Modulation of wave forces on kelp canopies by alongshore currents

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Abstract

The predominant view of the canopy-forming kelp’s mechanical response to water motion is that they sway passively under waves such that they are only rarely stretched out in flow, which reduces relative fluid velocities and decreases the applied force. Such a view is an appropriate first-order approximation but becomes conceptually problematic in the face of the net surface velocities (Stokes drift) that arise under waves of all but infinitesimal height, since such flows can tug organisms into fully extended positions, allowing forces to act unabated. Focusing on Nereocystis luetkeana, the bull kelp, this study examines quantitatively the capacity of alongshore currents to mitigate the consequences of Stokes drift by maintaining canopy-forming macroalgae in “neutral” positions with regard to the onshore–offshore orbits of the waves. Results indicate that alongshore currents can indeed substantially reduce the forces imposed on canopy-forming kelps, as well as decrease the levels of wave damping that result from the interaction of these organisms with the passing fluid.

Kelp forests provide essential habitat and food for hundreds of species of marine invertebrates and fish living in temperate nearshore waters (Foster and Schiel 1985). The forests’ proximity to the shore also makes them vulnerable to hydrodynamic forces imposed by surface gravity waves as these waves shoal into shallow water. Indeed, particularly during severe winter storms, large numbers of canopy-forming macroalgae such as Macrocystis pyrifera and Nereocystis luetkeana can be dissolved or destroyed by high-amplitude seas and swell (e.g., Seymour et al. 1989; Dayton et al. 1992). The ecological importance of these organisms, and their susceptibility to flow-driven disturbance in the face of a changing wave climate (Bacon and Carter 1991; Greve-meyer et al. 2000), suggests that efforts to understand the plants’ mechanical relationship to water motion are both valuable and timely.

The traditional view of the behavior of canopy-forming kelps in flow has been that they move passively with the fluid over substantial portions of each oscillatory wave cycle (i.e., they “go with the flow”), which results in a decrease in the speed of water relative to their fronds, thereby minimizing drag (Koehl 1984, 1986, 1999). In this scenario, it is only the most exceptional wave conditions that result in the imposition of dangerous forces (in nonwavy habitats, rapid tidal currents can also combine with accumulated grazer damage to cause significant mortality; in other cases, entanglements with already-dislodged individuals may be important [Koehl and Wainwright 1977; Dayton et al. 1992]). This general perspective is supported by observations of seaweed motion in nature (e.g., Koehl 1984), correlative patterns where kelp blades exhibit “slow-flow” morphologies even in moderately wavy locations (Koehl and Alberte 1988; Johnson and Koehl 1994), and a limited number of direct measurements of hydrodynamic forces acting on real organisms in the field (Denny et al. 1997; Gaylord and Denny 1997; Koehl 1999). Complementary flow data gathered using moored instruments also indicate that surface gravity waves are not noticeably damped in passing through kelp forests, which further supports this concept (Elwany et al. 1995).

However, simple dynamical models also suggest that, under certain conditions, large plants can acquire sufficient momentum and can translate far enough that they reach the limits of their range of motion, removing any slack in their stipes. Under such circumstances, decelerating individuals may impart on themselves an “inertial force” as they are jerked to a halt (Denny et al. 1997, 1998; Gaylord and Denny 1997; Gaylord et al. 2001; see also Mendez et al. 1999). At times, these inertial forces are predicted to outweigh the benefits of moving with the fluid. In addition, because such forces are of quite brief duration, they do not necessarily result in a large loss of wave energy and so can remain undetected in force-proxy indicators, such as wave damping estimates.

Such uncertainties in ascertaining the magnitudes of force imposed on canopy-forming kelps are further exacerbated by additional, subtler features of wave-driven water motion. In
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Nereocystis luetkeana is a subtidal brown alga of the Order Laminariales that grows with a long, ropelike stipe that extends from the seafloor to the water surface (Abbott and Hollenberg 1976; Koehl and Wainwright 1977). At the distal end of the stipe, an enlarged buoyant float (a pneumatocyst) supports 30–60 ribbonlike blades that together form the kelp’s canopy. The stipes of these organisms typically grow to lengths approximately equal to the water depth, commonly 10 m, which is the value employed for the present study.

Kelp dynamics

Unfortunately, the consequences of Stokes drift for increasing forces on kelp canopies and for modifying levels of wave damping have not been explored in a rigorous fashion over the length of any given individual. However, because the bulk of the mass of a Nereocystis is located at the distal end of the stipe, the summed effects of these forces can be approximated as if they all act on a point element of equivalent total mass to the whole frond, positioned at the site of the pneumatocyst. There are five external forces of note. The following description of each represents a brief summary of more detailed derivations in Gaylord and Denny (1997) and Denny et al. (1997).

The net buoyant force, \( \mathbf{F}_b \), is the difference between hydrostatic buoyancy and the weight of the organism and is positive upward. In Nereocystis, this force arises primarily from the kelp’s pneumatocyst. When the plant’s mass is completely below the water surface, \( \mathbf{F}_b \) equals \( \mathbf{F}_s \), its fully submerged value. However, if the pneumatocyst and blades begin to emerge from the water, as can occur in the trough of a wave, the net buoyancy decreases and is approximated by

\[
\mathbf{F}_b = \mathbf{F}_s \left( 1 - \frac{z - [d + \eta]}{0.75} \right)
\]

where \( z \) is the height of the plant’s frond mass above the seafloor and \( \eta \) is the sea surface elevation relative to the bottom. The net buoyant force, \( \mathbf{F}_b \), is the difference between hydrostatic buoyancy and the weight of the organism and is positive upward. In Nereocystis, this force arises primarily from the kelp’s pneumatocyst. When the plant’s mass is completely below the water surface, \( \mathbf{F}_b \) equals \( \mathbf{F}_s \), its fully submerged value. However, if the pneumatocyst and blades begin to emerge from the water, as can occur in the trough of a wave, the net buoyancy decreases and is approximated by

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mean water depth, \( d \), all measured in meters. The scaling factor (0.75) in the denominator accounts for the finite dimensions of the pneumatocyst and blades, which precludes an instantaneous exit of the full frond mass from the water. The magnitude of the scaling factor is based on observations of how far real plants in nature extend above the water surface during calm conditions on low tides. Note that all boldface quantities are vectors.

Drag, \( F_d \), results from water moving with respect to a kelp and applies a force in the direction of relative velocity,

\[
F_d = \frac{1}{2} \rho A S_a u t^{-1}
\]

where \( \rho \) is the density of seawater, \( A \) is the maximum projected blade area, \( S_a \) is a shape coefficient of drag, \( \gamma \) is a velocity exponent, and \( u \) is the relative velocity. Equation 2 is an equivalent, alternative form to the conventional velocity-squared expression of the engineering literature and has become standard in the biological arena because of its greater ease in parameterizing the processes of reconfiguration and streamlining (Denny 1995; Gaylord 2000).

Virtual buoyancy, \( F_{vb} \), derives from the pressure gradient that accompanies a spatially accelerating flow and points in the down-gradient direction (i.e., the direction of acceleration; Gaylord et al. 1994),

\[
F_{vb} = \rho V a
\]

where \( V \) is the volume of fluid displaced by the frond and \( a \) is the spatial acceleration of the flow relative to the earth.

An added mass force, \( F_{am} \), results from fluid accelerating relative to an organism and acts in the direction of that relative acceleration (Batchelor 1967; Gaylord et al. 1994),

\[
F_{am} = C_a \rho V a_t
\]

where \( C_a \) is an added mass coefficient and \( a_t \) is the total fluid acceleration relative to the plant.

Tension in the stipe of a seaweed, \( F_t \), acts as a restoring force when the stipe is extended. This force is modeled as if the stipe were an elastic, massless rope with material stiffness \( E \). Thus, tension is zero except when the stipe is stretched beyond its resting length, \( L \), under which conditions the force is given by

\[
F_t = EA_{st} \left( \sqrt{x^2 + y^2 + z^2} - L \right) / L
\]

where \( (x, y, z) \) indicates the position of plant mass in space, and \( A_{st} \) is the nominal cross-sectional area of the stipe. A traditional right-handed coordinate system is used in which the \( x \)-axis points toward shore parallel to the direction of wave propagation, and \( z \) increases upward from zero at the seafloor. \( F_t \) acts along the axis of the stipe and is therefore always directed toward the holdfast located at position \((0, 0, 0) \). The model also includes additional measures (as in Denny et al. 1997) for preventing unrealistic passage of the plant’s mass into the substratum, but because this issue does not arise for the cases examined in this study, these complexities are not discussed further.

According to Newton’s Second Law, the imposition of the forces above causes the kelp’s front mass, \( m \), to accelerate,

\[
a = \frac{F_v + F_d + F_{vb} + F_{am} + F_t}{m}
\]

where \( a \) is its acceleration (thus, even when all flow forces are zero, rapid decelerations can induce a finite \( F_v \) and thereby an inertial force). Equation 6 is then integrated numerically through time to track the plant’s instantaneous velocity and position. In practice, this task is accomplished through the use of a standard fourth-order Runge–Kutta algorithm with adaptive time step (Press et al. 1992). Note that this approach provides a detailed description of a kelp’s motion and the instantaneous forces imposed on it through time. That is, the analysis does not simply rely on time-averaged values, which are less relevant for understanding organism damage or dislodgment.

The parameter values used to model a typical mature \textit{Nereocystis} are listed in Table 1. All morphological values are extracted directly from the empirical allometric growth data of Denny et al. (1997), whereas the shape coefficient of drag is derived from measurements on current-swept \textit{Nereocystis} plants by Johnson and Koehl (1994). The drag exponent, \( \gamma \), is based on measurements conducted on \textit{Macroystis pyrifera} by Uther and Denny (1996) and on measurements using 12 other, somewhat smaller species of macroalgae by Gaylord (2000), as is the added mass coefficient. Note that although Stevens et al. (2001) suggest that the above drag parameters (which are identical to those originally used by Denny et al. [1997]) potentially underestimate force at slower relative velocities (<0.1 m s\(^{-1}\)) by about a factor of two, the alternative form they propose appears too small by almost a factor of 10 at relative velocities of 1 m s\(^{-1}\), and too small by as much as three orders of magnitude at relative velocities of 2 m s\(^{-1}\). This point derives from the observation that even smooth, flat plates aligned exactly with flow have drag coefficients that are several hundred times larger at such flow speeds (Schlichting 1979). Because quite substantial relative flow rates are expected for some wave conditions and at certain phases in any given oscillatory cycle, the original drag expression as employed by Denny et al. (1997)—and as validated in the field (see below)—is retained here.

The water velocities and accelerations at the location of the kelp’s pneumatocyst (i.e., the fluid motions responsible for the imposition of a major subset of the forces above) are estimated via Stokes second-order wave theory (Sarpkaya and Isaacson 1981). This theory uses a perturbation analysis
to improve accuracy over the more commonly used, and perhaps more familiar, linear approximations (e.g., Kinsman 1965; Denny 1988). Predicted wave-driven horizontal and vertical velocities \( \mathbf{u}_x \) and \( \mathbf{u}_z \), respectively, therefore become

\[
\mathbf{u}_x = \frac{\pi H \cosh(kz)}{T \sinh(kd)} \cos(kx - \omega t) + \frac{3}{4} \frac{\pi^2 H^2 \cosh(2kz)}{T^2 \sinh^2(kd)} \cos(2[kx - \omega t])
\]

\[
\mathbf{u}_z = \frac{\pi H \sinh(kz)}{T \sinh(kd)} \sin(kx - \omega t) + \frac{3}{4} \frac{\pi^2 H^2 \sinh(2kz)}{T^2 \sinh^2(kd)} \sin(2[kx - \omega t])
\]

where the second term in each expression represents the higher-order correction to the linear solution. \( H \) is the wave height (twice the wave amplitude), \( T \) is the wave period, \( \lambda \) is the wavelength, \( k \) is the wavenumber \( (2\pi/\lambda) \), \( \omega \) is the wave frequency \( (2\pi/T) \), \( t \) is time, and \( \sinh \) and \( \cosh \) are the hyperbolic sines and cosines, respectively. \( T, \lambda, \) and \( d \) are linked according to the dispersion relation

\[
C = \frac{\lambda}{T} = \frac{g}{\omega^2} \tanh(kd)
\]

where \( \tanh \) is the hyperbolic tangent. Fluid accelerations are then just the total derivatives, \( \partial \mathbf{u}_x / \partial t \) and \( \partial \mathbf{u}_z / \partial t \), of Eqs. 7 and 8. Monochromatic waves are employed to simplify interpretation of results, and an additional, steady alongshore current, \( \mathbf{u}_c = \mathbf{u}_{\text{current}} \), acts perpendicular to the oscillatory wave motions.

The use of Stokes theory is important because it provides a means of accounting for the tendency for real waves to induce a net mass transport (i.e., Stokes drift). In contrast to the idealized situation of fully linear waves with infinitesimal amplitude, fluid orbits under waves of finite amplitude are not quite closed. This feature results from the depth attenuation intrinsic to wave-driven flows, which causes fluid particles at the tops of their orbits to move forward slightly faster and for a longer time than they move backward at the bottoms of their orbits. The drift velocity that ensues can be calculated as (Komar 1998)

\[
\mathbf{u}_{\text{drift}} = \left( \frac{\pi H}{\lambda} \right)^2 C \cosh(2kz) \frac{\cosh^2(kd)}{2} \sinh(kd)
\]

Note that this velocity is maximal at the water surface, where it can interact with a kelp’s pneumatocyst and blades, and decreases rapidly below the surface. Thus, although this Stokes solution makes no allowance for a finite flow near the seafloor (a characteristic of more sophisticated theories; e.g., Longuet-Higgins 1953) and must be viewed as an approximation because of limitations on formal convergence of the second-order theory when applied to exceptionally steep waves (Sarpkaya and Isaacson 1981), the simpler form of Eq. 10 is sufficient for the purposes of this study, where all critical force balances operate high in the water column.

It should also be noted that, because wave-driven flows (either those associated with linear or Stokes waves) impose forces on a plant, a plant in turn applies forces on the water. This process generally results in a loss of kinetic energy from the fluid. The average rate of energy loss over a wave period is at most

\[
P_{\text{loss}} = \frac{1}{T} \int_0^T \mathbf{F}_d \cdot \mathbf{u} \, dt
\]

When compared to the energy flux associated with the passage of a wave train, this quantity provides a rough indication of the maximum possible level of wave damping caused by the kelp. In theory, it is also conceivable that plants could move in such a way so as to transfer some of their own kinetic energy (gained at the expense of wave energy) back to the water. However, the consequences of this plant-to-fluid kinetic energy exchange are assumed minor and are not explored in any detail here.

Field validation of the dynamical construct

A fully rigorous test of the above model across a complete range of conditions is not yet available because of the experimental and analytical difficulties that arise when confronting nonlinear waves. However, a preliminary check on the efficacy of the approach is possible for the subset of cases where the degree of nonlinearity is small. Gaylord and Denny (1997) and Denny et al. (1997) have conducted such tests previously, and a further example derived from these efforts is included here for completeness. Readers interested in greater detail should consult Denny et al. (1997).

Validation of the dynamical construct proceeded by mounting a 6.6-m-long Nereocystis individual on a force transducer positioned in 6.4 m of water within a small embayment at Hopkins Marine Station in Pacific Grove, California. The tensile force applied to the base of the stipe was recorded at 20 Hz by the transducer, and the subsurface pressure at the seafloor immediately adjacent to the plant was measured simultaneously. The sea surface elevation was then computed from the pressure record by decomposing 4,096-point segments of the time series into their Fourier components, correcting for the frequency-dependent depth attenuation that characterizes surface gravity waves and back-transforming (Kinsman 1965). The first 41 Fourier coefficients were used to define the component waves contributing to this variation in sea surface elevation, and the heights and periods of the waves were inserted into Eqs. 7 and 8 to calculate the corresponding velocity components and their respective phases (i.e., the monochromatic wave train assumption is relaxed here). Note, however, that because the Fourier partitioning of a random sea assumes linearity of the wave field (Kinsman 1965), just the first-order terms of the velocity equations were used. This approximation is appropriate in this context because the sea state during the field measurements was dominated by a 16-s period swell with a significant wave height of 0.8 m, which is only marginally nonlinear. The overall water motions at the location of the kelp were then estimated by summing all of the individual velocity components, and the summed values were inserted into the model together with the buoyancy term and flow factors involving derivatives of velocity (Eq. 863).
6) to predict the tensile forces acting on the plant. Finally, the predicted forces were compared, second by second, to the measured forces. As the example data presented in Fig. 2 indicate, although the general modeling approach is highly simplistic, it yields surprisingly accurate descriptions of actual flow forces imposed on kelps in nature.

An additional feature of the field experiments described above provides direct impetus for theoretical components of this study. The narrow embayment used for the force recordings is exposed to surface gravity waves propagating toward shore, but its geometry isolates it almost completely from larger scale alongshore currents. As a consequence, although the lack of alongshore fluid movement simplified the field logistics by eliminating the need to measure steady unidirectional flows (including Stokes drift because of the weak nonlinearity), it also precluded an empirical examination of more complex, three-dimensional motion of kelp individuals subjected simultaneously to both waves and currents. A primary purpose of the model results presented below, therefore, is to explore the consequences of coupled movement along three orthogonal axes at once.

Typical wave and current magnitudes

Wave conditions vary tremendously through time even at a single location; thus, kelp beds will generally experience a wide range of sea states. For example, Fig. 3a depicts the mean deep-water wave height spectrum measured offshore of Monterey Bay, California (National Data Buoy Center station 46042; 36°45.183′N, 122°25.350′W), during the winter months of 2001–2002. The error bars representing standard deviations show the high level of variability (which is greatest during this season), a characteristic also seen in plots of significant wave height ($H_s$, the average height of the highest one-third waves) measured hourly at the same location over the same duration (Fig. 3b). In general, the recorded dominant wave periods were ~10–12 s (i.e., wave frequencies 0.10–0.08 Hz), but shorter and longer period waves were common (e.g., $T \sim 5$–20 s). Significant wave
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Fig. 4. Rates of co-occurrence of waves and currents. Fraction of hours during the winter months of 2001–2002 that were characterized by specific combinations of significant wave height, dominant wave period, and alongshore current speed. For example, waves with a significant wave height of 0–2 m and a dominant period of 10 s were present together with a 10 cm s⁻¹ alongshore current during approximately 5% (60 h) of the winter (Fig. 4a). Similarly, waves with a significant wave height between 2 and 3 m and a dominant period of 12 s were associated with a current of 25 cm s⁻¹ during approximately 1% (12 h) of the winter (Fig. 4b). Although conditions during other years and months, or at other sites, will obviously differ somewhat from those shown (winter conditions tend to bound those of other seasons), these data provide a general sense of the range of wave–current climates that interact with subtidal macroalgae along substantial portions of the coast of North America.

Predicted forces on canopy-forming kelps and wave damping by them

The above empirical data (i.e., the field measurements of force, wave height, and current speed) have served primarily as validation for the dynamical model and justification for the parameter values employed. With this supporting information in hand, we now turn to a discussion of the model predictions themselves.

As can be seen in Fig. 5, the drift velocities of Eq. 10 induced by finite amplitude waves increase with wave steepness, which means that larger waves of shorter period pro-
duce faster net onshore currents. In some circumstances, these flow speeds are by no means trivial, approaching or even exceeding several centimeters per second. Such flow rates rival those associated with many other important nearshore fluid dynamic processes (e.g., geostrophic currents, buoyancy-induced flows, wind-driven circulation; see Pond and Pickard 1983). As a consequence, it is clear that the net fluid motions from surface gravity waves will potentially have strong biological import.

One arena where Stokes drift appears to influence canopy-forming seaweeds, as alluded to above, is with regard to the forces that act on them. If there is no net mass transport of water, which is the case for purely linear waves, then a strategy of “going with the flow” is often effective at reducing relative velocities and decreasing force. This is particularly true for longer period waves, where applied forces from the oscillations of linear waves are often smaller than the forces that would arise if those same peak orbital flows were applied as unidirectional currents (Fig. 6). This point has been made previously in a number of studies (Koehl 1984, 1986, 1999; Johnson and Koehl 1994; Denny et al. 1997; Gaylord and Denny 1997). The presence of Stokes drift, however, appears to offset many of these advantages. As Fig. 7 indicates, forces imposed on a typical mature Nereocystis individual by Stokes waves can exceed those imposed by linear waves by over a factor of four, depending on the wave height and period. The effect is particularly exacerbated under larger, longer period waves, exactly the conditions characteristic of storm waves, which are rarely sampled in the field but which indeed damage many plants (Seymour et al. 1989). In contrast, forces from shorter period Stokes waves might actually be lower than those associated with the linear case, although such situations often correspond to the scenario where moving with the fluid has already increased force because of the phenomenon of inertial loading (Fig. 6).

It is in this situation when Stokes waves are present where an alongshore current can come into play. As is indicated in Fig. 8, steady flows that act perpendicular to the axis of wave propagation can often reduce substantially the forces applied by Stokes waves. This effect typically becomes more pronounced as the magnitude of the alongshore current increases. With relatively rapid, but nonetheless common, alongshore flow rates of 0.3–0.5 m s$^{-1}$ (Figs. 3, 4; see also Gaylord et al. 2002 and references therein), forces can decline by as much as a factor of two. Note that this reduction occurs even though the summed magnitudes of the orbital velocities and alongshore current would otherwise suggest the potential for a much larger total relative velocity.

The general mechanisms by which alongshore currents ameliorate force can be isolated from a careful consideration of the trajectories of plant canopy displacement (Fig. 9). Typically, except under benign conditions where net buoyancy is the largest force, drag dominates the loading (magnitudes of virtual buoyancy and added mass forces vary with

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**Fig. 5.** Magnitude of the horizontal Stokes drift velocity at the water surface, as a function of wave height, for several wave periods, $T$. Water depth = 10 m.

**Fig. 6.** Ratio of the maximal force applied to a typical Nereocystis individual by linear waves to the maximal force from unidirectional flow for a range of wave heights and several wave periods, $T$. The unidirectional flows are assumed to have the same speeds as the peak orbital velocities associated with the corresponding waves. Water depth = 10 m, plant length = 10 m.

**Fig. 7.** Ratio of the maximal force applied to a typical Nereocystis individual by Stokes waves to the maximal force from linear waves for a range of wave heights and several wave periods, $T$. Water depth = 10 m, plant length = 10 m.

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**Fig. 8.** Magnitude of the horizontal Stokes drift velocity at the water surface, as a function of wave height, for several wave periods, $T$. Water depth = 10 m.
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Fig. 8. Ratio of the maximal force applied to a typical Nereocystis individual by Stokes waves in the presence of an alongshore current to the maximal force arising in the absence of a current, for a range of wave heights. Water depth = 10 m, plant length = 10 m. (a) Wave period = 5 s. (b) Wave period = 10 s. (c) Wave period = 20 s.

Fig. 9. Predicted trajectories of a typical Nereocystis canopy exposed to linear or Stokes waves of 2.5 m height and 10 s period, with or without a 0.3 m s\(^{-1}\) alongshore current. Notice that the presence of the current reduces the peak displacements (and thereby the stretch in the stipe) along the x- and z-axis, the two dominant directions in which drag is applied. The two-headed arrows in panels a and c indicate orbital motion in the vertical plane oriented parallel to the direction of wave propagation. (a) Trajectories viewed from above. (b) Trajectories viewed as if looking along the wave crests. (c) Trajectories viewed as if looking back along the axis of wave propagation. Water depth = 10 m, plant length = 10 m.

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Wave height (m)

Max force / Max force with zero current

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Wave forces on kelp canopies

Wave forces on kelp canopies

Wave forces on kelp canopies

Wave forces on kelp canopies

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alongshore component of force. This is possible because current velocities are typically smaller than wave-induced orbital velocities. The critical force amelioration therefore occurs as the kelp’s canopy is pushed off to one side by the current (Fig. 9c), where it lies both lower in the water column (reducing the degree to which the plant’s stipe is stretched vertically by the waves; Fig. 9b,c) and closer to its neutral position along the x-axis (reducing the extent to which the kelp is tugged by waves along the direction of wave propagation; Fig. 9a,b).

This basic phenomenon occurs across a variety of wave–current combinations, with reductions in force especially apparent in the case of shorter or intermediate-period waves ($5$ and $10$ s; Fig. 8a,b). For waves of $20$ s period, alongshore currents affect force much less strongly, and under some circumstances (i.e., smaller waves, faster currents) can actually increase force somewhat (Fig. 8c). This less typical outcome arises as a consequence of a kelp canopy now having sufficient time during the longer wave period to swing completely around from its neutral position off to one side, to where it can be fully extended along the axis of wave propagation. In such situations, the alongshore current loses its ability to offset the x-directed force and thus simply adds to the overall force total. In general, effects of alongshore currents appear to be greatest with smaller wave heights for wave periods of $5$ and $20$ s and with larger $H$ for waves of a period of $10$ s (Fig. 8). As is indicated in Fig. 4, shorter and longer period wave events in central California are indeed often characterized by smaller wave amplitudes, and the majority of large wave events are often characterized by wave periods between $10$ and $16$ s.

Such comparisons can also be extended to examine whether, in the face of Stokes drift, alongshore currents intrinsically improve a plant’s ability to oscillate passively with the fluid to avoid peak relative flows. This is analogous to the phenomenon explored in Fig. 6 for linear waves and no alongshore current. Data in Fig. 10 suggest that, even when Stokes drift is present, faster alongshore currents allow commonly for a robust drop in force relative to values that would arise in equivalent unidirectional flows (i.e., unidirectional flows with speeds equal to the peak wave velocities), where water motion relative to a plant is unavoidable. This is particularly the case for smaller waves of shorter period ($H < 2$ m, $T = 5$ s), where forces from Stokes waves in the absence of an alongshore current would be substantially larger than those that would arise in equivalent unidirectional flows (Fig. 10a). For longer period waves ($T = 20$ s), the effect of alongshore current speed is negligible and forces in oscillatory flow are universally less than those in unidirectional flow (Fig. 10c). Together, these patterns suggest that, regardless of wave conditions, the action of a sufficiently fast alongshore current can function to offset almost entirely the potential negative consequences of acquiring momentum. The final component of this conclusion is further supported by results of Fig. 11, which show canopy accelerations of kelps exposed to Stokes waves ($H = 2.5$ m, $T = 10$ s) with and without an alongshore current. The much smaller accelerations in the presence of the alongshore current indicate a greatly reduced susceptibility to inertial forces.

Passive movement in response to flow also has consequences for levels of damping experienced by waves passing through kelp forests. Under all wave and current conditions examined in this study, the kelp’s motion reduces the rate at which wave energy is lost to drag, relative to the rate of energy loss that would arise if the plants were stationary (Fig. 12). In most cases, predicted rates of energy loss are 2–20 times lower than they would be for rigid organisms. For waves of shorter period ($T = 5$ s; Fig. 12a), this ratio...
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Fig. 11. Acceleration of a typical Nereocystis canopy exposed to 2.5-m-high Stokes waves with a 10-s period in the presence or absence of an alongshore 0.3 m s\(^{-1}\) current. Note the much greater accelerations in the absence of the current, indicating an exacerbated vulnerability to inertial forces.

Fig. 12. Ratio of the rate of wave energy loss from a single Nereocystis, to the rate of energy loss that would arise if the plant didn’t move (aside from passively streamlining) in response to the passing waves, as a function of wave height and alongshore current speed. (a) Wave period = 5 s. (b) Wave period = 10 s. (c) Wave period = 20 s.

Results of this study therefore provide data on two general fronts. First, evidence presented here indicates that alongshore currents provide a robust mechanism for ameliorating forces imposed on canopy-forming kelps across a wide va-
Fig. 13. Ratio of the rate of wave energy loss during wave propagation through a *Nereocystis* bed relative to the incident wave energy flux, as a function of wave height and current speed. Each wave is assumed to propagate through 50 plants on its way to the shore. (a) Wave period $T = 5$ s. (b) Wave period $T = 10$ s. (c) Wave period $T = 20$ s.

A variety of incident wave conditions. Second, this study yields insight into how plants in turn influence the waves themselves through hydrodynamic feedback. Although such core model findings should be applied in their strictest sense only to *Nereocystis*, major themes might also repeat in other canopy-forming species as well. *Pelagophycus*, for example, maintains its blades near the water surface like *Nereocystis*, and probably responds similarly to flow. *Macrocystis* produces a cluster of fronds that extend throughout the entire water column and thus shows a somewhat different vertical architecture. However, as much as 70–80% of the biomass of individuals of this species can be held within the canopy (D. C. Reed unpubl. data), which suggests in turn that flow-induced motion of *Macrocystis* could be more similar to that of *Nereocystis* than might initially be expected. Additionally, although previous studies (e.g., Jackson and Winant 1983; Jackson 1998) have emphasized the exceptionally slow flows present within extensive *Macrocystis* forests in Southern California—which would suggest only a minor role for currents in affecting the motion of these organisms—beds of *Macrocystis* elsewhere are universally far smaller and could therefore damp currents much less. Thus, speeds of currents past *Macrocystis* plants in many locations along the coast of North America might be of sufficient magnitude to have effects similar to those predicted for *Nereocystis*. Until the necessary experiments have been conducted, however, such possibilities will remain in the realm of speculation.

Much of the work described here builds on previous models (e.g., Seymour and Hanes 1979; Dalrymple et al. 1984; Seymour 1996) in accounting explicitly for particular morphological features and dynamical behaviors (i.e., streamlining, acquisition of momentum, reorientation) that characterize canopy-forming kelps and control their mechanics of motion. The present work also complements recent studies on smaller, submergent macroalgae (e.g., *Laminaria hyperborea*) that exhibit somewhat different responses to flow (Asano et al. 1992; Kobayashi et al. 1993; Dubi and Torum 1994). As such, although it should be emphasized that the results presented above have not attempted to examine the full range of possible flow conditions and kelp sizes/shapes and have ignored complexities such as interactions among multiple individuals within dense kelp stands, this research brings us yet one step closer to a full understanding of how seaweeds in general and canopy-forming kelps in particular survive successfully in their fluid environments as they cope with the omnipresent waves that impinge on them. Of course, the topic of wave forces represents but one of a whole suite of factors influencing the population dynamics of these plants and their ecosystem functioning; clearly a full synthesis will require consideration not only of processes driving physical disturbance, but of all such factors.

**References**


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