectional area affecting the drag, they were able to estimate the drag force on an individual plant. For extreme tidally-driven currents of 10 cm s^{-1} , the drag force was given as 15.5 N (3.5 lbs) on a typical plant. The structure of the plant and its holdfast are clearly sufficiently strong to withstand loads of this magnitude. Even high current speeds have not been observed to cause mortality of adult *Macrocystis* (Foster & Schiel, 1985). Charters *et al.* (1969) studied the flow/structures interactions for more compact plants (*Eisenia arborea*) subjected to higher frequency (wave driven) oscillatory currents near the bottom. In this case, laboratory measurements were made of the drag of individual plants. Under conditions that were observable by divers in the field—maximum velocities of up to about 60 cm s^{-1} —these near-bottom oscillatory flows caused flexure of the stipe, some folding of the canopy to reduce drag—but no structural failures. The estimates of total

drag per plant, based upon the laboratory-derived drag coefficients and the field observations of velocity, range from 1.7 to 7.4 N (0.4–1.7 lbs). The plants studied in Charters *et al.* (1969) were short enough that they probably remained in the reduced-velocity bottom layer and certainly were not subjected to the high velocities associated with breaking waves at the surface. Neushul *et al.* (1967) measured forces of 2–9 kg on *Macrocystis* plants *in situ* under conditions of light to moderate currents and surge. Neushul (1972) measured a force of 0.1 kg transmitted down the stipe bundle to the holdfast when a moderate wave surge passed a *Macrocystis* at Anacapa Island.

Episodes or seasons of storm waves, which cause structural failure of giant kelp plants, are probably the most important source of mortality for adult *Macrocystis* in California (Zobell, 1971; Rosenthal *et al.*, 1974; Gerard, 1976; Foster, 1982; Reed & Foster, 1984; Dayton *et al.*, 1984; Tegner & Dayton, 1987). This mortality is dominated by failures of the holdfast attachment, with the next most important cause being tensile failure of the stipes such that the fronds are separated from the holdfast usually following entanglement with a drifting plant (Dayton *et al.*, 1984). Norton *et al.* (1982) discuss the importance of an effective holdfast attachment and the strength and elasticity of the stipe bundle to marine plants subject to strong flows. Koehl and Wainwright (1977) report that 90% of the solitary beachcast *Nereocystis leutkeana*, another surface canopy-forming kelp, had broken at flaws caused by grazing or abrasion. No studies have been discovered that are directed at the details of the flow/structure interactions between very large plants and the extremely energetic oscillatory currents produced by storm waves. Here we consider three different types of wave episodes observed in the 1980s and the resulting patterns of giant kelp mortality.

Wave-driven flows

Mature, undamaged *Macrocystis* plants have extensive surface canopies; 50% or more of the biomass is typically found in the upper 1 m of the water column (North *et al.*, 1982). While adult plants have many stipes, a simplified mechanical model might be a single flexible stem attached to a larger diameter, hydrodynamically-rougher and very flexible member that floats horizontally at or near the surface. Flows that vary slowly, such as tides, extend the surface canopy in the direction of flow until the tension in the stem (stipe bundle) equals the drag on the canopy. As discussed in Norton *et al.* (1982), a major survival strategy for most seaweeds appears to be the adoption of a configuration which minimizes the canopy drag, especially under conditions of unidirectional high flow speed. This class of flows varies so slowly that the plants can be assumed to respond without delay to changes.

As the form of a wave passes through water, the water particles are driven in circular orbits. Near the surface, the diameter of this orbit is equal to the wave height (the vertical distance between the crest and the trough). In deep water the magnitude of these orbital motions diminishes rapidly with depth until the motion becomes negligible at a depth about half of the wave length (horizontal distance between successive crests). As the wave moves into water shallower than this extinction depth, it begins to react with the bottom. The wave gets very slightly higher as it shoals, it moves at a slower speed (which means that its wave length must get proportionately shorter) and the circular orbits begin to flatten so that the horizontal motion becomes larger than the vertical motion (see Collins, 1976 for a general treatment of wave modeling and associated hydrodynamics). In very shallow water (e.g. 10 m for swell to 3 m or so for wind waves) there is essentially no

diminution with depth of the horizontal oscillations—they are constant throughout the water column. Further, these horizontal oscillations may now be five times or more as great as the wave height. Real ocean waves are made up of many, many individual wavelets, each with its own period, height, speed and direction. This causes the confused and chaotic situation in deep water where it is impossible to follow an individual crest for more than a few seconds. Close to shore, certain non-linear processes still not well understood tend to make all of the components in a neighbourhood clump together, form a relatively smooth wave and travel at the same speed and direction. Thus, engineers can make useful approximations of these complex waves near shore by assuming that they are a single wave with one height, period and direction. Using such a simplification, the horizontal water particle velocity in shallow water can be expressed as:

$$U_{\max} = 2\pi a_h / T \quad (1)$$

where U_{\max} = maximum horizontal orbital speed

a_h = amplitude of horizontal water motion

T = wave characteristic period = $1/f$

f = wave characteristic frequency.

From this we see that as the amplitude of motion (which is approximately proportional to the wave height for this particular depth and wave period) increases, the velocity increases linearly. As the period increases, however, the velocity decreases proportionally. In addition to these horizontal forces, vertical forces are imparted by the upward motion of the water under the crests. The value of the amplitude, a , in equation 1, however, is considerably smaller for the vertical motions than for the horizontal for shoaling waves.

For these wave-driven oscillatory flows, the direction of the motion may change so rapidly that the response time of the plant must be considered—especially for very large plants such as *Macrocystis*. Utilizing the simplified mechanical model for the kelp plant, the canopy will move downcurrent in response to wave-driven flows until the connection to the holdfast is stretched taut—provided that the direction of the flow is not reversed before this limit is reached. Until the stipe bundle is fully extended there is very little stress on the holdfast or the stipes. During the preliminary motion, for low frequency (long period) oscillations, the canopy closely mimics the motion of the surrounding water particles. Mature *Macrocystis* can have an effective canopy length of tens of meters. Therefore, very short period waves—in the range of 1–4 s—have wavelengths that are less than or equal to the canopy length. This results in a situation where the canopy can be put in tension by flows in opposing directions acting upon the same structure. Not surprisingly, the kelp fronds do not move very far in response to these high frequency flows. However, the relative velocities between the water and the fronds can be quite high. As was shown by equation 1, even small waves can produce respectable oscillatory speeds if their periods are small. Drag on the fronds is proportional to the square of this relative velocity as given in the classical quadratic drag law:

$$F_d = 0.5\rho C_d A U^2 \quad (2)$$

where F_d = drag force

ρ = density of water

C_d = drag coefficient

A = characteristic area opposing flow.

Drag power, or the time rate at which energy is being removed from the waves, is proportional to U^3 , resulting in very significant power losses with high relative flows. This power extraction process is approximately linear—that is, power is removed at the frequencies producing the relative velocities. The result, in the case of dense *Macrocystis* forests, is the almost complete removal of high frequency energy from the waves as they pass through the beds. This yields the familiar calm-appearing zones in the lee of kelp beds. However, because most of the wave energy is concentrated at lower frequencies which are largely unaffected by the kelp, there is little reduction of the total wave height (or wave energy) by this process.

As shown in equation 1, large oscillatory flow magnitudes can result from high wave frequencies or from large wave amplitudes, or both. Therefore, it is necessary to consider the case in which the wave length of the wave component of interest is much longer than the extended canopy length (> 4 s period for *Macrocystis*). Now the oscillatory flow will act in a coherent manner along the whole length of the canopy, stretching it downcurrent. In deep water, with long stipe bundles, this back and forth motion is still unlikely to move the canopy far enough in either direction to excessively load the holdfast—unless there is a biasing force which tends to make the canopy spend more time on one side or the other of center. In a storm there are at least two such biasing forces. The first can be a strong wind that results in a surface current tending to stretch the canopies in the cross-shore direction. Winant (1980) describes the measurement of onshore-directed surface flows (downwelling) associated with strong winds out of the south. With longshore wind components of about 10 m s^{-1} , longshore surface currents of 0.5 m s^{-1} and onshore surface currents of 0.2 m s^{-1} were measured. There was about a four hour lag between the onset of the shoreward current and the beginning of the wind forcing. However, because of the huge fetches available in the Pacific, very large waves in the form of swell can attack the kelp forests without an accompanying wind. The second source of bias results from whitecapping. When waves exceed a critical steepness in deep water or encounter water depths on the order of their height, they reduce their height by breaking. This is a very familiar process, evidenced by the appearance of whitecaps in a wind driven sea or of spilling breakers in a broad surf zone. When a wave travels in deep water, without breaking, there is a negligibly small transport of water in the direction of travel. In whitecapping, however, the top of the wave breaks off, entrains a significant amount of air in the form of bubbles, and surfs down the face of the wave form (Peregrine & Svendsen, 1978). This mass of water, referred to as a roller by coastal engineers, will move much further than the water particles below the surface which are oscillated by the wave passage. As the roller passes through the canopy it can have two significant effects. First, it can stretch the canopy shoreward much more than a non-breaking wave would so that the succeeding waves are more likely to fully extend the stipes and load the holdfast. Second, the water in the roller is moving at the same speed as the wave crest (called the phase speed) which will always be a higher speed than the oscillatory flows within a non-breaking wave. Therefore, the roller has the potential for exerting a very high drag force on the canopy. The uncertainty associated with the effects of the roller on the canopy arise from its lowered density because of air entrainment. It is not clear whether this density gradient is sufficient to prevent the nearly neutrally buoyant canopy from participating completely in the flow processes at the surface. Assuming that some significant interaction does occur, if there are a group of large waves that break successively, or if the wind is blowing with sufficient intensity to produce nearly continuous whitecapping, the canopy may be biased fully shoreward such that each wave stresses the stipe bundle and the holdfast. Any swimmer

or bodysurfer who has attempted to move offshore on the surface across a strong surf zone is well aware of this bias and has had the disconcerting realization that, in spite of strong swimming, progress away from the beach is often negative during sets of large waves.

Clearly, a combination of strong shore-directed wind-driven currents and breaking waves within the canopy will produce very high forces on the holdfast structure and is the situation most likely to result in structural damage to *Macrocystis* plants. Because the peak forces are proportional to U^2 , as given in equation 2, this parameter appears to be the most meaningful to evaluate the potential for damage among severe storms. It would be useful, however, to have a methodology for determining if waves were likely to break within the canopy independent of wind-driven whitecapping. It is generally accepted by coastal engineers that waves must break when they reach a depth which is about 1.4 times their height. Wave heights are not constant so they must be dealt with statistically. The common height parameter is significant height (H_s). The exact definition of H_s is the average of the 1/3 highest waves, but it is very closely approximated by 4σ , where σ^2 = variance of the sea surface elevation. This is not merely fortuitous, but arises from the theoretical adherence of wave heights to a Rayleigh (χ^2_2) distribution. Knowing an approximate distribution allows the estimation of extreme wave heights within a storm that has an assumed or measured H_s . For example, the one-wave-in-a-thousand height would be $1.86H_s$. Using the breaking depth criterion above, these extreme waves would then break at a depth equal to $2.6H_s$. Looking at this the other way, at depths of 10 m, significant wave heights of 3.8 m would produce at least one breaking wave out of every thousand. At 20 m the required wave height would be double. A thousand waves at 15 s intervals require about 4 h. Elgar and Seymour (1985) showed that waves are statistically stationary for this interval more than 80% of the time.

There is no theoretical basis for estimating the water velocity in the roller, except to assume that it is equal to the wave phase speed given by linear wave theory for a wave in that water depth with a period equal to the modal period of the spectrum. The actual velocity may exceed this slightly for a short period. However, there is a substantial uncertainty about the density of the flow because of bubble entrainment. Note that the drag force given by equation 2 is proportional to this density. Therefore, to allow some reasonable estimate of the drag under breaking wave conditions, it would seem prudent to assume the phase speed and a density of 0.8 times that of seawater. Note that this velocity, which could be expected to exceed the orbital velocity, exists only at the surface. It would not act on the stipe bundle or upon submerged fronds—which would feel only the orbital motion.

Extreme wave-driven flows in Southern California

As part of an extensive multistate network to gather coastal engineering data, wave measurements have been made in the vicinity of the Point Loma kelp bed for more than ten years. Wave data are acquired several times each day from a submerged pressure sensor array at the entrance to Mission Bay at a depth of about 10 m and also from a wave-following buoy about 13 km offshore at a depth of 170 m (Figure 1). A description of the data gathering system and the analysis techniques are given in Seymour *et al.* (1985). By applying linear wave theory to the wave height data gathered through this system, it is possible to calculate corresponding statistics of the wave-driven flows.

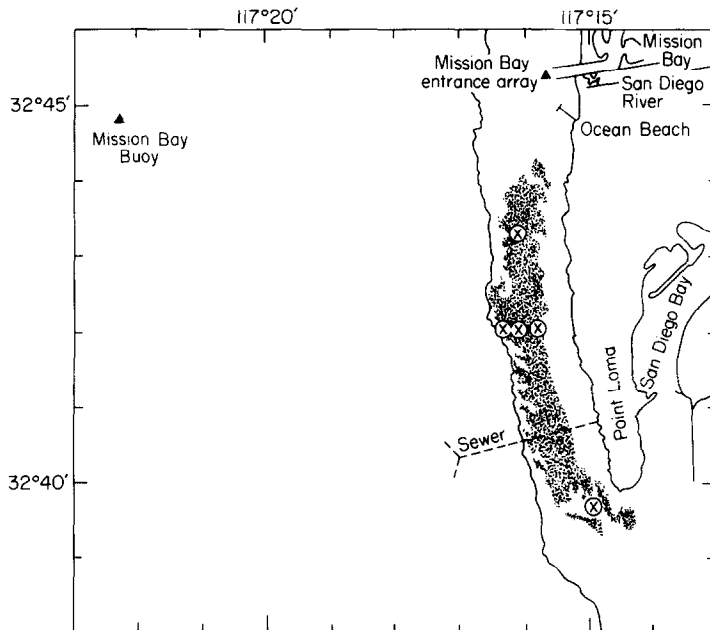


Figure 1. Location of wave sensors and study sites within the Point Loma kelp forest. The stippling represents the *Macrocystis pyrifera* canopy in 1980 and the contour line marks the 18 m (60 ft) depth contour.

Because spectral data are available, it is not necessary to use the singular wave approximation of equation 1. Manipulating the depth-dependent linear theory expression for the horizontal component of wave velocity yields:

$$(U_{\max})^2 = \beta \sum_{f=f_1}^{f_2} \frac{a^2(f)}{\lambda} \quad (3)$$

where U_{\max} = max wave-induced horizontal velocity

$$\beta = 9g\pi$$

g = gravitational constant

$a^2(f)$ = energy spectrum of local waves

λ = local wave length at frequency (f)

f_1, f_2 = frequency bounds of interest

The wave phase speed, designated C , is equal to λ_p/T_p , where the subscript p refers to the values at the peak of the spectrum.

During the previous decade, there have been a number of episodes of violent wave events, following a long period of relatively calm winters in Southern California. Seymour *et al.* (1984) describe the unusual series of six major storms exceeding significant wave heights of 6 m that occurred in the winter of 1982–83. There have been more than 10 of these huge wave events in the 1980s. There were none in the preceding two decades, as estimated by wave hindcasting techniques described in this study. In the 40 years preceding the decade of the 1980s, there were only four events in which the H_s was estimated to have exceeded 6 m, an order of magnitude reduction in the anticipated frequency compared to this decade.

The largest of the many large storms of 1982–83 occurred on 1–2 March, 1983. During the winter of 1985–86, the largest wave event was on 11 March, 1986 for the Mission Bay

TABLE 1. Highest waves measured at Mission Bay, CA for three winters seasons

Winter season	Maximum H_s (m) (peak period (s) in parentheses)	
	Mission Bay buoy	Mission Bay entrance
1982-83	4.8 (18)	4.6 (20)
1985-86	3.8 (15)	4.6 (17)
1987-88	6.7 (13)	6.1 (17)

TABLE 2. Breaking wave parameters at Mission Bay, CA for three winter seasons

Winter Season	1-in-1000 wave		Average 1-in-3 wave	
	Breaking depth (m)	Phase speed (m s ⁻¹)	Breaking depth (m)	Phase speed (m s ⁻¹)
1982-83	12.5	10.8	6.7	8.0
1985-86	9.9	9.6	5.3	7.1
1987-88	17.4	12.2	9.4	9.1

buoy and a month earlier on 16 February for the entrance gage. The highest waves of this decade, at the time of writing, occurred on 18 January, 1988. Outside the offshore islands, values of H_s exceeding 10 m were recorded. Table 1 shows the highest values of significant wave height measured at the two wave gages closest to the Point Loma kelp beds during these three peak events.

The wave gage at the entrance to Mission Bay is located on a fossil delta, formed when Mission Bay was the estuary of the San Diego River. This delta causes a focussing of wave energy, particularly at lower frequencies, making this a popular surfing site. The result of this focussing is that the wave height measured at this nearshore station is often greater than at the offshore buoy. Further, the peak period (the period corresponding to the maximum value in the energy spectrum) is typically greater as well—as shown in Table 1—because of preferential enhancement of the lower frequencies (higher periods). Therefore, it can be assumed that the buoy data will be more representative of the Point Loma kelp forest environment. Using the buoy values from Table 1 for each year, estimates of certain maxima can be made. From the maximum heights, the depth at which breaking will occur can be derived. From the depth at which the one-in-a-thousand wave breaks, the phase speed can be determined to allow an estimate of the maximum roller velocity. These parameters are shown in Table 2.

Using spectral information, the value of U_{\max}^2 can be calculated for the orbital motion. In Table 3, these peak flows are shown at three different water depths for the one in a thousand wave associated with each event in the three winter seasons.

Influence of water depth

In Table 3 the actual water depths (including tides) at the time of the peak wave heights were used in the analysis. The nominal depths shown in the header of the table refer to

TABLE 3. U^2 , Maximum surface flow speed squared (highest wave in a thousand) at various depths

Winter	Flow speed squared ($\text{m}^2 \text{s}^{-2}$) at nominal water depths (m) of		
	18	15	12
1982-83	5.34	4.73	3.36
1985-86	3.42	3.57	3.88
1987-88	10.11	8.99	6.42

mean lower low water (chart depth). In all cases the actual depths were at least 1 m greater than the nominal values. Considering the breaking depths shown in Table 2, it can be seen that depths less than about 17.5 m would not have seen the full height of the 1-in-1000 wave during the 1988 storm because it would have already partially broken and will have been reduced in size. The smaller waves in 1986 would not break at these depths and it can be seen that the values of U^2 increase in size with decreasing depth in this case as the horizontal orbital amplitudes increase. Conversely, the maximum values of U^2 for the other years decrease with decreasing depth because of the limiting height of waves that can exist at that depth. The 1983 storm maximum at the 12 m depth is less than that of 1986 because of the differences in the spectral shape.

Influence of island shadowing

As suggested in Figure 2, the coast of Southern California has substantial protection from the full onslaught of deep water waves through a series of offshore islands. Depending upon the direction of the incident waves, these islands provide complete or partial shade from swell generated seaward of them (Pawka, 1982; Pawka *et al.*, 1984). Inside the islands, there is a substantial fetch in the northwest-southeast direction which can result in very energetic wind waves during the infrequent occurrences of very strong local winds out of the northwest. During the many energetic storms of the winter of 1982-83, the dominant approach direction for big waves was out of the west from angles of about 260-295° (Seymour *et al.*, 1984). This resulted in the general lack of a shadowing pattern as shown in Figure 2a. During the January 1988 storm, a NOAA buoy moored north and west of Santa Catalina Island indicated that the dominant wave direction was out of the northwest on a bearing toward about 110° at the time of maximum wave height. As suggested in Figure 2b, this produces a vastly different shadowing pattern from the 1982-83 storms. Figure 2 is simplified in that the small effects of refraction in the lee of the islands and the major effects of diffraction are ignored. In the actual case, the shadows are narrowed as they approach the mainland. However, the basic differences between the two storm regimes are illustrated. In Figure 3 the maximum recorded significant wave heights, at a number of nearshore wave measuring stations, are indicated along an approximately 150 km section of Southern California coastline. This illustrates the effects of island shadowing on the wave intensity seen at other kelp forests to the north of Point Loma during this storm, as discussed below. Although the height differences might be suggestive of merely an increased fetch effect moving downwind, this could not have been the case because the observed wave periods were nearly constant for all stations. If fetch

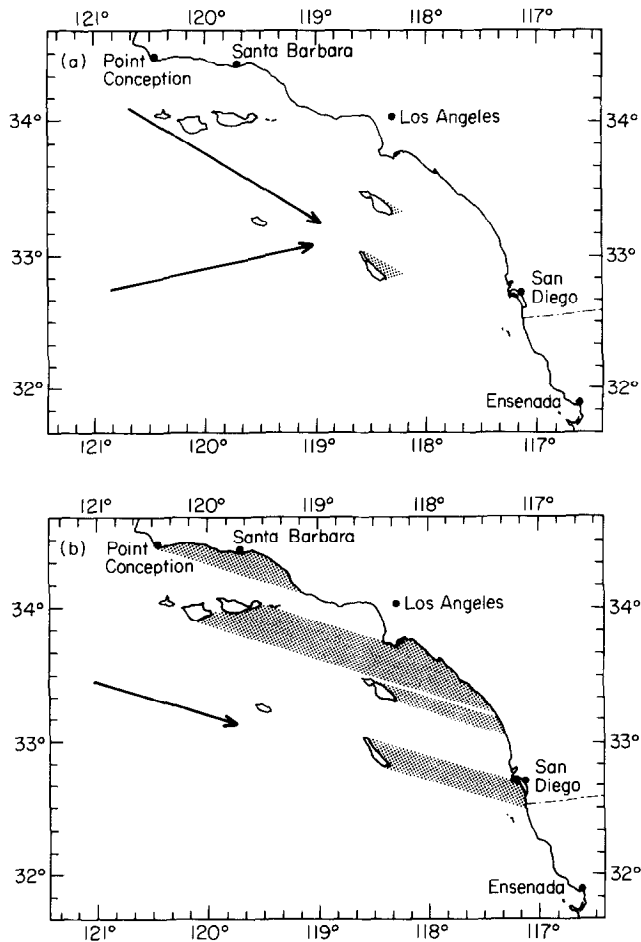


Figure 2. (a) The two vectors represent the extremes in the approach directions for waves in the storms of the winter of 1982–83. The limited areas in which complete island shadowing always occurred are suggested by the shading. (b) Typical island shadowing during the peak of the January 1988 storm, resulting in pronounced longshore variability in wave intensity.

difference had been significant, the northern stations would have had much smaller periods.

Wave forces on kelp canopies

As shown in equation 2, two parameters control the drag-induced tension in the stipe bundle. The first is the plant area, A , and the second is the square of the velocity, U^2 . Assuming to first order that the drag-affecting area of *Macrocystis* is, on the average, proportional to water depth, a prediction that maximum wave forces should be greatest at the greatest depths and should diminish as the depth decreases across the forest will result. However, because plants in the deeper portions of the Point Loma kelp forest tend to live longer, they have more stipes (and therefore a larger cross-sectional area) (Dayton *et al.*,

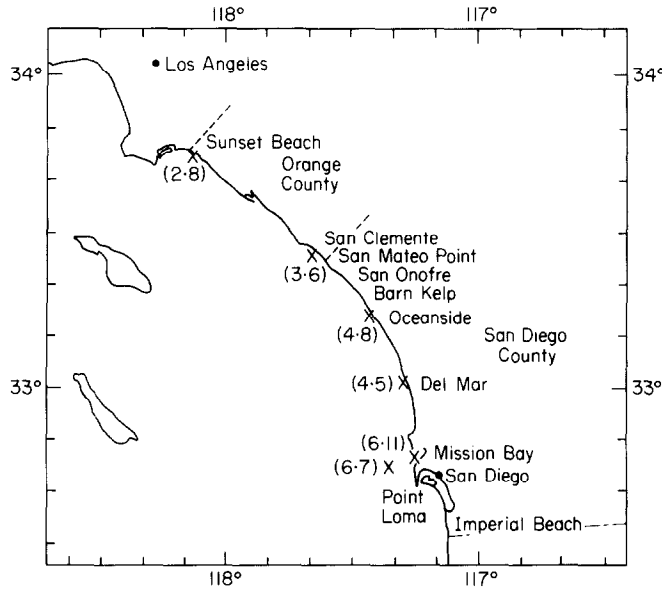


Figure 3. Coastline of Orange and San Diego Counties. Wave measurement stations are shown by (x) symbols. The maximum recorded significant wave height (m) during the January 1988 storm is shown in parentheses at each station.

1984). The average number of stipes per plant (based upon counts from the December mappings, 1984–87) was almost numerically equal to the depth in meters—except in the centre of the bed where the number exceeds this value by 20% or so. Assuming that, on average, all stipes have similar diameters—and, therefore, similar breaking strengths—yields the result that mortality caused by wave velocities ought to remain constant between the front and the back of the bed with a decrease predicted for the centre of the bed. This prediction requires, of course, that the holdfast scale its strength in proportion to the water depth as well. However, there is a further complication. As the holdfasts fail or the stipe bundles part, the drifter is now free to entangle its neighbour in the downwave direction, approximately doubling the available area and doubling the drag (Dayton *et al.*, 1984). It is clear that each iteration of this process results in an arithmetic progression of drag forces such that even the reduced values of velocity may be more than sufficient to fail the plants closest to shore. Furthermore, the potential for drifter mortality is also high in shallow water because younger stands of *Macrocystis* are more dense. Depending upon the degree of entanglement, virtually any increase in mortality can be predicted for the shallower depth plants.

Table 3 refers to the orbital flow speeds. Returning to Table 2 it can be seen that the speeds of the rollers—approximately the same as the phase speeds tabulated—are significantly higher than the orbital speeds. The square of these speeds is an order of magnitude greater than the corresponding values from Table 3. It is very difficult to predict just how these rapid, foamy flows will interact with the kelp canopy—if at all. Their density may be sufficiently low that the kelp fronds will not tend to rise into them and therefore will not feel their drag. With heavy breaking (as in 1983 and 1988) perhaps one wave in every five or six was breaking at a depth of 12 m. If the rollers do drag on the canopy, there certainly was ample opportunity during these storms.

TABLE 4. Percent of time during the year that H_t exceeds 3 m

Calendar year	% Exceedance	
	Mission Bay buoy	Mission Bay entrance
1981	2.2	0.8
1982	1.1	0.6
1983	4.4	5.5
1985*	0.4	0.2
1986	1.0	6.8
1987	1.0	0.6

*Insufficient data in 1984.

Influence of breaking waves on the inner boundary location

It may be that wave forces contribute to the establishment of the minimum depth for the giant kelp forests. In areas that are normally protected from severe wave events, dense *Macrocystis* beds are found as shallow as 2–3 m or even appear intertidally (North, 1971; Dayton, 1985a). In the Point Loma forest, the inner boundary of the giant kelp has varied from depths of about 8 to about 12 m. It is of interest to apply the principles evolved above to this observation. At a depth of 8 m, waves greater than 5.7 m in height would be expected to break. These are 1-in-1000 heights for wave fields having a significant height of 3 m. Table 4 shows statistics of occurrence of waves 3 m or greater at the two measurement points near the Point Loma bed. These data show that, in all but one of the six years observed, the significant wave height at one or both stations exceeded 3 m for more than 1% of the time. That is, for more than about 90 h each year there were breaking waves at 8 m. With the modal breaker period in this region of about 10 s, 90 h yields perhaps 32 000 waves—of which one in a thousand would be expected to break at a depth of 8 m. Allowing for high tide increasing the local water depth at the nominal depth of 8 m, there would still be on the order of ten such waves predicted each year at the point where the giant kelp plants disappear. This provides circumstantial evidence in support of the importance of wave breaking to kelp mortality and variability in the occurrence of these waves is probably the explanation for the fluctuating inner boundary of the forest. There are undoubtedly substrate, scouring and biotic effects such as competition and herbivory which also influence the inner boundary position, but our correlation strongly suggests that breaking waves help establish the large scale location.

Observations of kelp mortality

Macrocystis population dynamics have been followed at five sites in the Point Loma kelp forest near San Diego since the spring of 1983 [Dayton & Tegner, 1984; Tegner & Dayton, 1987; (unpublished data)]. These include three sites in the center of the normally 8–10 km long forest at depths of 12, 15 and 18 m, and two additional sites at 17 m at each end of the forest. Mortality of adult *Macrocystis* at the end of the 1982–83 storm season was assessed by comparing the densities of extant kelp plants and recently killed holdfasts and holdfast scars. Subsequently, four 25 m transects were installed at each site and kelp plants mapped

TABLE 5. Observed adult *Macrocystis* mortality in the Point Loma kelp forest for four winter seasons

Position	Percent mortality			
	1982-83	1985-86	1986-87	1988
Central stations				
18 m	13	36	2	65
15 m	47	31	9	69
12 m	66	37	29	94
End of the forest stations				
North (17 m)	40	23		89
South (17 m)	41	— ^a		87

^aNo adults prior to storms.

in 400 m² areas at intervals of two to six months. *Macrocystis* plants with four or more stipes (the stage at which sporophyll production begins) were considered to be adults. Mortality during the 1985-86 winter was based upon changes between December 1985 and April 1986. The 1986-87 census was taken in December 1986 and June 1987. The effects of the large storm of January 1988 were assessed by the changes between December 1987 and February 1988.

Adult *Macrocystis* mortality as a function of depth and location in the Point Loma kelp forest for these four seasons is shown in Table 5. In 1983 and 1988, mortality was highest at the shallow central site and decreased with depth. In both these years, mortality was higher at the north and south stations than at the central station of similar depth. In contrast, there was no apparent change in mortality with depth after the milder waves of 1986, and the north station exhibited higher survivorship than the central 18 m station. Because of an infestation of grazing amphipods in 1985, there were no adult *Macrocystis* at the south station before the storm season started (Tegner & Dayton, 1987). The data suggest that 1986-87 was a relatively benign storm season, yet the mortality rate at 12 m remained substantial. Clearly adult *Macrocystis* at this depth are turning over at a high rate. Data from 1988 suggest that mortality estimates from 1983 may be somewhat conservative. Up to 10% of the adult *Macrocystis* that disappeared in 1988 left no holdfast scars. However, because storm-induced damage to holdfasts in January may lead to further mortality in 1988, these estimates are also conservative.

Discussion

Macrocystis lives in a highly energetic environment and is dependent upon water motion to bring nutrients and to disperse its spores. Indeed most kelps show adaptation to winter storm disturbances by reproducing during this season (Dayton, 1985b) or, in the case of *Macrocystis* which tends to be reproductive all year, by having resting stages which can respond to appropriate windows of light availability (Deysner & Dean, 1986) often created by storm disturbances of existing canopies. The effects of storm waves vary with the degree of exposure and the frequency and intensity of the storms. While wave-induced canopy destruction is uncommon in Southern California, canopies are regularly lost to the more energetic fall and winter storms of Central California, and increasing wave intensity

may be why *Macrocystis pyrifera* does not occur in large stands north of Año Nuevo Island (Foster & Schiel, 1985).

Two population factors, the size and age structure of the stand of plants, affect the amount of damage storm waves cause. 1987 was an excellent year for kelp growth, and the *Macrocystis* canopy was very dense and larger in areal extent than it had been in many years. The high degree of frond intermingling observed in a dense canopy increases the probability of plants detached by the storm entangling others. Huge, tangled paddies of plants were observed floating away from forests or on beaches after the storm of January 1988. *Macrocystis* plants can live to seven years in Southern California (Rosenthal *et al.*, 1974) although a more realistic life expectancy is 4–5 years (Dayton *et al.*, 1984). Young plants with very small holdfasts are weakly attached and more easily ripped off the substrate (Norton *et al.*, 1982). Two and three year old *Macrocystis* survive better at Point Loma than other ages (Dayton *et al.*, 1984). The attachment of older plants gradually deteriorates as the center of the holdfast dies due to sedimentation or is eaten out by grazers (Ghelardi, 1971); this plus their higher biomass makes older plants more susceptible to storm waves. Moderate waves, such as those observed during the winters of 1985–86 and 1986–87, cause patchy detachment and entanglement and lead to a mosaic of cohorts. However, age structure appeared to have little effect on mortality patterns in 1988 as the average age of the plants at the north site was at least two years older than at the south site but the mortalities were virtually identical (Table 5). Massive wave events that cause widespread mortality act to homogenize age structure and tend to lead to oscillations in standing stock.

Local physical factors also affect the amount of damage storm waves cause. Hydrodynamically-propelled rock particles, ranging in size from sand grains through cobbles to small boulders, scour the bottom. The resulting abrasion of the base of kelp plants may contribute to stipe tensile failure under wave loading (e.g. Koehl & Wainwright, 1977). Dozens of cobbles in the order of 20 cm in diameter appeared in one of our study sites at the extraordinary depth of 22 m after the January 1988 storm; such missiles are capable of extensive damage. Rock particles can be moved by either drag forces, of the form shown in equation 2, or by inertial forces. In the latter case, the force tending to move the particle is proportional to the acceleration of the water mass surrounding it. The mathematics of wave motions is such that both the drag force and the inertial (acceleration) force are proportional to the square of the wave frequency. However, the drag force is also proportional to the square of the particle diameter multiplied by the square of the wave height, while the inertial force is proportional to the cube of the diameter times the wave height. The result of all this is that the wave-driven motions of small particles, like sand, are dominated by drag forces. Conversely, only large inertial forces can move cobbles and boulders. Large drag forces can result from either very high waves or short wave periods (or both). High inertial forces are more likely with short period waves of the kind found in the January 1988 storm. The geological damage was in fact the worst we have ever observed; whole reefs were destroyed, ledges broken off, and massive slabs overturned. The 1982–83 storms could have been expected to produce significant scour by sand, but far less damage by cobble and boulder displacement. The nature of the substratum also affects the nature of the wave damage. *Macrocystis* attached to hard rock bottoms are more susceptible to stipe breakage and canopy loss, whereas plants on soft, friable bottoms are more likely to be torn off completely (Foster, 1982).

The total observed mortality rate in the Point Loma bed during the three surveys discussed for the decade of the 1980s is predicted remarkably well by the statistic $(U_{\max})^2$,

calculated for the outer edge of the kelp forest from measured wave data in the vicinity. This parameter is proportional to the maximum drag force on the plant predicted from classical hydrodynamical theory. This agreement is achieved in spite of the differences in the relative abundance and age structure of plants among the surveys.

In addition to these contemporary observations, there are a number of historical accounts. Perhaps the most severe is Davidsons' (1889) report that the Point Loma kelp forest was completely torn away by storms during the winter of 1888–89. The San Diego Union of December 25, 1888 describes '30 foot waves' and 'thousands of tons of kelp on the beaches'. Historical weather records collected by the U.S. Army Signal Service in San Diego allow comparison of this storm to the January 1988 event. The atmospheric pressure low was 997 mb in 1888 and 989 mb in 1988. The pressure dropped 16 mb in 24 h in 1888 and 27 mb in 1988. There were strong coastal winds out of the south during both storms in advance of the low point in atmospheric pressure. The weather station in downtown San Diego measured peaks of 16 m s^{-1} from the south in 1888 and the airport (sheltered by Point Loma) measured 20 m s^{-1} in 1988. The January 1988 storm was clearly of greater intensity, perhaps the strongest ever recorded in Southern California.

The consistent increase in mortality with decreasing depth indicates that entanglement is an important factor. Without entanglement increasing the drag on succeeding holdfasts, mortality should, in most cases observed, decrease with decreasing depth. The combined effects of entanglement and of the assurance of breaking waves during every winter become so intense that an inner boundary is set for the *Macrocystis* at Point Loma at a nominal depth of about 8 m. First year plants reaching the surface have not developed sufficient stipe bundle or holdfast strength to survive the critical loads that will certainly be imposed in even a mild winter season.

Comparisons between the forcing function, U^2 , at the outer edge of the bed (18 m) in both the 1982–83 and the 1988 maximum events indicate that there should have been the observed significant difference in the mortality. However, factoring in the great number of storms in 1982–83 (Seymour *et al.*, 1984), a clear argument can be made for greater mortality in the earlier season. Yet the mortality in 1988 remains substantially higher (Table 5). Brandt (1923) suggests that *Macrocystis* mortality is higher in storms with wind out of the south than when the wind is from the north. This observation, which is consistent with the data reported here, suggests that the mechanism of stretching out the canopy by onshore-directed currents resulting from south winds may be very important in increasing the probability of holdfast or stipe bundle failures from wave loading.

Interannual variability in the wave climate incident on Southern California kelp beds is illustrated by Tables 1–4. It should also be understood that substantial variability can exist between storms in a single winter season and in the intensity of a single storm at different locations. If there is such an event as a typical winter storm in Southern California, it would be typified by large swell waves out of the northwest with little or no wind. These waves are generated at great distance from land—perhaps as much as 1000 km away—so that the high winds that caused them are typically not felt on shore. In El Niño years, the approach direction of the swell is more nearly directly from the west. Again, there tend not to be strong winds accompanying these large wave events. The January 1988 storm was distinguished from the typical storm in that it was intensely concentrated in a small area and its effects were very local. The large waves were generated much closer to shore and the center of the storm passed directly over Southern California rather than being deflected far to the north as in the typical winter storm scenario. The winds at the coast were unusually strong (gusts of 70 knots were measured at Scripps Pier on 17 January).

Because of the island shadowing illustrated in Figure 2b, mortality at Point Loma was substantially greater than at beds only tens of km away. W. North (personal communication) conducted aerial surveys before and after the January 1988 storm. He reported severe damage to canopies in the northern end of Orange County and the southern end of San Diego County. The canopies near San Clemente, San Mateo Point, San Onofre and Barn Kelp (a local place name), in southern Orange County and northern San Diego County (see Figure 3), were relatively intact after the storm. From Oceanside, the extent of canopy loss increased with distance to the south. Only traces remained at Point Loma and no kelp was visible from the air at Imperial Beach. During the 1982–83 winter, the dominant wave direction was roughly out of the west, but the directional variability inherent in the large numbers of storms (Figure 2b) resulted in a uniform and complete destruction of kelp forest canopies; no coastal canopies survived the winter of 1982–83 (R. McPeak, personal communication).

A hydrodynamical explanation was sought for the increase in mortality at the northern and southern extremes of the Point Loma bed at the 17 m depth. Kelp plants at the southern site would be streamed in the direction of wave travel (and breaking) by tidal flows into San Diego Bay, but the northern plants are too far south to be affected by similar flows into Mission Bay. Plants in intermediate depths appear, in general, to be more hardy than those in deeper water, perhaps because of optimal nutrient and light availability. Further, the plants at the extreme north and south are stressed by turbid tidal flows from Mission Bay and from San Diego Harbour. These factors probably control the longshore extent of the beds, which were known to extend much greater distances in both directions in earlier times (Dayton *et al.*, 1984).

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