*Annals of Botany* **XX**: 1–11, 2023
https://doi.org/10.1093/aob/mcad094, available online at www.academic.oup.com/aob

ANNALS OF
BOTANY
Founded 1887

# Wave damping by giant kelp, *Macrocystis pyrifera*

**Kristen Elsmore[1,*], Kerry J. Nickols[2], Luke P. Miller[3], Tom Ford[4], Mark W. Denny[5] and Brian Gaylord[1,6]**

*[1]Bodega Marine Laboratory, University of California at Davis, 2099 Westshore Road, Bodega Bay, CA 94923, USA, [2]Department of Biology, California State University, Northridge, 18111 Nordhoff Street, Northridge, CA 91330, USA, [3]Department of Biology, San Diego State University, 5500 Campanile Drive, San Diego, CA 92182, USA, [4]Coastal Research Institute, Loyola Marymount University, 1 Loyola Marymount Drive, Los Angeles, CA 90045, USA, [5]Hopkins Marine Station, Stanford University, 120 Ocean View Boulevard, Pacific Grove, CA 93950, USA and [6]Department of Evolution and Ecology, University of California at Davis, 1 Shields Avenue, Davis, CA 95616, USA*
*[*]For correspondence. E-mail keelsmore@ucdavis.edu*

Received: 9 March 2023 Returned for revision: 7 July 2023 Editorial decision: 10 July 2023 Accepted: 13 July 2023

- **Background and Aims** The increased likelihood and severity of storm events has brought into focus the role of coastal ecosystems in provision of shoreline protection by attenuating wave energy. Canopy-forming kelps, including giant kelp (*Macrocystis pyrifera*), are thought to provide this ecosystem service, but supporting data are extremely limited. Previous *in situ* examinations relied mostly on comparisons between nominally similar sites with and without kelp. Given that other factors (especially seafloor bathymetry and topographic features) often differ across sites, efforts to isolate the effects of kelp on wave energy propagation confront challenges. In particular, it can be difficult to distinguish wave energy dissipation attributable to kelp from frictional processes at the seabed that often covary with the presence of kelp. Here, we use an ecological transition from no kelp to a full forest, at a single site with static bathymetry, to resolve unambiguously the capacity of giant kelp to damp waves.
- **Methods** We measured waves within and outside rocky reef habitat, in both the absence and the presence of giant kelp, at Marguerite Reef, Palos Verdes, CA, USA. Nested within a broader kelp restoration project, this site transitioned from a bare state to one supporting a fully formed forest (density of 8 stipes $m^{-2}$). We quantified, as a function of incident wave conditions, the decline in wave energy flux attributable to the presence of kelp, as waves propagated from outside and into reef habitat.
- **Key Results** The kelp forest damped wave energy detectably, but to a modest extent. Interactions with the seabed alone reduced wave energy flux, on average, by 12 ± 1.4 % over 180 m of travel. The kelp forest induced an additional 7 ± 1.2 % decrease. Kelp-associated declines in wave energy flux were slightly greater for waves of longer periods and smaller wave heights.
- **Conclusions** *Macrocystis pyrifera* forests have a limited, albeit measurable, capacity to enhance shoreline protection from nearshore waves. Expectations that giant kelp forests, whether extant or enhanced through restoration, have substantial impacts on wave-induced coastal erosion might require re-evaluation.

**Key words:** Wave energy flux, wave damping, *Macrocystis pyrifera*, kelp, coastal protection, ecosystem service.

## INTRODUCTION

Canopy-forming macroalgae are found worldwide and operate as marine foundation species, creating underwater forests that provide structural habitat, shelter and food for numerous other taxa (North, 1971; Dayton, 1972; Miller *et al.*, 2018). In the case of *Macrocystis pyrifera*, the giant kelp, >800 other species can be supported by its presence (North, 1971; Schiel and Foster, 2015). These resident organisms experience environmental conditions that differ from those outside a forest. For instance, *Macrocystis* produces a dense network of floating surface blades that reduces light levels while simultaneously influencing seawater chemistry (Reed and Foster, 1984; Hirsh *et al.*, 2020; Traiger *et al.*, 2022). The blades and accompanying fronds of giant kelp that extend through the water column additionally slow current speeds and modify patterns of vertical mixing (Jackson and Winant, 1983; Gaylord *et al.*, 2004, 2007; Rosman *et al.*, 2007; Elsmore *et al.*, 2022).

*Macrocystis* and other forest-forming kelps are also impacted by ocean waves. Large waves generated by storms dominate the dynamics of abundance and primary production in giant kelps (Reed *et al.*, 2011; Castorani *et al.*, 2022), and interactions between waves and kelps have long inspired interest in the possibility that kelp forests might attenuate wave energy. Anticipated consequences of a changing climate, specifically rising sea levels and increasing storm frequency and severity (IPCC, 2019), have garnered a more recent interest in interactions among coastal vegetative ecosystems and wave energy (Hanley *et al.*, 2020). Although there is a growing sense of urgency to understanding the capacity for natural habitats to mitigate impacts of climate change, the idea that kelp forests might attenuate wave energy dates back to at least the 1800s, with historical records from Darwin (1839) noting ‘smooth water’ shoreward of kelp beds. To this day, surfers and coastal users note similar observations.

Despite such observations, the extent to which canopy-forming kelps might damp waves remains unclear. The ‘smooth water’ shoreward of kelp beds is most readily explained by the removal of capillary waves, i.e. small, centimetre-scale ripples, whose physics are governed by the surface tension of water. The bigger waves that characterize seas and swell, and which dislodge kelps and instigate shoreline erosion, are fundamentally different. Their behaviour is controlled by the restoring action of gravity, and they can be orders of magnitude larger and more powerful (Denny, 1988).

Quantitative assessments of wave attenuation by kelp and other seaweeds have been pursued in a number of studies. Early work took mathematical or laboratory approaches that modelled kelp forests as arrays of rigid cylinders or tethered floats (Seymour and Hanes, 1979; Dalrymple *et al.*, 1984; Kobayashi *et al.*, 1993). This research, much of which was applied to *M. pyrifera*, suggested that such arrays might reduce transmitted wave energy by 20–94 %. Related theoretical, laboratory and field experiments targeting much smaller seaweeds (i.e. ones without a surface canopy) have implied wave energy reductions of ≤85 % (Dubi and Tørum, 1996; Mork, 1996). Likewise, wave damping in seagrasses and saltmarshes has been shown to reach 40 % and 80 %, respectively, depending on the species (e.g. Mendez and Losada, 2004: Riffe *et al.*, 2011; Paul *et al.*, 2012; Houser *et al.*, 2015; Luhar *et al.*, 2017). Although the latter ecosystems differ from canopy-forming seaweeds in key ways, the sum total of this work has reinforced the idea that kelp forests might reduce levels of coastal wave action and thereby combat shoreline erosion (e.g. Arkema *et al.*, 2017).

Other lines of research, however, imply a substantially lower potential benefit of kelp forests for dissipating wave energy. This complementary axis of study emphasizes the structural and biomechanical traits of organisms. In particular, it highlights the capacity for canopy-forming kelps to sway passively back and forth with waves (Koehl, 1984), reducing the relative velocities between the kelp stipes and flow, and therefore hydrodynamic drag (Vogel, 1984). Numerical models that account for such flexible movement indicate strong dynamical effects, a portion of which could influence rates of wave energy loss (Denny *et al.*, 1998). This finding applies especially to large canopy-forming species (Denny *et al.* 1997), although there is relevance also to fully submerged taxa that do not interact with the surface of the water (Gaylord and Denny, 1997; Gaylord *et al.*, 2001). Laboratory measurements using scaled kelp mimics (Rosman *et al.* 2013) and field recordings (Gaylord *et al.*, 2008; Mullarney and Pilditch, 2017) support the applicability of such models for understanding flow–organism interactions. In cases where levels of expected wave damping have been computed explicitly, they appear limited (Gaylord *et al.*, 2003; Henderson, 2019). Wave dissipation by a subsurface species of kelp, *Ecklonia radiata*, also appears undetectable in most wave conditions (Morris *et al.*, 2020). Thus, ambiguity has persisted regarding the capacity of various species of kelp to damp wave energy.

In the case of *M. pyrifera*, the most widespread canopy-forming kelp along the US west coast, field experiments are sparse but tend to comport with prior dynamical models in suggesting small to negligible effects on transmitted wave energy (Elwany *et al.*, 1995; Rosman *et al.*, 2007). Elwany *et al.* (1995) relied on comparisons of wave energy at paired sites of similar bathymetry, where one site had kelp and the other did not. In this case, differences in energy between sites were insufficiently large to emerge from the statistical noise. Rosman *et al.* (2007) quantified wave energy at stations both outside and inside a forest and also did not see a strong indication of wave damping, although their study was not designed to distinguish between effects of waves propagating into shallower depths vs. dissipative effects of kelp. Difficulties in establishing adequate no-kelp controls against which kelp treatments could be matched directly are characteristic of all prior studies and have contributed to the challenge of drawing strong inferences about levels of wave damping by kelp forests (Tinoco *et al.*, 2020).

In the present study, we isolate the effects of giant kelp on wave attenuation explicitly, by collecting measurements in conjunction with a kelp forest restoration project in Palos Verdes, California. In the locality of this project, areas that were once overgrazed by the purple urchin, *Strongylocentrotus purpuratus*, and devoid of kelp (termed ‘urchin barrens’) returned to a kelp forest state after urchin densities were reduced through culling. The resulting transition from an urchin barren to a healthy kelp forest presented a unique opportunity to measure wave conditions before, during and after forest regeneration. In particular, it made possible a before–after design, whereby wave measurements could be collected both in the absence and in the presence of kelp at the same site, with bathymetry and other factors held constant. In this regard, this study was able to test unambiguously the physical effects of a canopy-forming kelp species on waves.

## MATERIALS AND METHODS

### *Study site*

Marguerite Reef (33.75712°N, −118.41842°W), along the Palos Verdes Peninsula of Southern California, USA, operated as the focal site for this study (Fig. 1). Bedrock and large boulders, common substrates for *M. pyrifera*, were interspersed with sandy patches. Unlike habitats with substrates dominated by fine sediments, which can shift through time, the bottom topography of this rocky reef remained static. Before the study, Marguerite Reef was blanketed by an urchin barren and devoid of a kelp forest. Urchins were subsequently removed as a part of a large-scale restoration of *M. pyrifera* that began in the autumn season of 2016 and continued into January 2017.

### *Kelp surveys*

Kelp forest regrowth after restoration activities was characterized monthly between November 2016 and November 2017 along eight evenly spaced transects (30 m long × 4 m wide, 30 m apart) oriented along an isobath spanning the cross-shore extent of the rocky reef. *Macrocystis pyrifera* individuals and stipes were counted within each transect to estimate the density of giant kelp. Only individuals with heights >1 m were included in these counts. The kelp forest density time series was then partitioned into categories describing the overall kelp conditions (i.e. No Kelp, Transition and Kelp), to allow for categorical assignment for statistical analyses outlined below. Time periods characterized as ‘No Kelp’ spanned from the start of the

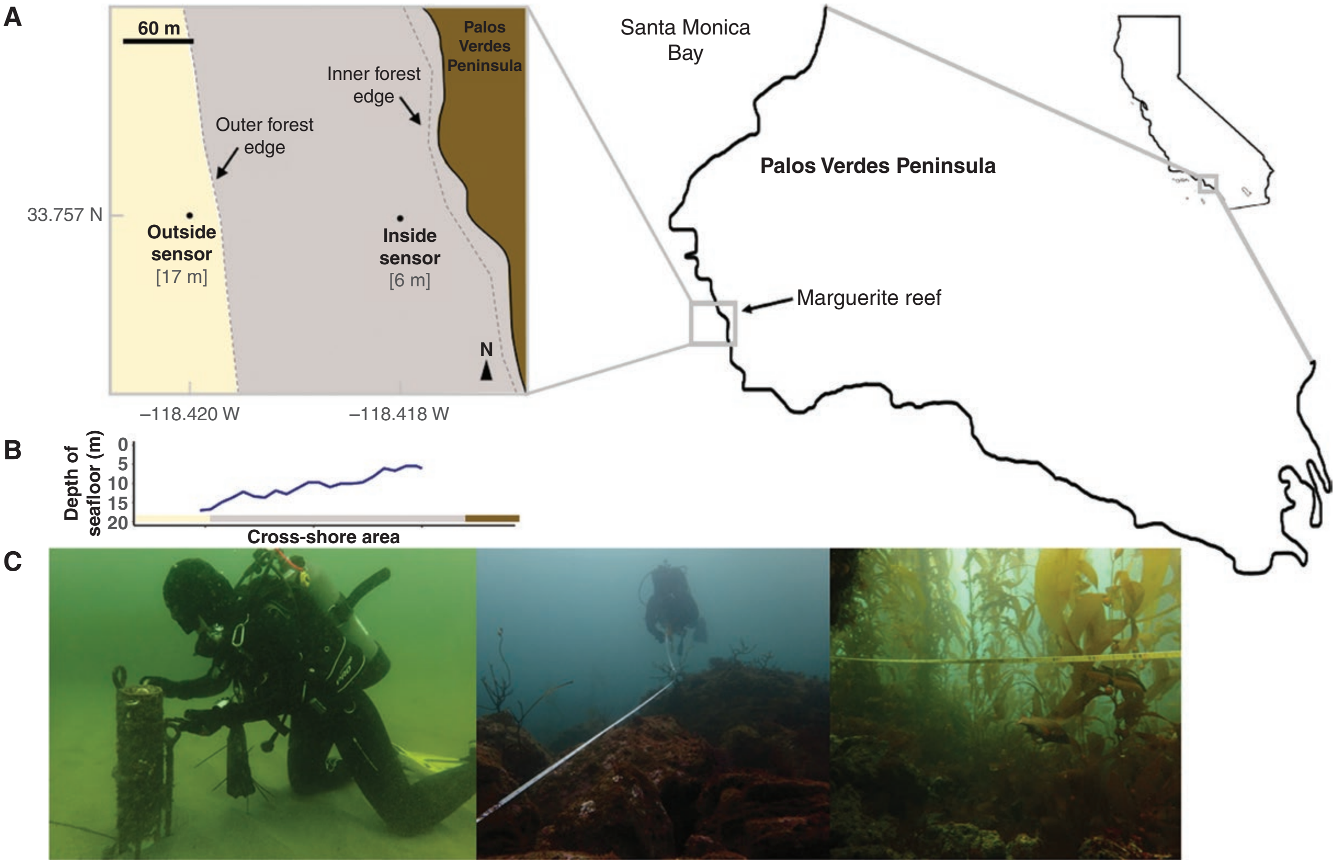

Fig. 1. (A) Map of Marguerite Reef, Palos Verdes, CA, USA, adapted from Elsmore *et al.* (2022), showing locations of the outside and inside pressure sensors, with their mean depths noted within square brackets. The outer and inner edges of the kelp forest, which generally follow seabed isobaths, are represented by dashed lines. During times when the kelp forest was present at this site, it extended across and beyond the full north–south domain depicted in the inset. (B) Cross-shore bathymetry estimated by divers. (C) Images, from left to right, outside the reef, inside the reef habitat during the No Kelp time period, and inside the reef habitat during the Kelp time period.

study in November 2016 to the first sightings of singled-bladed sporophytes on the sea floor, in April 2017. The 'Kelp' period began once stipes reached the surface and most kelp individuals had four stipes (a commonly used criterion for classifying individuals as adults; Dayton *et al.*, 1992), which occurred late in July 2017. The Kelp period ended in late October 2017; we terminated the study then to exclude subsequent sharp reductions in kelp density attributable to seasonal senescence characteristic of Southern California kelp forests (Rodriguez *et al.*, 2013). The 'Transition' period extended between the No Kelp and Kelp time periods, characterized by new forest growth and rapid changes in kelp density.

### *Wave theory*

Surface gravity waves, which comprise the seas and swell that interact most strongly with kelp and are of concern for coastal erosion, propagate as physical disturbances of the sea surface. They can be characterized by their height ($H$), wavelength ($L$) and frequency ($f$). The height is the difference in sea surface displacement between peak and trough, the wavelength spans the distance between successive peaks, and the frequency is the inverse of wave period ($T$), which is the time elapsed between the passage of one peak and the arrival of the next. As is detailed elsewhere (e.g. Kinsman, 1965; Denny, 1988), any such wave has kinetic and potential energy components that sum to yield a total energy per unit area of ocean surface ($E$):

$$E = \frac{1}{8}\rho g H^2 \tag{1}$$

where $\rho$ is the density of seawater and $g$ the acceleration attributable to gravity.

The rate at which the energy of a given wave propagates across space is the product of $E$ and the so-called group velocity ($C_g$), which is the speed at which packets of waves of similar physical characteristics travel, where:

$$C_g = \frac{C}{2}\left[1 + \frac{2kd}{\sinh(2kd)}\right] \tag{2}$$

Equation 2 contains several parameters, including the wave number, $k$ ($=2\pi/L$), and water depth, $d$. Sinh is the hyperbolic sine, where $\sinh(x) = 0.5(e^x - e^{-x})$. The quantity $C$ is the wave celerity, the speed of transit of an individual wave, which is always at least as fast as its corresponding wave packet; $C$ is defined by the wave dispersion relationship (Kinsman, 1965):

$$C = \left[\frac{g}{k}\tanh(kd)\right]^{1/2} \tag{3}$$

where tanh is the hyperbolic tangent, $\tanh(x) = (e^{x} - e^{-x})/(e^{x} + e^{-x})$.

The rate of transmission of wave energy per unit width of wave crest for a given wave, also called the wave energy flux (or wave power), is conserved in the absence of friction or dissipation. As alluded to above, this quantity, $P$, is given by:

$$P = C_g E \tag{4}$$

Because $C_g$ declines with decreasing water depth [eqn (2)], waves tend to shoal (increase in height) as they approach the shore, in order to meet the demand for conservation of wave energy flux.

The relationships of eqns (1)–(4) are most readily visualized in terms of an individually propagating wave. However, natural sea states include waves of many heights, wavelengths and frequencies, most of differing phase, which superpose on one another to yield a 'random sea'. The summed wave energy flux from all these constituents must be considered when evaluating any putative effects of kelp on wave attenuation. In practice, this task is accomplished using tools of spectral analysis to isolate from simple time series of sea surface displacement the contributions of waves of differing frequency. In particular, a time record of surface displacement, $\eta(t)$, can be represented in terms of a Fourier series:

$$\eta(t) = \sum_{i=1}^{N} a_i \cos(2\pi t i f_f - \phi_i) \tag{5}$$

Where $N$ is the number of waveforms of different frequencies or periods that sum to produce the overall record of surface displacement (note that these are harmonics of the fundamental frequency, $f_f$, which is the inverse of the total duration of the time series), $a_i$ is the amplitude ($a_i = H/2$) of a given waveform ($i$), $t$ is time, and $\phi_i$ is the phase shift appropriate to the waveform. By means of trigonometric identities this expression can also be rewritten:

$$\eta(t) = \sum_{i=1}^{N} (\alpha_i \cos 2\pi t i f_f + \beta_i \sin 2\pi t i f_f) \tag{6}$$

With this notation (taking note also that $a_i \neq \alpha_i$), the height of the waveform corresponding to frequency $i$ is given by:

$$H_i = 2\sqrt{{\alpha_i}^2 + {\beta_i}^2} \tag{7}$$

where $\alpha$ and $\beta$ are the so-called Fourier coefficients of eqn (6). The total wave energy flux, $Q$, accounting for the full complement of waves underlying the random sea, and combining eqns (1) and (7), is then computed as the sum of the energy fluxes from each underlying wave frequency component:

$$Q = \sum_{i=1}^{N} C_{g,i} E_i \tag{8}$$

where now the group velocities and energy fluxes associated with waves of differing frequency or period are tracked explicitly.

Relationships among the total wave energy flux, $Q$, outside and inside the reef, in the absence and presence of kelp, can be used to isolate dissipative losses attributable to kelp from other agents of energy loss. In the present experiment, $Q$ was quantified both at the station outside the kelp forest ($Q_{\text{outside}}$) and within the bed near its inshore edge ($Q_{\text{inside}}$). Time records of sea surface displacement, measured at each station, were used to compute the elements of $Q$ (i.e. $C_g$ and $E$), using the equations outlined above. The difference between $Q_{\text{outside}}$ and $Q_{\text{inside}}$ then quantifies the loss of wave energy flux as waves propagate from outside to inside the reef habitat. If no energy loss occurs, the values of $Q$ would be equal. However, energy losses always arise, and in the absence of kelp such losses are dominated by the effects of bottom friction. This baseline difference can then be compared with that arising in the presence of kelp, with any additional offset between $Q_{\text{outside}}$ and $Q_{\text{inside}}$ indicating the effects of kelp. We note that although refraction (waves 'bending' in shallow water until they propagate perpendicular to isobaths) can influence values of $Q$ at a given location, satellite imagery of our site indicates that wave crests have already refracted before reaching the study site and approach normal to shore by the outside station (Planet Team, 2020; Supplementary Data Fig. S1). More importantly, the key comparison of the above analysis is not between values of $Q$ at the two stations, but rather how the quantity ($Q_{\text{outside}} - Q_{\text{inside}}$) changes between times of No Kelp and Kelp. Scenarios of wave refractive processes modifying ($Q_{\text{outside}} - Q_{\text{inside}}$) in ways that are correlated with the presence or absence of kelp appear implausible. The rugose topography of the beach and its modest slope likewise minimize wave reflections that might otherwise influence values of ($Q_{\text{outside}} - Q_{\text{inside}}$).

### *Wave measurements and analyses*

In undertaking the calculations of $Q_{\text{outside}}$ and $Q_{\text{inside}}$, bottom-mounted pressure sensors (SBE-26 Seagauge Wave & Tide Recorder; Sea-Bird Scientific, Bellevue, WA, USA), were deployed inside and outside the kelp forest habitat at mean depths of 6 and 17 m, respectively. Both sensors were positioned outside of the surf zone, such that losses attributable to turbulent dissipation were negligible. Pressure measurements were taken throughout the duration of the project in both the absence and presence of kelp over a suite of incident sea state conditions. Seven instrument deployments were conducted, during which the SBE-26s recorded pressure at the seafloor at 4 Hz, over 17 min bursts, during four equally spaced periods each day, for a duration of 21 days per deployment.

Given that pressure signals of wave-driven surface displacements attenuate exponentially with depth, sea surface time series were reconstituted according to accepted methods by back-correcting the depth-attenuated records acquired by the sensors (Gaylord and Denny, 1997; Lyman *et al.*, 2020). The back-correction is frequency dependent, given that higher frequency waves attenuate faster with depth. Such higher frequency waves also have shorter wavelengths at a given water depth. For a specified wave frequency (or wavelength), the attenuation factor is (Denny, 1988):

$$K = \cosh(kz)/\cosh(kd) \tag{9}$$

where $z$ is the distance above the seafloor and cosh is the hyperbolic cosine, where $\cosh(x) = 0.5(e^{x} + e^{-x})$. The surface displacement associated with a wave of given frequency or period [eqn (5)] is therefore determined by dividing its at-depth pressure by the appropriate value of $K$ to reconstitute the attenuated waveform.

Given that any noise in the pressure record could yield spurious estimates of surface displacement if incorrectly reconstituted, the resolution of the sensors was also quantified by deploying them immediately below a Datawell Waverider MkIII buoy [maintained by the Scripps Institute of Oceanography Coastal Data Information Program (CDIP); CDIP buoy 158] that records sea surface heights directly, without any attenuation. This was done in water of the same depth as the outside station (17 m) (Lyman *et al.*, 2020). Using this procedure, it was possible to verify that the bottom-mounted sensors and the reconstitution protocol accurately estimated surface displacements associated with waves with periods >3.7 s. Therefore, in all subsequent analyses only waves with periods in excess of this cut-off were used. This exercise also allowed for an evaluation of how much wave energy might have been missed by the bottom-mounted pressure sensors owing to the loss of information about short-period waves (i.e. <3.7 s). The energy quantified for short-period surface waves in typical sea state conditions contributed <5 % of the total area under the spectral curve (Lyman *et al.*, 2020).

Statistical summary parameters were also computed at the outside station to characterize the incident sea state, before any potential physical interactions with kelp. In particular, significant wave height ($H_s$) and the dominant (or peak) wave period ($T_p$) were determined from the wave data, burst by burst, as:

$$H_s = 4\sigma \tag{10}$$

$$T_p = \frac{1}{f\,[\max(S)]} \tag{11}$$

where $\sigma$ is the standard deviation of the sea surface displacement and $f[\max(S)]$ is the wave period at which the power spectrum of sea surface displacement, $S$, exhibits its maximum.

Ultimately, as discussed above, the key quantity of interest is how the difference in wave energy flux between the outside ($Q_{\text{outside}}$) and inner edge of the forest ($Q_{\text{inside}}$) depends on the absence or presence of kelp. Given that incident wave conditions also vary through time (as indexed by changes in $Q_{\text{outside}}$ across bursts), the spatial differences in wave energy flux from outside to inside the forest can be normalized:

$$\Delta Q_{\text{norm}} = \frac{Q_{\text{outside}} - Q_{\text{inside}}}{Q_{\text{outside}}} = 1 - \frac{Q_{\text{inside}}}{Q_{\text{outside}}} \tag{12}$$

where $\Delta Q_{\text{norm}}$ is the change in energy flux from outside to inside, normalized by the incident energy flux, $Q_{\text{outside}}$. This quantity is therefore the proportional change in wave energy flux between the outside and inside stations, with positive values representing energy loss.

### *Influence of kelp on wave attenuation*

The value $\Delta Q_{\text{norm}}$ represents the wave energy flux lost owing to wave–benthos interactions plus any losses attributable to wave–kelp interactions. If *M. pyrifera* has no effect on wave conditions, given that the bottom terrain did not change during the shift between the absence and presence of kelp, the proportional change in wave energy flux would remain invariant.

To test statistically for differences in $\Delta Q_{\text{norm}}$ in the absence and presence of kelp, a linear regression was constructed, with proportional change in wave energy flux from outside to inside as the response variable and kelp condition (i.e. No Kelp and Kelp) as a predictor. This analysis yields a basic understanding of how the presence of kelp influences wave energy flux. However, kelp forests might attenuate waves of different height or period differently. To evaluate this possibility, the linear regression model was structured to include not only kelp condition (i.e. No Kelp and Kelp), but also the dominant wave period ($T_p$) and significant wave height ($H_s$) at the outside station, in addition to their associated interactions, as additional statistical predictors for the proportional change in wave energy flux from outside to inside. Finally, to check if the last model was overfitted, a backward stepwise model selection was conducted to determine the best-fitting model. Associated Akaike information criterion scores and models tested are shown in Table 1. The residuals in the model were tested for normality using a Shapiro–Wilk test and assessed for heteroscedasticity visually. Residuals appear homoscedastic, but do not fall within a normal distribution (Shapiro test, $P = 0.002$). Given the large sample size and the fact that a violation of non-normality would not change the point estimates, the model appears appropriate for describing the dataset, although the confidence intervals could be slightly inflated. Pairwise comparisons of the effect of kelp, between $H_s$ and $T_p$, were conducted using estimated marginal means with a Tukey correction. All statistical tests were accomplished in R v.3.6.1 (R Core Team, 2019), and pairwise comparisons were conducted using the package *emmeans* (Lenth, 2020).

## RESULTS

### *Kelp densities*

The benthos was devoid of vegetation throughout the No Kelp period. Single-bladed kelp recruits appeared at Marguerite Reef in April 2017 and grew to the surface throughout the following 7 months (Fig. 2). The overall stipe density of *M.*

TABLE 1. *Akaike's information criterion (AIC) scores, their degrees of freedom (d.f.) and predictors for each model in the backward stepwise model selection process. The final model selected is in bold. KelpCond is kelp forest condition (i.e. No Kelp or Kelp); Tp_Out is peak wave period outside the kelp forest; and Hs_Out is significant wave height outside the kelp forest.*

| | Model | d.f. | AIC |
|---|---|---|---|
| 1 | KelpCond × Tp_Out × Hs_Out | 9 | −301.7766 |
| 2 | (KelpCond + Tp_Out + Hs_Out)$^2$ | 8 | −302.1443 |
| 3 | KelpCond × Tp_Out + Tp_Out × Hs_Out | 7 | −300.9562 |
| 4 | KelpCond × Hs_Out + Tp_Out × Hs_Out | 7 | −295.7272 |
| **5** | **KelpCond × Tp_Out + KelpCond × Hs_Out** | **7** | **−303.7119** |
| 6 | KelpCond × Tp_Out + Hs_Out | 6 | −300.5064 |
| 7 | KelpCond × Hs_Out + Tp_Out | 6 | −296.6553 |

*pyrifera* increased rapidly throughout the Transition period (April–July 2017), reaching densities typical of mature *M. pyrifera* populations found in California (1.9–15 stipes m$^{-2}$; North, 1971; Elsmore *et al.*, 2022) by the Kelp period (Fig. 2A), which encompassed late July–October 2017. At the onset of the Transition period, the new kelp forest was composed of many small individuals, each consisting of one or two stipes per individual (Fig. 2B). Over time, the young individuals began to support more stipes per plant, such that most entered the adult classification (four or more stipes) early in the Kelp period. Throughout the experimental period, the understorey algal community was functionally absent, with the exception of extremely rare sightings of understorey species that often occupy Southern California's rocky reefs, including *Sargassum horneri*, *Sargassum muticum*, *Pterygophora californica*, *Eisenia arborea* and *Egregia menziesii*, even following re-establishment of the giant kelp canopy.

### *Wave conditions*

Coastal wave conditions varied appreciably throughout the study. Incident significant wave heights ($H_s$), as recorded at the outside measurement station and computed burst by burst, ranged from 0.34 to 4.3 m. Dominant wave periods ($T_p$) spanned 4.2–19.6 s. The modal incident significant wave height was 0.6 m, and the modal dominant wave period was 15 s. Conditions also encompassed both narrow-banded sea states dominated by single wave periods and broader-banded sea states where waves of a variety of periods arrived at the site.

Time series of sea surface displacement displayed a strong signature of waves both at the outside station and at the station located on the inshore edge of the forest domain (Fig. 3). However, this trend held regardless of whether kelp was present or not. If kelp had a dramatic damping effect, the amplitudes of the surface elevation record in the presence of kelp would have been greatly depressed, resulting in reduced deviations from the zero line. However, such a pattern did not manifest in our dataset, preventing simple comparisons of time series across the outside and inside stations from providing insight into potential levels of wave attenuation by *Macrocystis*. This pattern was not surprising given that as waves move shoreward, they increase in height through shoaling, while simultaneously experiencing bottom friction that tends to decrease their height. Owing to these contrasting processes, rudimentary comparisons of outside vs. inside records of sea surface displacement intrinsically provide a poor way to assess effects of kelp on wave energy attenuation (Fig. 3).

Likewise, more detailed spectral analyses showed overlap between outside and inside spectra, regardless of the presence or absence of kelp. This pattern begins to indicate a constrained capacity for giant kelp to damp waves. Spectral analyses allow the distribution of wave energy across a range of wave periods to be computed and highlight the wave periods that contribute most to the overall energy. In Fig. 4A, at the outside location in the absence of kelp, much of the energy in the wave field is associated with waves of 16 s periods, as indicated by the peak at 0.06 Hz. If kelp forests strongly attenuated wave energy, one would expect this peak to decline in the inside spectrum when kelp is present (i.e. larger differences between the outside and

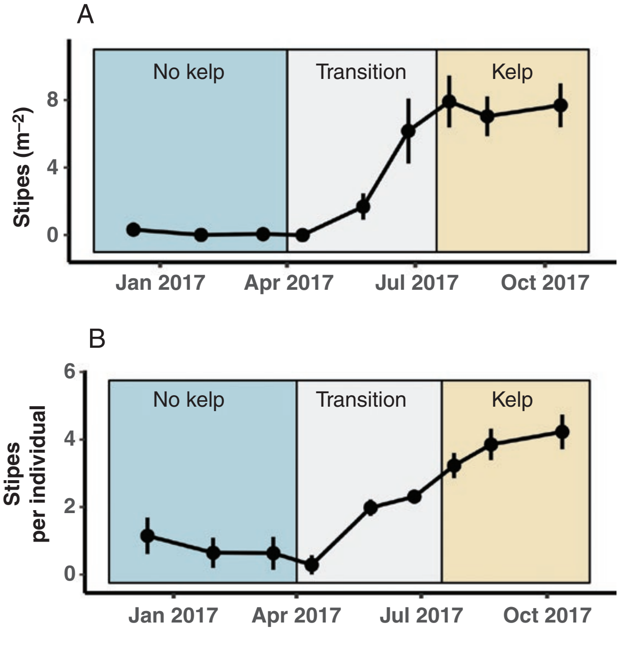

Fig. 2. Time series of *Macrocystis pyrifera* number of stipes per square metre (A) and number of stipes per individual (B) at Marguerite Reef throughout the duration of the study. Data points indicate means (±s.e.m.) averaged across the eight transects. Initial sightings of *M. pyrifera* recruits and onset of canopy formation were determined the beginning of the partitioned Transition and Kelp periods, respectively.

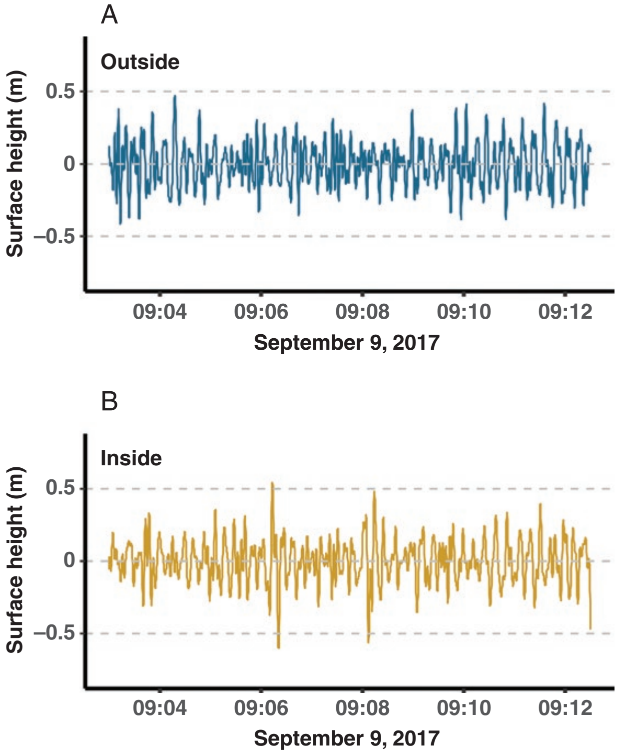

Fig. 3. Example time series of reconstituted sea surface elevations at Marguerite Reef at the outside (A) and inside (B) stations, in the presence of kelp.

inside spectra would appear in the presence of kelp). However, Fig. 4 demonstrates that this was not the case.

Although wave energy spectra are more valuable than simple time series for conveying information about sea state, they remain less than ideal for assessing the capacity for kelp to damp waves. This point follows from the fact that it is the rate of energy transfer through space (the wave energy flux) that is conserved in the absence of dissipation, rather than energy per se. As waves shoal, they increase in height as noted above, which increases their kinetic and potential energy per area. At first glance, this process seems non-physical, because it indicates greater energy in waves that have propagated further shoreward and thus (superficially) implies a violation of conservation laws. What reconciles the inconsistency is that as waves shoal, their passage across space also slows, which leads to the conservation of wave energy flux. We therefore used, as outlined in the Materials and Methods, differences between the wave energy flux outside and inside as a metric for effects of kelp on waves.

### *Wave damping by kelp*

In the absence of kelp, the site at Marguerite Reef exhibited an average reduction of 12.1 ± 1.4 % in wave energy flux between the outside and inside locations (Fig. 5A; Table 2; $P \leq 0.001$), probably attributable to effects of bottom friction. Importantly, an additional 7.2 ± 1.2 % was lost on average when kelp was present (Fig. 5A; Table 2; $P \leq 0.001$). The distribution of reductions in energy flux also varied substantially in both the absence and presence of kelp. However, some component of the breadth of the distributions is likely to reflect burst-level statistical uncertainty (e.g. owing to innate error associated with the spectral estimates), as evidenced by a portion of the distributions in Fig. 5B, C falling to the left of zero. Note that the rightward shift to higher losses in the kelp distribution highlights the additional loss in energy flux attributable to the presence of kelp (Fig. 5B, C).

The amount of energy dissipation attributed to kelp depended subtly on wave height and period, as revealed in the linear regression analysis (Table 3). Although shorter-period waves tended to lose relatively more energy while transiting between the outside and inside stations than longer-period

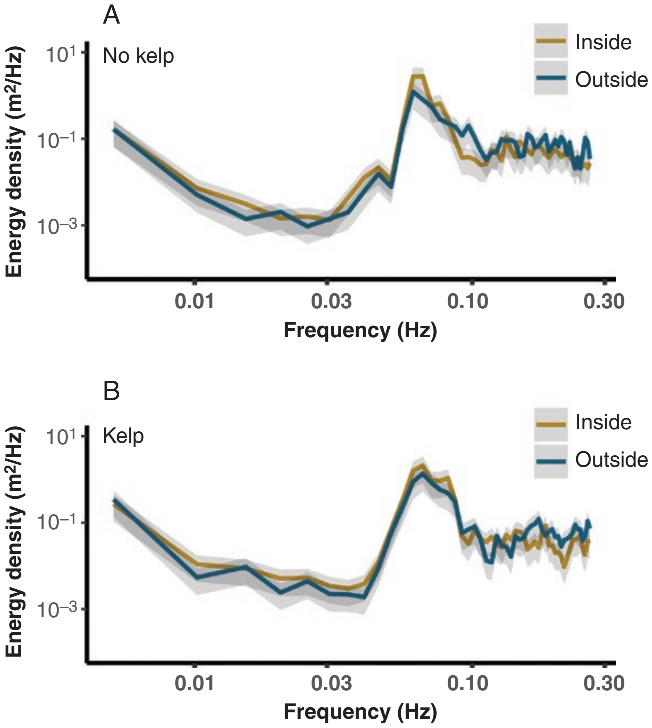

FIG. 4. Wave energy density spectra outside and inside Marguerite Reef, in the absence (15 February 2017, 00:12–00:29 h) and presence (31 October 2017, 05:45–06:02 h) of kelp. (A) Outside spectrum in the absence of kelp in blue (significant wave height, $H_s = 0.70$ m and dominant wave period, $T_p = 16.33$ s) and inside spectrum in the absence of kelp in yellow ($H_s = 0.88$ m and $T_p = 15.08$ s). (B) Outside spectrum in the presence of kelp in blue ($H_s = 0.73$ m and $T_p = 15.08$ s) and inside spectrum in the presence of kelp in yellow ($H_s = 0.84$ m and $T_p = 15.08$ s). Shading represents 95 % confidence limits of the spectral estimates.

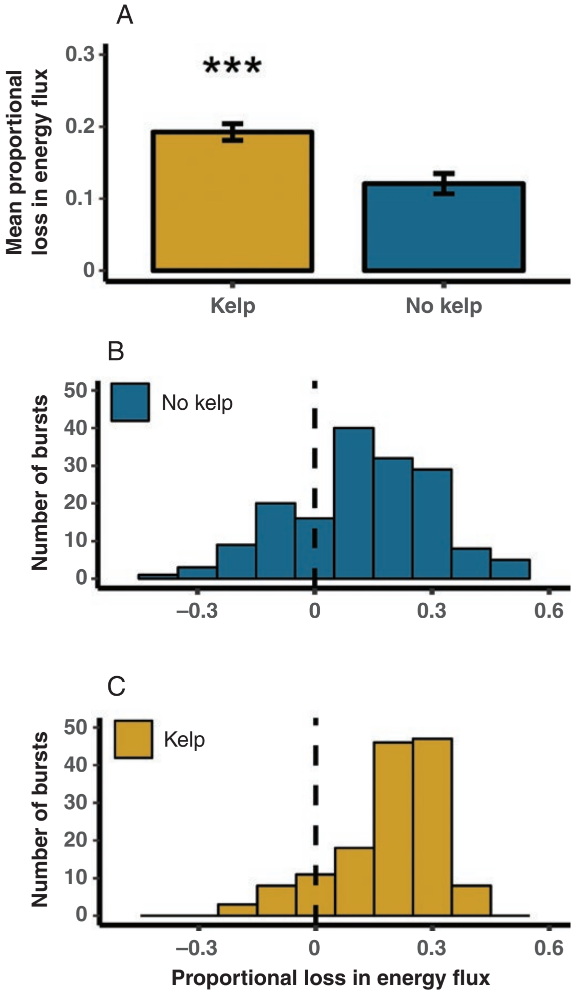

FIG. 5. Proportional loss in wave energy flux between outside and inside stations at Marguerite Reef in the absence and presence of kelp. For example, a value of 0.1 indicates that 10 % of the incident wave energy flux is lost as waves propagate from the outside to inside station. (A) Mean proportional loss in energy flux (±s.e.m.) averaged across all bursts from either the No Kelp or Kelp time periods. There was a significant difference between kelp conditions (***$P \leq 0.001$, d.f. = 302). (B) Full distribution underlying the No Kelp period of (A), where $n = 163$ bursts. (C) Full distribution underlying the Kelp period of (A), with $n = 141$.

TABLE 2. *Summary results for a linear model testing the effect of kelp presence on the proportional loss in wave energy flux. Bold values are statistically significant.*

| Parameter | Estimate | s.e. | *t*-value | *P*-value |
|---|---|---|---|---|
| Multiple $R^2 = 0.04734$; adjusted $R^2 = 0.04419$ | | | | |
| Intercept (No Kelp) | **0.12084** | **0.01262** | **9.577** | **<0.001** |
| Kelp | **0.07177** | **0.01853** | **3.874** | **<0.001** |

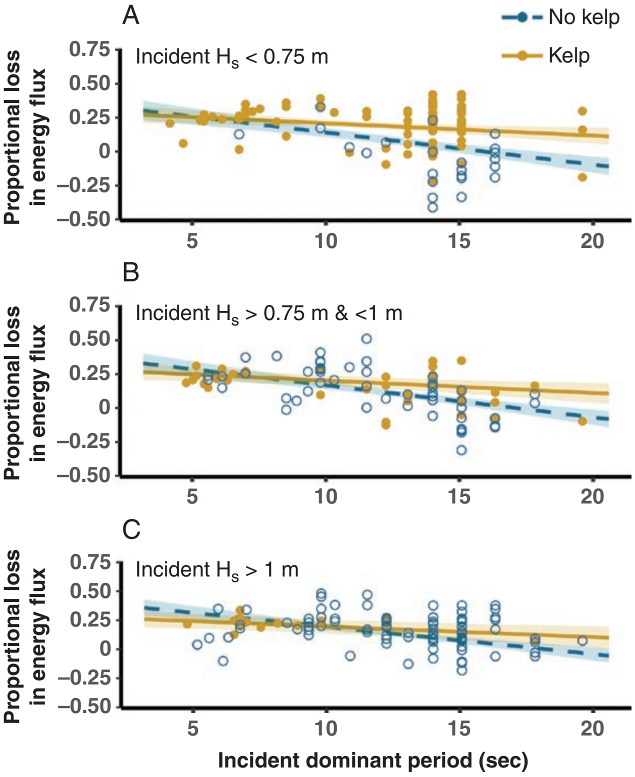

FIG. 6. Proportional loss in wave energy flux as a function of the dominant wave period ($T_p$) at the outside station. Dashed lines represent No Kelp conditions, and continuous lines represent Kelp conditions. Trends are shown for multiple ranges of significant wave heights ($H_s$) recorded at the outside station: (A) $H_s < 0.75$ m; (B) $H_s$ 0.76–1 m; and (C) $H_s$ 1.01–1.25 m. Shaded regions indicate 95 % confidence intervals. Filled and open data points correspond to Kelp and No Kelp conditions, respectively.

waves (note higher elevations of the leftmost portions of the curves in Fig. 6), kelp-associated decreases in wave energy flux were greater for waves of longer periods (the lines for Kelp and No Kelp deviate more strongly for longer period waves in Fig. 6). There was also a minor effect of incident wave height, with smaller waves (<0.75 m) exhibiting stronger damping by kelp on a percentage basis, in comparison to larger waves (>1 m). This effect is apparent as a flattening of the Kelp slopes, relative to the No Kelp slopes, across panels of Fig. 6.

In contrast to detectable effects of wave height and period on levels of attenuation by kelp, we saw no evidence that the directional character of waves kilometres offshore of the site strongly influenced the dissipation rates at our sensor locations (direction data derived from Datawell Waverider MkIII CDIP buoy 028; Supplementary Data Fig. S2A). The pattern held despite strong seasonal variation in the basin-scale wave climate, characterized by a bimodal distribution of offshore wave directions, such that offshore waves originated more often from the west in the winter and more often from the south and south-west in the summer (Supplementary Data Fig. S2A, C). As with the direction of waves while in deep water, regional wind fields (quantified using NDBC buoy station 46025) also appeared to play little role in influencing the levels of kelp damping (Supplementary Data Fig. S2B, D).

## DISCUSSION

In this study, we tested the physical effect of kelp on the local wave field explicitly, by measuring wave activity in the same topographically static site before and during the presence of a kelp forest. This approach allowed us directly to confront a persistent challenge to disentangling effects of kelp from other factors. In particular, it allowed us to separate the effects of kelp from those tied to seabed properties, which often differ between kelp and non-kelp sites owing to the preference of kelp for rock outcrops vs. less-consolidated substrata, such as cobble, sediment or sand. In our case, we found that a *M. pyrifera* forest in Palos Verdes, CA, USA had a detectable but limited capacity to damp wave energy. Wave interactions with the seafloor alone reduced wave energy flux, on average, by 12 ± 1.4 %, with an additional 7 ± 1.2 % reduction when an established kelp forest was present, over a propagation distance of 180 m.

### *Factors governing damping potential*

Although this study found that *M. pyrifera* forests have some capacity to damp waves, the magnitude of attenuation is small in comparison to that attributed to other forms of aquatic vegetation. Some kelps with stiffer support structures and which do not form floating surface canopies, such as *Laminaria hyperborea*, have been shown substantially to decrease wave heights (50 %; Dubi and Tørum, 1996) and/or damp wave energy (70–85 %; Mork, 1996; although these latter estimates include effects of bottom dissipation). Mangroves, which are considerably stiffer than kelps and protrude out of the water, can attenuate ≤72 % of incident wave energy (Horstman *et al.*, 2012). Salt marsh vegetation, which can also be emergent and only modestly flexible, has been shown to exhibit 60–80 % reductions in wave energy (Knutson *et al.*, 1982; Riffe *et al.*, 2011; Möller *et al.*, 2014). Seagrasses, which are more flexible, sometimes emergent, and found in substantially shallower waters relative to those in which *M. pyrifera* resides, have been shown to reduce wave energy by 20–40 % (Fonseca and Cahalan, 1992). We note, however, that these prior studies do not present information concerning vegetation-induced reductions in wave energy flux (as opposed to wave heights or wave energy per area), meaning that direct comparison with the present study is difficult.

The size of a vegetation assemblage or forest, its density, extent of submergence, morphology and the stiffness of seaweed or plant structures are all expected to affect the damping potential of various types of aquatic vegetation (Tinoco *et al.*,

TABLE 3. *Summary results for a linear model testing the effect of kelp presence, incident peak wave period* ($T_p$) *and incident significant wave height* ($H_s$) *on the proportional loss in wave energy flux and Tukey's HSD pairwise comparison.*

| **Parameter** | **Estimate** | **s.e.** | ***t*-value** | ***P*-value** |
|---|---|---|---|---|
| Multiple $R^2$ = 0.2392; adjusted $R^2$ = 0.2264 | | | | |
| Intercept (No Kelp) | 0.294377 | 0.052366 | 5.622 | <0.0001 |
| Kelp | 0.023085 | 0.083509 | 0.276 | 0.78241 |
| $T_p$ outside | −0.023637 | 0.003536 | −6.685 | <0.0001 |
| $H_s$ outside | 0.110327 | 0.022474 | 4.909 | <0.0001 |
| Kelp presence × $T_p$ outside | 0.014520 | 0.004837 | 3.002 | 0.00291 |
| Kelp presence × $H_s$ outside | −0.133661 | 0.058916 | −2.269 | 0.02400 |
| Tukey's HSD pairwise comparison with $H_s$ outside = 0.944 m; $T_p$ outside = 12.3 s; d.f. = 298 | | | | |
| **Contrast** | Estimate | s.e. | ***t*-ratio** | ***P*-value** |
| No Kelp vs. Kelp | −0.0755 | 0.0217 | −3.478 | 0.0006 |

2020). In particular, it is likely that the exceptionally large size, positioning of considerable kelp biomass at the surface of the water and the capacity for *M. pyrifera* to sway appreciably with passing waveforms together influence the interaction of this species with waves (see, e.g. scaling arguments of Denny *et al.*, 1998). However, determining which of these features contribute most strongly to the low levels of attenuation of wave energy flux observed here requires further study.

### *Wave vs. current damping*

The relatively low levels of wave damping observed in the present study might be at odds with the expectations of some kelp researchers, given the known ability of larger forests to slow currents (e.g. Jackson and Winant, 1983; Gaylord *et al.*, 2012; Elsmore *et al.*, 2022) and the common (although not universal) misconception that currents and waves will tend to interact in a similar manner with aquatic vegetation. Importantly, however, the time scale of currents and their reversals is distinctly different from that of wave-driven oscillations. In the case of nearshore currents, which typically change directions over hours in association with tides, considerable data indicate that these flows can indeed experience strong damping. This damping arises in aquatic vegetation as diverse as seagrass meadows (Fonseca *et al.*, 1982; Koch and Gust, 1999), turfy and understorey seaweeds (Carpenter and Williams, 1993) and inside forests of large canopy-forming macroalgae (Jackson and Winant, 1983; Gaylord *et al.*, 2007; Rosman *et al.*, 2007; Elsmore *et al.*, 2022). A key issue is that tidal currents flow in the same direction for sufficiently long durations that even canopy-forming kelps can be drawn out fully in the direction of flow, limiting the capacity for 'going with the flow' responses to reduce water speeds relative to the kelp (Koehl, 1984), such that drag can act on the stipes strongly.

Waves, in contrast, oscillate over seconds and reverse quickly enough that they are believed to have a much lower capacity to extend large, canopy-forming species fully to where they become stationary and subject to the maximal relative flow speeds that they can experience. This point has been discussed at length in the literature for many years (see, e.g. Koehl, 1984; Lowe *et al.*, 2005). Nevertheless, such fundamental differences between currents and waves are sometimes overlooked in considerations of how large canopy-forming kelps interact with water motions of different time scales.

### *Limitations of the study*

Although this study documented a relatively modest capacity for kelp to reduce wave energy flux, the underlying measurements were conducted in only a single forest. The degree to which a given *M. pyrifera* forest might modify wave energy flux could vary according to a number of site-specific and forest-specific characteristics. The forest used in this study, although within the range of plant and stipe densities characteristic of many *M. pyrifera* forests, was a medium-sized forest in terms of spatial extent (180 m in cross-shore width). A forest with greater cross-shore canopy extent would impose a greater total amount of damping, even given an identical rate of decrease in wave energy flux per metre of transit through a forest. We also acknowledge that Southern California generally experiences more benign sea state conditions than some other locales and, consequently, the incident wave conditions observed throughout our study did not include extreme wave heights associated with the largest of storms. That said, sea state conditions much in excess of those we recorded are associated with dislodgement of kelp from the substrate (Seymour *et al.*, 1989). The potential for appreciably greater magnitudes of wave energy attenuation by giant kelp therefore appears limited.

### *Conclusion*

This study quantified the effect of a giant kelp forest on surface gravity waves using field measurements of waves at a single site in the absence and presence of kelp. Kelp-associated effects were isolated from those attributed to interactions with the seafloor using a before–after experimental design. Kelp-associated reductions in wave energy flux were detectable, but not substantial, and varied with impinging wave heights and periods. Waves of smaller heights and longer periods exhibited the most damping in the presence of kelp. Although giant kelp does cause wave attenuation, the degree of damping is small in comparison to multiple other types of aquatic vegetation. These findings reinforce and confirm previous work, conducted without the advantage of an explicit no-kelp–with-kelp experimental design, suggesting limited potential for wave attenuation by giant kelp. Benefits of *M. pyrifera* forests for shoreline protection therefore appear modest, other valuable features of such forests notwithstanding. High expectations for using giant kelp restoration as a tool for protection against wave-induced coastal erosion might require careful scrutiny, and further work regarding the role of vegetation in coastal defence, as advocated by others (e.g. Hanley *et al.*, 2020; Morris *et al.*, 2020) is warranted.

## SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following.

Figure S1: example Planet satellite imagery showing waves impinging on Marguerite Reef across three dates spanning the study period. Figure S2: proportional loss in wave energy flux as a function of the dominant offshore wave direction at the 028 CDIP buoy; the offshore wind speed at the station 46025 NDBC buoy; the dominant offshore wave direction at the NDBC buoy; and the offshore wind gust speed at the NDBC buoy.

## FUNDING

This work was supported by the California State Coastal Conservancy [grant number 15-013], National Science Foundation (NSF) [grant numbers OCE-1636191 and OCE-2129942], University of Southern California, Sea Grant [grant number NA180AR4170075] and Dolby Laboratories. K.E. was additionally supported by an NSF Graduate Research Fellowship, a Bilinski Fellowship and a Norcal Society of Environmental Toxicology and Chemistry grant.

## ACKNOWLEDGEMENTS

We are grateful to M. Anghera, A. Barilotti, H. Burdick, B. Burford, B. Cohn, K. Dubois, B. Grimes, T. Herzik, J. Hollarsmith, P. House, G. Ng, A. Ninokawa, B. Sterling and G. Thompson for field and logistical assistance. There are no conflicts of interest.

## LITERATURE CITED

**Arkema KK**, **Griffin R**, **Maldonado S**, **Silver J**, **Suckale J**, **Guerry AD. 2017**. Linking social, ecological, and physical science to advance natural and nature-based protection for coastal communities. *Annals of the New York Academy of Sciences* **1399**: 5–26. doi:10.1111/nyas.13322.

**Carpenter RC**, **Williams SL. 1993**. Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. *Limnology and Oceanography* **38**: 687–694. doi:10.4319/lo.1993.38.3.0687.

**Castorani MCN**, **Bell TW**, **Walter JA**, **Reuman DC**, **Cavanaugh KC**, **Sheppard LW. 2022**. Disturbance and nutrients synchronise kelp forests across scales through interacting Moran effects. *Ecology Letters* **25**: 1854–1868. doi:10.1111/ele.14066.

**Dalrymple RA**, **Kirby JT**, **Hwang PA. 1984**. Wave diffraction due to areas of energy dissipation. *Journal of Waterway, Port, Coastal and Ocean Engineering* **110**: 67–79. doi:10.1061/(ASCE)0733-950X(1984)110:1(67).

**Darwin C. 1839**. *The Voyage of the Beagle*. (Reprinted in 1962, The Harvard Classics). New York: P.F. Collier & Son Company.

**Dayton PK. 1972**. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. In: **Parker BC**, ed. *Proceedings of the Colloquium on Conservation Problems in Antarctica*. Lawrence, KS: Allen Press, 81–96.

**Dayton PK**, **Tegner MJ**, **Parnell PE**, **Edwards PB. 1992**. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecological Monographs* **62**: 421–445. doi:10.2307/2937118.

**Denny MW. 1988**. *Biology and the Mechanics of the Wave-Swept Environment*. Princeton, NJ: Princeton University Press.

**Denny MW**, **Gaylord BP**, **Cowen EA. 1997**. Flow and flexibility II. The roles of size and shape in determining wave forces on the bull kelp *Nereocystis luetkeana*. *The Journal of Experimental Biology* **200**: 3165–3183. doi:10.1242/jeb.200.24.3165.

**Denny M**, **Gaylord B**, **Helmuth B**, **Daniel T. 1998**. The menace of momentum: dynamic forces on flexible organisms. *Limnology and Oceanography* **43**: 955–968. doi:10.4319/lo.1998.43.5.0955.

**Dubi A**, **Tørum A. 1996**. Wave energy dissipation in kelp vegetation. *Proceedings on Coastal Engineering* **3**: 2625–2639. doi:10.1061/9780784402429.203.

**Elsmore K**, **Nickols KJ**, **Ford T**, **Cavanaugh KC**, **Cavanaugh KC**, **Gaylord B. 2022**. *Macrocystis pyrifera* forest development shapes the physical environment through current velocity reduction. *Marine Ecology Progress Series* **694**: 45–59. doi:10.3354/meps14107.

**Elwany MHS**, **O'Reilly WC**, **Guza RT**, **Flick RE. 1995**. Effects of Southern California kelp beds on waves. *Journal of Waterway, Port, Coastal and Ocean Engineering* **121**: 143–150. doi:10.1061/(asce)0733-950x(1995)121:2(143).

**Fonseca MS**, **Cahalan JA. 1992**. A preliminary evaluation of wave attenuation by four species of seagrass. *Estuarine, Coastal and Shelf Science* **35**: 565–576. doi:10.1016/s0272-7714(05)80039-3.

**Fonseca MS**, **Fisher JS**, **Zieman JC**, **Thayer GW. 1982**. Influence of the seagrass, *Zostera marina* L., on current flow. *Estuarine, Coastal and Shelf Science* **15**: 351–364. doi:10.1016/0272-7714(82)90046-4.

**Gaylord B**, **Denny MW. 1997**. Flow and flexibility I. Effects of size, shape and stiffness in determining wave forces on the stipitate kelps *Eisenia arborea* and *Pterygophora californica*. *The Journal of Experimental Biology* **200**: 3141–3164. doi:10.1242/jeb.200.24.3141.

**Gaylord B**, **Hale BB**, **Denny MW. 2001**. Consequences of transient fluid forces for compliant benthic organisms. *The Journal of Experimental Biology* **204**: 1347–1360. doi:10.1242/jeb.204.7.1347.

**Gaylord B**, **Denny MW**, **Koehl MA. 2003**. Modulation of wave forces on kelp canopies by alongshore currents. *Limnology and Oceanography* **48**: 860–871. doi:10.4319/lo.2003.48.2.0860.

**Gaylord B**, **Reed DC**, **Washburn L**, **Raimondi PT. 2004**. Physical–biological coupling in spore dispersal of kelp forest macroalgae. *Journal of Marine Systems* **49**: 19–39. doi:10.1016/j.jmarsys.2003.05.003.

**Gaylord B**, **Rosman JH**, **Reed DC**, ***et al*. 2007**. Spatial patterns of flow and their modification within and around a giant kelp forest. *Limnology and Oceanography* **52**: 1838–1852. doi:10.4319/lo.2007.52.5.1838.

**Gaylord B**, **Denny MW**, **Koehl MAR. 2008**. Flow forces on seaweeds: field evidence for roles of wave impingement and organism inertia. *The Biological Bulletin* **215**: 295–308. doi:10.2307/25470713.

**Gaylord B**, **Nickols KJ**, **Jurgens L. 2012**. Roles of transport and mixing processes in kelp forest ecology. *The Journal of Experimental Biology* **215**: 997–1007. doi:10.1242/jeb.059824.

**Hanley ME**, **Bouma TJ**, **Mossman HL. 2020**. The gathering storm: optimizing management of coastal ecosystems in the face of a climate-driven threat. *Annals of Botany* **125**: 197–212. doi:10.1093/aob/mcz204.

**Henderson SM. 2019**. Motion of buoyant, flexible aquatic vegetation under waves: simple theoretical models and parameterization of wave dissipation. *Coastal Engineering* **152**: 103497. doi:10.1016/j.coastaleng.2019.04.009.

**Hirsh HK**, **Nickols KJ**, **Takeshita Y**, ***et al*. 2020**. Drivers of biogeochemical variability in a Central California kelp forest: implications for local amelioration of ocean acidification. *Journal of Geophysical Research, Oceans* **125**: 1–22. doi:10.1029/2020JC016320.

**Horstman EM**, **Dohmen-Janssen M**, **Narra P**, ***et al*. 2012**. Wave attenuation in mangrove forests; field data obtained in Trang, Thailand. *Coastal Engineering Proceedings* **1**: 40. doi:10.9753/icce.v33.waves.40.

**Houser C**, **Trimble S**, **Morales B. 2015**. Influence of blade flexibility on the drag coefficient of aquatic vegetation. *Estuaries and Coasts* **38**: 569–577. doi:10.1007/s12237-014-9840-3.

**IPCC. 2019**. Summary for policymakers. In: **Pörtner H-O**, **Roberts DC**, **Masson-Delmotte VP**, ***et al.***, eds. *IPCC special report on the Ocean and Cryosphere in a changing climate*. Geneva: IPCC.

**Jackson GA**, **Winant CD. 1983**. Effect of a kelp forest on coastal currents. *Continental Shelf Research* **2**: 75–80. doi:10.1016/0278-4343(83)90023-7.

**Kinsman B. 1965**. *Wind waves*. New York, NY: Dover.

**Knutson PL**, **Brochu RA**, **Seelig WN**, **Inskeep MR. 1982**. Wave damping in *Spartina alterniflora* marshes. *Wetlands* **2**: 87–104. doi:10.1007/bf03160548.

**Kobayashi N**, **Raichle AW**, **Asano T. 1993**. Wave attenuation by vegetation. *Journal of Waterway, Port, Coastal and Ocean Engineering* **119**: 30–48. doi:10.1061/(asce)0733-950x(1993)119:1(30).

**Koch EW**, **Gust G. 1999**. Water flow in tide- and wave-dominated beds of the seagrass *Thalassia testudinum*. *Marine Ecology Progress Series* **184**: 63–72. doi:10.3354/meps184063.

**Koehl MAR. 1984**. How do benthic organisms withstand moving water? *American Zoologist* **24**: 57–70. doi:10.1093/icb/24.1.57.

**Lenth R. 2020**. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.5. https://CRAN.R-project.org/package=emmeans

**Lowe RJ**, **Koseff JR**, **Monismith SG. 2005**. Oscillatory flow through submerged canopies: 1. Velocity structure. *Journal of Geophysical Research, Oceans* **110**: C10016. doi:10.1029/2004JC002788.

**Luhar M**, **Infantes E**, **Nepf H. 2017**. Seagrass blade motion under waves and its impact on wave decay. *Journal of Geophysical Research, Oceans* **122**: 3736–3752. doi:10.1002/2017jc012731.

**Lyman TP**, **Elsmore K**, **Gaylord B**, **Byrnes JEK**, **Miller LP. 2020**. Open Wave Height Logger: an open source pressure sensor data logger for wave measurement. *Limnology and Oceanography: Methods* **18**: 335–345. doi:10.1002/lom3.10370.

**Mendez FJ**, **Losada IJ. 2004**. An empirical model to estimate the propagation of random breaking and nonbreaking waves over vegetation fields. *Coastal Engineering* **51**: 103–118. doi:10.1016/j.coastaleng.2003.11.003.

**Miller RJ**, **Lafferty KD**, **Lamy T**, **Kui L**, **Rassweiler A**, **Reed DC. 2018**. Giant kelp, *Macrocystis pyrifera*, increases faunal diversity through physical engineering. *Proceedings of the Royal Society B: Biological Sciences* **285**: 20172571. doi:10.1098/rspb.2017.2571.

**Mork M. 1996**. The effect of kelp in wave damping. *Sarsia* **80**: 323–327. doi:10.1080/00364827.1996.10413607.

**Morris RL**, **Graham TDJ**, **Kelvin J**, **Ghisalberti M**, **Swearer SE. 2020**. Kelp beds as coastal protection: wave attenuation of *Ecklonia radiata* in a shallow coastal bay. *Annals of Botany* **125**: 235–246. doi:10.1093/aob/mcz127.

**Mullarney JC**, **Pilditch CA. 2017**. The differential response of kelp to swell and infragravity wave motion. *Limnology and Oceanography* **62**: 2524–2537. doi:10.1002/lno.10587.

**Möller I**, **Kudella M**, **Rupprecht F**, ***et al*. 2014**. Wave attenuation over coastal salt marshes under storm surge conditions. *Nature Geosciences* **7**: 727–731. doi:10.1038/ngeo2251.

**North WJ. 1971**. The biology of giant kelp beds (*Macrocystis*) in California. *Nova Hedwigia* **32**: 1–600.

**Paul M**, **Bouma TJ**, **Amos CL. 2012**. Wave attenuation by submerged vegetation: combining the effect of organism traits and tidal current. *Marine Ecology Progress Series* **444**: 31–41. doi:10.3354/meps09489.

**Planet Team. 2020**. *Planet application program interface: in space for life on Earth*. San Francisco, CA. https//api.planet.com.

**R Core Team. 2019**. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

**Reed DC**, **Foster MS. 1984**. The effects of canopy shadings on algal recruitment and growth in a giant kelp forest. *Ecology* **65**: 937–948. doi:10.2307/1938066.

**Reed DC**, **Rassweiler A**, **Carr MH**, **Cavanaugh KC**, **Malone DP**, **Siegel DA. 2011**. Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. *Ecology* **92**: 2108–2116. doi:10.1890/11-0377.1.

**Riffe KC**, **Henderson SM**, **Mullarney JC. 2011**. Wave dissipation by flexible vegetation. *Geophysical Research Letters* **38**: 1–5. doi:10.1029/2011gl048773.

**Rodriguez GE**, **Rassweiler A**, **Reed DC**, **Holbrook SJ. 2013**. The importance of progressive senescence in the biomass dynamics of giant kelp (*Macrocystis pyrifera*). *Ecology* **94**: 1848–1858. doi:10.1890/12-1340.1.

**Rosman JH**, **Koseff JR**, **Monismith SG**, **Grover J. 2007**. A field investigation into the effects of a kelp forest (*Macrocystis pyrifera*) on coastal hydrodynamics and transport. *Journal of Geophysical Research* **112**: C02016. doi:10.1029/2005JC003430.

**Rosman JH**, **Denny MW**, **Zeller RB**, **Monismith SG**, **Koseff JR. 2013**. Interaction of waves and currents with kelp forests (*Macrocystis pyrifera*): insights from a dynamically scaled laboratory model. *Limnology and Oceanography* **58**: 790–802. doi:10.4319/lo.2013.58.3.0790.

**Schiel DR**, **Foster MS. 2015**. *The Biology and Ecology of Giant Kelp Forests*. Oakland, CA: University of California Press Books. doi:10.1525/9780520961098.

**Seymour RJ**, **Hanes DM. 1979**. Performance analysis of tethered float breakwater. *Journal of the Waterway, Port, Coastal and Ocean Division* **105**: 265–280. doi:10.1061/jwpcdx.0000153.

**Seymour RJ**, **Tegner MJ**, **Dayton PK**, **Parnell PE. 1989**. Storm wave induced mortality of giant kelp, *Macrocystis pyrifera*, in Southern California. *Estuarine, Coastal and Shelf Science* **28**: 277–292. doi:10.1016/0272-7714(89)90018-8.

**Tinoco RO**, **San Juan JE**, **Mullarney JC. 2020**. Simplification bias: lessons from laboratory and field experiment on flow through aquatic vegetation. *Earth Surface Processes and Landforms* **45**: 121–143. doi:10.1002/esp.4743.

**Traiger SB**, **Cohn B**, **Panos D**, ***et al*. 2022**. Limited biogeochemical modification of surface waters by kelp forest canopies: influence of kelp metabolism and site-specific hydrodynamics. *Limnology and Oceanography* **67**: 392–403. doi:10.1002/lno.11999.

**Vogel S. 1984**. Drag and flexibility in sessile organisms. *American Zoologist* **24**: 37–44. doi:10.1093/icb/24.1.37.