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Contrasting mechanisms of dislodgement and erosion contribute to production of kelp detritus

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Abstract

We quantified simultaneously dislodgement and erosion for a dominant kelp species (*Ecklonia radiata*) over 1 yr, and related both to potential explanatory factors (wave exposure, temperature, and kelp fecundity). Erosion was the largest contributor of detritus, accounting for 80% of annual production. Most erosion occurred as a major pulse in autumn, whereas dislodgement was a minor and constant process throughout the year. Neither erosion nor dislodgement was correlated with water velocity (as often proposed), and this finding contradicts the common assumption that high dislodgement rates during peak wave action account for the bulk of detrital production. Together with low growth, the high erosion rate led to a severe reduction of individual kelp biomass in autumn (from 600 g to 300 g fresh weight kelp^{-1}), reducing drag forces on kelp thalli by ~ 50%, likely reducing their susceptibility to dislodgement during peak wave action. Instead, a pulse of detrital production coincided with periods of peak kelp fecundity. We propose that sporogenesis weakens the tissue, making *E. radiata* more susceptible to erosion, and that the ensuing changes in kelp morphology decouple detrital production from the wave-action forces.

The distribution of primary production across landscapes is usually heterogeneous, with adjacent habitat patches often differing markedly in rates of productivity (Pickett and Cadenasso 1995). Patches within landscapes are connected by the flow of matter across their boundaries, and this process can subsidize secondary productivity in recipient habitats where primary productivity is low (Polis et al. 1997). Such cross-habitat trophic subsidies are disproportionately important in aquatic ecosystems because of their greater connectivity and faster rate of nutrient recycling compared with many terrestrial systems (Giller et al. 2004).

Kelp detritus is a key vector of trophic connectivity in many coastal ecosystems (Krumhansl and Scheibling 2012). Kelp beds (stands of large brown algae of the order Laminariales) are among the most highly productive habitats on earth, with rates of productivity up to 1500–2500 g C m^{-2} yr^{-1} (Mann 1973); these rates rival the most productive terrestrial ecosystems, including tropical rain forests (up to 1500–1700 g C m^{-2} yr^{-1}; Schuur 2003). In some cases, when grazers are abundant, kelps are among the primary producers most strongly affected by herbivory (Poore et al. 2012). However, similar to many terrestrial ecosystems, it is often the case that only 10–15% of the production from kelp beds is consumed locally by herbivores, while 85–90% of the production is not directly consumed and becomes detritus (Cebrian 1999), which is frequently exported from the kelp beds to distant habitats where it is consumed (Vanderklift and Wernberg 2008). Consequently, kelp detritus subsidizes a large variety of habitats, including beaches, intertidal rocky shores, distant reefs, submarine canyons, seagrass beds, and small islands (Polis et al. 1997; Krumhansl and Scheibling 2012).

Kelp detritus is generated primarily through two different mechanisms (Krumhansl and Scheibling 2012): either the dislodgement of entire thalli including very large fragments (usually leading to the death of the kelp; Seymour et al. 1989), or fragmentation of parts of the thalli through erosion and pruning (Krumhansl and Scheibling 2011). Detritus generated through these different mechanisms is likely to be exported to different places and might support different sets of consumers, because the difference in particle sizes (whole thalli to small fragments) will influence mechanisms of transport and the types of consumers that can eat them. In contrast to extensive studies on kelp productivity, the production of kelp detritus has been less frequently studied. Some studies have quantified dislodgement (Gerard 1976; Seymour et al. 1989) and erosion (Newell et al. 1982; Krumhansl and Scheibling 2011), but their relative contribution to detrital production has rarely been investigated simultaneously (but *see* Gerard 1976; Newell et al. 1982). Gerard (1976) found that dislodgement of the giant kelp, *Macrocystis pyrifera,* in California was three times greater than erosion; whereas, Newell et al. (1982) found erosion to be 10 times greater than dislodgement for *Ecklonia maxima* and *Laminaria pallida* in South Africa.

Wave exposure is frequently viewed as the main influence on production of kelp detritus because of higher kelp mortality during peak wave action (Seymour et al. 1989), frequent accumulation of drift algae in nearshore habitats after storms (Colombini and Chelazzi 2003), and

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the hypothesized physical abrasion of kelp tips during high wave activity, which has been advanced to explain the lower individual kelp biomass during certain times of the year (Wernberg and Goldberg 2008). Other studies have found erosion rate to be positively related to water temperature (Krumhansl and Scheibling 2011), leading to peak erosion during warmer months. Rates of erosion might also be linked to seasonal patterns in kelp maturity and sporulation. Many species of kelps exhibit a strong seasonal reproductive synchrony (Mohring et al. 2012). In order for spores to be released, abscission of reproductive sori (clusters of spores) frequently occurs, probably caused by a combination of a structural weakening and mechanical scouring from water motion (Walker 1980). Hence, it can be hypothesized that erosion rate will peak at the same time.

Accumulations of beach-cast kelp on the shore frequently consist mainly of large fragments or entire kelp (Colombini and Chelazzi 2003). One possible explanation for this is that the dislodgement of whole kelp is the dominant mechanism fueling this coastal detrital pathway. Because the observations of drift-kelps usually coincide with storms (Seymour et al. 1989), it is generally recognized that physical forcing of waves and currents generate pulses of kelp-dislodgement, rather than a more continuous erosion rate and minor contributor to detritus production. Nevertheless, the high productivity of kelps and their limitation in sizes (Mann 1973) imply relatively high erosion rates, which might also be an important contributor to detrital production. However, no studies have assessed the magnitude and relative contributions of dislodgement and erosion to detrital production over a year for any kelp species. As pointed out by the review of Krumhansl and Scheibling (2012), such understanding is required to assess the importance of the energy flow related to this detrital matter through coastal systems.

Here, we determine the contribution of dislodgement and erosion to kelp detritus production over 1 yr for nine sub-tidal reefs. Furthermore, we test how well three hypothesized drivers of detrital production (water velocity, seawater temperature, and kelp fecundity) explained measured dislodgement and erosion losses of kelps from these nine reefs. The study region exhibits maximum seawater temperature in the austral summer (i.e., December to February [Kirkman 1984; Smale and Wernberg 2009]), frequent storms generate large swell and waves in austral winter (i.e., June to August; Lemm et al. 1999), and the peak of fecundity for the kelp studied, *Ecklonia radiata,* shows a seasonal peak in spore production and release in autumn (Mohring et al. 2012). Therefore, the detrital production will peak (1) in winter if dislodgement and erosion are controlled by water velocity; (2) in summer if the erosion depends on the seawater temperature; (3) in summer and winter if both temperature and water velocity are determinant; and (4) in autumn if erosion is related to kelp fecundity and spore release.

Methods

Study site characteristics—Southwestern Australia is strongly influenced by waves, both swell and wind-generated waves, but is dominated by oceanic swell from the west and southwest (Lemm et al. 1999). In summer (December–February), sea breezes generate moderate waves; whereas, in winter (June–August), frequent storms generate large swell and waves. The configuration of the coastline, with successive lines of submerged limestone reefs running parallel to the shore, dissipates hydrodynamic forces as waves approach the coast, and generate a gradient of wave exposure (Thomson et al. 2012). Therefore, wave exposure varies both seasonally and spatially. Our study took place in Marmion (31°480′18″S, 115°420′11″E), which comprises a mosaic of different habitats (reefs, seagrass meadows, sand) at relatively shallow depth (< 15 m deep). Nine sub-tidal reefs (8–11 m deep) with dense kelp beds (6–10 kelp adults m^{-2}; Wernberg 2009) were chosen to encompass a broad range of water velocities at the sea floor (Fig. 1). Dislodgement and erosion were estimated for these nine reefs for each season (autumn, winter, spring 2010, and summer 2011) over 1 yr. In southwestern Australia, grazing by fish and sea urchins is low and little of the biomass produced by kelp is grazed directly, except for some inshore reefs where grazing can be greater (Vanderklift et al. 2009). Instead, the majority of the sea urchins in this region (*Heliocidaris erythrogramma*) feed only on drift material and did not affect the kelp beds (Vanderklift and Wernberg 2008).

Biomass accumulation—Biomass accumulation (= primary productivity) was measured every 3 months for 15 kelps at each site, using the traditional hole-punch method (Kirkman 1984). Individual kelps were punched with two holes into the central lamina. The first hole was located 5 cm from the junction between the stipe and the lamina and the second hole was 5 cm from the first one. The distance from the first hole to the junction between the stipe–lamina and the distance between the two holes were measured in the laboratory. The thallus extension was calculated by subtraction of the sum of these two measures by 10 cm. The segment (5 cm) of maximum biomass (for the first 30 cm) was then used to calculate biomass accumulation (BA or kelp productivity, g fresh weight [fresh wt] $kelp^{-1}$ d^{-1}) as BA = X fresh wt/5T, where X is the thallus extension (cm), the fresh weight (g) of the heaviest strip, and T is the number of days between punching the holes and collecting the kelp (Vanderklift et al. 2009). To convert fresh weight to carbon content, we applied conversion factors of 5.27 fresh weight : dry weight (dry wt; T. Wernberg unpubl. mean of 250 kelps from 25 sites across southwest Australia) and 2.78 dry wt : C (35% carbon of dry weight for *Ecklonia radiata* in the same region [Atkinson and Smith 1983]).

Dislodgement—At each of the nine reefs, four circular plots (2 m diameter) were established; and within each plot, 15 adult kelps (stage 3; Kirkman 1984) with distinct holdfasts (no fused holdfast) were tagged around the stipe, with cable ties inserted through fluorescent latex surgical tubing. A subset of 50% of all kelps at four reefs (two out of four plots at each reef, n = 120 kelps) were double-tagged to test for tag loss. After a 3 month trial, 100% of

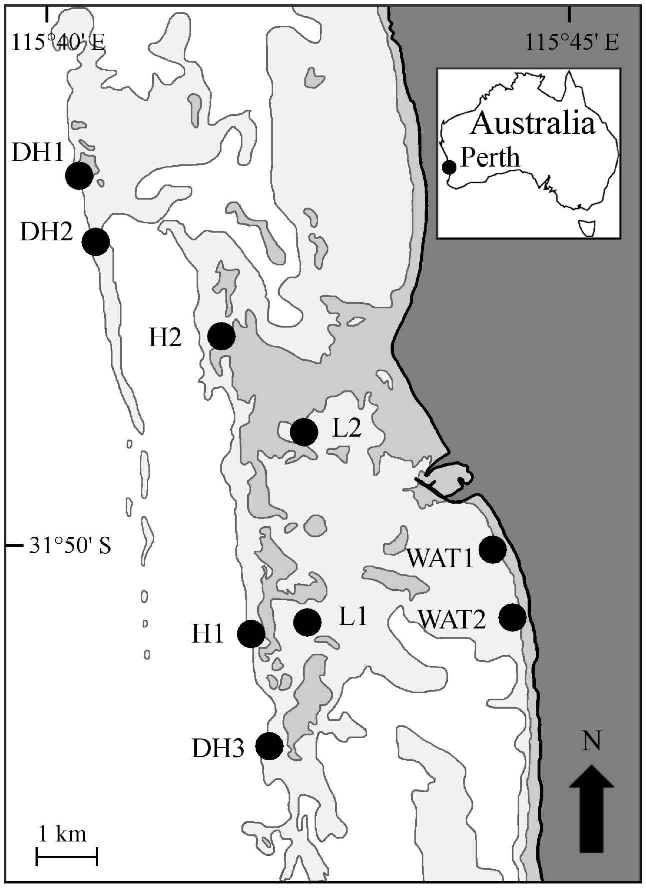

Fig. 1. Map of Marmion indicating the location of the nine sites included in this study. The grey scale shows the bathymetry, depth 0–5 m in light grey and 5–10 m darker. WAT1, WAT2, L1, L2, H1, H2, DH1, DH2, and DH3 are the study sites. Inset shows location of Marmion.

the kelp recovered had double tags, indicating that tag loss was non-existent. Every 3 months, four new randomly located plots (n = 60 kelps per reef) were set up at each reef. For each plot, the tagged kelps were relocated and counted; dislodgement was inferred from an inability to relocate a tagged plant, which implied a breakage at the holdfast–reef, along the stipe, or at the stipe–lamina junction. Each plot was counted three times to avoid any over-estimation of dislodgement. The kelp dislodgement rate (D, loss kelp plot^{-1}) was defined as the difference in tagged kelps over the 3 month period. The rate of detrital production (DP_D, g m^{-2} d^{-1}) was then derived as

$$DP_D = \frac{D \times \overline{WW} \times K}{T \times N \times A} \quad (1)$$

where $\overline{WW}$ is the mean individual biomass (n = 15) of adult kelp at the tagging; T is the duration in days; K is the number of adult kelps within the circular plot; A is the area of the circular plot of 1 m radius (A = 3.14 m^{-2}); and N is the number of kelp tagged within the plot (n = 15). The four plots were then averaged to get a single value per reef for each season.

Erosion—To obtain rates of erosion for morphologically complex kelps such as *Ecklonia radiata,* a new approach was developed based on the biomass per unit length (fresh weight: lamina length every 5 cm; fresh wt : l) plotted against distance from the base of the blade (Fig. 2). According to Mann and Kirkman (1981), each thallus can be divided into three zones: (1) a zone of secondary growth, where fresh wt : l increases with distance from the blade; (2) a zone of maximum biomass where fresh wt : l is relatively constant; and (3) a zone of erosion in which fresh wt : l decreases. In order to obtain an average biomass profile at the beginning of each sampling period for each site, 15 adult kelps were harvested (15 kelps at the beginning of the experiment and the same kelps used for measurement of biomass accumulation at the end of each productivity measurement period), each lamina length was measured, and 12 5 cm segments of each thallus were weighed (six sections working progressively upward from the base and six downward from the top). For each site and time, these segments were averaged to obtain a representative partitioning of biomass per unit length for an 'average thallus length' adult kelp (average n = 15 lamina lengths). Each biomass profile was plotted with a missing section between the two sets of segments (basal and distal) depending of the average lamina length when > 60 cm (Fig. 2).

According to the overall shape of the biomass profile, a polynomial cubic regression was chosen ($r^2 > 0.98$, $p < 0.001$) to model the variation of weight along the thallus. Each averaged biomass profile was expressed as a cubic polynomial function after regression, with $y = 0$ at both ends of the profile (Fig. 2). The erosion of kelp at each reef was then estimated as the area under the profiles of two consecutive times, as shown in Fig. 2, with the biomass profile of the starting time moved along the x-axis according to the averaged thallus extension between the two times. The erosion was estimated for each combination of reef × time (n = 36) as

$$\sum_{i=5}^{L_1+G} [Y_1(x_i) - Y_2(x_i)].\ \Delta x, \quad \Delta x = 5\ \text{cm}, \quad (2)$$
$$\text{for } Y_1(x_i) - Y_2(x_i) > 0$$

with L_1 being lamina length at time 1; G being the thallus extension between time 1 and time 2; Y_1 (x) and Y_2 (x) being the polynomial function of the biomass profiles at time 1 and 2 (Fig. 2).

The rate of detrital production from erosion (DP_E, g m^{-2} d^{-1}) was then derived as

$$DP_E = \frac{E \times K}{T \times A} \quad (3)$$

Where E is the average individual erosion rate (g kelp^{-1}); T is the duration in days; K is the number of adult kelps within the circular plot; and A is the area of the circular plot of 1 m radius (A = 3.14 m^2).

Drivers of kelp detrital production—To test for possible relationships with potential drivers of detrital production,

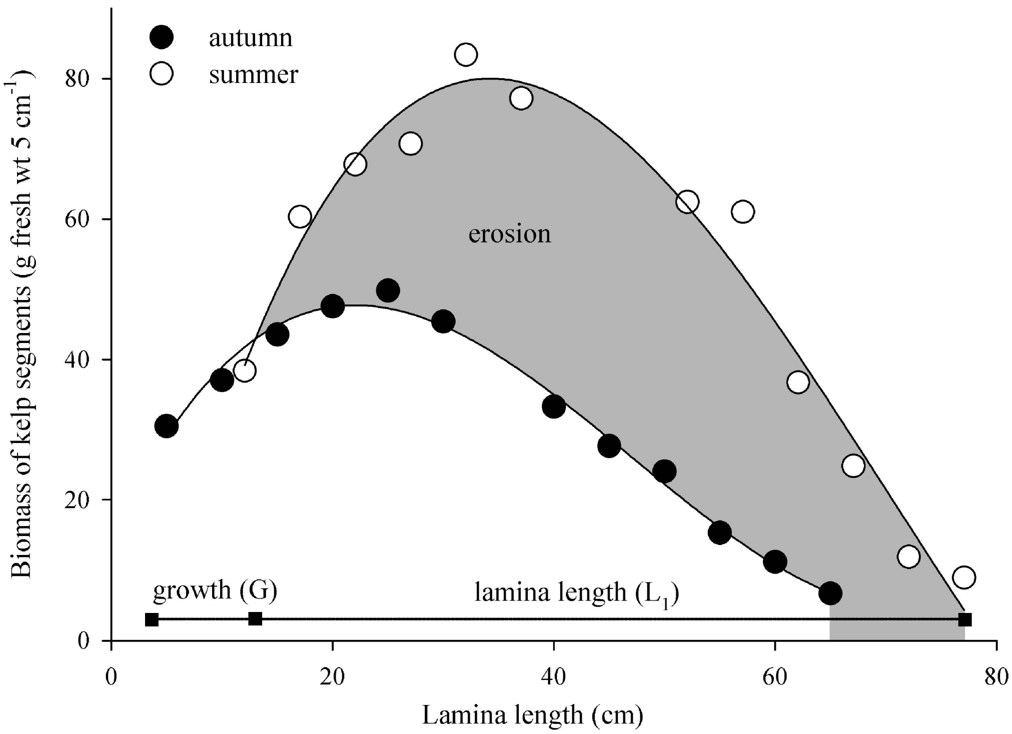

Fig. 2. Diagram representing the erosion as the area between the two biomass profiles from two different times (data used from reef DH1, to calculate autumn erosion with profiles of late summer and late autumn 2010). Each dot (black or white) represents the average weight of the different 5 cm segments of an average kelp (n = 15). The biomass profile is displayed from left to right, from the basal to the distal part of the kelp thallus.

erosion and dislodgement were regressed against temperature, water velocity, and kelp fecundity.

Temperature: Temperature (°C) was monitored every 10 min at each site with data loggers (onset HOBO® data loggers Pendant Temp-Light, Onset Computer Corporation) and averaged for each site and season.

Water velocity: Water velocity at the seafloor was calculated using the recognized and tested numerical model for the region, the simulating waves nearshore (SWAN) model (Booij et al. 1999). SWAN was run for the period March 2010 to February 2011 within the 30 × 30 m high resolution grid of the model domain, encompassing 161.78 km^2 of Marmion (Thomson et al. 2012). The model was forced at its western (seaward) boundary using daily averaged wave height, period, and direction obtained from the Rottnest wave buoy (Department for Planning and Infrastructure-Western Australia, located 20 km southwest of the study area). Daily model outputs of average bottom-water velocity were extracted from the model grid cell nearest to each of our nine reefs. These values were then used to obtain the 95th percentile of bottom-water velocities at each site for each season.

Kelp fecundity: Kelp fecundity was measured two times during each season. Four thalli were harvested for seven of the nine reefs (L1, L2, H1, H2, DH1, DH2, DH3; Fig. 1) and kelp fecundity was determined as zoospore release density (Mohring et al. 2012). From each thallus, 10 discs of tissue of 27 mm diameter (total 11,451.1 mm^2) were punched from the central lamina and placed in a cup to facilitate zoospore release. After 20 min, 1 mL of the zoospore solution was placed in a Neubauer counting chamber and the number of zoospores determined and converted to density of spores released per area of lamina. For each reef, the results from the eight thalli were averaged for each season and expressed as a proportion of the total spore density observed during the year (%) at that reef and time (i.e., for each reef × time[season]), as an index of kelp fecundity.

Results

Biomass accumulation, erosion, and net productivity—Biomass accumulation was highest in spring 2010 (mean = 3.84 ± 1.53 standard deviation [SD] g fresh wt kelp^{-1} d^{-1}, intermediate in winter 2010 and summer 2010–2011 (respectively, 1.75 ± 0.58 and 1.95 ± 0.54 g fresh wt kelp^{-1} d^{-1}), and lowest in autumn 2010 (0.89 ± 0.17 g fresh wt kelp^{-1} d^{-1}; Fig. 3a). Erosion peaked in autumn (4.8 ± 1.69 g fresh wt kelp^{-1} d^{-1}), decreased in winter (2.12 ± 0.84 g fresh wt kelp^{-1} d^{-1}), and reached a minimum in spring and summer (respectively, 0.70 ± 0.45 and 0.97 ± 0.81 g fresh wt kelp^{-1} d^{-1}; Fig. 3b). The opposing temporal patterns of biomass accumulation (BA) and erosion (E) led to marked temporal differences in net productivity (BA–E; Fig. 3c), with negative (−3.93 ± 1.61 g fresh wt kelp^{-1} d^{-1}) and positive (+3.15 ± 1.32 g fresh wt kelp^{-1} d^{-1}) peaks in autumn and spring, respectively. In winter and summer, the differences between biomass

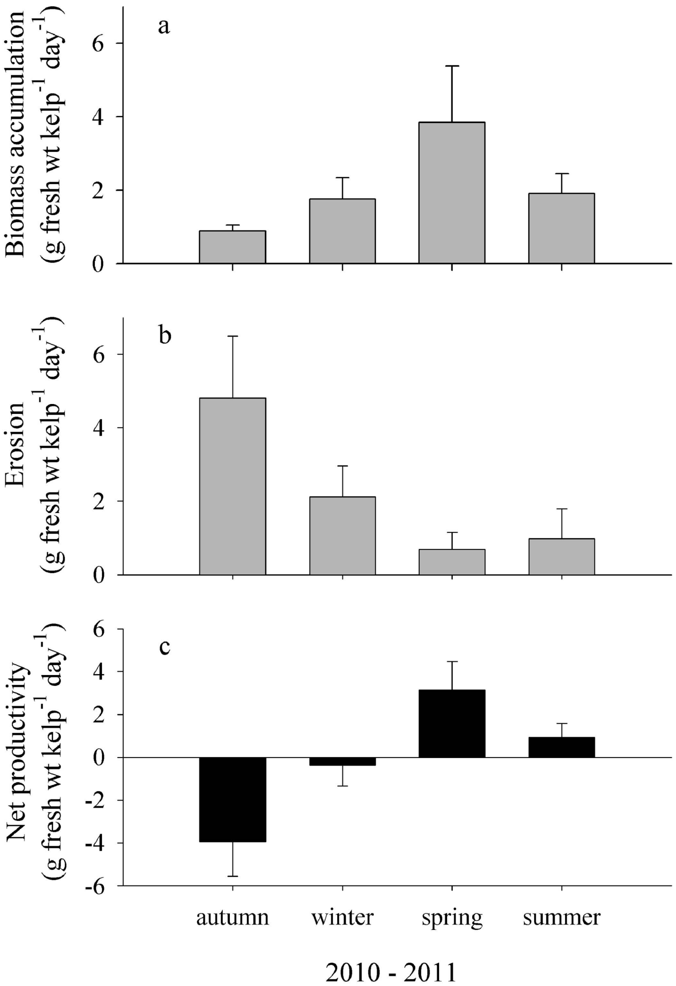

Fig. 3. Seasonal variation in individual (a) biomass accumulation (BA); (b) erosion (E), and (c) net productivity (BA–E; mean and SD across the nine sites).

accumulation and erosion were lower, resulting in intermediate net productivity estimates (−0.37 ± 0.97 and 0.93 ± 0.64 g fresh wt kelp^{-1} d^{-1}, respectively; Fig. 3c).

Dislodgement and erosion—Kelp density did not change during the study period, with adult density between 7 kelp m^{-2} and 8 kelp m^{-2} (Fig. 4a). However, there was strong temporal variation in the biomass of individual kelps, with a minimum in late autumn and late winter 2010 (355 and 285 g fresh wt kelp^{-1}, respectively), and a maximum in early autumn 2010, late spring 2010, and late summer 2011 (606, 554 and 648 g fresh wt kelp^{-1}, respectively; Fig 4b).

For all sites, there was no remaining tagged kelp with large pieces of missing lamina, which implied that large pieces of drift kelp resulted primarily from breakage at the reef–holdfast junction or structural failure along the stipe and at the stipe–lamina junction (described as dislodgement of adult kelps). The mean dislodgement rate was constant throughout the sampling period, though there was greater variation among sites in spring and summer 2010–2011 and least variation in winter 2010 (Fig. 4c). In contrast, there was a strong temporal variation in the mean individual

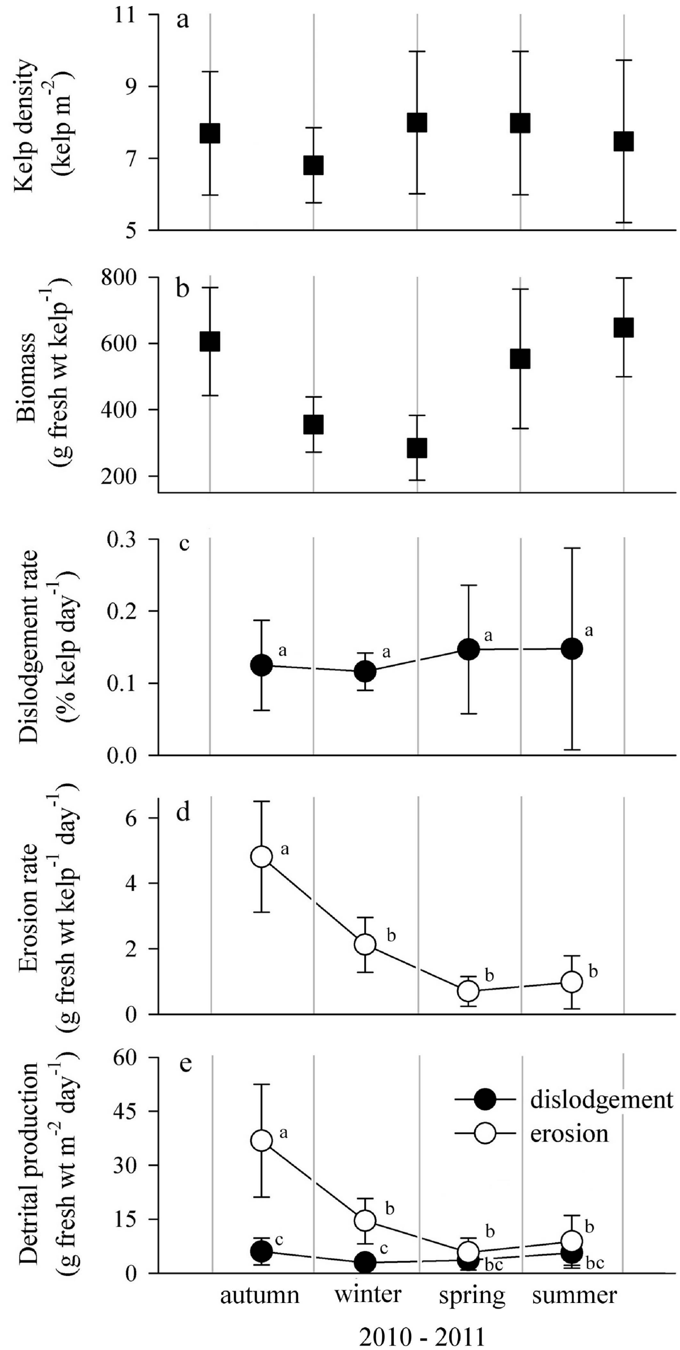

Fig. 4. (a) Kelp density, (b) individual kelp biomass, (c) dislodgement rate, (d) individual erosion rate, and (e) detrital production generated through dislodgement and erosion (mean and SD across the nine sites). Letters above symbols indicate the significant differences between seasons and mechanisms (analysis of variance, $p < 0.05$).

erosion rate, with a peak in autumn 2010 (4.8 ± 1.69 g fresh wt kelp^{-1} d^{-1}). The measured kelp densities, biomass, dislodgement rates, and the derived erosion rates (Fig. 4a–d) were used to estimate the production of kelp detritus through dislodgement and erosion (Fig. 4e). The two mechanisms of detrital production (dislodgement and erosion) exhibited different temporal patterns (Fig. 4e).

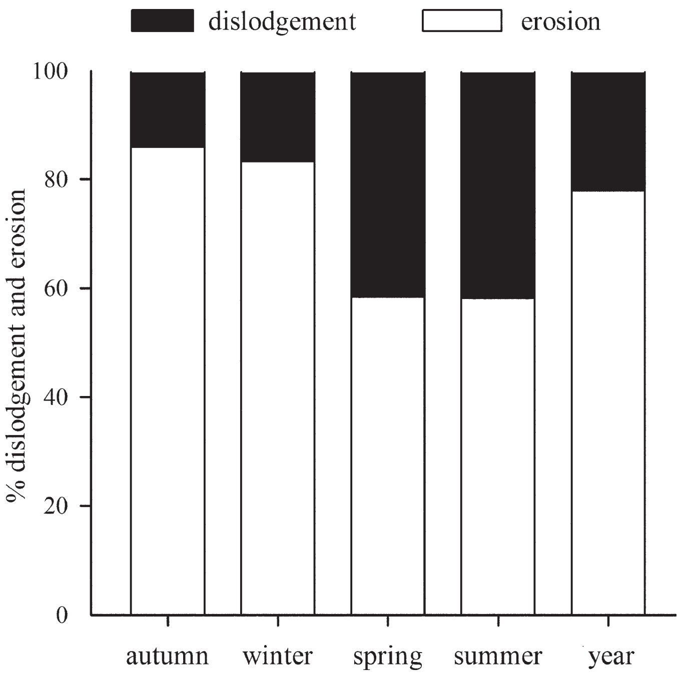

Fig. 5. Relative proportions of the two mechanisms of kelp detrital supply (dislodgement and erosion) for every season in 2010–2011 and for the whole year.

Kelp detritus production through dislodgement was constant over the year (mean ± SD = ~ 4.5 ± 2.8 g fresh wt m^{-2} d^{-1}); whereas, the detrital production via erosion peaked in autumn 2010 (~ 40 ± 15 g fresh wt m^{-2} d^{-1}), decreased but remained high in winter (14.5 ± 6.3 g fresh wt m^{-2} d^{-1}), and then fell to similar production rates as dislodgement in spring and summer (Fig. 4e). The detrital production via erosion was the product of the individual erosion rate (g fresh wt $kelp^{-1}$ d^{-1}; Fig. 4d) and the kelp density at the beginning of each time (Fig. 4a), and the kelp density was constant over the year; therefore, changes in this detrital production were explained only by changes in individual erosion rate (Fig. 4d).

The average annual detrital production, for the nine sites, was 7391 (± 2762) g fresh wt m^{-2} yr^{-1}, of which 1593 (± 758) g fresh wt m^{-2} yr^{-1} was derived from dislodgement and 5798 (± 2081) g fresh wt m^{-2} yr^{-1} from erosion (Fig. 5). This dominance of erosion as the contributor was consistent throughout the year, accounting for > 80% of the total detrital supply in autumn and winter 2010, and about 60% of total in spring and summer 2010–2011 (Fig. 5). Therefore, the contributions of dislodgement and erosion for the total kelp detrital production were on average 109 ± 52 and 396 ± 142 g C m^{-2} yr^{-1}, respectively, and 505 ± 189 g C m^{-2} yr^{-1} in total.

Potential drivers—There were no significant relationships between water velocity (wave exposure) and either dislodgement or erosion rates (Fig. 6a,b). Similarly, there was no relationship between seasonal variation in mean temperature and erosion (Fig. 6c) because maximum erosion occurred around 22°C and not at the maximum temperature recorded (> 24°C; Fig. 6c). However, there was a strong positive correlation between kelp fecundity and erosion rate (Fig. 6d), with the kelp fecundity index explaining 76% of the variation in erosion (Fig. 6d).

Discussion

Erosion accounted for almost 80% of the annual kelp detrital production from the reefs studied. This input of detritus was not constant over time, but occurred as a pulse of erosional losses from March to June (autumn) providing on average 40 g fresh wt m^{-2} d^{-1} of kelp detritus (up to 50 g fresh wt m^{-2} d^{-1}), making a considerable contribution to the whole coastal system (4–6 times greater than other times of the year). In contrast, kelp loss through dislodgement was less and constant throughout the year. These findings contrast with large canopy kelp species (e.g., *Macrocystis pyrifera*), which exhibit seasonal wave dislodgement peaking in winter and greater than erosion (Krumhansl and Scheibling 2012). However, even if the timing of kelp dislodgement differs, its ecological consequences for recipient habitats can be similar if previous dislodged kelps are wave-driven transported at the same time in winter.

The amount of detrital material produced annually from erosion (254–538 g C m^{-2} yr^{-1}) was in the same range as reported for *Ecklonia radiata* in New Zealand (~ 450–645 g C m^{-2} yr^{-1}; Novaczek 1984), a mixed stand of *Saccharina longicruris* and *Laminaria digitata* in Nova Scotia (150–513 g C m^{-2} yr^{-1}; Krumhansl and Scheibling 2011), a mixed stand of *Ecklonia maxima* and *Laminaria pallida* in South Africa (~ 343 g C m^{-2} yr^{-1}; Newell et al. 1982), and monospecific stands of *Lessonia nigrescens* and *Lessonia traberculata* in Chile (~ 553 and 524 g C m^{-2} yr^{-1}, respectively; Tala and Edding 2007). However, the detrital production via erosion was much lower than a previous estimate for *Ecklonia radiata* from a single reef in the same region (~ 1725 g C m^{-2} yr^{-1}; Kirkman 1984). This discrepancy between Kirkman's (1984) and our estimates can be explained by a very high density of kelps at his site (density of 26 kelp m^{-2} vs. 8 in our study), which is not representative of most reefs in the region (Wernberg 2009).

The constant rate of dislodgement (% of kelp density dislodged) throughout the year (~ 4% kelp loss.$month^{-1}$) contrasted with our expectation of increased dislodgement coinciding with peak water velocity and storms that remove whole thalli from the reefs. However, this can be explained by the interaction between kelp growth dynamics, erosion losses, and the factors that determine drag forces acting on kelps. At peak bottom-water velocities characteristic of winter storms in the region (2–4 m s^{-1}), the drag acting on a kelp, and its likelihood of dislodgement, is largely a function of kelp biomass (de Bettignies et al. 2013). However, in autumn and winter, when the storm-induced water flows are at their greatest, the individual kelp biomass is at its minimum due to the high erosion (5 g fresh wt d^{-1}) and low biomass accumulation (0.9 g fresh wt d^{-1}) in early autumn. This temporal growth dynamic and autumn–winter decrease of individual biomass has been noted in previous studies (Kirkman 1984). Therefore, we propose that the reduction of biomass through erosion

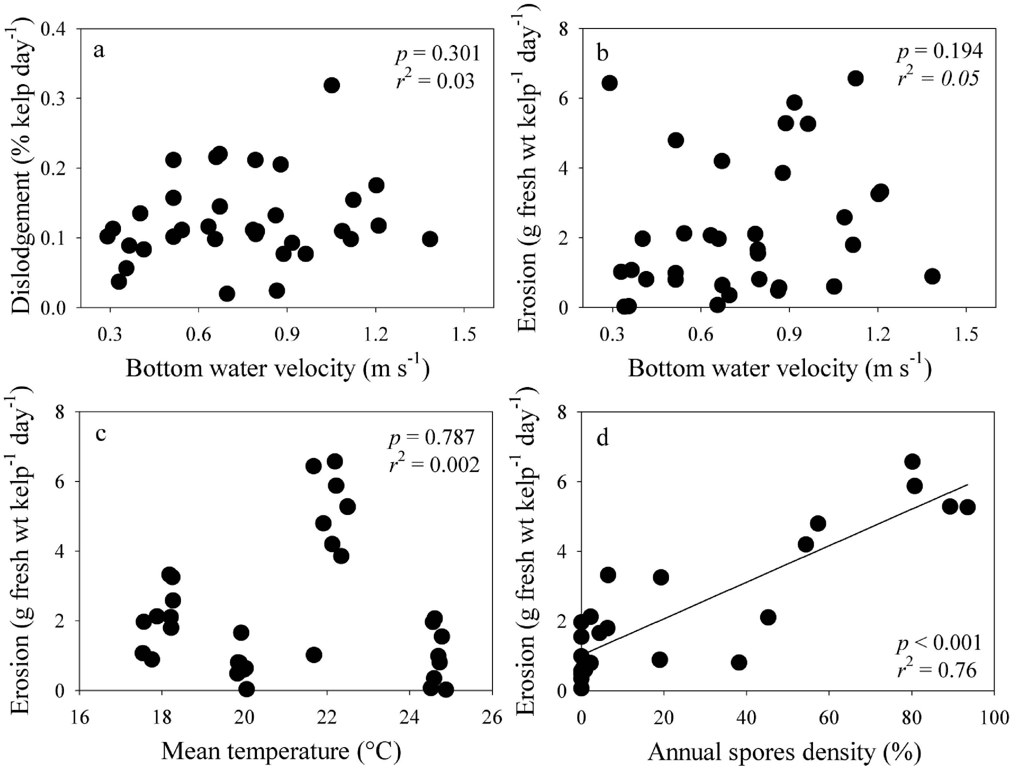

Fig. 6. Relationship between detrital production mechanisms (dislodgement and erosion) and measures of wave exposure, temperature, and kelp fecundity. (a) Dislodgement vs. average bottom-water velocity; (b) erosion vs. average bottom-water velocity; (c) erosion vs. temperature, and (d) erosion vs. kelp fecundity, with p and r^2 from the respective linear regressions.

minimizes the drag forces acting on kelps during storms, explaining the lower than expected dislodgement rates observed in winter.

Because the erosional defoliation of adult kelps is severe, such a reduction in cover of the dominant canopy-forming species will affect the local communities. First, this reduction can maximize the recruitment and recruit growth of *Ecklonia radiata* itself, similar to the effect of canopy removal (Wernberg and Goldberg 2008). Because this process occurs together with spore formation and release, this timing is important for kelp bed dynamic, and subsequent recruit survival and canopy renewal. Because ambient diurnal light is lower during this period (autumn–winter), recruits will not suffer from excessive photoinhibition and photostress that can be critical for their survival (Toohey and Kendrick 2007). Finally, any change in kelp canopy cover (canopy removal or defoliation) will have flow-on effects for the other reef-associated communities (Wernberg et al. 2013). Canopy-forming kelps influence the diversity and turn-over of the understory algal communities because they modify the physical environment (Reed and Foster 1984; Irving and Connell 2006). Kelp canopies, such as *Ecklonia radiata,* have been shown to increase physical abrasion via thallus scour, and to reduce sub-canopy light (Irving and Connell 2006). These modifications can affect negatively the recruitment, survival, and physiological performance of the understory algal communities. However, the extent of the seasonal pruning and severe decrease in individual biomass of the dominant kelp canopy species can balance this negative effect, and make space available for colonization, increase light penetration for growth, and reduce thallus scouring. Wernberg and Goldberg (2008) demonstrated that increase and decrease of cover and biomass of *Ecklonia radiata* affected the species richness and assemblage structure of other macroalgae, resulting in high species-turnover on the reef, similar to the canopy-gap mosaic that maintains species richness across spatial landscapes.

The pulse of erosion-driven detrital production in autumn (March–June) was associated with increasing kelp fecundity (the number of zoospores released from kelp tissue), but not with wave exposure or seasonal variation in mean temperature, as has previously been proposed (Seymour et al. 1989; Krumhansl and Scheibling 2011, 2012). However, the duration and magnitude of extreme temperature warming can lead to large mortality or defoliation of kelp, directly through physiological stress (Wernberg et al. 2013) or altered species interactions, such as heavy fouling by bryozoans during warm periods (Krumhansl and Scheibling 2012). Instead, we hypothesize that the peak in kelp erosion in autumn was largely facilitated by zoospore release, because this has previously been shown for *Nereocystis luetkeana* in British Columbia and Central California (Walker 1980). In *N. luetkeana,* tissue necrosis leading to dissolution of the cuticle covering the sori (Walker 1980) produces structural weakening so that water motion causes the sori to abscise from the blade (Walker 1980). Although portrayed by previous authors as a rare mechanism in kelp (Walker 1980), it may be broadly applicable in kelps with vegetative and reproductive tissues that are not physically separated on the thallus. In *Ecklonia radiata,* sori are distributed throughout the distal end of the thallus, and it is plausible that a similar weakening of the reproductive tissue might have affected the vegetative tissue of *Ecklonia radiata,* leading to increased erosion of the thallus. We have previously documented how the amount of damage and wounds to kelp tissue was highest in autumn (300–400 holes per thallus; de Bettignies et al. 2012), and that simulation of equivalent wounding led to kelp fragmentation at much lower than expected hydrodynamic forces (de Bettignies et al. 2012). Similarly, Krumhansl and Scheibling (Krumhansl and Scheibling 2011, 2012) found tissue weakening caused by encrusting bryozoans and grazing snails to facilitate detrital production in Nova Scotian kelp beds.

In conclusion, this work presents one of the first accounts of the relative importance of both erosion and whole kelp dislodgement to detrital supply from a kelp bed over a year. We conclude that erosion of distal parts of thalli accounted for the overwhelming proportion ($\sim$ 80%) of the annual detrital production, delivered as a peak pulse in autumn. The results contrast with the common perception that waves drive detrital production through dislodgement of whole thalli. We conclude that water velocity and storms are less important as drivers of dislodgement than previously thought, but emphasize they may play an important role in delivering detritus to recipient consumers.

The large pulse of detritus in autumn via erosion is conceptually comparable to the seasonal input of leaf fall from deciduous trees in autumn, which strongly affects temperate freshwater and terrestrial ecosystems such as streams and lakes (Nakano and Murakami 2001). Because of the magnitude of kelp tissue loss, the high density of kelps, and the large surface area of reefs in some temperate zones, these detrital inputs will likely propagate through the entire coastal food web. These erosion losses can also benefit the local reef because they subsidize the associated reef communities, make the kelp less susceptible to storms in winter (minimize drag forces), facilitate kelp recruitment and recruit growth, and increase the species-turnover of understory algal communities.

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