Limnol. Oceanogr., 38(2), 1993, 396–407 © 1993, by the American Society of Limnology and Oceanography, Inc.

A dynamic model for wave-induced light fluctuations in a kelp forest

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Abstract

We formulated a dynamic model with linear wave theory to predict the effects of wave height, wave length, and water depth on modulation of the local surface cover in a Macrocystis pyrifera canopy. This model was incorporated into a general model for attenuation of photosynthetically active radiation (PAR) in a M. pyrifera forest with particular emphasis on light reaching understory algae. The model predicts that the period of fluctuations of PAR on the bottom matches that of the dominant wave period and that the amplitude of irradiance peaks is increased by positive local surface areal stain during the trough of a wave. Field measurements of instantaneous irradiance and surface elevation and simultaneous video recording of the surface canopy allowed investigation of these predictions. Cross-correlation analysis on irradiance and surface elevation measurements showed a significant negative correlation between surface elevation and PAR reaching the understory. This correlation cannot be attributed to the decrease in lightpath length alone, but can be explained by the change in M. pyrifera surface cover. Measured changes in instantaneous fractional canopy cover exceeded theoretically predicted values by a factor of as much as 3. Consequently, the intensities of light flecks exceeded predictions. A combination of mechanisms, as well as assumptions of the model, may explain the deviation between the magnitudes of predicted and measured fluctuations in canopy cover and light. The dominant period of ocean swells is typically in the range of 5-20 s, and light flashes with these periods have been shown to effect significant gains in light utilization efficiency by certain algae.

In the understory of multilayered forests, transient bursts of intense direct illumination (known as sun flecks) occur for seconds to several minutes as gaps in the canopy line up with the sun (Pearcy 1988). These sun flecks may compose a large portion of the daily irradiance reaching understory species in both terrestrial hardwood forests and marine kelp forests (Pearcy 1990; Gerard 1984), and their photon flux density and frequency can change the photosynthetic capacity of understory plants (Pearcy 1988, 1990; Chazdon 1988). For instance, physiological responses to sun flecks by rain forest understory plants suggest that these plants make efficient use of high intensity photosynthetically active radiation (PAR) of short duration (5–20 s) (Chazdon and Pearcy 1986*a*,*b*). Similar results have been found for some marine algae (Dromgoole 1987, 1988; Greene and Gerard 1990; Wing unpubl. data). In both terrestrial and marine systems, forests with highly variable PAR may support higher understory productivity than forests with similar average irradiance but lower variance.

In the marine environment much of the variance in PAR is caused by surface waves that can focus PAR (Dera and Gordon 1968; Snyder and Dera 1970; Fraser et al. 1980) or increase its penetration into algal stands by mechanical disruption of self-shading (Koehl and Alberte 1988; Leigh et al. 1987). Consider, for example, the "forest" formed by the giant

Acknowledgments

We acknowledge the advice and assistance of the following persons; Bob Pearcy, Jim Quinn, Mark Patterson, Lou Botsford, Jim Dykes, Laurie Sanderson, Jim Watanabe, Rodger Phillips, Emily Bell, John Lee, and Peter Edmunds. Data on wave parameters from Montercy Bay, and light measurements at Pt. Joe were provided by the Monterey Bay Aquarium Research Department.

This work was supported in part by a Sigma Xi Grantin-Aid of Research, University of California Reserve System grant 54354-8, and a University of California Jastro-Shield Grant-in-Aid of Research to S.R.W., and NSF OCE 90-16721, and NSF OCE 87-16688 to M.W.D. J.J.L. was supported by a Friend's of Hopkins Marine Station fellowship.

kelp Macrocystis pyrifera. A large portion of PAR attenuation occurs in the floating canopy. where light penetration decreases exponentially with canopy cover (Gerard 1984). Consequently PAR beneath undisturbed M. pyrifera canopies may be reduced to only 1-5% of surface irradiance (Reed and Foster 1984). However, under normal conditions the canopy is constantly disturbed by surface waves and PAR may be highly variable in the understory. We have noticed that photon flux density beneath the canopy varies on a scale of minutes as large patches of canopy drift back and forth with the arrival of sets of waves (surf beat). Light intensity also varies on a scale of seconds as the distribution of gaps between floating algal blades varies due to the action of individual surface waves. These latter fluctuations occur over a frequency range (1-0.05 Hz) that may affect gains in the efficiency of light fleck utilization of understory macroalgae (Dromgoole 1987; Greene and Gerard 1990). We modeled the effects of surface waves on light levels under floating algal canopies and compared the predictions of the model with data collected beneath a *M. pyrifera* canopy and from a nearby area without kelp in Monterey Bay, California.

A dynamic model of PAR in an understory kelp environment

Instantaneous photon flux density at a point below a floating macroalgal canopy is a function of four factors: ambient irradiance above the air-water interface, penetration of the water's surface, attenuation of light by algal tissues at the surface, and attenuation with depth.

Light penetration of a flat water surface depends on ambient levels of direct downward irradiance $E_d(sun)$, diffuse downward irradiance $E_d(sky)$, and T_s , the transmittance for the total downward irradiance through the surface:

$$E_d(0) = [E_d(\operatorname{sun}) + E_d(\operatorname{sky})]T_s.$$
(1)

Here $E_d(0)$ is downward irradiance just below the water's surface (μ Einst m⁻² s⁻¹).

Transmittance of light through the surface (T_s) is a function of albedo (defined as the ratio of upward radiation flux to the amount of radiation incident on a surface.) In most cases reflected radiation dominates the upward radiation flux (i.e. albedo $\approx \rho$) (Jerlov 1976). The

albedo of a smooth ocean surface varies with sun zenith angle from 0.04 at zenith angle of 0° (solar noon) to 0.28 at zenith angle of 80° (Holmes 1957). If the water's surface is not flat, Eq. 1 is not strictly accurate. Typical surface waves, such as those we measured in Monterey Bay, may influence albedo at high zenith angles and albedo may increase as much as 10% on a choppy day with white caps (Lobban et al. 1981). However, whitecaps are not common in dense kelp beds as short period choppy waves are damped by floating algal canopies.

Transmittance by light-absorbing objects floating at the water's surface depends on the percent cover of the objects and their absorption properties:

$$T_c = (1 - bA) \tag{2}$$

where T_c is transmittance through the canopy, b the fractional canopy cover, and A absorptance by the canopy. Absorptance of single M. pyrifera blades has been measured as 66% of incident light (Gerard 1984). In addition, attenuance may be enhanced by local reflection and backscattering by plant tissue in the canopy (Gerard 1984).

Following penetration of the water surface and algal canopy, PAR decreases exponentially in water with uniform particulate concentration (Jerlov 1976):

$$E_d(z) = E_d(0)\exp(-zk_d) \tag{3}$$

where $E_d(z)$ is irradiance at depth z (µEinst $m^{-2} s^{-1}$) and k_d the vertical irradiance attenuation coefficient for zenith sun (m^{-1}). This equation assumes that attenuation across depth strata is dominated by absorption and there is only a small percentage of backscatter in the total radiation flux (Jerlov 1976). Over the range of PAR, extinction is usually highest in the top few meters of water and falls progressively lower with depth as high-energy wavelengths are attenuated. Transmittance through the water column (T_w) is represented by $exp(-zk_d)$.

Seasonal changes in PAR attenuation through the water column in *M. pyrifera* forests are correlated with changes in sediment flux (Dean 1985). However, attenuation may also be influenced by vertical *M. pyrifera* fronds in the water column, particularly close to the upright portion of the fronds (Gerard 1984).

Multiplying Eq. 1, 2, and 3, we can approx-

imate steady state irradiance for a point below the surface as a function of depth:

$$E_d(z) = [E_d(\operatorname{sun}) + E_d(\operatorname{sky})]T_sT_cT_w.$$
 (4)

The parameters $E_d(sun)$, $E_d(sky)$, T_s (as a function of solar elevation), and k_d (in T_w) vary over long periods of time relative to the wave period. For example $E_d(sun)$, $E_d(sky)$, and T_s have components that change in a predictable fashion over a diel cycle, and k_d may vary between days. However, these factors as well as water depth (z), alignment of surface fronds with the sun, and fractional canopy cover (b)may change over shorter periods as well, for example as waves pass through the canopy. These short period fluctuations conspire to produce a highly complex and variable light environment in the understory of kelp forests. Major components of this variance may be correlated, however, with wave period and amplitude.

Two wave-induced mechanisms for irradiance fluctuations are due solely to the optical properties of seawater. First, path length of direct light changes over the period of a wave (the path length is long under a crest, short under a trough), producing fluctuations that are 180° out of phase with the water's surface elevation when the sun is directly overhead. The magnitude of these fluctuations is directly related to attenuance of the water column (Nikolayev et al. 1971). Second, waves may act as lenses that focus light at some depth dependent on wave height, wave length, and the zenith angle of the sun (Snyder and Dera 1970). The combination of these two mechanisms produces a spectrum of light fluctuations with two conspicuous peaks at shallow depths (<21m) (Nikolayev et al. 1971). The first peak is correlated with the dominant wave frequency and is caused by the fluctuating light path length. The second peak, at higher frequency, is apparently due to lens effects from surface waves (Nikolayev et al. 1971; Nikolayev and Khulapov 1976). Over the range of depths considered here (5-10 m), these two frequency peaks are distinguishable.

Two other mechanisms driving short period irradiance fluctuations are produced by movement of kelp fronds. First, on cloudless days clumps of blades may block direct lighting from the sun. When waves move the canopy as a whole, irradiance on the bottom varies according to the spatial distribution of fronds on the surface and alignment of clumps of blades with the sun. Under dense canopies, when there are only small gaps between blades, we expect that wave-induced translation of the canopy will produce light fluctuations of a frequency much higher than the dominant wave frequency. Second, as a wave passes through the canopy, we expect b to vary as the water's surface is stretched and compressed, producing light fluctuations at the same frequency as the waves.

In this study, we concentrate on the second mechanism of variation in canopy cover as a source of fluctuation in subcanopy PAR. We model the variation in kelp canopy cover with a hypothetical canopy consisting of a uniform distribution of light-absorbing fronds. Initially fronds float on a still water surface, to which we then impose a sinusoidal wave form. A wave crest is an area where water is pushed together and therefore up; conversely a trough is an area where water is pulled aside and the surface is lowered locally. As a result of these wave-induced motions of the surface water, floating fronds are pushed together near the crests and pulled apart in the troughs. In our calculations wave-induced movement of fronds is approximated by assuming that fronds are free to move with the water in which they float, thus the horizontal and vertical displacement of fronds is modeled by the horizontal and vertical displacement of the surface water.

The equations of linear wave theory can be used to predict vertical (z) and horizontal (x-y)plane) particle displacement during passage of a wave, given a set of crucial assumptions about the nature of the wave form and the fluid through which it moves (Denny 1988). We assume that wave height H is small relative to the wave length L, that L is large enough so that capillary effects are negligible (L > 0.1 m), that all variation in surface elevation is in the plane of wave propagation (x-z) (i.e. variance in surface elevation along the y-axis, perpendicular to propagation, is negligible), and that water motion is irrotational. As defined by linear wave theory, instantaneous horizontal (x), and vertical (z) displacements for a particle at the water surface moving along its orbital path are

horizontal displacement

$$=\frac{\mathrm{H}}{2\tanh(kd)}\sin(kx-\omega t),\qquad(5)$$

and vertical displacement

$$=\frac{H}{2}\cos(kx-\omega t)\tag{6}$$

where d is the depth of water below still water level (in m), $k = 2\pi/L$, $\omega = 2\pi/T$, and T is the wave period.

Consider a small rectangular area of the water surface with length (l) along the x-axis and width (w) along the y-axis. As a wave crest passes, the length and therefore the area of the rectangle decreases. As a wave trough passes, the length (and area) expand. Because an ideal wave has no components of velocity parallel to the wave crest, the width of the rectangle remains constant. The magnitude of expansion and contraction of the length depends on the strain (ϵ_x) imposed on local water surface area during a wave cycle.

Now envision two points on the undisturbed water surface, one at x = 0 and the other at a distance D along the x-axis. In the presence of surface waves the distance Ψ between the points along the x-axis varies as points are moved horizontally by waves. Equation 5 gives the instantaneous horizontal displacements for the two points x = 0 and D. Thus at any time t

$$\Psi = \left[\frac{-H}{2 \tanh(kd)}\sin(kD - \omega t) + D\right]$$
(7)
$$+ \left[\frac{H}{2 \tanh(kd)}\sin(-\omega t)\right].$$

The change in distance between the points is their instantaneous distance Ψ minus the original distance D. Thus, noting that $\sin(-\omega t) = -\sin(\omega t)$ and rearranging terms,

$$\Delta \Psi = \frac{-H}{2 \tanh(kd)} [\sin(kD - \omega t) + \sin(\omega t)].$$
(8)

Engineer's strain (ϵ_x), the fractional stretching of the water's surface in the x-direction, is defined as $\Delta \Psi/D$, so

$$\epsilon_x = \frac{-H}{2D \tanh(kd)} [\sin(kD - \omega t) + \sin(\omega t)].$$
(9)



Fig. 1. Relationship between surface areal strain (ϵ_x) (dimensionless) and surface elevation as predicted by Eq. 9. ω (radian wave frequency) multiplied by time (*l*) gives the phase of a wave form in radians. Amplitude and phase of maximum strain is dependent on the ratio of gap distance (*D*) and local wave length (*L*). For the simulation, H = 1.0 m, L = 100 m, and d = 10 m. Surface elevation is represented by the dashed line.

When D is small, engineer's strain plotted against time varies sinusoidally through the period of the wave, with the maximum in the trough when particles are below their still water position and the minimum strain at the wave crest as the particles are above it (Fig. 1). Maximum strain increases with H and decreases with an increase in L.

Note that the wavelength is a monotonically increasing function of wave period:

$$L = \frac{gT^2}{2\pi} \tanh(kd) \tag{10}$$

so that strain decreases with wave period.

The magnitude of strain (ϵ_r) is sensitive primarily to changes in H and water depth (Fig. 2). Note also the dependence of strain on the scale of D/L, evident from Fig. 1. The larger the D one chooses, the smaller the average strain over that length as surfaces with different phases are added together. Note also that the phase at which the maximum strain occurs depends on the scale of D/L. If D/L is small, but not zero, there is a slight phase shift in maximum strain away from 180°. To take an extreme example, if D = L the two points move in phase and $\epsilon_x = 0$. For kelp canopies, D is a measure of the distance between clumps of functionally unconnected blades along the x-axis. This distance is usually small relative to wave length (D/L < 0.01). Therefore in our



Fig. 2. Sensitivity of local surface areal strain (ϵ_x) (dimensionless) from Eq. 9 to changes in wave height (H) (m), water depth (d) (m), and wave length (L) (m). ω (radian wave frequency) multiplied by time (t) gives the phase of a wave form in radians. Strain is most sensitive to changes in H, followed by d, and L. Normal values (except when changed) are H = 1.0 m, d = 10.0 m, and L = 100.0 m.

model the strain is estimated as D approaches 0.

Noting by algebraic identity that

$$\sin(kD - \omega t) = \sin(kD)\cos(\omega t) - \cos(kD)\sin(\omega t)$$

and that as D approaches 0, sin(kD) approaches kD and cos(kD) approaches 1, for small D,

$$\sin(kD - \omega t) \approx kD\cos(\omega t) - \sin(\omega t).$$

Therefore

$$\epsilon_{x,D \to 0} = \frac{-Hk}{2 \tanh(kD)} \cos(\omega t).$$
(11)

Noting that $k = 2\pi/L$ (definition) and $\cos(\omega t) = \cos(-\omega t)$, we arrive at an expression for strain as *D* approaches zero:

$$\epsilon_{x,D \to 0} \cong \frac{-\pi H}{L \tanh(kd)} \cos(-\omega t).$$
 (12)

From Eq. 6, we calculate that at x = 0 (where we calculate the strain) the surface elevation for the wave is

$$\eta = \frac{H}{2}\cos(-\omega t). \tag{13}$$

Thus, solving for $\cos(-\omega t)$ and substituting in Eq. 11,

$$\epsilon_x = \frac{-2\pi}{L \tanh(kd)} \,\eta. \tag{14}$$

In other words, the strain is 180° out of phase with the surface elevation, as we expect, and the extreme local strain is

$$\epsilon_{x,\max} = \pm \frac{\pi H}{L \tanh(kd)}.$$
 (15)

Note also that the total change in strain through the wave period is

$$\Delta \epsilon_{x,\max} = \frac{2\pi H}{L \tanh(kd)}.$$
 (16)

In deep water, where d > L/2, $tanh(kd) \approx 1$, so

$$\Delta \epsilon_{x,\max} \cong \frac{2\pi H}{L}.$$
 (17)

In shallow water, where d < L/20, $\tanh(kd) \approx 2\pi d/L$, so

$$\Delta \epsilon_{x,\max} \cong \frac{H}{d}.$$
 (18)

If we assume that blades of the algal canopy are uniform light-blocking objects that never overlap, the area of surface canopy is constant while the area of the water's surface changes with time, dependent on local wave-induced strain. As a result, local fractional canopy cover (b) varies with time. Instantaneous b is thus a function of surface strain:

$$b(t) = \frac{b_0}{(1 + \epsilon_x)} \tag{19}$$

where b is a function of time t, b_0 is b at still water, and $(1 + \epsilon_x)$ the extension ratio.

It now becomes clear that the ratio of direct $[E_d(sun)]$ to diffuse $[E_d(sky)]$ radiation incident on the water surface is important for the appropriate choice of an equation for strain in Eq. 19. On a clear day where direct radiation is the dominant component of PAR from the surface most of the PAR reaching an understory kelp comes from one particular angle (i.e. effective D is small), and Eq. 12 is an appropriate estimate for the strain used in Eq. 19. However, if the PAR reaching an understory kelp is derived from a large area of the surface. such as on a cloudy day when diffuse radiation is the dominant component of PAR, and D is effectively increased, the effect of local canopy strain on irradiance at the bottom will be smaller, as D is effectively increased. In this case, D is a measure of the total gap distance along the x-axis from which light comes, and Eq. 9 allows for a more appropriate estimate of average surface areal strain over this distance.

A fundamental simplification in our model is that blades of kelp do not overlap and are free to move with the surface water. In reality, blades can overlap when the surface is compressed, and their motion can be constrained by their stipes, which are tethered to the bottom. However, our video records taken in the field show that stipes are typically long enough to allow surface fronds to "go with the flow," and that the simplifications made in our model are appropriate for present purposes. Note that in very shallow water horizontal displacements in waves are magnified (Eq. 5) and waves may break. Under these conditions, the assumption of independent motion by the fronds is clearly violated and our model is inappropriate.

Field measurements of instantaneous pho-

ton flux density, surface elevation, and simultaneous video recording of the surface canopy allowed us to compare the general predictions of our model against actual wave-induced light variation beneath a *M. pyrifera* canopy.

Methods

We measured PAR under M. pyrifera canopies to determine the relative influence of surface fronds (Eq. 2) vs. midwater vertical fronds on PAR attenuation through the water column. PAR was measured at a depth of 13 m at three adjacent sites (A, B, and C) under a monospecific M. pyrifera canopy at Pt. Joe near Monterey (35°36.5'N, 121°57.5'W). The sites were of similar algal density (~ 0.5 individuals m^{-2}), depth (within 0.5 m), and bottom profile and were separated by no more than 100 m. PAR measurements on the bottom were collected simultaneously at each study site with three LiCor LI-193SA 4π light sensors interfaced with LI-1000 data loggers in waterproof housings. Site A was cleared of M. pvrifera by removing algae at the holdfast in a circular area with radius ~ 20 m around the light sensor. At site B, the floating surface fronds were cut away leaving the upright fronds and holdfast intact over an area of similar size around a second light sensor. At site C the canopy was left untouched over a third light sensor. PAR was integrated for 0.5-h intervals at each site for a period of 2 weeks. These data were then used to partition the effects of upright and floating algae on attenuation of light beneath the canopy. Differences in irradiance between sites were tested with a Friedman's rank sum test (Sokal and Rohlf 1981). Hours were averaged over the 2-week period and considered as blocks, and sites as the treatment effects. For the pairwise tests between sites a sequential Bon Ferroni correction procedure was used to minimize type 1 statistical error (Rice 1989).

To demonstrate the relative amount of variance in irradiance between the three sites we calculated the mean C.V. (SD \times 100/mean) for each daylight hour for the 2-week period. This measure allows us to compare the variance of sites with greatly different mean irradiance.

To investigate the predictions of our dynamic model of local areal strain we measured PAR on the bottom under a surface canopy of M. *pyrifera* while simultaneously measuring the height of waves passing through the canopy and recording a video image of the percent cover of the canopy. A 12-bit A/D converter and microprocessor supporting 28 kilobytes of static RAM (Onset Computer Corp.) sampled PAR from a LiCor 190SA 2π irradiance sensor, and hydrostatic pressure (a measure of wave height) from an Omega PX176-50psi pressure transducer at a frequency of 10 Hz. The A/D converter-microprocessor, light, and pressure sensors were housed inside an Ikelite 5810 strobe housing and the sampling period was started by closing a magnetic proximity reed switch that completes a circuit powering the A/D converter. Calibration of the light meter was performed against a NBS-traceable calibrated LiCor LI-193SA 4π quantum sensor in a collimated beam of light. In collimated light these two sensors measure the same irradiance. The pressure transducer was calibrated against a ScubaPro oil-filled depth gauge. Calibration was performed for 10 points for both light and pressure sensors across a range of values exceeding that measured in the field and both calibration curves were significant with r^2 values in excess of 0.97 (light $r^2 = 0.99$, P < 0.0001, pressure $r^2 = 0.98$, P < 0.0001).

Hydrostatic pressure on the bottom is an accurate predictor of wave height, but because wave-induced changes in pressure are attenuated with depth, the pressure record must be corrected with a depth-dependent scaling factor to determine actual wave heights (Denny 1988):

$$\Delta P_{\min,\max} = \frac{\rho g H}{2} \left[\frac{\cosh(ks)}{\cosh(kd)} \right]$$
(20)

where s is vertical distance from the bottom (in m) at which the sensor is located, g the gravitational acceleration (m s⁻²), and ρ the density of seawater (kg m⁻³).

Light and wave data were collected from 11 sites underneath *M. pyrifera* canopies ranging in depth from 6 to 10 m and situated along the shore from Hopkins Marine Station to Pt. Pinos, ~ 3 km to the north. Light and pressure data were also collected from two sites at 8-m depth with no *M. pyrifera* present. Maximum wave heights ranged from 0.34 to 1.28 m. The light and pressure sensors were positioned on the bottom 2-4 m away from the nearest *M. pyrifera* holdfast under canopies with an average density of 0.41 individuals m⁻² and average dry biomass of 91.5 g m⁻². In all cases there was a dense monospecific surface canopy with > 50% blade cover. Water clarity afforded 10-12 m of visibility. The instruments were positioned during midday (1130–1330) with SCUBA and sampling lasted 20 min at each site (12,000 data points for each sensor per sample). In all cases the sky was free of clouds during the measurement period. To investigate the predictions of the surface strain model, we compare measured changes in light levels on the bottom with predictions based on both predicted (Eq. 19) and measured changes in surface canopy cover. Predicted light levels were calculated with Eq. 4 assuming that the terms $[E_d(sun) + E_d(sky)], T_s$, and T_w remain constant over short time periods while T_c changes with canopy cover according to Eq. 2.

The study sites are characterized by a dense growth of *M. pyrifera* with a surface canopy and numerous understory species including *Rhodymenia arborescens, Dictyoneuropsis reticulata, Dictyoneurum californicum, Laminaria dentigera,* and *Desmarestia ligulata* (Harrold et al. 1988). The portion of the shore closest to Hopkins Marine Station is partly sheltered from ocean waves by Pt. Pinos; the area closest to Pt. Pinos is more exposed to open ocean swell (Harrold et al. 1988).

We performed cross-correlation analysis on the surface elevation-irradiance data from all sites to determine correlation between surface elevation and PAR. These analyses enabled us to test our predictions (Fig. 1) that the two series are cyclic with a phase lag of ~180°. Cross-correlation values were computed for lags (τ) from zero to twice the dominant wave period (T) as

$$R_{xy}(\tau) = \sum_{t=1}^{n} \frac{(x_t - m_x)(y_{t-\tau} - m_y)}{\sigma_x \sigma_y (n - \tau)} \quad (21)$$

where *n* equals the number of data points in the series, σ_x is the SD of the PAR values, σ_y the SD of the surface elevation values, m_y the mean of the surface elevation values, m_x the mean of the PAR values, and *t* the time increment of the data set (Kope and Botsford 1990).

The correlation values were then tested for significance by computing the variance of the cross-correlation with the statistic $\operatorname{var}[R_{xv}(\tau)]$

$$\approx \frac{1}{\gamma} \sum_{i=1-n}^{n-1} \left(1 - \frac{|i|}{\gamma} \right) \rho_{xx}(i) \rho_{yy}(i) \quad (22)$$

where γ is the number of data pairs $(n - \tau)$, i varies between 1 - n and n - 1, ρ_{xx} is the autocorrelation of the PAR values, and $\rho_{\nu\nu}$ the autocorrelation of the wave-height values. The test statistic uses the function $\left[(1 - |i|) \right]$ $\gamma \rho_{xx}(i) \rho_{yy}(i)$ to reduce error imposed on the cross-correlation values by positive autocorrelation in each time series x and y. Thus the intraseries correlation of each data set is accounted for in the test statistic (Kope and Botsford 1988). Note that this function represents 1 SE of a Gaussian distribution around zero. Therefore, in order for the cross-correlation values to be considered significant at the 0.05 level they must be greater in magnitude than 1.96 times the variance computed here. In the absence of intraseries correlation the expression becomes

$$\operatorname{var}[R_{xy}(\tau)] \approx \frac{1}{\gamma}.$$
 (23)

Fast Fourier transformations (FFT) were performed on the autocorrelation functions and the cross-correlation function to obtain the cross-spectral density between the two data sets (PAR and surface elevation) and the spectral density within each data set (PAR and surface elevation). This analysis allows one to determine the frequency range of variance that is positively correlated between the two data sets as indicated by the cross-correlation analysis.

To further our analysis of the strain model we examined the correlations between local surface area strain, ϵ_x (as indicated by changes in percent cover), and irradiance and between ϵ_x and surface elevation. Video records were collected simultaneously with the light and pressure record at five sites to determine time variance of local surface canopy cover. An 8-mm underwater video camera was positioned on the bottom pointing up at the canopy and synchronized with the light-pressure record. Frames from the video record were then digitized on an Apple Macintosh IIcx through a RasterOps 24-bit color frame grabber and analyzed for changes in percent cover of surface fronds with the NIH image analysis program Image 1.29. Frames were digitized of an $\sim 10 \text{ m}^2$ square patch of canopy directly above the sensor array at a frequency of 0.5 Hz. Each frame was then imported into the image analysis program and converted to gray scale. An index of percent cover was determined from the gray-scaled images where 0% is open water at the surface and 100% is total frond cover. The frames were analyzed with a column-averaging algorithm that averages the density of pixels across a specified area of the frame. Values for percent cover were then temporally matched with the light and pressure record.

Results

Shading by floating vs. midwater algal fronds-Averaged hourly irradiances at each of the three sites at Pt. Joe were computed for the 2-week sampling period and pairwise comparisons were made between sites. Results from the Friedman's rank sum tests of A vs. B, B vs. C, and C vs. A indicate that site C (the control, all fronds intact) is significantly different from site B (all surface fronds removed) (df = 1, P < 0.005) and from site A (surface and subsurface fronds completely removed) (df = 1, P < 0.005). Sites A and B are not significantly different from each other (df = 1, P >0.5). These analyses suggest that the upright fronds of *M. pyrifera* have relatively little influence on light penetration to the bottom compared with the floating canopy fronds. In light of this result, in our model (Eq. 4) we deal only with fractional cover changes in the canopy (b) and ignore the comparatively small influence of upright fronds on the extinction coefficient of light (k_d) in the water column.

Averaged irradiance at each hour of the day is more variable between days in areas with kelp than in clear areas. With the exception of a dip during the 1600-hour record for site C, the averaged C.V. for the 2-week period is high during all hours of the day for sites C (kelp intact), intermediate for site B (surface fronds removed), and consistently low in site A (cleared of all kelp) (Fig. 3). Cross-correlation analysis on wave and light data collected at two 8-m sites where *M. pyrifera* was absent showed no significant correlation between light and pressure.

Testing the predictions of the surface strain model—Autocorrelation of wave height and



Fig. 3. Plot of C.V. of PAR (μ Einst m⁻² s⁻¹) vs. time of day for three sites in a *Microcystis pyrifera* forest near Pt. Joe, Monterey Bay. Site A was cleared of all kelp and shows the lowest variation in PAR. Site B was cleared of floating surface fronds and shows intermediate variation in PAR. At site C the canopy was left intact and shows high variation during most of the day, except for a drop at 1600 hours for unknown reasons. Each site had a dense canopy of *M. pyrifera* before manipulations.

values of the cross-correlation of wave height and PAR [with lag (τ) from 0 to twice the wave period (T)] are cyclic and $\sim 180^{\circ}$ out of phase with each other. The peak cross-correlation values ranged from 0.01 to 0.35. Cross-correlation and autocorrelation averaged for all 11 samples were determined to be significantly different from zero with a triangular weighting function (Kope and Botsford 1990) (Fig. 4). FFT analysis of the autocorrelation of light and pressure and cross-correlation between light and pressure produce spectral density and cross-spectral density functions of the data. The spectral density results show that the variance in the light record that is correlated with surface elevation occurs at the same frequency as the dominant wave period.

Video images of the surface enabled us to measure an index of percent cover at five sites and to synchronize this record with the light and pressure record. We hypothesize that the index of percent cover is an inverse measure of the engineers strain (ϵ_x) at the water's surface. After image analysis the data for percent cover were plotted against the light and pressure records to explore the relationship between the percent cover of fronds on the surface directly over the light and pressure sensor and the light and pressure record. In all cases investigated, the percent cover index shows an



Fig. 4. Averaged cross-correlation coefficients (line C) between surface elevation and PAR (μ Einst m⁻² s⁻¹) on the bottom and averaged autocorrelation coefficients (line A) of surface elevation are ~180° out of phase. Values were averaged from 11 sites, with depth range from 6 to 10 m, average *Microcystis pyrifera* density 0.4 individuals m⁻² at each site. The sample size was 12,000 measurements for each sensor. Dashed lines indicate the variance in the cross-correlation statistic as calculated by Eq. 22 (cross-correlation values 1.96 times the variance are significant at the 0.05 level).

inverse relationship with the light record. However, the amplitude of changes in fractional canopy cover (b) tended to exceed theoretical predictions. For example, Fig. 5 displays a representative sample of data and corresponding theoretical estimates of changes in b. The phase of the changes in measured b corresponds with the theoretical prediction of Eq. 14-19. While the range of measured instantaneous canopy cover around the mean of 0.46 is 0.34-0.57, the predicted range is 0.42-0.49. The range of light levels around the mean of 54.7 μ Einst m⁻² s⁻¹ is 36–111, with transient peaks occurring on a frequency range of 5-10 Hz. When these high frequencies are filtered out with a 5-s moving average (dashed line in Fig. 5), the range is $41.5-72.2 \mu$ Einst m^{-2} s⁻¹. The range of predicted light levels calculated from the predicted changes in canopy cover is 54.0–55.6 μ Einst m⁻² s⁻¹, while the range of predicted light levels from the measured changes in canopy cover is 52.3-57.3 μ Einst m⁻² s⁻¹.

Discussion

The model—Models of light in M. pyrifera forests (e.g. Jackson 1987; Nisbet and Bence 1989) and empirical studies (Dean 1985) have described steady state extinction of light through the canopy with depth by means of simple exponential models (e.g. Eq. 3). This general approach has been questioned by investigators concerned with photosynthesis by plants exposed to transient bursts of sunlight (e.g. Pearcy 1990). For example, Gerard (1984) examined the variability of irradiance in M. pvrifera forests and concluded that temporal and spatial variability of PAR is extremely high and may influence the light utilization efficiency of algae in these environments. Here we investigated explicit mechanisms by which waves moving through the canopy may produce fluctuations in photon flux density on the bottom. The results are most applicable to studies concerned with light environment in the understory of kelp forests and utilization of fluctuating light by understory kelp species.

Analysis of our field data supports two general predictions of the surface areal strain model. Time-series analysis demonstrates that the dominant components of light fleck period beneath the algal canopy matches the period of waves passing through the canopy and that peaks in PAR are correlated with wave troughs (Figs. 1, 4, and 5). That no significant correlation between light and pressure existed for two areas without M. pyrifera suggest variation in light path length and focusing by waves can account for only a small fraction of the fluctuation in PAR. However, we do not dismiss fluctuating path length as a factor contributing to the total variance in light. Video records demonstrate that gaps between M. pyrifera blades widen in wave troughs and narrow as strain is relaxed over wave crests. However, the magnitudes of measured changes in canopy cover and of light flecks are greater in most cases than our model of strain predicts. Although the surface strain model is supported by the temporal correlation between local strain and PAR on the bottom, a combination of mechanisms may explain the observed patterns and the magnitude of light flecks.

One alternative explanation for the observed temporal changes in local percent cover and PAR on the bottom is that wave-driven horizontal transport of the canopy moves dense patches of canopy in and out of the reference frame of the video camera or back and forth in front of the sun. From the predictions of linear wave theory, one can see that the period



Fig. 5. Theoretical values for fractional canopy cover (line A, upper panel) are plotted with field measurements. This representative sample of fractional canopy cover (line B, upper panel), surface elevation (C), and PAR (D, solid line) shown in real time demonstrates the cyclic nature of each data series. Dashed-line D shows PAR with highest frequencies of variation filtered out with a 5-s moving average. These data were taken at an 8-m site near Hopkins Marine Station on 3 June 1990 at 1330 hours. The sensors were placed within 2-3 m of the nearest Microcystis pyrifera holdfast in an area with an average density of 0.4 individuals m⁻². Notice that there is a phase shift between the crests of waves and the corresponding peak in fractional canopy cover (b) and drop in PAR. The theoretical values for b were computed with Eq. 14 and 19 with surface elevations from curve C.

of horizontal particle displacement is matched with the period of surface waves. Consequently, one might predict that PAR on the bottom will fluctuate with the same period as surface elevation. Consider a kelp canopy with b = 0.5and haphazard placement of fronds in the canopy. Looking straight up from the bottom, there is an equal probability that a gap, or a clump of fronds, will line up with the sun at solar noon under still water conditions. There is thus an equal probability that the sun will be blocked during the crest of a wave or during the trough of a wave as the surface canopy is washed back and forth. If horizontal displacement of clumps of fronds governs light penetration through the canopy in this manner, the inverse relationship between PAR and surface elevation consistently observed in our data sets (Fig. 4) would not be expected. However, random phase lag caused by this mechanism is indistinguishable from phase lag caused by changes in solar elevation or variance in the D: L ratio.

Fluctuations in the path length of light as a

wave passes may introduce changes in irradiance on the bottom out of phase with surface elevation. For example, in previous studies of light in the ocean (e.g. Nikolayev et al. 1971), investigators found significant inverse crosscorrelations between light and pressure at the dominant wave period for the depths with which we are concerned (5-10 m). Further, in a 2-yr study of submarine irradiance at a 13.2-m site adjacent to a southern California kelp forest, Dean (1985) recorded coefficients of extinction (k) ranging from ~ 0.2 to 0.5. These values will produce changes in irradiance at 5-10 m ranging from 47 to 69% for a 1-m change in light path length. In our study we recorded cyclic changes in irradiance from 50 to 250% for similar changes in depth (6-10 m) and path length (0.5–1.25 m). Thus, fluctuating path length alone cannot explain the magnitude of these observed cyclic changes in irradiance.

At the depth range considered here, fluctuations in irradiance faster than the dominant wave frequency may be caused by lens effects from surface waves (Nikolavev et al. 1971). The focal length of these waves is subject to change with the zenith angle of the sun and the azimuthal orientation of the wave form with the sun. Small, high-frequency waves and the correspondingly high-frequency focusing patterns that they produce may be damped in dense kelp forests, but focusing patterns may well contribute to fluctuations observed in our data at frequencies in excess of the wave frequency, and we cannot dismiss this mechanism as a contributor to some of the highfrequency fluctuations we observed.

An explanation of the model's tendency to underestimate fractional canopy changes may lie in the assumption that kelp blades are uniform light-blocking objects that never overlap and that the area of the surface canopy is constant while that of the water's surface changes with surface strain (Eq. 19). Clearly, surface blades can overlap, and the area of floating canopy may not be entirely independent of surface strain. If blades are partially overlapping at their still water position (zero strain), their overlap will increase at maximum strain in wave crest and decrease in wave troughs, vielding a greater change in fractional canopy cover than the nonoverlapping model can predict. An understanding of the dynamics of kelp blade movement under the influence of surface waves could be an interesting focus of future investigations. However, the details of this problem are likely to be extremely complex.

The biological effects of light fluctuations – Distribution and abundance of benthic marine algae are strongly influenced by submarine irradiance (Luning 1981). Within multilayered stands of kelp, understory species may be shaded out by dense growths of canopy species, indicating that interspecific competition for light is an important structuring mechanism in these assemblages (Dean and Jacobsen 1984; Dayton 1985; Dean et al. 1989). Because surface waves predictably affect the delivery of light to the understory, M. pyrifera forests are an ideal system for the study of the physical dynamics of light flecks in an algal system and of the utilization of fluctuating irradiance by understory species. While light flecks beneath terrestrial plant canopies may be stochastically generated by heterogeneity of gap sizes in the canopy or disruption of the canopy by wind (Pearcy 1990), waves passing through M. pyrifera canopies typically produce light flecks on the bottom of relatively predictable, short duration and regular period (4-16 s). Light flecks in this range of duration are known to enhance the efficiency of light fleck utilization of three species of benthic macroalgae: Carpophyllum maschalocarpum, Hormosira banksii, and Ecklonia radiata (Dromgoole 1988). In these studies, efficiency of light fleck utilization is a dimensionless ratio of photosynthetic rate under fluctuating PAR and the photosynthetic rate predicted from steady state values (e.g. Chazdon and Pearcy 1986a). Greene and Gerard (1990) found that growth rates of Chondrus crispus were elevated under high-frequency (1 Hz) light fluctuations, above saturation irradiance, but not under light fluctuations below saturation irradiance. The results of Greene and Gerard (1990), and Dromgoole (1987, 1988) have ecological significance in the context of a multilayered stand of macroalgae with environmental frequency and amplitude modulation of PAR by ocean waves. Differences in the period and amplitude of wave-modulated light flecks along a wave exposure gradient formed by geomorphological characters of the shoreline may result in differences in the photosynthetic capacity of understory algae across these environments.

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Submitted: 6 February 1991 Accepted: 30 June 1992 Revised: 23 October 1992