

2013

Sources and supply of kelp detritus : quantifying mechanisms of production

Thibaut de Bettignies
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**SOURCES AND SUPPLY OF KELP DETRITUS:
QUANTIFYING MECHANISMS OF PRODUCTION**

by

Thibaut de Bettignies

Master of Science (M.Sc.)

**This thesis is presented in fulfilment of the requirements
for the degree of Doctorate of Philosophy**

**Faculty of Computing, Health and Science
Edith Cowan University**

January 2013

DECLARATION

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ABSTRACT

In temperate waters, rocky reefs dominated by extremely productive kelp beds export considerable primary production. Despite the extensive body of work on kelp detritus as a trophic subsidy, many questions remain about the production of this detritus. The aim of this thesis was to determine the rate and mechanisms of kelp detritus production, for *Ecklonia radiata*, the dominant kelp species in temperate Australia. Most of the work was conducted in Marmion Lagoon located 20 km North of Perth, south-western Western Australia, a region strongly influenced by oceanic swell and winter storms. The study comprised of four major components: the impact of kelp morphology on the drag forces acting on kelp thalli; investigation of wound patterns in kelp tissue and the biomechanical implications for kelp detritus production; the relative contribution of erosion of frond material and dislodgement of whole thalli to detritus production; and the relationship between kelp dislodgement and peak water velocities, implemented with a kelp dislodgement model.

The initial work in chapter 1 revealed that only size (total area), not morphology, was important in determining the drag acting on *E. radiata* at peak velocities. This implied that at storm velocities the only way drag forces acting on a kelp can be reduced is by a reduction of total thallus area (biomass) and not by modification of thallus shape. These results constituted the first step to build a mechanistic model of kelp dislodgement.

In chapter 2, it is shown that wounds were highly abundant on kelps before peaks in winter storms and that simulated wounds caused significant loss of tissue integrity and strength. Collectively, these findings suggest that accumulation of wounds over summer results in kelp pruning (tissue fragmentation) in early winter. Paradoxically, this may increase kelp survival during winter storms because the biomechanical drag is much lower on small, pruned kelps (lower biomass).

Results presented in chapter 3 indicated that erosion accounted for 80% of the annual detrital production with a pulse in autumn, whereas dislodgement accounted for a smaller and more constant proportion throughout the year. Neither erosion nor dislodgement correlated with increasing water velocity. Instead, the pulse of detrital

production coincided with sporogenesis, leading to the hypothesis that weakening of structural tissue through the formation and release of spores made *E. radiata* more susceptible to wound accumulation (Ch. 2) and erosion.

In chapter 4, results are presented that show no increase in kelp dislodgement with increasing water velocity, except during the most severe storms. The dislodgement model indicated that the seasonal variation in individual kelp biomass, resulting from erosion of frond tissue (Ch. 3), resulted in lower susceptibility to dislodgement (lower biomass) at times of peak water velocities. The benefit of erosion in reducing drag acting on the thallus, as proposed in the previous chapters, was therefore demonstrated by the model.

The commonly accepted model of wave-driven mortality of kelp during storms in winter was refined by the results. The experimental, field sampling and modelling studies have been synthesised into an alternative model of kelp dislodgement, in which kelp beds are in dynamic equilibrium with wave disturbance. This equilibrium is mediated through erosion-driven adjustment of individual kelp biomass in autumn-winter which lowers drag on kelp thalli during the period of peak water velocity. This relationship between erosion and the susceptibility of *E. radiata* to dislodgement suggests an adaptation of the kelp *E. radiata* to its environment, critical to kelp survival in one of the most hydrodynamically challenging environment.

AKNOWLEDGEMENTS

I dedicate this PhD thesis to the captain Joseph le Bourdiec,

my grandfather, a catalyst for discovering the marine world

& to Marcelle le Bourdiec,

my grandmother, who initiated me to the living and love by the sea.

“It is good to have an end to journey toward; but it is the journey that matters, in the end.” (*Ernest Hemingway*); and I can say, it has been a great journey!

I would first and foremost like to thank my supervisors, Thomas Wernberg, Paul Lavery and Mat Vanderklift who dedicated a lot of their time, expertise and enthusiasm to guide me thoroughly through this PhD, often beyond expectations. It has been a great honour and pleasure to work with you and learn from you. I am particularly indebted to Thomas Wernberg, without him nothing would have been possible from the beginning to the end, from designing the project to the finalisation of manuscripts. After showing the relentless fight with the swells for the beauty of kelp and turning my fr-english into a well written manuscript, your mentoring has definitely served as foundation for becoming a skilled early-career scientist.

Big thanks to all the volunteers: Margie Mohring, Pierre Bouvais, Sabrina Luret, Sandra Luret, Phil Van Dyk, Scott Bennett, Dan Smale, José Escaño Roepstorff (alias Pin), Sabrina Luret, Sandra Luret, Bastien Debeuf, Jeremie Godefroy, Guilhem Marre, Aldo Turco, Federico Vitelli, Oriol Mascaró Vidal, Pearse Buchanan, Heather Dunham, Tomaso Minutoli Tegrimi, Brezo Martinez, Michael Rule, Karina Inostroza and Audrey Cartraud. Undoubtedly, you guys have been an invaluable support for boating, diving and processing samples, and you made this project possible.

Thank you to the School of Natural Sciences (ECU) and the Western Australian Marine Science Institution for funding support. The Centre for Marine Ecosystems Research, the School of Natural Sciences and Edith Cowan University in general, for providing

great facilities to conduct such intense field-based research, which, I wish strongly, will still profit to the future students and researchers.

In my daily life, I'm thankful to my great housemates and friends who prevented from the insanity side of research and reminded me about the importance of balance in life. Among them, special thanks to Sharon Smart, José Escaño Roepstorff, Anxo Casal, Miriam Cortes, Pierre Bouvais, Nader Mustafa, Federico Vitelli, Federica Micheli, Oriol Mascaró Vidal and to Florian and Tiphaine de Bettignies, my brother and sister, and many more...

Thanks Australia for welcoming me and Sabrina.

Thanks *Ecklonia radiata* and to all of them who gave their life to Science.

Last but not the least, I am entirely indebted to my parents for supporting me throughout my 'relatively' long studies and to my girlfriend, Sabrina, for her infinite support and love.

LIST OF PUBLICATIONS INCLUDED

- de Bettignies T**, Wernberg T, Lavery PS (2012a) Size, not morphology, determines hydrodynamic performance of a kelp during peak flow. *Marine Biology* (in press) doi: 10.1007/s00227-012-2138-8
- de Bettignies T**, Thomsen MS, Wernberg T (2012b) Wounded kelps: patterns and susceptibility to breakage. *Aquatic Biology* **17**: 223-233, doi: 10.3354/ab00471
- de Bettignies T**, Wernberg T, Lavery PS, Vanderklift MA, Mohring M. Contrasting mechanisms of dislodgement and erosion contribute to production of kelp detritus. *Limnology and Oceanography*, accepted 7/05/13
- de Bettignies T**, Wernberg T, Lavery PS, Vanderklift MA, Gunson J, Symonds G. An equilibrium hypothesis of kelp dislodgement and wave disturbance (to be submitted)

STATEMENT OF CONTRIBUTION

To whom it may concern,

I, Thibaut de Bettignies, contributed to conceiving, designing, and performing the experiments, analysing the data, and writing all manuscripts included in this thesis, as well as writing the thesis itself.

Date 15 / 01 / 13

I, as a supervisor and co-author on all publications included here, endorse that this level of contribution by the candidate indicated above is appropriate.

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LIST OF CONFERENCE PRESENTATIONS

de Bettignies T, Wernberg T, Lavery PS, Vanderklift MA, Symonds G & Gunson J (2012) An equilibrium hypothesis of kelp dislodgement and wave disturbance redefines the model of kelp forest dynamic. *Annual UNESCO IOC Perth / IMarEST Western Australian Marine Studies Awards*, Fremantle.

Wernberg T, **de Bettignies T**, Mohring M & Bennett S (2011) Continental-scale pattern of ecological processes in kelp beds. *Third Annual ANNIMS Conference 2011*, Perth.

de Bettignies T, Wernberg T, Lavery PS & Vanderklift MA (2011) Spatial subsidies provided by organic matter export from kelp forests: importance of storm-driven pulses verses chronic export. *Third Annual ANNIMS Conference*, University of Western Australia; *International Temperate Reef Symposium*, Plymouth.

de Bettignies T, Wernberg T, Lavery PS & Vanderklift MA (2010). The importance of storms in driving export of organic matter (kelp wrack) from rocky reefs. *Australasian Society for Phycology and Aquatic Botany (ASPAB) conference*, Rottnest Island; *WAMSI Young Career Researchers Symposium*, Joondalup.

de Bettignies T, Godefroy J, Wernberg T & Vanderklift MA (2010). Changes in growth, erosion, productivity and morphology of *Ecklonia radiata* along a hydrodynamic gradient. *ASPAB conference*, Rottnest Island.

Vanderklift MA, Babcock R, Bearham D, **de Bettignies T**, Kendrick G & Wernberg T (2010) A single species, the kelp *Ecklonia radiata*, is disproportionately important in coastal marine ecosystems. *ASPAB conference*, Rottnest Island.

de Bettignies T, Wernberg T, Lavery PS & Vanderklift MA (2009) Sources and supply of wrack: quantifying vectors of habitat connectivity. *Australian Marine Sciences Association annual conference*, Adelaide; *Annual Royal Society of WA Postgraduate Symposium*, Curtin University; *AMSA-WA student workshop*, Rottnest Island.

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GENERAL INTRODUCTION

1 Background

In most natural ecosystems, movement of resources (nutrients, detritus and prey) and consumers across habitat boundaries are common (Polis et al. 1997). These cross-ecosystem transfers of energy and nutrients, that may be variable in time and space, play a key role in linking habitats and can dramatically affect trophic and community dynamics. Such spatial flows are called “spatial subsidies” when local productivity is enhanced by resources originating from elsewhere (Polis et al. 1997). This phenomenon has been well documented especially for heterogeneous landscapes with marked differences in productivity (Pearson and Brawley 1996; Polis and Hurd 1996; Polis et al. 1997).

2 Ecological significance of kelp detritus

Resource heterogeneity is particularly high in the coastal zone, which often comprises several discrete habitats with different levels of productivity, such as beaches, unvegetated subtidal areas, seagrass meadows and reefs. In temperate coastal regions, kelps - large brown algae in the order Laminariales - often dominate rocky substrata, where they can occur in high densities as “kelp forests” or “kelp beds” (Steneck et al. 2002). Kelp forests are among the most productive components of marine ecosystems capable of producing more than $1 \text{ kg C m}^{-2} \text{ y}^{-1}$, significantly higher than the 0.1 to 0.3 $\text{kg C m}^{-2} \text{ y}^{-1}$ attributed to temperate-water phytoplankton (Mann 2000). Waves and currents often impose large hydrodynamic forces on kelp forests. In a wave swept environment, subtidal kelps experience peak water velocities over 2 m s^{-1} , comparable to a force exerted by a wind of 200 km h^{-1} on land (Denny and Gaylord 2002), whereas intertidal and surface canopy-forming kelp (e.g. *Macrocystis pyrifera*) can experience the full force of breaking waves that can reach up to $15\text{-}25 \text{ m s}^{-1}$ (Denny 1988; Denny and Gaylord 2002). Such water velocities can result in severe hydrodynamic forces that can physically damage, prune or remove macro-algae from the reef (Seymour et al. 1989; Dayton et al. 1992; Krumhansl and Scheibling 2012). Therefore, the combination of high rates of productivity and susceptibility to dislodgement and tissue fragmentation, provides the opportunity for a strong subsidy from kelp beds to adjacent, relatively low-productivity habitats.

Cross habitat resource subsidies mediated by kelp detritus have been demonstrated for a large variety of habitats and food webs; from terrestrial habitats, beaches and intertidal rocky/sandy shores to subtidal reefs, seagrass meadows and submarine canyons (see details in Table 1). The large spectrum of subsidised habitats and organisms highlights the widespread impact of kelp detritus and its ecological significance in temperate coastal regions (Table 1). Delivery of kelp into a recipient habitat can enhance secondary production through the provision of food for detritivores and the microbial community (Linley et al. 1981; Duggins et al. 1989; Bustamante et al. 1995). For example, in beach ecosystems, the spatio-temporal variation in kelp detritus delivery strongly influences the persistence of populations, species diversity, community structure and dynamics, and the evolution of specific life history traits (Colombini and Chelazzi 2003). An important feature of this spatial subsidy is that consumers in the recipient habitat do not control the magnitude of inputs. On the contrary, the magnitude of allochthonous production controls the abundance of consumers if local productivity is low, termed “bottom up control” (Menge 1992; Polis et al. 1997), which may influence even higher trophic levels (e.g. Dugan et al. 2003) and create hotspot of secondary production (e.g. Vetter 1994).

3 Origin of kelp detritus

The ecological consequences of spatial subsidies from kelp detritus has been the focus of extensive research (see Table 1), but the mechanisms that lead to the formation of kelp detritus have been comparatively less investigated. The literature indicates that kelp detritus can be generated primarily through two different mechanisms: dislodgement of entire kelp thalli (usually leading to the death of the individual) (Dayton et al. 1992; Graham et al. 1997), and fragmentation of parts of the thallus through erosion and pruning (Newell et al. 1980; Krumhansl et al. 2011).

A large body of work has reported direct and indirect evidence for wave-driven kelp dislodgement and suggested that dislodgement is more important than erosion for the production of kelp detritus. This includes direct observations of kelp dislodgement from the reef (Seymour et al. 1989; Dayton et al. 1992; Graham et al. 1997; Filbee-Dexter and Scheibling 2012); inferences derived from observations from the recurrence of

patches devoid of kelp (Connell and Irving 2008; Wernberg and Connell 2008; Thomson et al. 2012) and accumulation of drift kelps in adjacent habitats directly after storms (Colombini and Chelazzi 2003; Filbee-Dexter and Scheibling 2012). The current paradigm, therefore, implies that kelp detritus primarily is produced through storm-waves, more frequent in winter, that tear individual kelps from reefs, once hydrodynamic forces surpass kelp attachment or tissue strength (threshold response, Dayton 1985; Seymour et al. 1989). Because the dislodgement process can be viewed as the balance between attachment and dislodgement forces, the supply of kelp detritus can be investigated through a mechanistic approach and “survival models”.

The high productivity of kelps (Mann 1973), however, and their relatively constant size (Steneck et al. 2002) implies relatively high erosion, which may also be an important contributor to detrital production. Indeed, a recent review that compiled kelp erosion and dislodgement rates from around the world found that erosion was on average two times higher than dislodgement (448 ± 455 vs. 257 ± 206 g C m⁻² year⁻¹, Krumhansl and Scheibling 2012).

Table 1 - Review of trophic subsidies provided by kelp detritus (non-exhaustive list).

<i>Recipient habitats</i>	<i>Subsidised organisms</i>	<i>Kelp species</i>	<i>Regions</i>	<i>References</i>
Sandy beach	Diptera, beetle	<i>E. radiata</i>	Western Australia, Australia	Ince et al., (2007)
	Earthworm	<i>E. radiata</i>	Western Australia, Australia	Coupland & McDonald (2008)
	Bacteria	<i>E. maxima</i>	West coast, South Africa	Koop et al. (1982a; 1982b)
	Bivalve	<i>E. maxima, L.pallida</i>	West coast, South Africa	Soares et al.(1997)
	Amphipod, coleoptera	<i>M. pyrifera</i>	New Zealand	Inglis (1989); Marsden (1991)
	Amphipod, isopod, diptera, shorebird	<i>M. pyrifera</i>	California, USA	Dugan et al. (2003)
	Amphipod	<i>N. luetkeana, M. integrifolia</i>	British Columbia, Canada	Mews et al. (2006)
Intertidal rocky shore	Limpet	<i>E. maxima, L. pallida</i>	West coast, South Africa	Bustamante et al. (1995)
	Mussel, colonial polychaete	<i>E. maxima, L. pallida</i>	West coast, South Africa	Bustamante & Branch (1996)
	Sponge, polychaete, barnacle, crab, mussel, bryozoan, sea squirt	<i>L. digitata</i>	Brittany, France	Schaal et al. (2009; 2010)
	Sea urchin	<i>L. nigrescens, L. trabeculata</i>	central coast, Chile	Rodriguez (2003)
Subtidal reef	Mussel, polychaete	<i>L. groenlandica, A. marginata</i>	Washington State, USA	Duggins & Eckman (1997)
	Abalone	<i>M. pyrifera, E. arborea</i>	California, USA	Tutschulte & Connell (1988)
	Mussel	<i>L. pallida</i>	West coast, South Africa	Stuart et al. (1982; 1982)
	Mussel, barnacle, amphipod, soft coral	<i>L. groenlandica, L. longipes, A. fistulosa</i>	Aleutian Islands, USA	Duggins et al. (1989)
	Limpet, sea urchin, sponge, sea squirt, bacteria	<i>E. maxima, L. pallida</i>	West Coast, South Africa	Newell et al. (1982) Linley et al. (1981)
	tube-dwelling polychaete worm	<i>M. pyrifera</i>	California, USA	Kim (1992)
	Sea urchin	<i>E. radiata</i>	Western Australia, Australia	Vanderklift et al. (2008)
Seagrass meadows	Herbivorous fish	<i>E. radiata</i>	Western Australia, Australia	Wernberg et al. (2006)
	Seagrass, epiphyte, gastropod	<i>E. radiata</i>	Western Australia, Australia	Hyndes et al. (2012)
Submarine canyon	Amphipod, leptostracan crustacean	<i>M. pyrifera</i>	California, USA	Vetter (1994; 1998)
	Amphipod, polychaete, crustacean	<i>M. pyrifera</i>	California, USA	Okey (2003)
	Sea urchin, holothurian, crab, fish	<i>M. pyrifera, E. menziesii</i>	California, USA	Vetter & Dayton (1999)
Deeper reef	Sea urchin	<i>S. latissima, L. digitata</i>	Nova Scotia, Canada	Filbee-Dexter et al. (2012)
Island	Spider	<i>M. pyrifera</i>	California, USA	Polis et al. (1995)
Surf-zone	Amphipod, fish	<i>E. radiata</i>	Western Australia, Australia	Crawley et al. (2007; 2009)

4 Wave disturbance and kelp dislodgement

Wave- and current-driven water motion has substantial consequences for benthic marine plants especially on macroalgae (Hurd 2000). While some water motion is beneficial for nutrient uptake (Wheeler 1988), photosynthesis (Wheeler 1980; Wheeler 1982), and transport of gases, gametes and spores (Pearson and Brawley 1996), intense water motion can physically damage or dislodge macroalgae (Denny 1995; Utter and Denny 1996). Because of the magnitude of hydrodynamic stress in coastal regions Denny and co-workers (Denny 1994; Gaylord et al. 1994; Denny et al. 1997; Gaylord and Denny 1997) have argued for a mechanistic approach, incorporating biomechanical models, to describe the survival mechanisms and dislodgement characteristics of sessile organisms. This approach has been widely used in studies of algae to understand a variety of ecological questions including survival mechanisms, adaptation to water motion, species distributions and population dynamics (Table 2). According to this approach, the likelihood of dislodgement depends principally on the balance between hydrodynamic forces experienced by the algae, and the force required to break or dislodge the algae, related to its material properties and attachment strength to the substratum (Fig.1, Thomsen 2004).

Table 2 - Focus of recent studies (from 1990 to 2012 using a biomechanistic approach to understand how water motion affects macroalgae (Non-exhaustive list).

	<i>Species</i>	<i>I-S*</i>	<i>References</i>
Survival mechanisms and Adaptations to water motion	<i>Chondrus crispus</i>	I	Dudgeon & Johnson (1992)
	<i>Fucus gardneri</i>	I	Blanchette et al. (2002)
Species distribution	<i>Gigartinacea (3 sp.)</i>	I	Bell (1999)
		I/S	Denny & Gaylord (2002)
	<i>Chondrus crispus</i>	I	Boller & Carrington (2006b)
	<i>Mastocarpus pappilatus</i>	I	Kitzes & Denny (2005)
	<i>Egregia menziesii</i>	I/S	Blanchette et al. (2002)
	<i>Laminaria japonica</i>	S	Kawamata (2001)
	<i>Laminaria pallida</i>	S	Molloy & Bolton (1996)
	<i>Chondrus crispus</i>		Pratt & Johnson (2002)
	<i>Mastocarpus stellatus</i>	I	
	<i>Mazzaella linearis</i>		Shaughnessy et al. (1996)
Population dynamics	<i>Mazzaella splendens</i>	I	
Effects of the canopy	<i>Nereocystis luetkaena</i>	S	Duggins et al. (2001)
Sensibility of aquaculture algae	<i>Chondrus crispus</i>	I	Boller & Carrington (2006a)
Change in attachment strength	<i>Saccharina latissima</i>	S	Buck & Buchholz (2005)
	<i>Ecklonia radiata</i>	S	Thomsen et al. (2004), Wernberg (2005)

* I-S: “I” for intertidal species and “S” for subtidal species

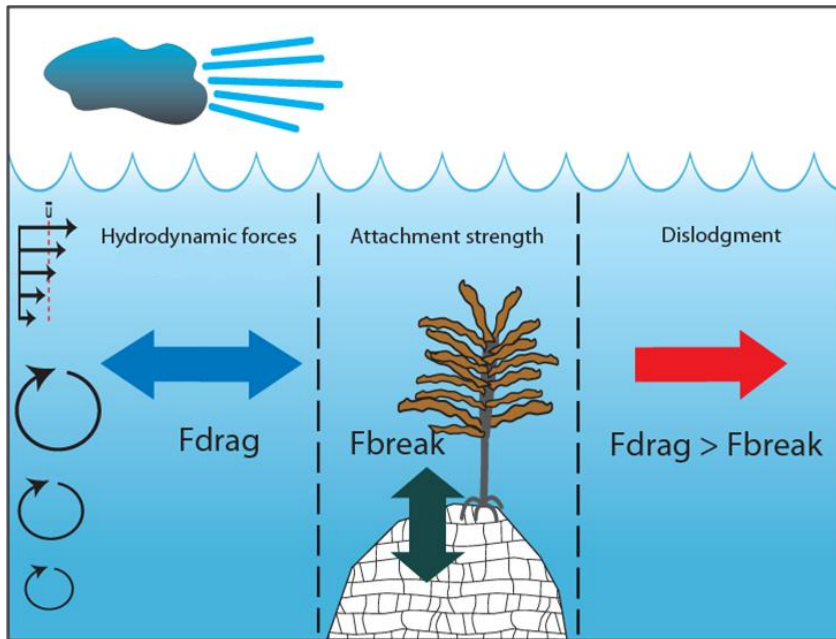


Figure 1 - Conceptual model of algal dislodgement driven by wave disturbance, showing the sequence of processes from left to right that result in kelp dislodgement. F_{drag} is the drag force acting on an individual kelp thallus and F_{break} is the break force or attachment/tissue strength of the same kelp. When F_{drag} exceeds F_{break} it results in kelp dislodgement [equivalent to Environmental Safe Factor (ESF) = $F_{break}/F_{drag} < 1$].

The different forces acting on a sessile organism are drag, lift and acceleration; however it is a common practice to focus only on drag which is quantitatively the only force on non-buoyant kelp (Gaylord 2000; Denny and Gaylord 2002). The drag force (F_{drag}) is usually measured directly by pulling the alga through water, attached to a dynamometer, at known velocities (Koehl 2000; Milligan and De Wreede 2004). Drag force represents the resistance of an object to fluid movement (Fig. 1) and is due to two components of the object: the shape (form drag) and the surface of the body (skin drag). The dimensionless drag coefficient (C_{drag}) is a property of these two drag features, and can be derived from the standard empirical drag equation (Vogel 1984; Denny 1995):

$$F_{drag} = \frac{1}{2} \rho \times U^2 \times C_{drag} \times A \quad (\text{Equation 1})$$

where F_{drag} is the drag force (Newton), ρ the density of seawater (1026 kg m^{-3}), U the water velocity (m s^{-1}), C_{drag} the drag coefficient (dimensionless) and A the object area

(m²), which can be measured directly (morphologically simple algae) or derived by proxy of biomass (morphologically complex algae, e.g. *Ecklonia radiata* in Wernberg 2005).

The force required to break algae (break force; F_{break}) represents the strength of the algae, and combines both tissue strength and attachment strength (Fig.1). F_{break} can be measured by pulling the algae with a dynamometer until it breaks. For subtidal kelps this test is performed underwater (Thomsen et al. 2004; D'Amours and Scheibling 2007). Whereas several macroalgae species break at the stipe or holdfast-stipe junction (Shaughnessy et al. 1996; Duggins et al. 2001), *Ecklonia radiata* in Western Australia is more often dislodged (~70%) at the holdfast-reef location (Thomsen et al. 2004). However, this is likely the consequence of the hardness of the substrat (mostly limestone) and not the attachment strength of kelp holdfasts as suggested by Thomsen et al. (2004). Once F_{drag} and F_{break} are established, the water velocity required to break or dislodge a thallus (Fig. 1, break velocity; U_{break} , m s⁻¹) can be determined as:

$$U_{\text{break}} = \left[\frac{(2 \times F_{\text{break}})}{(C_{\text{drag}} \times A \times \rho)} \right]^{0.5} \quad (\text{Equation 2})$$

Consequently, the cumulative frequency of dislodgement as a function of water velocity can be estimated according to frequency distribution of attachment strength and resulting drag forces (Fig. 2).

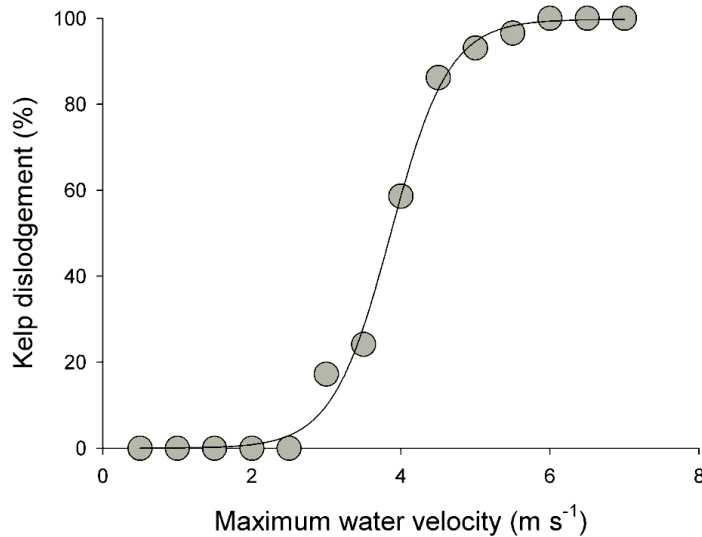


Figure 2 - Theoretical cumulative probability curve of kelp dislodgement

Moreover, dislodgement characteristics may change if the physical attributes of the kelp change. For example, change in kelp morphology can alter the resulting drag or wounds that weaken kelp tissue can impact kelp attachment strength (Fig. 1) resulting in modifying the model and probability of kelp dislodgement (Fig. 2).

5 The coastal marine system of south-western Western Australia

Coastal marine systems of temperate Western Australia are a mosaic of different habitats and communities. The two main vegetated communities are seagrass meadows in sandy areas and kelp-dominated reefs. *Ecklonia radiata* (C. Agardh) J. Agardh is the most abundant macroalga by biomass (Steinberg and Kendrick 1999) and a dominant habitat-former across subtidal reefs of temperate Australia (Kennelly and Underwood 1992; Wernberg et al. 2003a; Wernberg et al. 2003b). On the reefs, physical disturbances drive kelp dynamics (i.e. productivity, recruitment, mortality) which in turn influence species richness and assemblage structure of the understory communities (Wernberg and Goldberg 2008).

South-western Australia is strongly influenced by both swell and wind-generated waves, but dominated by oceanic swell from the west and south-west (Searle and Semeniuk 1985; Lemm et al. 1999). In summer (December-February), regular strong sea breezes generate moderate waves whereas in winter (June-August), frequent storms generate large swell and waves locally. As a result, wave characteristics vary seasonally with

means significant wave heights and wave periods of 1 to 2 m and <8 s in summer and 1.5 to 2.5 m and >8 s in winter (Lemm et al. 1999). However, the configuration of the coastline with successive lines of reefs running parallel to the shore, dissipate the hydrodynamic forces as waves approach the coast. These features generate a gradient of wave exposure (Lemm et al. 1999; Smale et al. 2011).

6 Aims

This thesis investigates the mechanisms that generate kelp detritus from *Ecklonia radiata* beds. To achieve this objective, there are six specific aims:

1. Understand how kelp morphology affects drag force at peak water velocities (Chapter 1).
2. Examine the implication of wounds for kelp survival and detrital production (Chapter 2).
3. Compare the relative contribution of dislodgement and erosion to kelp detrital production (Chapter 3).
4. Investigate the relationship between kelp dislodgement rate and wave disturbance *in-situ*, in order to test the current paradigm of wave-generated kelp dislodgement (Chapter 4).
5. Build a model of dislodgement as a function of kelp morphology, attachment strength and water velocity to explain the observed kelp dislodgement (Chapters 1 and 4).
6. Identify drivers of kelp detrital production through dislodgement and erosion (Chapters 2, 3 and 4).

7 Thesis overview

Each of the chapters 1, 2, 3 and 4 is written in a format for publication as individual studies. Chapter 1 and 2 are already published, chapter 3 is in review and chapter 4 is close to submission.

Chapter 1

Wave energy is a strong driver of intra-specific variation in algal morphology, which is usually implied to minimize drag forces acting on the kelp thallus. However, this understanding is largely based on work focused at relatively low water velocities. This

chapter examines how morphological variation affects drag forces at storm generated water velocities. Peak water velocities are measured *in-situ*, and the relationship between morphological characters and drag is tested experimentally by subjecting kelps of different morphologies to hydrodynamic drag. The relationships found between kelp morphology and drag force (first part of the dislodgement conceptual diagram, Fig. 1) provides baseline knowledge to build the dislodgement models used later in Chapter 4.

Chapter 2

Kelps are not generally undamaged in nature because physical and biological processes (i.e. sand abrasion, whiplash and grazing) can wound and weaken kelp tissue. Depending on the wound location, it can influence the dislodgement of entire kelps or erosion of kelp tissue, and therefore impact the rate of kelp detrital production. This chapter examines wound patterns in kelps and tests the effect of wounds on the biomechanical properties of kelp tissue and its implications for generating kelp detritus. This study is centred on winter, the period when the interactions between wounds, wave forcing and kelp detrital production is thought to be predominant.

Chapter 3

Despite the rich body of work on kelp detritus as a trophic subsidy (Table 1), little is known about the quantity of kelp detritus and its origin. Dislodgement of whole individuals and erosion of distal end portions of blades are the two mechanisms generating kelp detritus. This chapter aims to disentangle the origin of kelp detritus and the spatio-temporal contribution of these two mechanisms, with emphasis on potential drivers of dislodgement and erosion. In order to compare both mechanisms, dislodgement and erosion rate are measured simultaneously for nine reefs of different environmental conditions over a year. Wave disturbance is currently proposed as the main driver of the production of kelp detritus but other potential explanatory factors might be important to consider (temperature and kelp fecundity). Also, this chapter investigates if these factors are related to the rate of kelp dislodgement and erosion.

Chapter 4

The last data chapter focuses on the dislodgement of *E. radiata*, using experimental and theoretical approaches to test hypotheses about wave-driven dislodgement and the

impact of increasing wave forcing intensity. The experimental kelp dislodgement rate and its relationship with increasing water velocity are explained in the light of biomechanical model outputs of kelp susceptibility to dislodgement. The combination of results from chapter 1, water velocity data from a wave model of the study region and the frequency distribution of kelp break force data is used to develop a dislodgement model (Fig.1 and 2).

General Discussion

Finally, the results from these different studies are drawn together to propose an original and novel model of kelp detritus production related to kelp biology, biomechanics and environmental forcing. Based on these results, the discussion highlights how these individual studies are inter-related. Furthermore, the general discussion highlights implications for fate of kelp production and kelp detritus.

CHAPTER 1

Size, not morphology, determines hydrodynamic performance of a kelp during peak flow

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Key words: Functional morphology, drag, C_{drag} , *Ecklonia radiata*, shape index, reconfiguration, storm, dislodgement.

The work contained in this chapter is published ('Online first') as:

de Bettignies T, Wernberg T, Lavery PS (2012a) Size, not morphology determines hydrodynamic performance of a kelp during peak flow. *Marine Biology* doi: 10.1007/s00227-012-2138-8.

1.1 Abstract

The morphology and shape of algae can affect their survival in wave swept environments because of the hydrodynamic drag created by water flow. Studies of morphology and drag are typically conducted at relatively low water velocities and the influence of algal morphology on drag, over the range of water velocities algae must cope with in their natural environment, remains unclear. Here, we tested the link between morphological variation and hydrodynamic drag for a dominant kelp with complex morphology (*Ecklonia radiata*), over a range of water velocities representative of conditions on wave swept reefs. Our results indicated that kelps on subtidal reefs must withstand maximal orbital water velocities in excess of 2-3 m s⁻¹. Our measurements of drag, resulting from flows ranging from 1 to 3 m s⁻¹, revealed that shape and width-related thallus and lamina characters were important to drag at low speed, but that total thallus area (or biomass) was the main determinant of drag at high flow. Drag coefficients converged at increasing speed suggesting that, at high flow, significant thallus reconfiguration (more streamlined shape) decoupled drag from morphology. This implies that, at peak velocities, only size (total area), not morphology, is important to drag and the probability of dislodgement.

1.2 Introduction

Important questions in ecology and evolution centre on the relationship between an organism's morphology and its performance. Different morphological characters can lead to different performances, making a specific morphology more suitable to a given environment through enhanced survival and fitness (Koehl 1996; Wainwright 1996). For sessile marine organisms, morphology has critical implications for their likelihood of dislodgement or survival when experiencing intense hydrodynamic forces, driven by waves and currents (Denny 2006). Macroalgae such as kelps are found across different hydrodynamic environments and exhibit great intra- and inter-specific morphological variation (Johnson and Koehl 1994; Roberson and Coyer 2004; Wernberg and Vanderklift 2010). Consequently, they are good models for studying the ecological implications of morphology.

Differences in algal morphology are thought to be the consequence of a trade-off between limiting drag forces, which prevent breakage and dislodgement for wave

exposed morphotypes (Kawamata 2001; Blanchette et al. 2002; Buck and Buchholz 2005); and maximizing light capture and transfer of gas and nutrients for photosynthesis and growth for sheltered morphotypes (Koehl and Alberte 1988; Stewart and Carpenter 2003; Haring and Carpenter 2007). Therefore, it is generally accepted that algae from sheltered environments have wide, thin and undulate thalli which are often bushy whereas algae from exposed environments have narrow, thick and flat thalli with thick stipes and a more streamlined shape. Several studies have demonstrated that the hydrodynamic forces resulting from waves are strong drivers of this variation (Wernberg and Thomsen 2005; Fowler-Walker et al. 2006; Wernberg and Vanderklift 2010; Krumhansl and Scheibling 2011a), either as a consequence of pruning and tattering (Dudgeon and Johnson 1992; Blanchette 1997; Carrington et al. 2001; Mach et al. 2007), which limit size and shape mechanically, or genotypic or phenotypic adaptation towards characters that minimize hydrodynamic drag (Fowler-Walker et al. 2006; Krumhansl and Scheibling 2011a). The major physical force acting on a subtidal kelp is the hydrodynamic drag, created by water flow, which pulls the alga downstream (Gaylord et al. 1994; Denny and Gaylord 2002). The magnitude of the force is proportional to the velocity of the water and depends on the size and shape of the alga (Vogel 1984; Denny 1995; Thomsen et al. 2004). Moreover, the shape of most algae can reconfigure in response to increasing flow into a more streamlined and homogeneous shape ('reconfiguration', Vogel 1994; Harder et al. 2004; Wernberg 2005) and the effects of morphology on drag may therefore change with water velocity.

The kelp *Ecklonia radiata* (C. Agardh) J. Agardh is a dominant habitat-former on the temperate subtidal reefs of Australasia (Wernberg et al. 2003b; Fowler-Walker et al. 2006; Connell and Irving 2008). *E. radiata* is probably the most abundant macroalga in Australia and it forms large beds on moderate- to rough-water coasts (Connell and Irving 2008; Wernberg and Connell 2008). It can reach a length up to 2 m and has a thallus with a terete basal stipe that bears a flattened blade with ramified lateral branches which often create a complex 3-dimensional shape (Wernberg et al. 2003a). Despite extensive knowledge of the relationships between wave exposure and morphological variation for this species (Wernberg and Thomsen 2005; Fowler-Walker et al. 2006; Wernberg and Vanderklift 2010), little is known about how this affects drag. In this study we tested how morphological variations and shape affects the

hydrodynamic drag experienced under different hydrodynamic conditions, and more specifically at velocities typical of storms.

To test our main hypothesis, that morphological changes affect the hydrodynamic drag, and to determine if there is ‘an object area’ to be incorporated in the drag equation (Equation 2) for *E. radiata*, we subjected thalli of differing morphologies to a range of water velocities, representative of field conditions, and measured the resultant drag. Ultimately, we tested if the coefficient of drag changes with water velocity.

1.3 Materials and Methods

1.3.1 Water velocities

The measurements took place in Marmion Lagoon, 20 km north of Perth, Western Australia (32° S latitude). (Smale et al. 2011; de Bettignies et al. 2012a). This coastline is characterised by a series of successive high relief reef ridges (reef lines) run parallel to the shore, dissipating the hydrodynamic forces as waves approach the coast, creating a gradient in wave exposure (Phillips et al. 1997; Smale et al. 2011). This region is strongly influenced by westerly and south-westerly wind and swell generated-waves (Searle and Semeniuk 1985; Lemm et al. 1999) with prevalent storms in winter (waves >4 m, up to 8-9m offshore). We investigated the range of water velocity experienced by *Ecklonia radiata* in the study region, particularly during storms in winter (Lemm et al. 1999), when maximum velocities are usually recorded and hence when morphological variation may be critical for survival. The instant water velocities were measured every 30 sec at 4 reefs of different wave exposure in Marmion Lagoon. Measurements were done with gravitational data loggers (HOBO Pendant G, Onset Computer Corporation, Bourne, MA, USA) mounted on a 40 cm flexible aerial with blades (for technical details see ‘H2OMotionV1 design’ in Evans and Abdo 2010). Prior to the deployment, the devices were calibrated in the field against an Acoustic Doppler Velocimeter (ADV, D. Thomson-CSIRO) to obtain the corresponding water velocity (m s^{-1}). The loggers were deployed for one week in winter (July 2010), a period that encompassed both general winter wave patterns and a significant storm (south-westerly swell), as indicated by a maximum 7 m wave height (averaged per hour) and 12-17 s wave period as measured by an offshore wave rider buoy. This event was similar to the frequent storms associated with mid-latitude depressions that occur in winter (>20 events year⁻¹, Lemm et al. 1999)

and therefore, the range of velocities encompassed during this week is typical of what velocities kelp can experience in winter.

1. 3. 2 Kelp collection

Adult kelp thalli with thallus fully differentiated into complex laterals (stage 3 sporophytes, N = 45, Kirkman 1981) were collected from subtidal reefs (~8 m depth) between April and May 2009 (austral autumn) by carefully cutting immediately above the holdfast. To obtain a maximum range of morphotypes, the collections targeted kelps from Hamelin Bay (34°14'S; 115°01'E) and Marmion Lagoon (31°50'S; 115°42'E), two locations known to have morphologically distinct kelps (Wernberg et al. 2003a). The algae were kept moist during transport in an oxygenated cool box with ice packs and seawater, and were stored *in-situ* in underwater cages for one night before undertaking drag measurements the following day.

1. 3. 3 Drag and water velocity measurements

Drag was measured while towing kelps behind a boat at known speeds in an experimental set up similar to that used by Utter & Denny (1996) with *Macrocystis pyrifera* and Koehl (2000) with *Chondracanthus exasperatus*. Individual kelp thalli were tied to a non-flexible cord running through a metal pole and pulled through the water horizontally at a depth of about 1 m, a distance from the boat of 1.5 m on the side and 4 m downstream from the pole to avoid surface and wake effects generated by the boat and equipment. The cord was connected to a 5 kg, high precision, Pesola spring scale (Baar, Switzerland) to record maximum drag forces (drag pointer) encountered by the kelp during a 30 s. run at relatively constant speed. Concurrently, water velocity was measured with a current velocity meter (model OSS-PC1, Hydrological Services Pty Ltd) placed 10 cm above the alga. For each thallus, the drag force was measured at four water velocity intervals (1-1.5, 1.5-2, 2-2.5 and 2.5-3 m s⁻¹), representative of velocities encountered by kelps in winter during high wave action (results from the HOBO loggers, Fig. 1). Speeds > 3.0 m s⁻¹ could not be reliably measured due to turbulence around the kelp produced by the set up. This experiment was run inside Ocean Reef Harbour 10 km north of Marmion Lagoon (Western Australia), protected by a rocky sea wall to minimize effects of wind and waves.

1. 3. 4 Morphology

For each kelp thallus, 10 morphological characters describing the gross morphology were measured. An additional three derived area measures and two shape indices were calculated (Table 1, Wernberg et al. 2003a). Immediately after collection, the algae were weighed and a photo taken of each thallus by holding it upside down against a white background. The picture was analysed with *ImageJ 1.41 (Image processing and Analysis in Java)* and calibrated against a known area. Three different measures of area were derived per thallus based on past drag studies on seaweed (Carrington 1990; Denny 1994; Wernberg 2005). Two measures were obtained by analysing the photography (Planform area and Frontal area) and the total area was obtained from a biomass-area relationship. Planform and Frontal Area (or profile area) are, respectively, the orthographic projection of the thallus on a plane either perpendicular or parallel to the direction of motion induced by the water current (= direction of the kelp held upside down). The Frontal Area was calculated as the circular cross sectional area with the maximum thallus width as the diameter, obtained from the thallus photography. The planform area was calculated as the thallus area seen on the picture. Finally, the Total Area was obtained from the biomass (wet weight, WW) by applying WW:AREA from small batches of laterals and lamina of known areas (19.63cm²) for 25 plants (3 from laterals and 3 from lamina haphazardly taken from each thallus). Lamina and laterals accounted for 11.7% (± 2.95 , N = 25) and 87.2% (± 3.12 , N = 25) of thallus biomass respectively, with mean biomasses per cm² of 0.20 g (lamina, ± 0.05 , N = 25) and 0.10 g (laterals, ± 0.03 , N = 25). Stipes accounted for only 1.1% of the total biomass and were ignored. From these measures, the Total Area was calculated as:

$$\text{Total Area (cm}^2\text{)} = \frac{(0.1172 \times \text{WW})}{0.2} + \frac{(0.8721 \times \text{WW})}{0.1} \quad (\text{Equation 1}),$$

, with WW, the total wet weight (g) of a thallus. The two shape indices were the Bushiness Index and the Flatness Index (BI and FI, Table 1). The Bushiness Index (BI), calculated as the circumference (with maximum thallus width as the diameter) to length ratio of the thallus, indicates how streamlined a kelp is (Begin and Scheibling 2003; D'Amours and Scheibling 2007) and the Flatness Index (FI) represents the degree to which a plant grows as a flat sheet (Gaylord 2000).

Table 1 - Description of morphological characters, shape index and the procedures to measure or calculate them.

<i>Morphological characters</i>	<i>ID</i>	<i>Measurement</i>
Primary morphology		
Total Length (cm)	TL	Length of the thallus to the distal end of the frond (without stipe)
Thallus width (cm)	TW	Greatest width of the thallus when holding it upside down
Lamina length (cm)	LL	From where the stipe widens and flattens into the frond to the distal end of the central lamina
Lamina width (cm)	LW	Width measured at an arbitrarily selected place on the mid-1/3 of the central lamina
Lamina twist (count)	LT	Number of full rotations of the central lamina
Lateral density (number.cm ⁻¹)	LAD	Density of secondary laterals (except were heavily eroded) protruding from the central lamina
Lateral length (cm)	LAL	Average length of 3 laterals arbitrarily selected from the mid-1/3 of the central lamina
Lateral width (cm)	LA W	Width of the selected (cf. lateral length) secondary lateral at its widest place
Lateral ramifications (count)	LAR	Number of ramifications for 3 consecutive laterals. Arbitrarily, from the mid-1/3 of the central lamina
Wet weight (g)	WW	Thallus wet weight after collection
Derived areas		
Total area (cm ²)	TA	Biomass converted to area by applying WW:AREA obtained from small batches of lateral and lamina.
Planform area (cm ²)	PA	Projected area of one side of an alga hold upside down by analysing pictures.
Frontal area (cm ²)	FrA	Orthographic projection of the thallus on a plane perpendicular to the direction of motion or frontal area.
Shape Indexes		
Bushiness Index	BI	Circumference (calculated with TW as diameter) / Total Length
Flatness Index	FI	Planform Area ^{3/2} / Volume (volume for <i>E.radiata</i> thallus was calculated as the volume of 2 cones joint by their base when kelp held upside down)

The drag equation

Drag is due to two components of an object, shape (form drag) and surface of the body (skin drag) (Vogel 1994). In biomechanical studies, drag is defined from the standard empirical drag equation (Vogel 1984; Denny 1995) as:

$$F_{\text{drag}} = \frac{1}{2} \rho \times U^2 \times C_{\text{drag}} \times A \quad (\text{Equation 2})$$

where F_{drag} is the drag force (Newton), ρ the density of seawater ($1,026 \text{ kg m}^{-3}$), U the water velocity (m s^{-1}), C_{drag} the drag coefficient (dimensionless) and A the ‘object area’ (m^2).

1. 3. 5 Data analysis

An ordination was performed for 45 thalli, each described by 15 morphological variables (Table 1) to verify that the kelps sampled did not cluster into similar morphological groups. The ordination was performed using a PCO based on a Euclidian distance matrix. To examine the impact of morphological variation on drag, morphological data were \log_{10} transformed to obtain normalised multivariate data. Euclidian distance was used as the dissimilarity measure for drag measures. The DISTLM (Distance-based linear models) routine, based on the AICc model selection criterion with a Forward selection procedure (McArdle and Anderson 2001; Anderson 2003), was then used to examine the impact of algal morphology on drag. The selection criterion employed in this analysis was a modified version of the information criterion (AIC) (Akaike 1973), namely AICc, used where the number of samples (n) relative to predictor variables (q , the 14 morphological variables) is small (i.e. $n / q < 40$) (Burnham and Anderson 2002).

1. 4 Results

1. 4. 1 *In-situ* orbital water velocity

During one week in winter (July 2010), the four reefs exhibited differences in orbital velocities, ranging from less than 1 m s^{-1} for the onshore reef to more than 3 m s^{-1} with few peaks reaching 4 m s^{-1} for the mid-shore outer reef (Fig. 1). While water velocity generally increased with distance of the reefs offshore, the most offshore site (Fig. 1D) did not show a higher velocity than the mid-shore outer reef (Fig. 1C), possibly due to differences in depth. The first three reefs had depths of 7 to 8 m while the deeper offshore reef was at 10-11 m, therefore wave energy being more dissipated. A shift from general winter conditions to a storm period after 6 days of deployment was observed (Fig. 1). The loggers registered maximum orbital velocities of 3 to 4 m s^{-1} at the most exposed reef (Fig. 1C) and on average 1.5 to 2 m s^{-1} regardless of the reef (Fig. 1). Unfortunately, the memory capacity of the loggers was exceeded before the end of the storm so it is possible that higher velocities may have occurred.

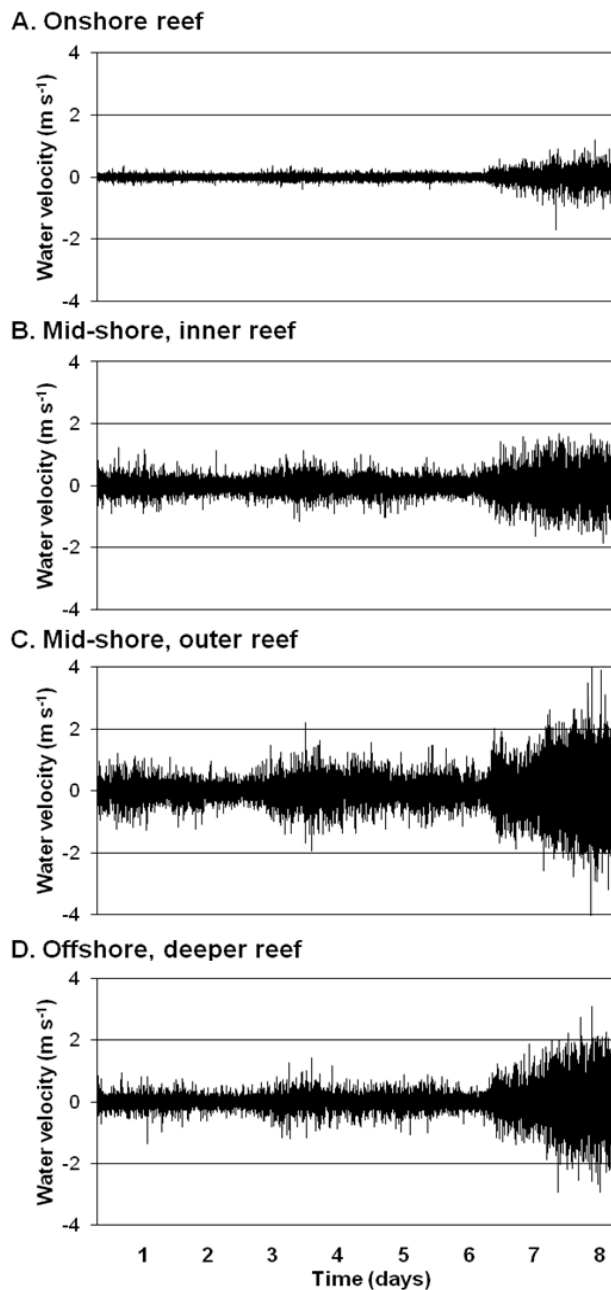


Figure 1 - Orbital water velocities recorded at four reefs over 8 days including a storm event, from the 2nd to 10th of July 2010, using a 30 s sampling rate.

1. 4. 2 Morphological determinant of drag

Prior to analysing the morphological determinants to drag, the kelp collected were viewed with a PCO based on a Euclidian distance matrix according to their morphological attributes to explore their morphological variations. The first two axes of the PCO explained 64.9% of the total variation inherent in the resemblance matrix and the thalli did not cluster into discrete groups (Fig. 2). The population of kelps (stage 3)

was taken across different environments (different reefs, wave exposures and distances from shore) and was likely to approximate the maximum morphological variations occurring *in-situ*.

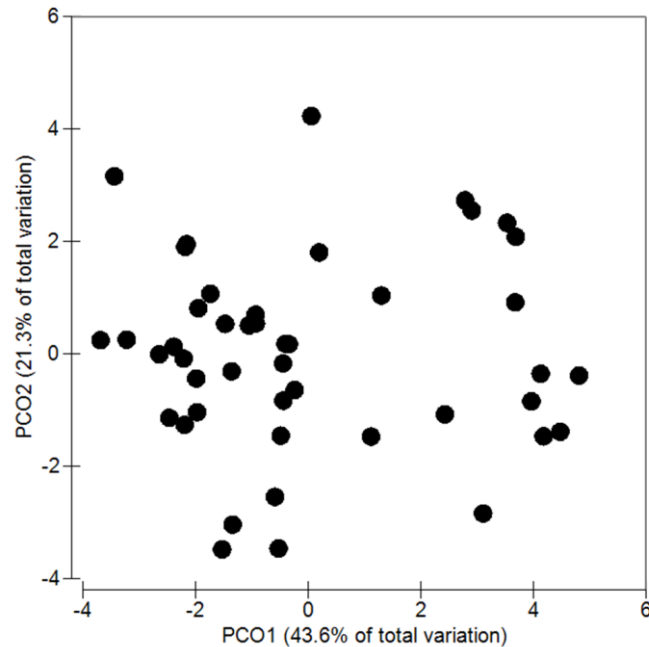


Figure 2 - Principal Component Ordination (PCO) of morphological variation (15 morphological characters) among *Ecklonia radiata* thalli (n=45) used for drag measurement.

Drag forces increased as velocity increased with values (mean \pm SD, N) of 16.43 ± 6.03 N (N = 45), 25.61 ± 7.81 N (N = 45), 34.98 ± 10.35 N (N = 45) and 46.70 ± 15.65 N (N = 45) for the respective classes of water velocities 1-1.5, 1.5-2, 2-2.5 and 2.5-3 m s^{-1} . All morphological parameters were included in the multivariate multiple regression model (Forward DISTLM in PRIMER) except for thallus biomass (Total area being a proxy for the biomass). The correlation of morphological variables with drag increased from 0.41-0.37 to 0.50-0.71 (r^2 , Table 2) as velocity increased beyond 2 m s^{-1} , indicating a growing importance of morphological parameters at higher water velocity. At the lowest speed (1 to 1.5 m s^{-1}) thallus width characteristics, such as Lamina width and Thallus width were determinant of drag, but not thallus area (Table 2). However, the drag at higher velocities was strongly related to change in Total Area (proxy of Biomass) with an r^2 up to 0.59 for the model at high speed (2.5 to 3 m s^{-1} , Table 2). The increase of the r^2 , for the overall model at higher velocities was explained by the

increased ability of the Total Area to explain drag (r^2 increased from 0.26 to 0.59, Table 2) whereas addition of other morphological variables improved the model by only 10% on average. Lamina width was an important parameter in the models at all speeds, though its contribution to explaining drag was greater at lower speed.

Table 2 - Outputs from sequential tests of the multivariate analysis for a linear model using forward selection (DISTLM-Forward in PRIMER) at each water velocity class. All morphological variables (Table 1) were entered into the analysis.

<i>Velocity</i>	<i>Model</i>	<i>AIC_c</i>	<i>SS (trace)</i>	<i>Pseudo-F</i>	<i>P_i</i>	<i>r²</i>
1-1.5 m s ⁻¹	LW	134.9	518.7	20.4	.0002	.34
	LW + TW	132.9	100.3	4.3	.04	.41
1.5-2 m s ⁻¹	TA	161.4	665.3	13.7	.001	.26
	TA + LW	157.2	282.2	6.65	.01	.37
2-2.5 m s ⁻¹	TA	168.2	1915.3	30.2	.0001	.44
	TA + LW	166.1	253.6	4.4	.04	.50
2.5-3 m s ⁻¹	TA	179.6	5458.1	51.3	.0001	.59
	TA+ LAL	175.9	563.7	6.0	.02	.65
	TA + LAL + LW	171.2	565.7	7.1	.01	.71

AIC_c modified Akaike Information Criterion, SS (trace) portion of sum of squares related to the analysed predictor variable, r^2 percentage of variance explained by the variables selected in the model, P_i probability for the model. TA = Total Area, LW = Lamina width, TW = Thallus width and LAL = Laterals length (see Table 1).

1. 4. 3 Variation of C_{drag} with water velocity

According to our results, C_{drag} was estimated using the measure of total thallus area for the ‘Object area’ (Equation 2). The overall C_{drag} value and variance for the 45 kelps tested at the four velocities decreased with increasing water velocity following a negative power regression curve ($p < 0.001$, Fig. 3). However the correlation coefficient was relatively low ($r^2 = 0.14$, Fig. 3). At low velocity (1-1.5 m s⁻¹), C_{drag} values were highly variable ranging from 0.02 to 0.10 (0.037 ± 0.020 , N = 45; mean and SD for C_{drag} between 1-1.5 m s⁻¹) converging to 0.024 (± 0.011 , N = 45; mean and SD for C_{drag} between 2.5 to 3m.s⁻¹, Fig. 3) as velocity increased. According to the regression equation ($C_{drag} = 0.041 \times \text{Water velocity}^{-0.634}$, Fig. 3), C_{drag} values varied from 0.037 at

1-1.5 m s⁻¹ to 0.022 at 2.5-3 m s⁻¹. During the storm monitored, the range of maximum water velocities was 2 to 3 m s⁻¹ which resulted in an averaged C_{drag} of 0.025 (Fig. 1 and 3).

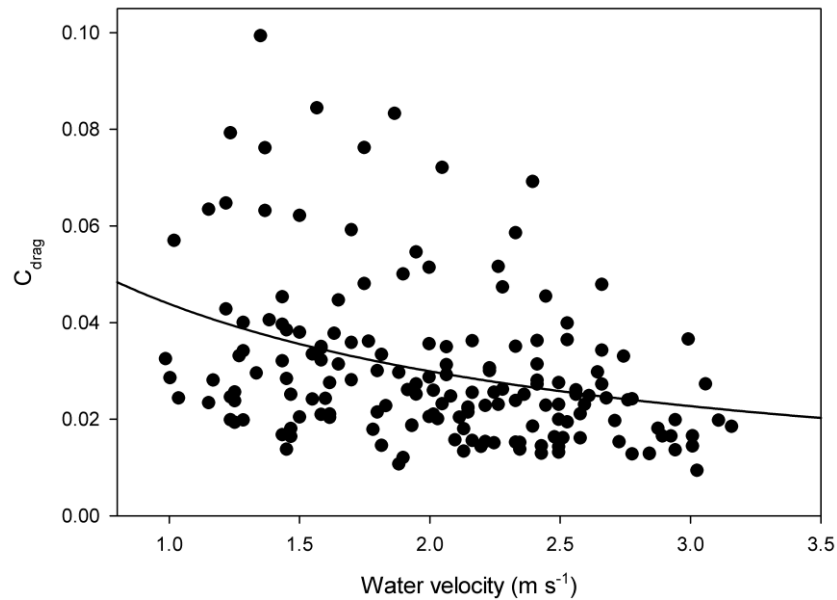


Figure 3 - Variation of drag coefficient (C_{drag}) with water velocity. Negative power regression curve displayed ($C_{\text{drag}} = 0.041 \times \text{Water velocity}^{-0.634}$, $P < 0.001$, $r^2 = 0.14$, $N = 167$).

1.5 Discussion

This study was the first worldwide to record continuously orbital water velocity generated by storm on temperate subtidal reef *in-situ*. During the storm we monitored, kelp experienced orbital water velocities over 2 m s⁻¹ (up to 3-4 m s⁻¹); comparable to the velocities we applied to kelp of different morphologies. Knowing the range of *in-situ* velocities provided ecological content for the simulation of storm velocities on individual kelp thalli. Once kelp was subjected to these high water velocities, total thallus area or biomass became the main determinant of drag and not the morphological variation in shape. Variables related to the shape of the algae were important at low speed only. These findings, together with the observed decrease of C_{drag} with speed, highlight the significant reconfiguration of the thallus occurring at high water velocity. This reconfiguration in high flow resulted more likely in the algae equally streamlined despite further increases in velocity, effectively decoupling hydrodynamic forces such as drag from algae shape.

The morphological determinants of drag, and their relationship with drag, varied with water velocity. At speeds that were low in the experiment, but in an ecological context are relatively high (1 to 1.5 m s⁻¹), the width of the lamina and thallus were the two most important variables explaining pressure drag, related to the form of the object. This is typically the case for algae with a flat, strap-like morphology, where width of the thallus is a crucial morphological parameter (Koehl and Alberte 1988), or for small bushy algae (*Codium fragile*), where the circumference to length ratio or bushiness index drives changes in drag (D'Amours and Scheibling 2007). At higher velocities, the lamina width remained an important parameter in the model. This indicated that the lamina width may limit the potential of the thallus to reconfigure under high water velocities. The effect of this variable for *Ecklonia radiata* has been suggested previously by Wernberg et al. (2005) who found a trend of narrower lamina and laterals for kelps on exposed reefs. However, once the velocity reached 1.5 m s⁻¹, the main determinant of drag became the total area of the thallus or biomass. Milligan & De Wreede (2004) found similar results comparing morphotypes of an intertidal alga, *Hedophyllum sessile*, and showed that morphological variations in shape did not reduce the drag stress when water velocity reached 4 m s⁻¹. In theory, two forms of drag can be distinguished (Vogel 1994): drag caused by build-up of pressure in front of the body and a decrease in pressure behind the body, called *pressure drag* or *form drag*; and the viscous resistance of the fluid along the surface of the body, called *skin drag* or *friction drag*. The results indicated that friction and pressure drag could act together in complex algae like *Ecklonia radiata*, but their relative importance changes with water velocity. At low speed the lamina and thallus width best explained drag (pressure drag), but as water velocity increased the total area (combining both drags) was better related to drag. Indeed, the ability of flexible organisms to reconfigure reduces the size of the wake downstream, thereby reducing form drag at high flow (Carrington 1990; Koehl 2000).

The decrease of the drag coefficient with increasing velocity is consistent with the findings for drag force and corresponds to a reconfiguration of the algae to a more streamlined and compact shape (Koehl 1984; Koehl and Alberte 1988; Gaylord et al. 1994; Denny and Gaylord 2002). This implies that kelp morphology changes with the flow and therefore morphological determinant of drag must vary with water velocity

(what we found). Similar to other studies, C_{drag} tends to reach an asymptote at higher velocities and the effects of shape change were greatly reduced (Carrington 1990; Gaylord et al. 1994; Bell 1999; Boller and Carrington 2006a). This can be explained by the flexibility of algae due their relatively simple shape and the compliance of their materials that enables algae to reconfigure in rapid steady flows. This extreme reconfiguration in high flows can result in decoupling of hydrodynamic forces such that drag becomes relatively independent of the apparent differences of algae shape (Denny and Gaylord 2002). Past studies demonstrated similar results of converging C_{drag} for different morphotypes of a species (*Pachydictyon coriaceum*, Haring and Carpenter 2007) and for different species (Carrington 1990). Although the drag coefficient can be calculated from different measures of thallus areas (Carrington 1990; Denny 1994; Wernberg 2005), the value obtained for C_{drag} (0.025) using the Total Area in our study was very similar to drag coefficients for several kelps under high flow regime: 0.01-0.05 (Koehl 2000; Kawamata 2001; Thomsen 2004).

The simulated unidirectional steady flow used in our experiments was a simplification of the oscillatory motion that occurs under wave action. Because waves generate orbital water flow, the reorientation of the plant and its ability to ‘go with the flow’ is likely to more efficiently reduce hydrodynamic forces (acceleration forces) than “drag reducing shape”. Indeed, Wernberg and Vanderklift (2010) showed that morphological characters of *E. radiata*, associated with overall size, increased with increasing wave exposure. This could be an adaptation to follow the orbital flow, preventing the thallus being stretched out fully before the flow reverses, and reducing the forces experienced (Denny 1998; Koehl 1999). However, the combination of long wave periods during storm (~13 to 17 s, <http://www.dpi.wa.gov.au> and Lemm et al. 1999) and the relative small size of *Ecklonia radiata* (<1 m, Wernberg and Vanderklift 2010) should always result in the kelp being totally stretch out and experiencing the total force of the waves (Gaylord et al. 1994; Koehl 1999). Further investigation is needed to test the reciprocal impact of morphology on hydrodynamic forces via this strategy of ‘going with the flow’.

These results confirm the importance of the object area as a determinant of drag, principally at high speed, and the importance of other morphological variables related to the width, which probably limits the compaction of the object at lower speed. However,

these morphological variables only had a minor effect on drag and C_{drag} converged at water velocities characteristic of storms due to the algae being equally streamlined at these higher velocities. Consequently, drag is decoupled from the shape and other morphological variables of the thallus, with the exception of Total Area, a function of biomass. Given this, the only way of minimizing drag forces at storm velocities is by a reduction of thallus area (biomass) and not by modification of thallus shape. Along the Western-Australian coastline, storms associated with mid-latitude depression are common in winter (Lemm et al. 1999) and generally algal dislodgement occurs during such severe storms, which generate high water velocities (Seymour et al. 1989; Dayton et al. 1992; Blanchette 1997). However, the temporal growth-erosion dynamic and the resulting decrease in individual kelp biomass (i.e. Total area) for *Ecklonia radiata* in autumn-winter (Kirkman 1989; de Bettignies et al. 2012b) will minimize the drag force, and might offset the increase in water velocities during the storms and the risk of dislodgement. Ultimately, the survival of *E. radiata* will depend of the balance between the drag force (as the main hydrodynamic force) and the force required to break or dislodge the algae (break force), related to its material properties and attachment to the substrate.

1.6 Acknowledgements

TdB was funded through an ECU postgraduate award. Additional funding was obtained from the Western Australian Marine Science Institution (TdB). TW was funded by The Australian Research Council. We thank J. P. Escaño Roepstorff, T. Minutoli Tegrini, F. Vitelli, S. Luret and P. Bouvais for assistance in the field, D. Goodall and G. Maguire for comments on the early manuscript and editing, and D. Thomson for the calibration of the accelerometers.

CHAPTER 2

Wounded kelps: patterns and susceptibility to breakage

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Key words: Seaweed biomechanics, *Ecklonia radiata*, wounds, biomass loss, pruning, survival, Western Australia

The work contained in this chapter is published as:

de Bettignies T, Thomsen MS, Wernberg T (2012b) Wounded kelps: patterns and susceptibility to breakage. *Aquatic Biology* 17 :3 223-233 doi: 10.3354/ab00471

2. 1 Abstract

Kelps are highly productive seaweeds predominantly found in wave-exposed environments. Physical and biological processes such as sand abrasion, whiplash and grazing can wound kelp tissue, potentially weakening its ability to withstand wave forces. Despite the ecological importance of kelp tissue loss, few studies have quantified wounding patterns in kelps or how wounding might affect the biomechanical properties of kelps. We quantified the prevalence of wounds on 360 *Ecklonia radiata* kelps collected across 3 different reef lines (levels of wave exposure) in April (autumn), June (early winter), August (winter) and October (early spring) (i.e. before, during and after peak wave activity). Small holes in the centre of laterals dominated the wounds. Wounding pattern did not differ between reef lines but changed over time, with most in early winter and least in early spring (from 285 to 71 wounds kelp⁻¹). This pattern suggests that wounds accumulate over summer and that highly wounded parts of the frond (but not the entire kelp) break off when encountering the first storms. Biomechanical break-force tests assessed the effect of experimental wounds on the forces required to break kelp tissue. These tests showed that holes or horizontal cuts to the edge of the kelp frond dramatically reduced the strength, extensibility, toughness and stiffness of the tissue. We conclude that wounds are common in *E. radiata* and that the resulting loss of tissue integrity, caused by even small damages, can dramatically increase the susceptibility to breakage. Our findings may have important ecological implications; the peak in wounds in early winter is likely to increase fragmentation of the kelp, thereby reducing its size and hydrodynamic drag, and, paradoxically, reducing the risk of fatal dislodgement during severe winter storms.

2. 2 Introduction

Kelp forests are highly productive and ecologically important habitats along rocky coastlines in polar to warm temperate regions where they influence ecosystem dynamics (Mann 2000; Steneck et al. 2002). Kelps are common in wave-exposed environments where they experience extreme forces (Denny 1994; Thomsen et al. 2004) that can cause loss of parts of the thalli (pruning) and loss of the entire thalli (dislodgement) (Seymour et al. 1989; Dayton et al. 1992; Thomsen and Wernberg 2005) resulting in canopy loss on reefs and accumulation of drift kelp in adjacent habitats (Wernberg et al. 2006) and on the shore (Ince et al. 2007). Canopy loss and accumulation of drift kelp

are important ecological processes that underpin much of the community dynamics on reefs (Dayton et al. 1992; Wernberg and Connell 2008) and in adjacent habitats (Bustamante et al. 1995; Wernberg et al. 2006). It is therefore important to understand the factors that influence the rate of kelp pruning and dislodgement. Conceptually, the mechanical process whereby entire kelps are dislodged from reefs is well understood (Denny 1995) but much less is known about pruning. In particular, the range and exact nature of mechanisms that influence the susceptibility of kelps to pruning are unclear.

To cope with extreme hydrodynamic forces, kelps can adjust their morphological (Roberson and Coyer 2004; Fowler-Walker et al. 2006; Wernberg and Vanderklift 2010) and/or material properties (Denny et al. 1989; Harder et al. 2006). Kelps can be described as “shock absorbers” that absorb energy through tissue extension before breaking (Johnson and Koehl 1994). Due to the absence of stiff structural tissue components such as lignin in higher plants, kelp tissues are relatively weak, with a low breaking stress ($\sigma_{\text{brk}} = 1$ to 5 MN m^{-2}). On the other hand, kelps are highly extensible with a high breaking extension or breaking strain ($\epsilon_{\text{brk}} = 0.3$ to 0.75) compared to, for example, trees (wood, $\epsilon_{\text{brk}} = 0.01$) (Harder et al. 2006). For instance, the stipe of the kelp *Nereocystis luetkeana* can extend up to 40% without sustaining cellular damage (Koehl and Wainright 1977). Moreover, kelps have typically streamlined morphologies with long, flat fronds and long stipes (Gerard and Mann 1979; Wernberg and Thomsen 2005; Wernberg and Vanderklift 2010) making them flexible and able to dissipate wave energy by “going with the flow” (Friedland and Denny 1995). It has been proposed that this combination of high extensibility and flexibility explains the paradoxical existence of some of the largest plants on earth, in one of the most hydrodynamically challenging environments (Koehl 1984; Denny et al. 1989).

Kelps are under constant pressure from external stressors such as waves, abrading sediments, scouring fronds, grazers and pathogens. These physical and ecological stressors can wound and cause damage to the kelp through cuts, holes and scars in the kelp tissue (Dayton 1985; De Wreede et al. 1992; Krumhansl and Scheibling 2011b), likely affecting tissue properties such as strength and extensibility, and potentially making kelp tissue more prone to structural failure and crack propagation leading to tissue loss (Holbrook et al. 1991; Duggins et al. 2001). Depending on where on the

plant the tissue the impact occurs, this might result in mortality (breakage of holdfast or stipe below the meristem = dislodgement) or lead to significant loss of biomass via pruning without necessarily killing the alga. Most previous studies have been concerned with processes that affect the survival of kelps only, and these studies have focused on, and simulated, stipe damage (Biedka et al. 1987; Denny et al. 1989; Duggins et al. 2001; Harder et al. 2006). However, it is also relevant to understand the susceptibility of kelps to non-fatal biomass loss to better understand detrital production and biomass export from kelp forests to adjacent habitats (Colombini and Chelazzi 2003; Vanderklift and Wernberg 2008; Kelly et al. 2012). Wounding processes can be particularly important if wounds weaken the tissue and increase rates of pruning and fragmentation of blades, thus affecting rates of export of kelp biomass from reefs to adjacent habitats. Indeed, it has been demonstrated that only 10% of kelp biomass is consumed directly by herbivores (Mann 2000), with the other 90% entering the coastal food web through the detrital component as particulate and dissolved organic matter (POM and DOM respectively, Mann 1982; Duggins et al. 1989). This kelp-derived detritus can constitute the main source of carbon for detritivores in adjacent recipient habitat: in the supralittoral zone (Polis and Hurd 1996), intertidal zone (Bustamante et al. 1995; Bustamante and Branch 1996), seagrass meadows (Wernberg et al. 2006), distant reefs (Vanderklift and Wernberg 2008) and deeper habitats (Vetter 1994; Kelly et al. 2012).

Winter is a key period for kelp detrital production when large waves associated with winter storms tear blades and plants off (Seymour et al. 1989; Graham et al. 1997; Reed et al. 2011). At the same time, tissue wounding is likely to be higher at more wave exposed sites and in winter with increasing physical disturbance (i.e. scouring, whiplash). Therefore, this study aimed to, firstly, quantify spatio-temporal patterns around winter, in the prevalence of wounds in different kelp tissues, and secondly, test for effects of different types of wounds (simulated damage from cuts and holes at different positions on the tissue) on the strength, extensibility, stiffness and toughness of kelp tissues. We hypothesized (1) that wounds would be most prevalent in kelps from exposed reefs during winter months when storm activity and sand abrasion peak (Lemm et al. 1999; Li et al. 2011), and (2) that wounds would influence tissue biomechanical properties dramatically.

2. 3 Materials and Methods

2. 3. 1 Study site

This study took place in Marmion Lagoon, Perth, Western Australia (32° S latitude). This region is strongly influenced by westerly and south-westerly wind and swell generated-waves (Searle and Semeniuk 1985; Lemm et al. 1999). Wave characteristics vary seasonally, but waves are largest in winter (June to August) when the average wave height is 1.5 to 2.5 m; storms (waves >4 m) occur ~30 times per year with a peak frequency in winter (Lemm et al. 1999). A series of successive high relief reef ridges (reef lines) run parallel to the shore, dissipating hydrodynamic forces by 50 to 75 % as waves approach the coast, creating a gradient in exposure to wave forces (Phillips et al. 1997; Smale et al. 2011). Reefs throughout temperate Australia, including Marmion Lagoon are dominated by the small kelp *Ecklonia radiata* (1 to 2 m) which has a terete basal stipe that bears a flattened blade (lamina) with ramified laterals (Wernberg et al. 2003a) (see also Fig. 1A).

2. 3. 2 Experimental design

Kelps were sampled at 6 reefs (depth range from 8 to 10 m) with 2 reefs nested in 3 reef lines (protected midshore reefs, exposed midshore reefs and deep offshore reefs). Their respective wave exposures were measured as acceleration of the water flow (0.15 ± 0.02 , 0.19 ± 0.04 and 0.16 ± 0.02 m s⁻²) during 1 week in winter (2 to 9 July 2010) with the '*H₂O Motion VI design*' (Evans and Abdo 2010). Kelps (n = 15) were collected from each reef in April (autumn), June (early winter), August (late winter) and October (spring). These sample times were targeted because wave-induced damage is most likely to occur late in the season when the kelp thalli (Wernberg and Goldberg 2008) and waves (Lemm et al. 1999) are largest.

2. 3. 3 Kelp wounds

We counted all macroscopic wounds (visible to the naked eye) on all stipes, laminae and subsamples of 3 laterals of similar surface area (5 to 7 cm x 15 to 20 cm) in the middle of the thallus from all 360 kelps. Wounds were classified as 'holes' (Fig. 1D,E,F,G,H), 'tears' (large piece of tissue torn off; Fig. 1A,G,I), and 'cuts and scars' (Fig. 1B,C). These wound types were quantified for different kelp tissues (stipe, lamina, and laterals), and for laminae and laterals the 'positions' of wounds were recorded as

either on the ‘edge’ or in the ‘centre’ of the tissue. Most wounds were circular holes (Fig. 1D,E,G), and these were categorised into 2 size-groups: small and large holes (<10 and >10 mm diameter, respectively). In total, 9 wound variables were measured, representing observed combinations of wound type, tissue, position and size.

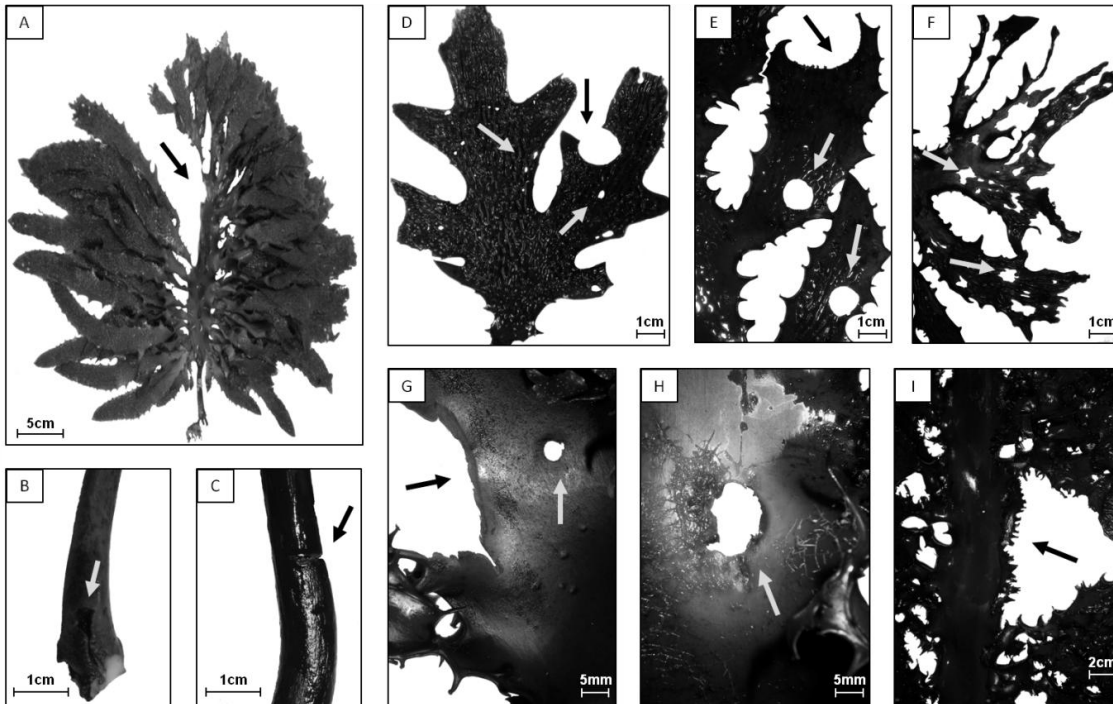


Figure 1 - *Ecklonia radiata*. Photographs of different types of damage recorded: (A) tear along the lamina; (B,C) stipe scars; (D,E,F) holes within and on the edge of the laterals; and (G,H,I) holes and tears within and on the edge of the lamina. Black and grey arrows indicate locations of damage.

2. 3. 4 Biomechanical tests of effects of tissue wounding.

Whole plants of *Ecklonia radiata* were collected from Marmion Lagoon and kept fresh until used for tensile tests within 24 h. Strips of healthy lamina tissue were cut into hourglass shapes, ca. 12 cm long and ca. 3 cm wide, narrowing to 3-8 mm width at the mid-section to facilitate controlled test-breakage at this tissue position (Fig. 2). Tensile tests were performed using *Shimpo* mechanical force gauges (*Shimpo*, $\pm 0.2\%$ precision). One end of the tissue was fixed between a pair of neoprene coated clamps to ensure that the tissue was firmly attached but did not break around the attachment point. This clamping device was attached to the force gauge. A standardized strain rate was applied by pulling the tissue by hand with a slowly increasing sweeping motion until the

tissue broke (typically after 8 to 10 s). This strain rate aimed to mimic typical benthic surge created by waves (~ 5-12 sec wave period, Lemm et al. 1999) and kelp frond reconfiguration (Wernberg 2005). The break extension was recorded by observing the exact point of tissue breakage against a background-ruler (Fig. 2). Tests in which breakage occurred near the attachment point of the clamp were discarded. Tensile tests of non-wounded controls (n = 52 successful tests) were compared to 3 types of artificially induced wounding (Fig. 2): 2 mm circles positioned centrally (n = 16), 2 mm half circles positioned along the edge (n = 15) and 2 mm linear cuts positioned along the edge (n = 17). These experimental wounds mimicked wounds seen *in situ*, likely reflecting grazing marks from mesograzers (holes, centre), fish (half circles, edge) or mechanic damage (cuts) (Fig. 2). Following breakage the tissue width and tissue depth at the exact break location was measured using callipers. From these data, strength (standard stress at breaking), extensibility (strain at breaking), stiffness (ratio of stress/strain at breaking) and toughness (work of fracture) were calculated, (Harder et al. 2006). The standard stress (MN m^{-2}) was obtained by dividing the force at breaking by the cross-sectional area of tissue where it breaks. The strain at breaking was the ratio of the extension of the tissue at breaking to the initial tissue length (12 cm). Because the strain at breaking is dimensionless, the ratio of stress to strain (stiffness) has the dimension of stress (MN m^{-2}). The work of fracture was calculated as the area under the stress-strain curve (MJ m^{-3}).

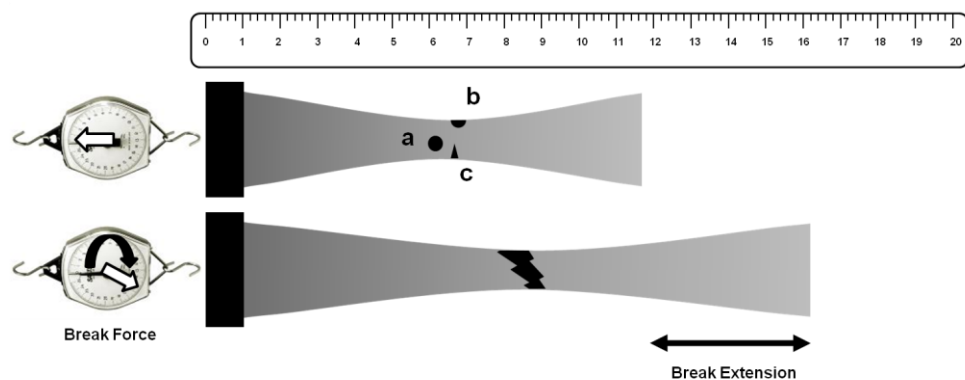


Figure 2 - Schematic view of the tensile test before and after the pull test. A strip of tissue (12 cm long) was clamped to a mechanical gauge and pulled manually until breakage. The letters a, b and c represent the 3 types of artificially induced wounding, i.e. hole in the middle, and hole or cut at the edge of kelp tissue. Each type of damage was made on different test pieces

2.3.5 Statistical analyses

The 9 wound variables were square root transformed to down-play the importance of small abundant wounds over large and less frequent wounds and to reduce potential differences in the dispersion of the data. Euclidian distances were calculated between each reef-time combination. Permutation based multivariate analysis of variance (PERMANOVA; Anderson et al., 2008) was used to partition variation between sampling 'Times' (fixed factor = April, June, August, October), 'Reef line' (fixed factor = protected midshore reefs, exposed midshore reefs, and deep offshore reefs) and 'Reefs' nested within reef lines (random factor, $n = 2$). Subsequently, pairwise comparisons were performed for the significant factors. The key results of wounding pattern were visualised by constrained analysis of principal coordinates (CAP, Anderson et al. 2008), and vectors for strongly correlated variables ($r > 0.5$) were overlaid to identify the wound variables potentially driving the patterns. The PERMANOVA and CAP analyses revealed that, by far, the most multivariate data variability was explained by Time on 3 of the 9 wound variables (see 'Results'). We therefore proceeded with 1-way ANOVAs on the Time tests factor (on square root-transformed data) followed a by post hoc test (Tukey) on these 3 wound variables. We also used 1-way ANOVAs to test for effects of simulated wounding on kelp tissue biomechanical properties. When homogeneity of variance could not be met even after transformation (square root), significance was interpreted conservatively at $p < 0.01$ (Underwood 1997).

2.4 Results

2.4.1 Field survey of wounds

The majority of the thalli analysed had wounds in their tissue (93 to 100% for each of 24 combinations of reefs and times). There was a high variability in wounding at different times and reef lines as suggested by the highly significant Time x Reefs nested in Reef lines ($p = 0.009$; Table 1). However, as the 2-way interaction between Time and Reef lines was marginally non-significant ($p = 0.074$) and accounted for very little variation relative to time (MSs of 108.3 vs. 18.5; Table 1), we proceeded to analyse the single-factor effects of Time and Reef lines. There was strong temporal variation in wounding pattern ($p = 0.001$), but no difference with reef lines ($p = 0.407$; Table 1). The

wounding patterns were similar in April and June ($p = 0.287$), but different between all the other months ($p < 0.05$; Table 1). Three distinct groups for the factor Time were also seen from the CAP analysis (Fig. 3), with April and June grouped together and August and October separated. Three wound variables were strongly correlated with the multivariate wounding patterns ($r > 0.5$; Fig. 3): $>10\text{mm}$ holes in the centre of laminae, and $< 10\text{mm}$ holes and $> 10\text{mm}$ holes in the centre of laterals. There was strong temporal variation in the severity of wounding for these 3 variables ($p < 0.003$; Table 2 and Fig. 4) and differences in wounds between the 4 months (Fig. 4). In general, there was a significant decrease in number of wounds at the different times, with a minimum in October (Fig. 4). Interestingly, the highest number of wounds was not observed in August when wave energy peaks, but in April and June (Fig. 4). We subsequently used our wounding data to calculate the total number of wounds an ‘average kelp’ with 1 stipe, 1 lamina and ca. 40 laterals (Wernberg and Vanderklift 2010) is expected to have (Fig. 4D). For this average kelp, we observed almost the same pattern as for the small holes ($< 10\text{ mm}$) at the centre of laterals (which dominated the number of wounds, see Fig. 4D). The total number of wounds on an average kelp was significantly higher in April (285 ± 47 , mean \pm SE) and June (256 ± 25) compared to August (123 ± 11) and October (71 ± 8) (Fig. 4D).

Table 1 - PERMANOVA, testing for differences in wounding patterns between Time (April, June, August, October; fixed factor), Reef lines (1 to 3 from inshore to offshore; fixed factor) and 2 Reefs nested within each reef line (random factor).

<i>Source of variation</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Time	3	108.32	12.12	0.001
Reef line	2	15.76	1.54	0.407
Reefs(RL)	3	10.18	2.10	0.041
T \times RL	6	18.50	2.07	0.074
T \times R(RL)	9	8.95	1.84	0.009
Residual	325	4.84		
Pair-wise test for Time				
<i>Time</i>	<i>t</i>	<i>p</i>		
April vs. June	1.22	0.287		
April vs. August	2.96	0.038		
April vs. October	3.96	0.020		
June vs. August	2.97	0.042		

June vs. October	4.60	0.017
August vs. October	3.13	0.021

Table 2 - One-way ANOVA results for the effect of Time (April, June, August and October) on the 3 wound variables found to correlate ($r > 0.5$) with wounding patterns. Homogeneity of variance could not be met even after transformation; significance was therefore interpreted conservatively as $p < 0.01$.

<i>Variables</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Lamina (centre), large holes,	3	1.79	4.68	0.003
residual	345	0.38		
Lateral (centre), small holes,	3	5032.09	14.95	<0.001
residual	345	336.59		
Lateral (centre), large holes,	3	24.34	13.24	<0.001
residual	345	1.83		

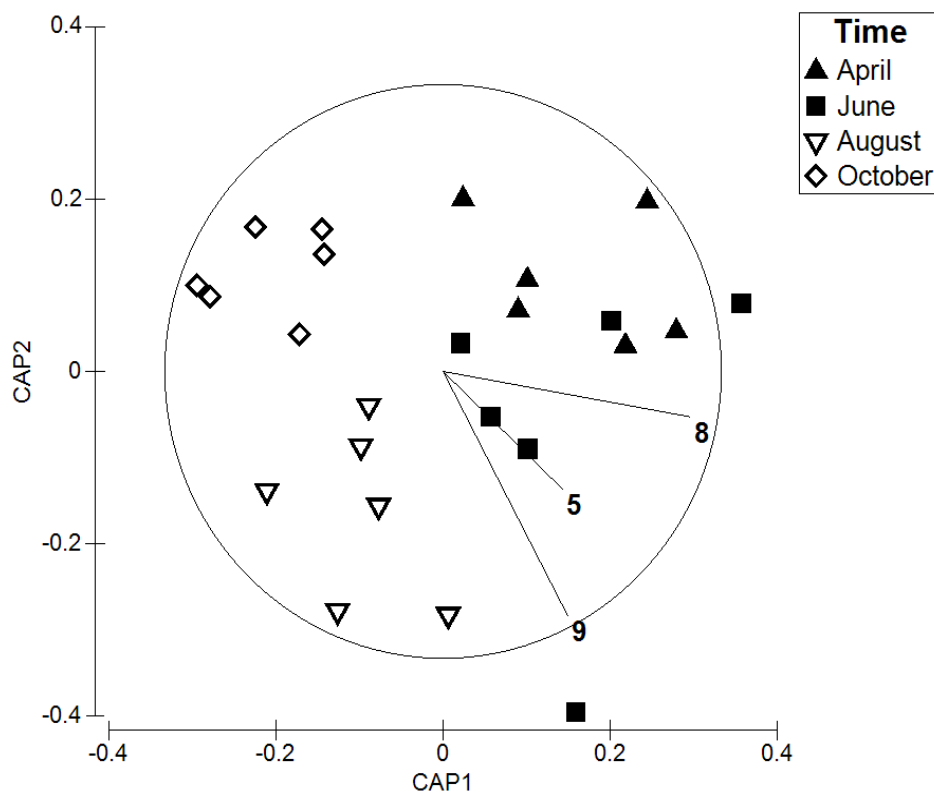


Figure 3 - Ordination (constrained analysis of principal coordinates; CAP) of kelps from Marmion Lagoon based on their wounding patterns constrained by sampling times and vector overlays with selection criterion at Pearson coefficient >0.5 (3 variables). Variables 5, 8 and 9 correspond, respectively, to >10 mm holes in the centre of lamina,

and <10 mm holes and >10 mm holes in the centre of laterals. The squared correlation coefficient and result of leave-one-out allocation success were $\delta^2 = 0.78$ and LoA = 79.2%, respectively, using $m = 6$, where m is the number of axes.

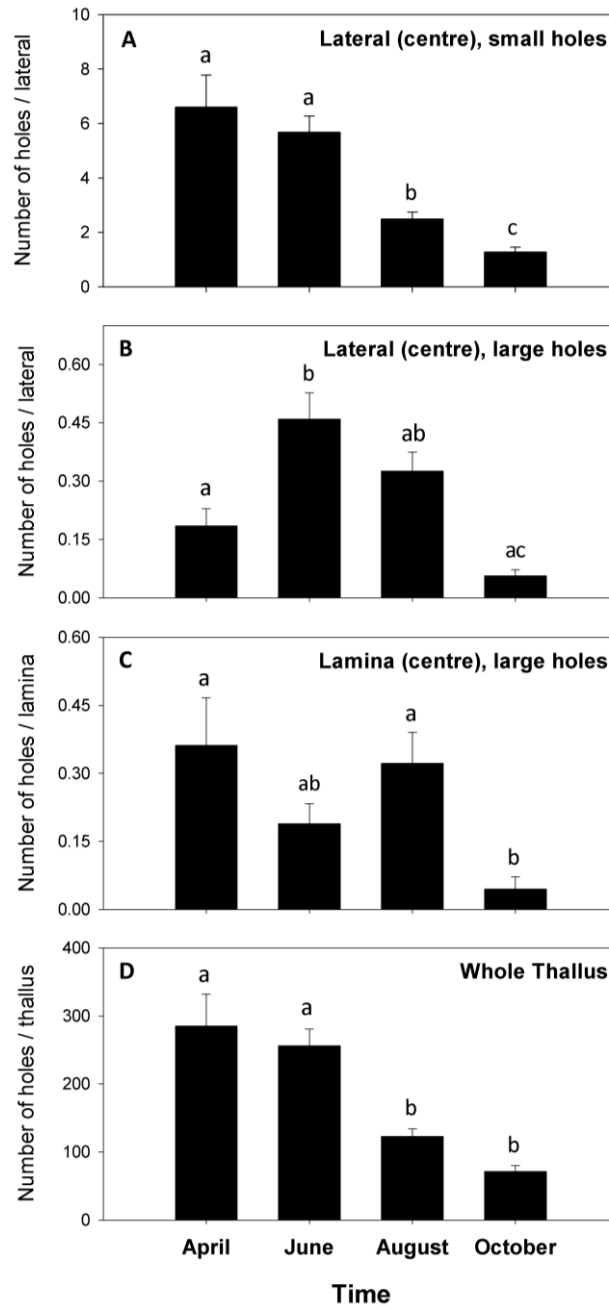


Figure 4 - Changes in wounds at different times (mean \pm SE) for (A) small holes in laterals, (B) large holes in laterals and (C) large holes in lamina. These 3 variables explained most of the multivariate wounding pattern for the 4 sampling times (April, $n = 83$; June, $n = 90$; August, $n = 87$; October, $n = 89$). (D) shows the total number of wounds extrapolated to an ‘average-sized kelp for each month’ (see ‘Materials and

methods'). Letters above bars indicate significantly different treatments (on square-root-transformed data) from Tukey's post hoc tests ($p < 0.01$)

2. 4. 2 Biomechanical tissue tests of wounding effects

The tissue properties of intact strips of lamina had a relatively low standard stress at breaking ($3.91 \pm 1.11 \text{ MN m}^{-2}$, mean \pm SD; Fig. 5A) but high extensibility (0.32 ± 0.08 , Fig. 5B) and stiffness ($12.65 \pm 3.96 \text{ MN m}^{-2}$; Fig. 5C) and therefore also a high toughness ($0.65 \pm 0.29 \text{ MN m}^{-2}$; Fig. 5D). We found that wounding significantly reduced these biomechanical properties (Table 3), showing a gradient in severity with centred holes and edge cuts having the least and most severe impacts, respectively (Fig. 5A to D). For toughness, all wounding treatments differed from each other ($p < 0.01$, Tukey test; Fig. 5D). However, for extensibility, 'centred holes' did not differ from unwounded tissue (Fig. 5B). Similarly, for stiffness and strength at breaking, 'centred holes' did not differ from 'edge holes' ($p > 0.01$; Fig. 5 A,C). Finally, centred-holes, edge holes and edge cuts reduced the energy required to break healthy kelp tissue by 43, 75 and 92 %, respectively (Fig. 5D). To summarize schematically how wounding influenced these key biomechanical properties (Fig. 5A to D), we also plotted 'simplified standard stress-strain curves' (Fig. 6).

Table 3 - One way ANOVA results for effect of different simulated wounds (no wounding, centred hole, edge hole and edge cut) on 4 biomechanical properties (Strength at breaking, Extensibility, Stiffness and Toughness) of lamina tissue.

<i>Variables</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Strength at breaking	3	6.12	116.02	<0.001
residual	96	0.53		
Extensibility	3	0.17	61.65	<0.001
residual	96	0.003		
Stiffness	3	6.97	31.39	<0.001
residual	96	0.22		
Toughness	3	1.66	83.14	<0.001
residual	96	0.20		

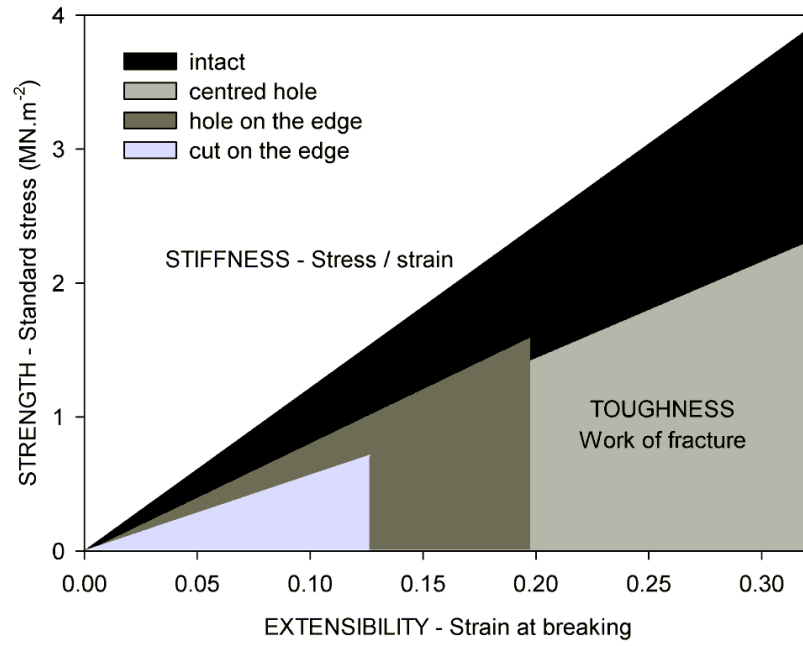


Figure 6 - Summary of changes in tissue properties after wounding. Strain and standard stress at breaking of wounded tissues are displayed on the figure; stiffness and toughness were obtained from stress-strain curves, respectively, as the slope of the stress-strain curves and the area under the curves.

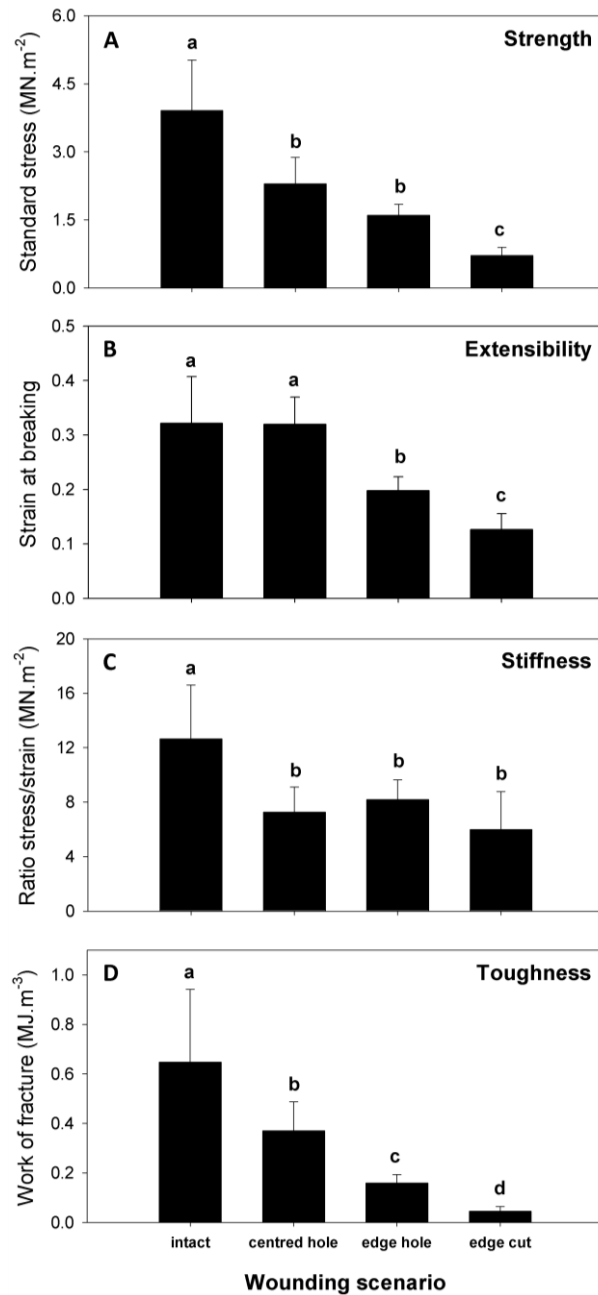


Figure 5 - Impact of simulated wounding on lamina tissue properties: (A) strength (= standard stress at breaking), (B) extensibility (= strain at breaking), (C) stiffness (= ratio stress/strain) and (D) toughness (= work of fracture); n = 52, 16, 15 and 17 for ‘intact’ ‘centred hole’, ‘edge hole’ and ‘edge cut’, respectively. Letters above bars indicate significantly different treatments (on square-root-transformed data) from Tukey's post hoc tests (p < 0.01).

2.5 Discussion

We found that average *Ecklonia radiata* kelps (i.e. with 1 stipe, 1 lamina and ca. 40 laterals; Wernberg & Vanderklift, 2010) can sustain from ~300 wounds thallus⁻¹ in April to ~70 thallus⁻¹ in October from relatively wave-exposed reefs. We are not aware of any studies to have reported whole-thallus wounding patterns, and we can therefore not evaluate if these numbers are representative for other species, regions or habitats. In addition, we found that simulated wounds (holes or cuts) greatly affected the biomechanical properties of kelp tissue, reducing the energy required to break it by 45 to 82%. Overall, these findings indicate that wounds are very common on all kelps before winter and that wounds likely result in greatly increased kelp pruning rates for *E. radiata* beds. The high incidence of wounding implies that physical damage is a ubiquitous and constant pressure on kelps, which might, in turn, limit their size. Paradoxically, wounding may thereby increase kelp survival during storms, because drag and dislodgement is typically lower for small (pruned) than large (intact) kelps.

2.5.1 Wounding patterns

Our study indicated that wounds occur in most kelp thalli (93 to 100%) and in all different kelp tissues (although rarely on stipes), where the vast majority of wounds were small holes located on laterals. Wounds were frequent, diverse and exhibited a complex temporal and spatial pattern around winter. Interestingly, we did not find support for the hypothesis that wounds would be most prevalent in kelps from exposed reefs during winter. Instead, we found no effects of wave exposure and a general peak in wounds in April to June (autumn to early winter), dropping off in August (mid-winter) and reaching a minimum in October (spring). This strong temporal pattern was mainly driven by small and large holes within the lateral tissue and, to a lesser extent, by large holes in the lamina. The only difference between June and April was a higher number of large holes in June, likely a result of ‘wounding growth’ of many small holes in April (abundant small holes in April propagating into larger holes in June). This overall high number of wounds in early winter could be the consequence of accumulation of wounds over time due to relatively low growth during this period (Kirkman 1984; Kirkman 1989), increasing the exposure time of kelp tissue to damage. This accumulation of wounds has previously been shown to be associated with higher degradation of aged kelp tissue and a general decrease in toughness (Norderhaug et al.

2003; Molis et al. 2010). Wound accumulation could also constitute a natural seasonal senescence process in late austral autumn, when growth is inhibited by high temperature. Indeed, past research from south-western Western Australia has documented severe reduction in individual biomass in March to July (around 40 to 50% losses) (Kirkman 1984; Kirkman 1989). Furthermore, grazing rates are generally very low in this system and decrease with increased wave action (Vanderklift et al. 2009); the seasonal pattern found here is, therefore, unlikely to be driven by grazers (we rarely found grazers associated with wounds). However, other studies have found herbivores such as sea urchins (Tegner et al. 1995), mesograzers (Duggins et al. 2001; Krumhansl and Scheibling 2011b), or fishes (Taylor and Schiel 2010) to be important wound generators. Our data suggest that wounds accumulate over time, that highly wounded individuals are likely to be ‘weeded out’ during storms and that wave exposure appears to be much less important than season in generating wounds.

2. 5. 2 Biomechanical tests

Our hypothesis that even small wounds would influence tissue biomechanical properties was supported. The tensile tests confirmed that tissue properties were significantly impacted with a loss of strength at breaking, extensibility, stiffness and toughness of up to 82, 57, 53 and 92%, respectively. Previous studies have demonstrated similar impacts of simulated wounds on kelp tissue (Biedka et al. 1987; Mach et al. 2007). Our tests showed that kelps like *Ecklonia radiata* are highly extensible and generally compliant with a low breaking strength, as documented for other macroalgae (Carrington et al. 2001; Denny and Gaylord 2002; Pratt and Johnson 2002). Because of these material properties, macroalgae are susceptible to propagation of small initial damages (Denny et al. 1989; Mach et al. 2007). Moreover, the type of wounding and its position had clear implications for the biomechanical properties. As expected, a cut on the edge resulted in the most dramatic effects. When kelps are wounded by cuts, crack propagation occurs easily and typically causes tissue breakage (Denny et al. 1989; Mach et al. 2007). Therefore, holes or cuts on the edge of the tissue are likely to cause the substantial loss of laterals associated with the part of lamina being torn off, as observed for some of the kelp sampled. Previous studies have shown that wounding can increase tissue loss and therefore decrease plant biomass (Toth and Pavia 2006; Krumhansl et al. 2011; Krumhansl and Scheibling 2011a) without affecting overall survival. However, the

response might be slightly more complex with several factors interacting. Indeed, our study did not take into consideration the repetitive loading characterizing hydrodynamic wave forces. Interestingly, Mach et al. (2007) found that repeated loading by sub-lethal force eventually caused complete failure of tissue by fatigue. However, it is also possible that fatigue can be countered by wound-healing and induction of increased strength and toughness as demonstrated for other kelp species (Lowell et al. 1991; De Wreede et al. 1992; Lüder and Clayton 2004), whereby wounding ultimately minimizes the risk of breakage.

Overall, we found that kelps were highly wounded in April to June before the peak of storm-generated waves in winter (July to August), with a high number of small holes within the lateral tissue. Additionally, we showed that simulating wounding significantly decreased tissue break forces and the extensibility of *Ecklonia radiata*. It has been shown that wave-swept algae, typically, are ‘mechanically over-designed’ (Denny 2006; Mach et al. 2007) and that they can cope with extreme drag forces. However, we demonstrated that even small individual occurrences of tissue damage can reduce kelp material properties dramatically and lead to breakage at much lower-than-expected hydrodynamic forcing. This could have severe consequences for the fitness and survival of kelps, making them more susceptible to wave force. However, wounds may also increase pruning rates, resulting in decreased total kelp biomass and thereby also decreased drag. Similarly, grazing damages and associated wounds have been found to increase kelp erosion and consequently decrease individual kelp biomass (Black 1976; Krumhansl and Scheibling 2011a). Black (1976) suggested this similar paradoxical beneficial function of reducing drag and increased survival for an intertidal kelp, *Egregia menziesii*. Previous research in the same region (Kirkman 1984; Kirkman 1989; Wernberg and Vanderklift 2010) found a strong temporal growth pattern with a decrease in individual kelp biomass from March to July (autumn to winter). More specifically, Wernberg & Vanderklift (2010) investigated how seasonal growth influenced morphological variation in *E. radiata* and suggested that low growth and high erosion during the autumn to winter period leads to a minimum kelp individual biomass coinciding with the peak wave period. This reduction in biomass, via wounding-mediated erosion, reduces hydrodynamic drag forces and may also reduce dislodgement, resulting in increased survival during peak wave action. The net result of

wounding-induced biomass pruning may thereby, paradoxically, lead to an increase in kelp survival during winter storms. Simultaneously, the resulting increase in detrital supply to adjacent habitats results in higher trophic connectivity within the coastal system during this period of peak wave action. Interestingly, climate-change modelling generally predicts an increase in storm frequency and intensity (Emanuel 2005), and the ecological implications of wounding, pruning, increased survival of pruned kelps and kelp detritus export could therefore become even more important in the future.

2.6 Acknowledgements

TdB was funded through an ECU postgraduate award. Additional funding was obtained from the Western Australian Marine Science Institution (TdB) and The Australian Research Council (TW). We thank J. Godefroy for field and laboratory assistance, and P. Lavery and S. Bennett for comments on the manuscript.

CHAPTER 3

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

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Key words: kelp bed, *Ecklonia radiata*, Australia, trophic connectivity, spatial subsidy, detrital production, erosion, dislodgement

The work contained in this chapter is in review as:

de Bettignies T, Wernberg T, Lavery PS, Vanderklift MA, Mohring M Contrasting mechanisms of dislodgement and erosion contribute to production of kelp detritus.

3. 1 Abstract

We quantified simultaneously dislodgement and erosion for a dominant kelp species (*Ecklonia radiata*) over one year, 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 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

3. 2 Introduction

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 to 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 to 2500 g C m⁻² year⁻¹ (Mann 1973), rates which rival the most productive terrestrial ecosystems, including tropical rain forests (up to 1500-1700 g C m⁻² year⁻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, like 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 subsidises a large variety of habitats, including beaches (Colombini and Chelazzi 2003), intertidal rocky shores (Bustamante et al. 1995), distant reefs (Vanderklift and Wernberg 2008), submarine canyons (Vetter 1994), seagrass beds (Wernberg et al. 2006), and small islands (Polis et al. 1997).

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 2011a). 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 2011a), 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 ten 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 the hypothesised physical abrasion of kelp tips during high wave activity, 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 2011a), 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 (Reed et al. 1997; 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 hypothesised that erosion rate will peak at the same time.

Accumulations of beach-cast kelp on the shore are frequently comprised 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 fuelling this coastal detrital pathway. Because the observations of drift-kelps usually coincide with storms (Seymour et al. 1989; Filbee-Dexter and Scheibling 2012), it is generally recognised 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 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 one year for nine subtidal reefs. Furthermore, we test how well three hypothesised 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.

3.3 Materials and methods

3.3.1 Study site characteristics

South-western Australia is strongly influenced by waves, both swell and wind-generated waves, but dominated by oceanic swell from the west and south-west (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° 48' 18" S, 115° 42' 11" E), which comprises a mosaic of different habitats (reefs, seagrass meadows, sand) at relatively shallow depth (<15 m deep). Nine subtidal reefs (8-11 m deep), with dense kelp beds (6 to 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 9 reefs for each season (autumn, winter, spring 2010 and summer 2011) over one year. In south-western 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 do not affect the kelp beds (Vanderklift and Wernberg 2008).

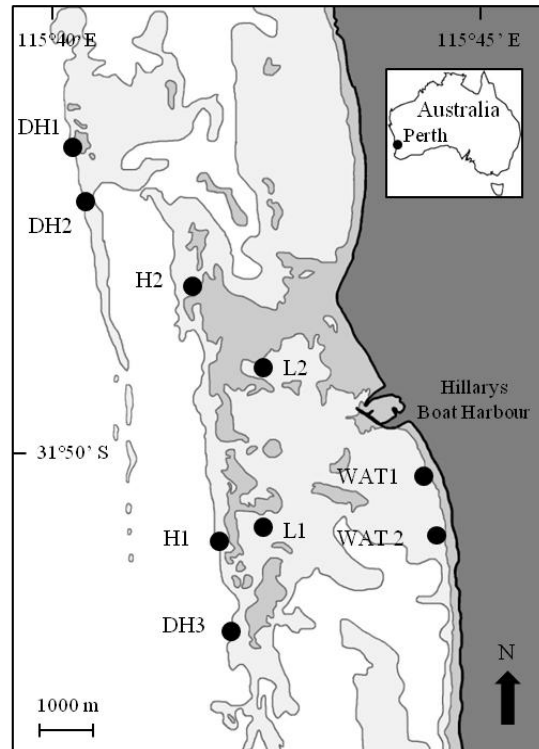


Figure 1 - Map of Marmion indicating the location of the 9 sites included in this study. The grey scale shows the bathymetry, depth 0 to 5 m in light grey and 5 to 10 m darker. WAT1, WAT2, L1, L2, H1, H2, DH1, DH2 and DH3 are the study sites. Inset shows location of Marmion.

3. 3. 2 Biomass accumulation

Biomass accumulation (=primary productivity) was measured every 3 months for 15 kelps at each site, using the traditional hole-punch method (Mann and Kirkman 1981). Individual kelps were punched with 2 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 kelp⁻¹ day⁻¹) as $BA = X.FW/5T$, where X is the thallus extension (cm), FW is 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 (T. Wernberg unpubl.

data, mean of 250 kelps from 25 sites across southwest Australia) and 2.78 DW:C (35% carbon of dry weight for *Ecklonia radiata* in the same region (Atkinson and Smith 1983)).

3.3.3 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 1981) 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 4 reefs (2 out of 4 plots at each reef, $n = 120$ kelps) were double-tagged to test for tag loss. After a three-month trial, 100% of the kelp recovered had double tags, indicating that tag loss was non-existent. Every three months, 4 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 3 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} , the mean individual biomass ($n = 15$) of adult kelp at the tagging; T , the duration in days; K , the number of adult kelps within the circular plot; A , the area of the circular plot of 1 m radius ($A = 3.14$ m²); and N is the number of kelp tagged within the plot ($n = 15$). The 4 plots were then averaged to get a single value per reef for each season.

3.3.4 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 5cm; 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 twelve 5 cm-segments of each thallus were weighed (6 sections working progressively upward from the base and 6 downwards 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 $> 60\text{cm}$ (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 (Mann and Kirkman 1981). 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 2 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 2 times. The erosion was estimated for each combination of reef x time ($n = 36$) as:

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

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

The rate of detrital production from erosion (DP_E , $\text{g m}^{-2} \text{d}^{-1}$) 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 , the duration in days; K , the number of adult kelps within the circular plot; and A , the area of the circular plot of 1 m radius ($A = 3.14 \text{ m}^2$).

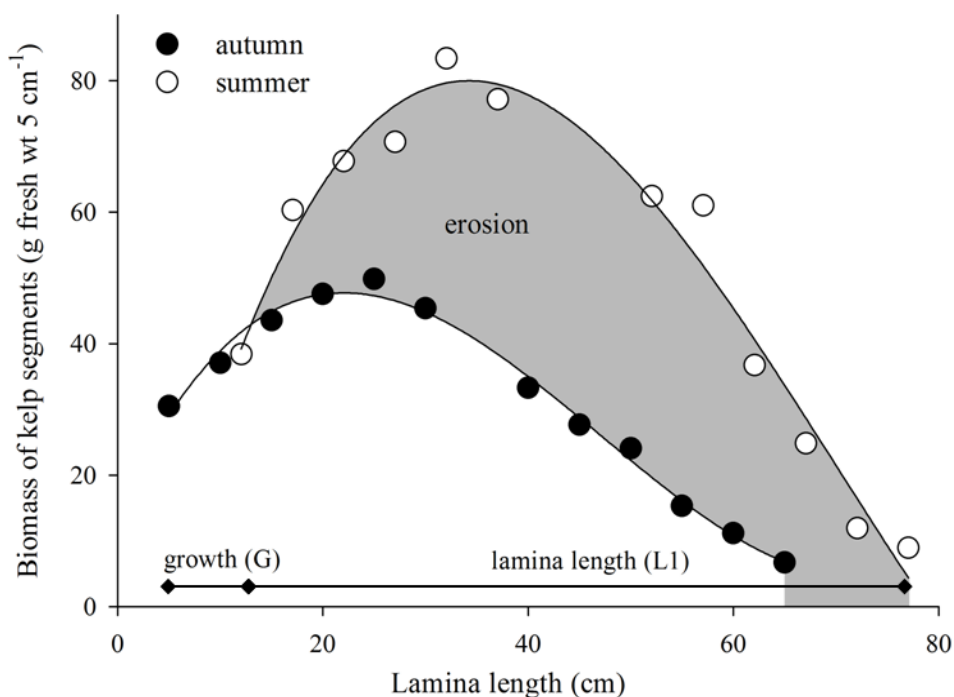


Figure 2 - Diagram representing the erosion as the area between the 2 biomass profiles from 2 different times (data used from reef DH1, to calculate autumn erosion with profiles of late summer and late autumn 2010). Each dot (black or white) represents the average weight of the different 5 cm segments 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.

3. 3. 5 Drivers of kelp detrital production

To test for possible relationships with potential drivers of detrital production, erosion and dislodgement were regressed against temperature, water velocity and kelp fecundity.

Temperature

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

Water velocity

Water velocity at the seafloor was calculated using the recognised and tested numerical model for the region, the simulating waves nearshore (SWAN) model (Booij et al. 1999) (Simulating WAVes Nearshore, Booij et al. 1999). SWAN was run for the period

March 2010 to February 2011 within the 30 x 30 m high resolution grid of the model domain, encompassing 161.78 km² 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 Rottneest wave buoy (Department for Planning and Infrastructure-Western Australia, located 20 km south-west 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 (U_{bot95}) at each site for each season.

Kelp fecundity

Kelp fecundity was measured two times during each season. Four thalli were harvested for 6 of the 9 reefs (L1, L2, H1, H2, DH1, DH2, DH3; Fig. 1) and kelp fecundity determined as zoospore release density (Mohring et al. 2012). From each thallus, ten 27 mm diameter discs of tissue (total 11451.1 mm²) were punched from the central lamina and placed in a cup to facilitate zoospore release. After 20 minutes, one 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 8 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 x time(season)), as an index of kelp fecundity.

3. 4 Results

3. 4. 1 Biomass accumulation, erosion and net productivity

Biomass accumulation was highest in spring 2010 (3.84 ± 1.53 g Fresh wt kelp⁻¹ d⁻¹, mean, SD), 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 and erosion led to marked temporal differences in net productivity (BA-E, Fig. 3c), with negative (-3.93 ± 1.61 g Fresh wt kelp⁻¹ day⁻¹) and positive ($+3.15 \pm 1.32$ g Fresh wt kelp⁻¹ day⁻¹) peaks in autumn and spring, respectively. In winter and summer, the differences between

biomass 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).

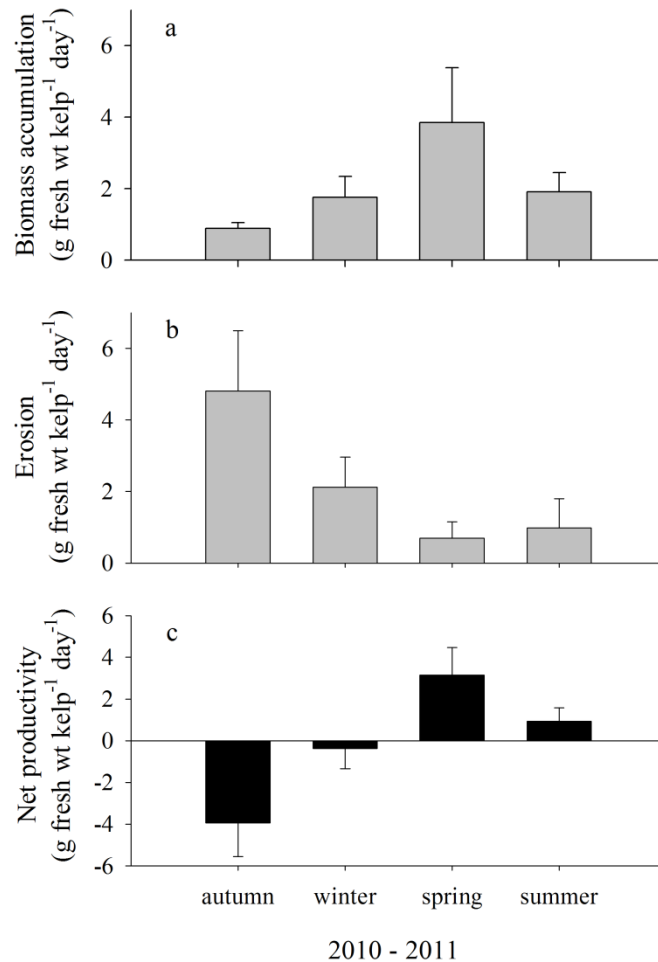


Figure 3 - Seasonal variation in individual (a) biomass accumulation (BA); (b) erosion (E), and (c) net productivity (BA-E) (mean and SD across the 9 sites).

3. 4. 2 Dislodgement and erosion

Kelp density did not change during the study period, with adult density between 7 to 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 mostly 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 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). Kelp detritus production through dislodgement was constant over the year (mean \pm SD = $\sim 4.5 \pm 2.8$ g Fresh wt m⁻² d⁻¹) whereas the detrital production via erosion peaked in autumn 2010 ($\sim 40 \pm 15$ g Fresh wt m⁻² d⁻¹), decreased but remained high in winter (14.5 ± 6.3 g Fresh wt m⁻² day⁻¹), and then fell to similar production rates as dislodgement in spring and summer (Fig. 4e). Since 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 because the kelp density was constant over the year, changes in this detrital production were explained only by changes in individual erosion rate (Fig. 4d).

The average annual detrital production, for the 9 sites, was $7391 (\pm 2762)$ g Fresh wt m⁻² yr⁻¹, of which $1593 (\pm 758)$ g Fresh wt m⁻² yr⁻¹ was derived from dislodgement and $5798 (\pm 2081)$ 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 more than 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.

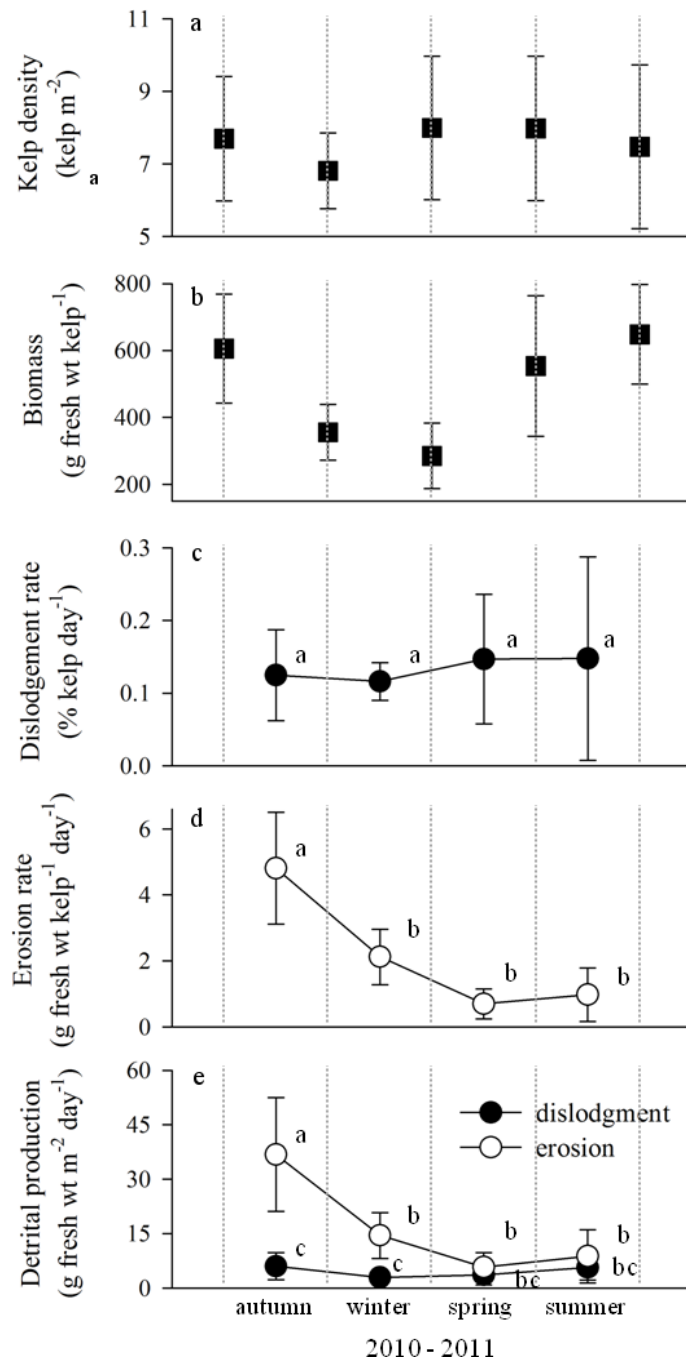


Figure 4 - (a) Kelp density, (b) individual kelp biomass, (c) dislodgement rate, (d) individual erosion rate, and (e) detrital production generated through dislodgement and erosion (mean and SD across the 9 sites). Letters above symbols indicate the significant differences between seasons and mechanisms (Analysis of Variance, $p < 0.05$).

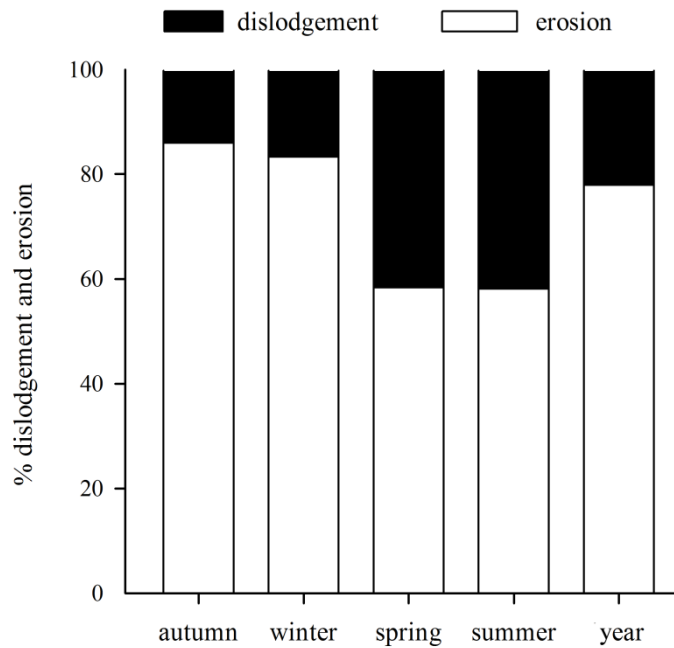


Figure 5 - Relative proportions of the two mechanisms of kelp detrital supply (dislodgement and erosion) for every season in 2010-2011 and for the whole year.

3. 4. 3 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) as maximum erosion occurred around 22°C and not at the maximum temperature recorded (>24°C, Fig. 6c). However, there was a strong positive relationship between kelp fecundity and erosion rate (Fig. 6d), with the kelp fecundity index explaining 76% of the variation in erosion (Fig. 6d).

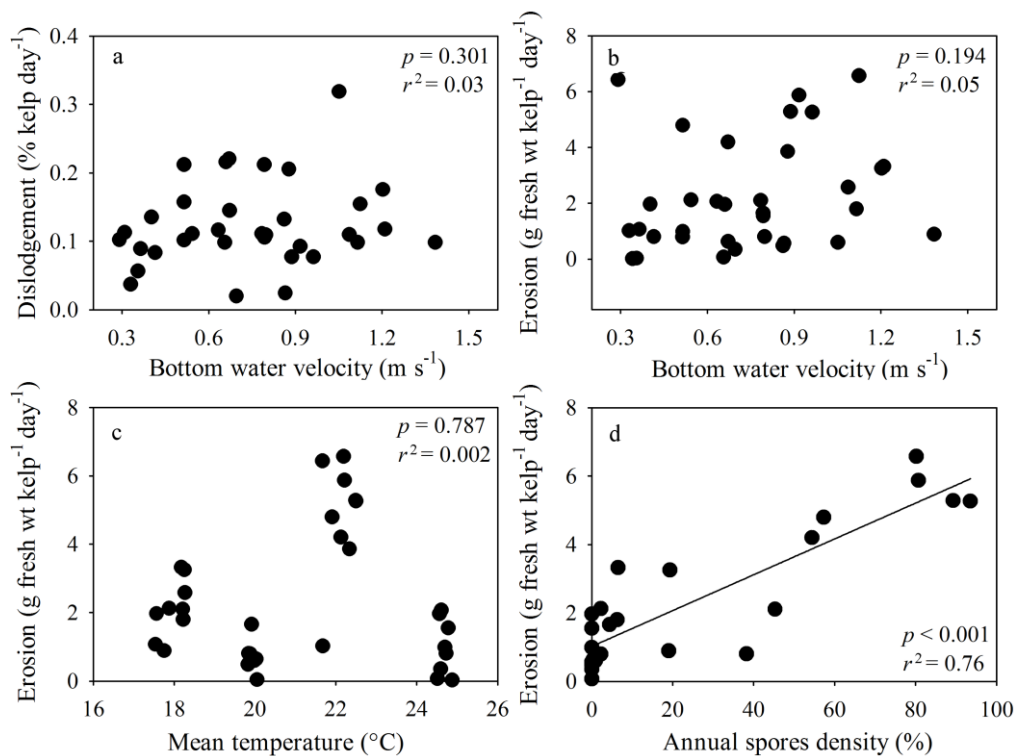


Figure 6 - Relationship between detrital production mechanisms (dislodgement and erosion) and measures of wave exposure, temperature, and kelp fecundity. (a) dislodgement vs. average bottom water velocity; (b) erosion vs. average bottom water velocity; (c) erosion vs. temperature and (d) erosion vs.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

3.5 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 $40 \text{ g Fresh wt m}^{-2} \text{ d}^{-1}$ of kelp detritus (up to $50 \text{ g Fresh wt m}^{-2} \text{ d}^{-1}$), making a considerable contribution to the whole coastal system (4 to 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, 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 to 538 g C m⁻² yr⁻¹) was in the same range as reported for *Ecklonia radiata* in New-Zealand (~ 450 up to 645 g C m⁻² yr⁻¹, Novaczek 1984), a mixed stand of *Saccharina longicuris* and *Laminaria digitata* in Nova Scotia (150 to 513 g C m⁻² yr⁻¹, Krumhansl and Scheibling 2011a), 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 to 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; Wernberg and Vanderklift 2010). Therefore, we propose that the reduction of biomass through erosion 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 reduce sub-canopy light (Toohey et al. 2004; 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 2011a; Krumhansl and Scheibling 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 2011a). Instead, we hypothesise that the peak in kelp erosion in autumn was largely facilitated by zoospore release, as 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). While 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 to 400 holes per thallus, de Bettignies et al. 2012a), and that simulation of equivalent wounding led to kelp fragmentation at much lower-than-expected hydrodynamic forces (de Bettignies et al. 2012a). Similarly, Krumhansl et al. (Krumhansl et al. 2011; Krumhansl and Scheibling 2011a) 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 (~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 emphasise 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, 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.

3.6 Acknowledgements

We are grateful to P. Bouvais, A. Turco, P. Van Dyk, J. Godefroy, K. Inostroza, G. Mare, B. Debeuf, H. Dunham, and P. Buchanan for assistance with the diving and boating. J. Gunson and G. Symonds (Commonwealth Scientific and Industrial Research Organisation) are acknowledged for providing wave data from the Simulating WAVes Nearshore wave model. TdB was funded through an Edith Cowan University postgraduate award. Additional funding was obtained from the Western Australian Marine Science Institution (TdB) and The Australian Research Council (TW).

CHAPTER 4

Disturbance in kelp forest and susceptibility of kelps to wave-driven dislodgement

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Key words: kelp bed, *Ecklonia radiata*, Australia, dislodgement, wave disturbance, storm, biomechanics, drag force, break force

The work contained in this chapter is close to submission as:

de Bettignies T, Wernberg T, Lavery PS, Vanderklift MA, Gunson J, Symonds G.
Disturbance in kelp forest and susceptibility of kelps to wave-driven dislodgement

4.1 Abstract

Dislodgement of canopy-forming kelp is an important ecological process which can alter the biodiversity and functioning of reef systems and increase production in coastal systems adjacent to reefs. Our current understanding is that winter storms tear kelps from reefs once hydrodynamic forces exceed kelp attachment or tissue strength - a threshold response which implies a pulsed relationship between wave forces and dislodgement, peaking in winter. Here, we challenge this understanding by showing how kelp phenology decouples susceptibility to dislodgement from seasonal patterns in wave forces. We measured kelp dislodgement rates and hydrodynamic forces at 9 reefs over 2 years. Contrary to expectation, we found relatively low and constant dislodgement for all reefs (mean per season \pm SD, 13% \pm 2.8) in spite of a strong temporal pattern in wave-action and extreme water velocities (winter peaks up to 3 - 4 m s⁻¹). A biomechanical model, based on the balance between kelp attachment strength and hydrodynamic drag forces, demonstrated that severe reduction in individual kelp biomass towards winter (> 50% decrease for all sites) minimized drag forces and made the kelps less susceptible to peak flow during storms, thus allowing individuals to survive storm velocities over 3 - 4 m s⁻¹. We conclude that, the timing of susceptibility to disturbance, through the seasonal reduction of individual kelp biomass to coincide with times of peak flows, is critical to the dynamics of kelp dislodgement and survival. We propose that phenological processes maintain many kelp beds in a higher degree of equilibrium with hydrodynamic forces than previously believed. This is likely to have implications for kelp ecosystems as climate change and climate variability disrupts the timing, frequency and magnitude of storms.

4.2 Introduction

Disturbance shapes ecosystems by providing a framework upon which ecological processes and interactions between species occur (Pickett and White 1985). Most notably, disturbances that affect foundation species have cascading impacts on ecosystem structure and function (Hughes 1994; Ellison et al. 2005; Halpern et al. 2007). Kelps are foundation species and loss of kelps generally lead to a shift in community structure (Graham 2004; Byrnes et al. 2011; Moy and Christie 2012; Wernberg et al. 2013). Kelps inhabits one of the most mechanically challenging environments on earth, where wave forces are severe, and the risk of disturbance

through dislodgement of individual kelps is great (Seymour et al. 1989; Dayton et al. 1992; Graham et al. 1997).

Direct and indirect inferences of kelp dislodgement have emphasized the dynamic nature of kelp forests, constantly being reshaped by disturbances (Dayton et al. 1992). In temperate regions, large waves associated with storms usually dominate in winter and often tear off kelp from the reef, reducing their abundance (Graham et al. 1997). Wave driven dislodgement of kelps in winter has been directly observed for large kelp species such as *Macrocystis pyrifera* (Seymour et al. 1989; Dayton et al. 1992; Graham et al. 1997). Inferences of wave driven kelp dislodgement include the occurrence of patches devoid of kelp at wave-exposed reefs (Wernberg and Connell 2008; Thomson et al. 2012) and the accumulation of drift kelps in adjacent habitats directly after winter storms (Colombini and Chelazzi 2003; Filbee-Dexter and Scheibling 2012). Collectively, these observations suggest that dislodgement occurs as a threshold response to wave energy which, by definition, is triggered when the force exceeds the capacity to resist the perturbation (Romme et al. 1998; Turner and Dale 1998). From a theoretical perspective, the dislodgement of kelps, and the threshold response, can take one of several forms in response to the magnitude of perturbation (Fig. 1). Either (1) pulses of kelp dislodgement are determined by storm intensity (i.e. when water velocity and the resulting force exceeds the strength of kelp attachment, Fig. 1a) or a disproportional pulse accounting for the majority of kelp dislodgement when the first significant storm of the season occurs (similar to “First Flush Theory” of Lee et al. 2004) (Fig. 1b). The “first flush” scenario will occur when a large portion of individuals weakly attached to the reef are dislodged during the first major storm of the season, leaving only individuals that are firmly attached to the reef, which will resist the subsequent storms. Both scenarios are hypothesized to happen in winter, a period of frequent severe storms in temperate regions. Another scenario implies that kelp attachment remains greater than forces generated by storms, and therefore kelp dislodgement stays low and constant throughout the year (scale-independent response, Fig. 1c).

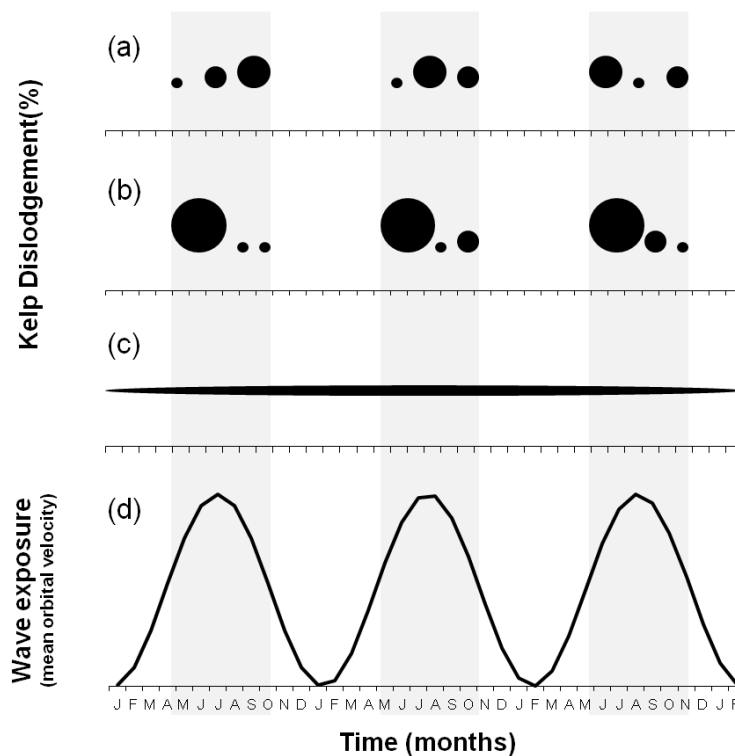


Figure 1 - Theoretically possible kelp dislodgement scenarios in relation to water velocity. (a) Pulsed dislodgement above a threshold perturbation, (b) First flush scenario, with large dislodgement at first perturbation exceeding the threshold, and subsequent lower rates, (c) low and constant dislodgement of kelp independent of the intensity of perturbation, (d) modelled average bottom water velocity, with peak in the winter months. The circular black shapes in (a), (b) and (c) represent the dislodgement of kelp and their sizes are proportional to the quantity of kelp dislodged.

Dislodgement and survival of sessile organisms such as macroalgae can be investigated through a mechanistic approach which considers the dislodgement process a balance between the hydrodynamic forces experienced by the organism, and the force required to break the organism off (break force), which in turn is related to kelp tissue properties and attachment to the substrate (Gaylord et al. 1994; Denny and Gaylord 2002). The different forces acting on a sessile organism are drag, lift and acceleration, however the major force exerted on subtidal macroalgae is the hydrodynamic drag force (Denny and Gaylord 2002) which represents its resistance to the fluid movement. This approach has been widely used in studies of algae to answer a variety of ecological questions such as survival mechanisms and adaptation to water motion (Blanchette 1997; Thomsen 2004; Boller and Carrington 2006a).

In this study, we examined in detail the relationship between wave-generated perturbation to kelp beds and the nature of the ensuing disturbance. More specifically, we tested if the relationship between peak water velocity and magnitude of kelp dislodgement best resembled pulsed (Fig. 1a), first flush (Fig. 1b) or constant (Fig. 1c) scenario. To address this main objective we first characterised maximum *in-situ* water velocities with different methods (wave model and wave gauges) at each season during 2 years and during the most severe storm; we measured kelp dislodgement for 9 reefs over a gradient of wave exposure and related it to water velocities to examine which scenario kelp dislodgement follows. Finally, we explained the causes of this relationship with a biomechanical model which estimated the seasonal, spatial and monthly risk of kelp dislodgement.

4.3 Materials and Methods

4.3.1 Study site

The study was conducted in Marmion Lagoon, 20km north of Perth, south-western Australia (Fig. 2). This region is strongly influenced by waves, both swell and wind-generated waves. In the austral summer (December-February), strong sea breezes generate moderate waves (up to 2 m) whereas in the austral winter (June-August), frequent storms generate large swell (up to 8-9 m, Searle and Semeniuk 1985; Lemm et al. 1999). The configuration of the coastline dissipates hydrodynamic forces, mainly due to the presence of successive lines of limestone reefs running parallel to the shore (Fig. 2). These features generate a gradient of wave exposure (Phillips et al. 1997; Smale et al. 2011; Thomson et al. 2012) and 9 sites (depth range 8 to 10 m) were selected along this gradient (Fig. 2).

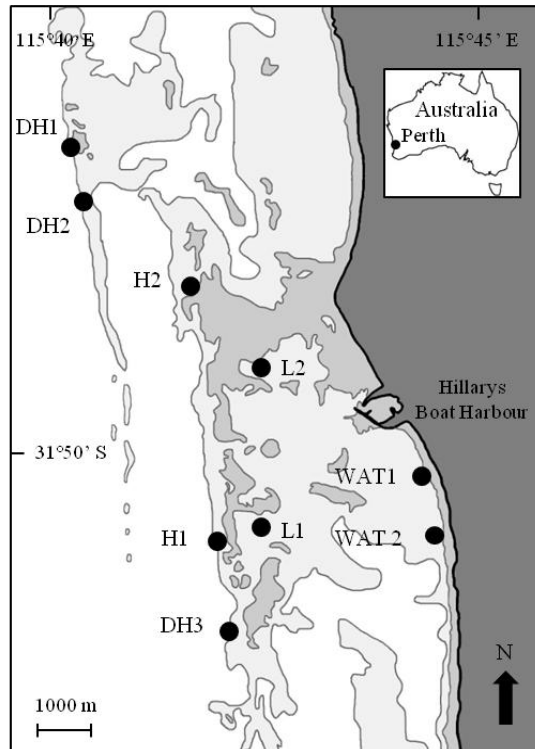


Figure 2 - Map of Marmion Lagoon indicating the location of the 9 sites included in this study. The grey scale shows the bathymetry, depth 0 to 5m in light grey and 5 to 10m darker

4. 3. 2 Peak water velocities

Wave Model

Water velocity at the seafloor was estimated using the SWAN model (Simulating WAVes Nearshore, Booij et al. 1999). SWAN is a third generation spectral wave model used to obtain estimates of wave parameters in coastal areas which has been constructed specifically for the Marmion Lagoon area. Drawing on local bathymetry and oceanography it simulates wave generation, propagation and dissipation across the shallow coastal area when forced at its western boundary by daily-averaged wave height, period and direction obtained from an oceanic wave buoy (located 20 km south-west of the study area). The SWAN-predicted wave heights compared favourably with daily-averaged wave height measured by an AWAC instrument located in Marmion lagoon for 2007-2008 ($r^2 = 0.80$, see Annexe 1). The SWAN model was run for the period from September 2008 to September 2011, over a 18 km (north-south) by 11 km (east-west) grid encompassing all of Marmion Lagoon, with grid cells of 30 m \times 30 m. The model produced wave parameters for each of the grid cells for each day. We extracted the

orbital water velocity at the bottom (U_{bot} , m s^{-1}) calculated from the significant wave height, period and wavelength (Holthuijsen 1997) and obtained the maximal values of U_{bot} for each reef \times time combination ($U_{\text{bot}}^{\text{max}}$, $N = 72$), and calculated maximum individual water velocity as $U_{\text{max}} = 2 \times U_{\text{bot}}^{\text{max}}$ (Holthuijsen 1997).

In-situ wave gauges

Within the kelp bed at each reef, a 3 m diameter area was cleared of all macroalgae for the deployment of an array of hydrodynamic recorders consisting of dynamometers and gravitational data loggers. The dynamometers measures maximum drag force through drag in a sphere, which can be converted maximum water velocity using the calibration curves of Bell & Denny (1994). The gravitational loggers were mounted on a flexible bar with blades to continuously measure horizontal acceleration (Evans and Abdo 2010; de Bettignies et al. 2013), which was converted to water velocity from a previous calibration using an Acoustic Doppler Velocimeter (ADV). Three dynamometers and two accelerometers were deployed in each array for one week in winter (July 2010), a period that encompassed a substantial storm event (wave rider buoy: 6 to 7 m averaged wave height at 10 - 14 sec period, offshore of Marmion Lagoon, Fig. 5a).

4. 3. 3 Dislodgement rate

At each of the nine reefs, four circular plots (2 m diameter) were established and within each plot 15 adult kelps (stage 3, Kirkman 1981) with distinct holdfasts (no fused holdfasts, Wernberg 2005) were tagged around the stipe with cable ties inserted into fluorescent latex surgical tubing ($N = 540$ kelps). A 50% subset of all kelps at 4 reefs (2 out of 4 plots at each reef, $N = 120$ kelps) were double-tagged to test for tag loss. After a three months trial, 100% of the kelp recovered had double tags, indicating that tag loss was negligible. Every three months, 4 new randomly located plots ($n = 60$ kelps per reef) were set up on each reef. For each plot, the tagged kelps were relocated and counted; dislodgement was inferred from an inability to relocate a tagged individual. Each plot was searched and counted 3 times to ensure all surviving kelps were located and avoid any over-estimation of dislodgement. For each season, the kelp dislodgement rate from a plot was defined as the percentage of tagged kelps lost (from the 15 kelps tagged) after 3 months. Dislodgement rate of the nine reefs was also measured during the most severe storm of the study period.

4. 3. 4 Biomechanical dislodgement model

A biomechanical dislodgement model, based on the balance between the hydrodynamic force exerted on a kelp thallus (drag force; F_{drag}) and the force required to break the thallus (strength of the tissue and/or attachment to the reef; break force; F_{break}), was used to evaluate the risk of dislodgement at different water velocities. According to this biomechanical relationship, dislodgement occurs when F_{drag} is greater than F_{break} .

Drag is the only quantitatively important hydrodynamic force on a non-buoyant subtidal kelp (Denny and Gaylord 2002). F_{drag} (Newton) can be derived from the standard empirical drag equation (Vogel 1984; Denny 1995):

$$F_{\text{drag}} = \frac{1}{2} \rho \times U^2 \times C_{\text{drag}} \times A \quad (\text{Equation 1})$$

where ρ is the density of seawater (1026 kg m^{-3}), U the water velocity (m s^{-1}), C_{drag} the drag coefficient (dimensionless) and A an area measure of the thallus (m^2). At high water velocities (over 2 m s^{-1}), drag can be predicted with A , the total area of the thallus and a coefficient of drag (C_{drag}) of 0.025 for *Ecklonia radiata* (de Bettignies et al. 2013). The total area was obtained from the biomass (wet weight, WW) by applying WW:AREA relationship found for adult kelps (de Bettignies et al. 2013). F_{break} was measured *in-situ* by pulling kelps off the reef with a *Pesola* dynamometer (Thomsen et al. 2004). These biomechanical break tests were performed on 60 kelps per reef: 30 in early winter (early June 2010) and 30 at the end of winter (early August 2010), from a subset of 4 reefs of different wave exposure (WAT1, L2, H2 and DH1).

First, the cumulative probability of dislodgement with increasing water velocity was calculated at these 4 reefs for early winter 2010. This was done by re-arrangement of the drag equation to output the water velocity required to dislodge a kelp individual (U_{break}):

$$U_{\text{break}} = \left[\frac{(2 \times F_{\text{break}})}{(C_{\text{drag}} \times A \times \rho)} \right]^{0.5} \quad (\text{Equation 2})$$

The dislodgement curves in winter were then obtained by estimating the cumulative frequency of dislodged kelp for theoretical water velocities with an increment of 0.5 m s^{-1} from 0 to 10 m s^{-1} (from F_{break} values in early August 2010, $N = 30$ per reef, at

WAT1, L2, H2 and DH1). The other dislodgement curves for spring, summer and autumn were obtained by re-calculating the U_{break} by assigning new total thallus area estimated from the thallus total area in winter multiplied by the percent different in biomass between seasons.

Subsequently, the dislodgement risk that wave induced water velocities impose on kelp individuals was investigated in detail (*R software version 2.15.2*). Drag forces were predicted from a combination of thallus biomass and water velocity measurements. Thallus biomasses were obtained from a 3 year data set (2009, 2010 and 2011) of monthly individual kelp biomass (M. Vanderklift, T. de Bettignies and T. Wernberg unpublished data, $N = 749$) and seasonal maximum water velocities (U_{max}) from the SWAN model for 3 sites with enough biomass and break force data available (i.e. L2, H2 and DH1). For each predicted drag force (each kelp thallus), a break force value was randomly generated from the normal distribution of break forces at each site (obtained with *R software version 2.15.2*). The Environmental Stress Factor (ESF), a measure of the resistance to detachment, was calculated as the ratio of break force to drag force for individual kelps (Johnson and Koehl 1994; Stewart 2006). When the $ESF \leq 1$, the kelp is dislodged from the reef. A second scenario was run with the maximum biomass maintained throughout the year, to look at the effect of change in biomass on the dislodgement pattern of kelp. The month with the maximum averaged biomass was applied to the other months and the ESF was calculated the same way as the original scenario.

4.3.5 Statistical analysis

To investigate the spatio-temporal pattern of kelp dislodgement, data were analysed by permutational analyses of variances (PERMANOVA) following two experimental designs, focusing on seasons and the most severe storm, respectively. The first experimental design included three factors: Year (random factor with 2 levels), Season (fixed factor with 4 levels, crossed with year) and Reef (random factor with 9 levels, crossed with Year and Season) and the second design included only one factor: Reef (random factor with 9 levels).

4.4 Results

4.4.1 Water velocities across the lagoon

Variation in model-generated $U_{\text{bot}}^{\text{max}}$ (Fig. 3) reflected the offshore-onshore gradient in significant wave height (combined with the wave period) and bathymetry. The $U_{\text{bot}}^{\text{max}}$ was lower in summer (0 to 0.5, up to 1 m s^{-1} for the most exposed part of the lagoon; Fig. 3b,f), intermediate in autumn and spring (larger areas up to 1 m s^{-1} ; Fig. 3a,c,e,g), and greater in winter with velocities between 1-1.5 m s^{-1} for most of the lagoon and reaching up to 2 to 2.5 m s^{-1} (Fig. 3d,h). Water velocity varied spatially over the study site particularly in winter with the two most offshore reef lines relatively exposed and then relatively lower water velocity zones, at the back of the mid-shore reefs (dark blue, Fig. 3d,h).

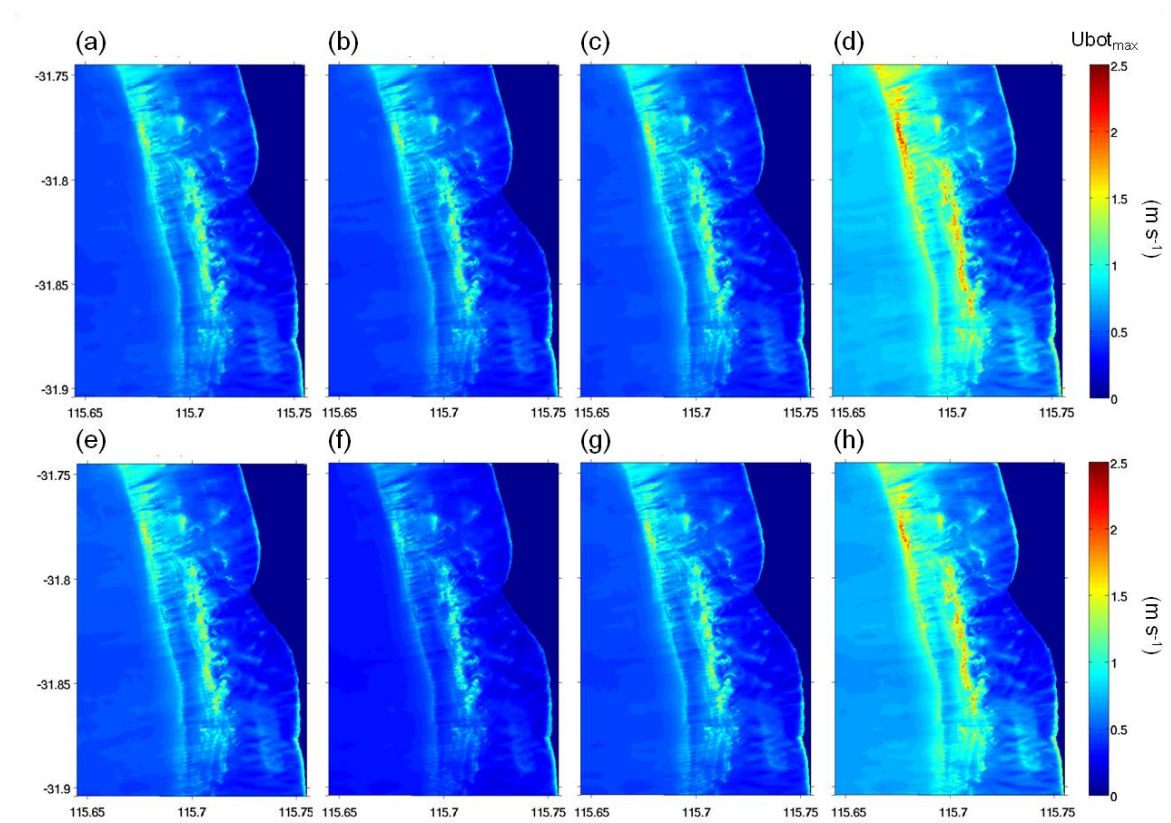


Figure 3 - Maps of maximum daily averaged water velocity for each season ($U_{\text{bot}}^{\text{max}}$ in m s^{-1}) generated by the SWAN model for the study period (spring 2009 to winter 2011): (a) spring 2009, (b) summer 2009-2010, (c) autumn 2010, (d) winter 2010, (e) spring 2010, (f) summer 2010-2011, (g) autumn 2011 and (h) winter 2011. The summer months are December, January and February; the spring months are September, October

and November; the autumn months are March, April and May; and winter months are June, July and August.

4. 4. 2 Kelp dislodgement vs. water velocity - season

Maximum bottom velocities of the 9 reefs (Fig. 4a) highlighted the strong seasonality in wave exposure from spring 2009 to winter 2011 (Fig. 3) with peak velocities in winter (Fig. 4a). However, the most protected reefs did not exhibit any significant increase in U_{\max} in winter (L2, WAT1 and WAT2; Fig. 4a). WAT1 and WAT2 always experienced $U_{\max} < 1 \text{ m s}^{-1}$; L2 experienced slightly higher U_{\max} , just over 1 m s^{-1} . U_{\max} increased farther offshore but there were no major differences in maximum values between the mid-shore outer reefs and the deep offshore reefs (H1, H2 vs. DH1, DH2, DH3; Fig. 4a). Their velocity ranges were between $1.5\text{-}2 \text{ m s}^{-1}$ in summer, $2\text{-}2.5 \text{ m s}^{-1}$ in spring and autumn, and up to $3\text{-}3.5 \text{ m s}^{-1}$ in winter (Fig. 4a).

In contrast to the strong seasonality in water velocities (Fig. 4a), the dislodgement rate did not increase in winter or for the most wave-exposed reefs (DH1, DH2, DH3, H1, and H2; Fig. 4b). Instead, winter 2010 had relatively low and similar dislodgement rates for the 9 reefs ($8\text{-}16\%$ kelps season^{-1} , Fig. 4b) and winter 2011 did not show any major differences from the other seasons. In general, kelp dislodgement rate varied from nearly 0% up to 30% , with an average of $13.4\% \pm 6.5$ ($N = 70$) kelps dislodged season^{-1} (Fig. 4b).

There was no relationship between maximum water velocity and kelp dislodgement rate when considering all combinations of reef \times season ($r^2 < 0.001$, $P = 0.954$, $N = 69$; Fig. 4c), and there was no peak in dislodgement rate for the highest water velocities in winter (Fig. 4a,b,c). The three-way factor PERMANOVA confirmed that the reef differences was negligible (Reefs, $P = 0.278$; Table 1) and indicated that seasonal patterns in dislodgement was not the same in each year (Year \times Season, $P = 0.012$; Table 1).

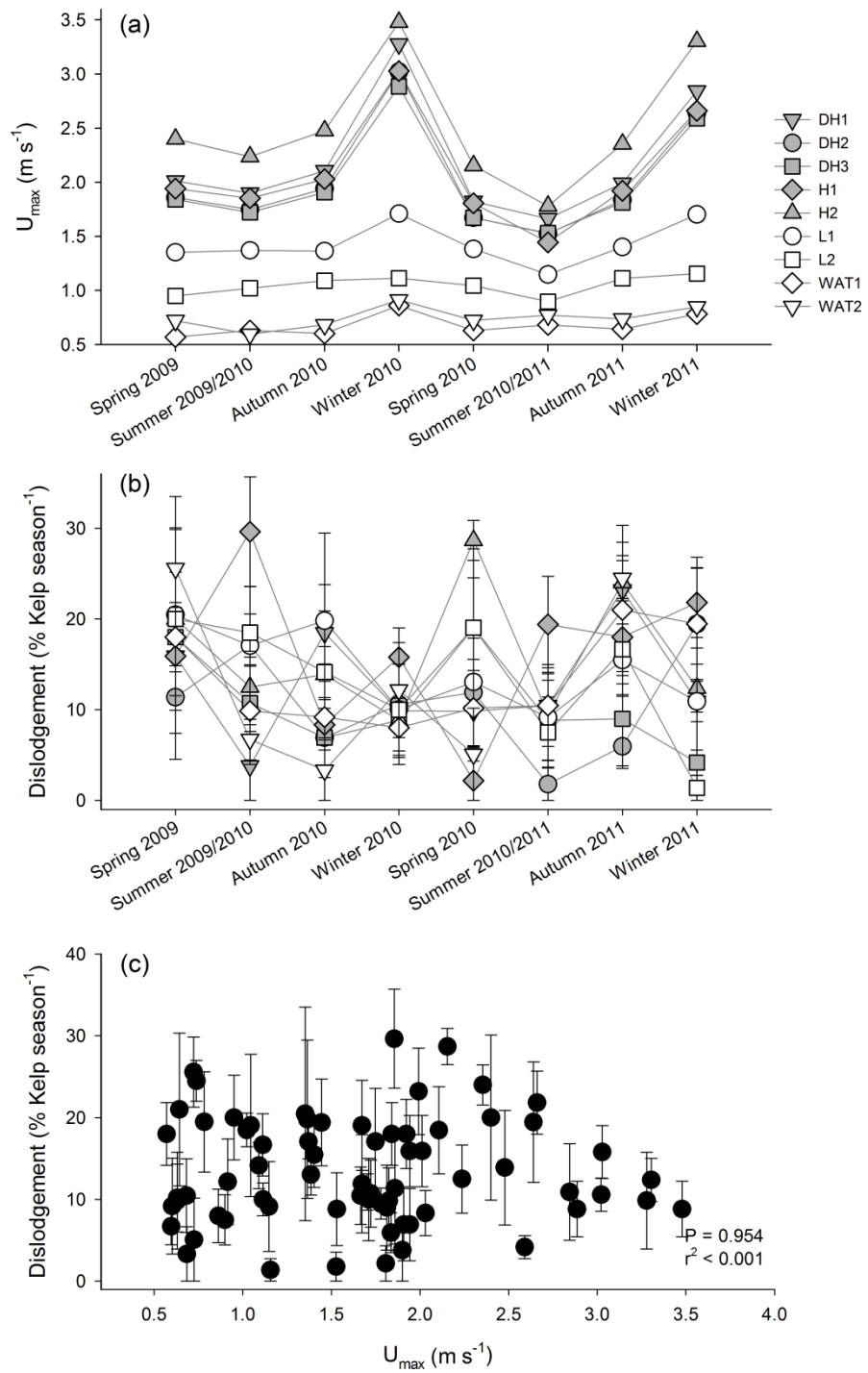


Figure 4 - Relationship between water velocities and kelp dislodgement rate. (a) Seasonal variation of water velocities at the 9 reefs, (b) seasonal variation of kelp dislodgement rate (mean and SE) at the 9 reefs and (c) response of kelp dislodgement rate (mean and SE) to increasing water velocity. Grey and white filled symbols (a, b) represent respectively the more exposed and more sheltered sites.

Table 1 - PERMANOVA analysis testing for differences in kelp dislodgement across seasons.

Source	df	MS	Pseudo-F	P
Year (Ye)	1	1.32E-3	0.15	0.710
Season (Se)	3	3.00E-3	0.56	0.839
Reef (Re)	8	1.39E-3	1.56	0.278
Ye x Se	5	5.66E-3	4.49	0.012
Ye x Re	8	8.94E-3	0.90	0.509
Se x Re	24	1.91E-3	1.51	0.170
Ye x Se x Re	22	1.26E-3	1.27	0.182
Residual	208	9.88E-3		

4. 4. 3 Kelp dislodgement vs. water velocity - during a storm

The storm monitored in July 2010 was the most severe during the 2-year study period (November 2009 to September 2011) with offshore waves up to 7 m high (averaged per hour, non directional wave data from the Rottnest wave buoy, Fig. 5a). The storm encompassed two discrete events: first a peak of 5.5 m wave height on 10th July 2010, followed by a calmer period with wave heights of ~3 m, and then a second peak, larger than the first one with waves up to 7 m high on 12th July (Fig. 5b). Water velocities were so severe that several of the wave gauges reached their limit. Due to the limited memory capacity of the HOBO G-loggers, the sampling period of the accelerometer encompassed the first storm peak only (Fig.5b, c). The values from the dynamometers (black dots, Fig. 5c) were however the maximum velocities recorded for the entire storm period. We did not get any results for site DH3 because the hydrodynamic gauges were not recovered.

Maximum water velocities estimated from the SWAN wave model (Fig. 4a) and measurements *in-situ* (Fig. 5c) were similar, up to 3-3.5 m s⁻¹ for the most exposed sites (H1, H2, DH1 and DH2; Fig. 5c) with few extreme peaks at 4 m s⁻¹ for H1 and H2 (see annexe 2).

The site, WAT2, was removed from the analysis because of sudden overgrazing by sea urchins (*Holopneustes sp.*) that ate the kelps during the same period (pers. obs.). In contrast to the seasonal kelp dislodgement rate, we found a positive linear relationship

between dislodgement rate and increasing water velocity during the storm ($r^2 = 0.52$, $P = 0.0044$, Fig. 6).

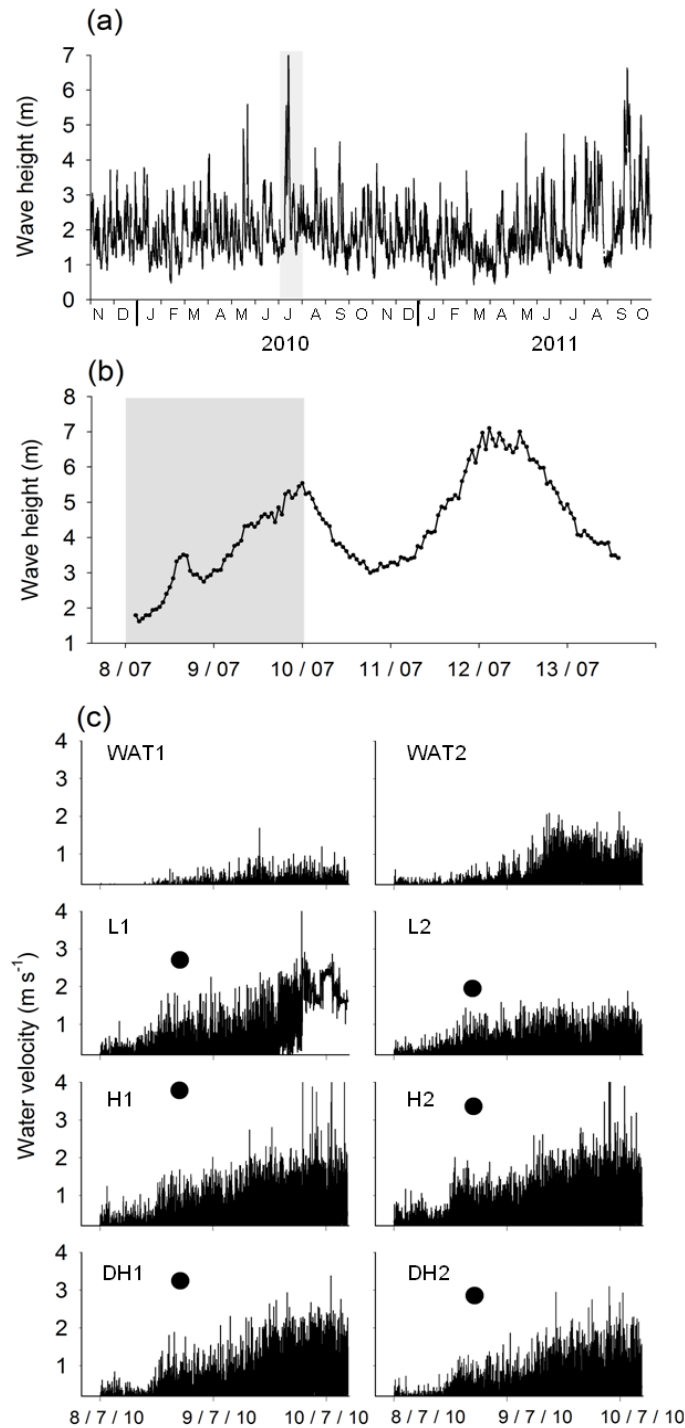


Figure 5 - Wave height and resulting orbital water velocity in kelp beds. (a) Significant wave height (averaged per hour) from the non directional wave data of the Rottnest Directional wave buoy (<http://www.dpi.wa.gov.au/imagery/19219.asp#Rottnest>). (b) Significant wave heights for a storm period in early July 2010. (c) Continuous

measurements of water velocity (30sec sampling rate, on 8 of the 9 reefs) calculated from gravitational loggers and black dots for results from maximum velocity recorders (mean), during the storm. The grey shaded areas in (a) and (b) indicate the period encompassed by measurements of water velocity in (c).

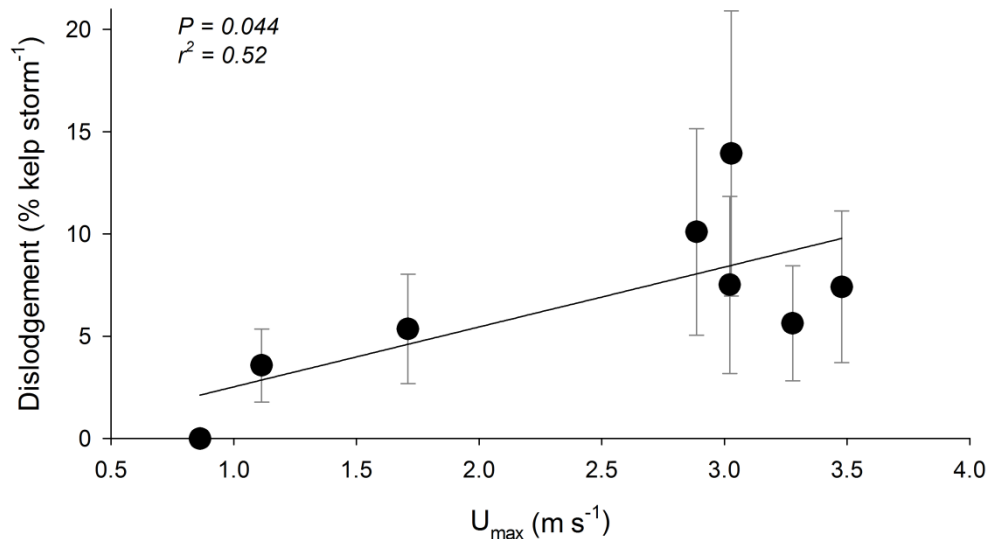


Figure 6 - Relationship between dislodgement (mean and SE) and water velocity during the most severe storm in winter 2010 with p and r^2 from the linear regression. Water velocity is the maximum estimate from the SWAN model for the corresponding reef.

4.4.4 Biomechanical model

Break force tests

There was no change over time in the attachment and tissue strength of kelp before and after winter ($P = 0.22$, Table 2). Break force differed between reefs ($P < 0.001$, Table 2), and this was driven by difference between the most onshore site (WAT1) against the other three reefs (L2, H2 and DH1; pair-wise tests, $P < 0.001$, Table 2). Kelps at WAT1 had lower break force (Mean \pm SD, 126.8 ± 55.0 N) than L2, H2 and DH1 (respectively $162.5 \text{ N} \pm 59.7$, $173.5 \text{ N} \pm 54.2$ and $174.5 \text{ N} \pm 50.5$). In subsequent models, break force measurements from different times were pooled for each reef.

Table 2 - Two-way PERMANOVA analysis testing for differences in kelp break forces between sampling Time and Reefs (both fixed factors).

Source	Df	MS	Pseudo-F	P
Time	1	47.66	1.46	0.220
Reef	3	333.30	10.26	0.0001
Time x Reef	3	24.15	0.74	0.526
Residual	234	32.49		

Pair-wise tests	
Groups	P
WAT1, L2	< 0.001
WAT1, H2	< 0.001
WAT1, DH1	< 0.001
L2, H2	0.296
L2, DH1	0.154
H2, DH1	0.712

Cumulative probability of kelp dislodgement with increasing water velocity

The first model predicted no kelp dislodgement in winter for velocities up to 3 m s⁻¹ for WAT1 and 4 m s⁻¹ for L2, H2 and DH1 (Fig. 7b). The significant variation of thallus biomass (proxy for total thallus area) throughout the year (decrease of ~50% in autumn-winter) led to a large shift of modelled dislodgement curves towards lower water velocities in spring and summer when the biomass was the largest (Fig. 7a,b). Maximum water velocities registered in winter will be critical for kelp at the most exposed sites (Fig. 7b, H2 and DH1) if they occur in spring or summer, which can result in 10 to 50% and 10 to 80% kelp dislodgement for H1 and DH1 respectively (Fig.7b). The model indicated that kelp at the most sheltered sites (WAT1 and L2) will not be impacted even if their biomasses remain at their maximum (Fig. 7b).

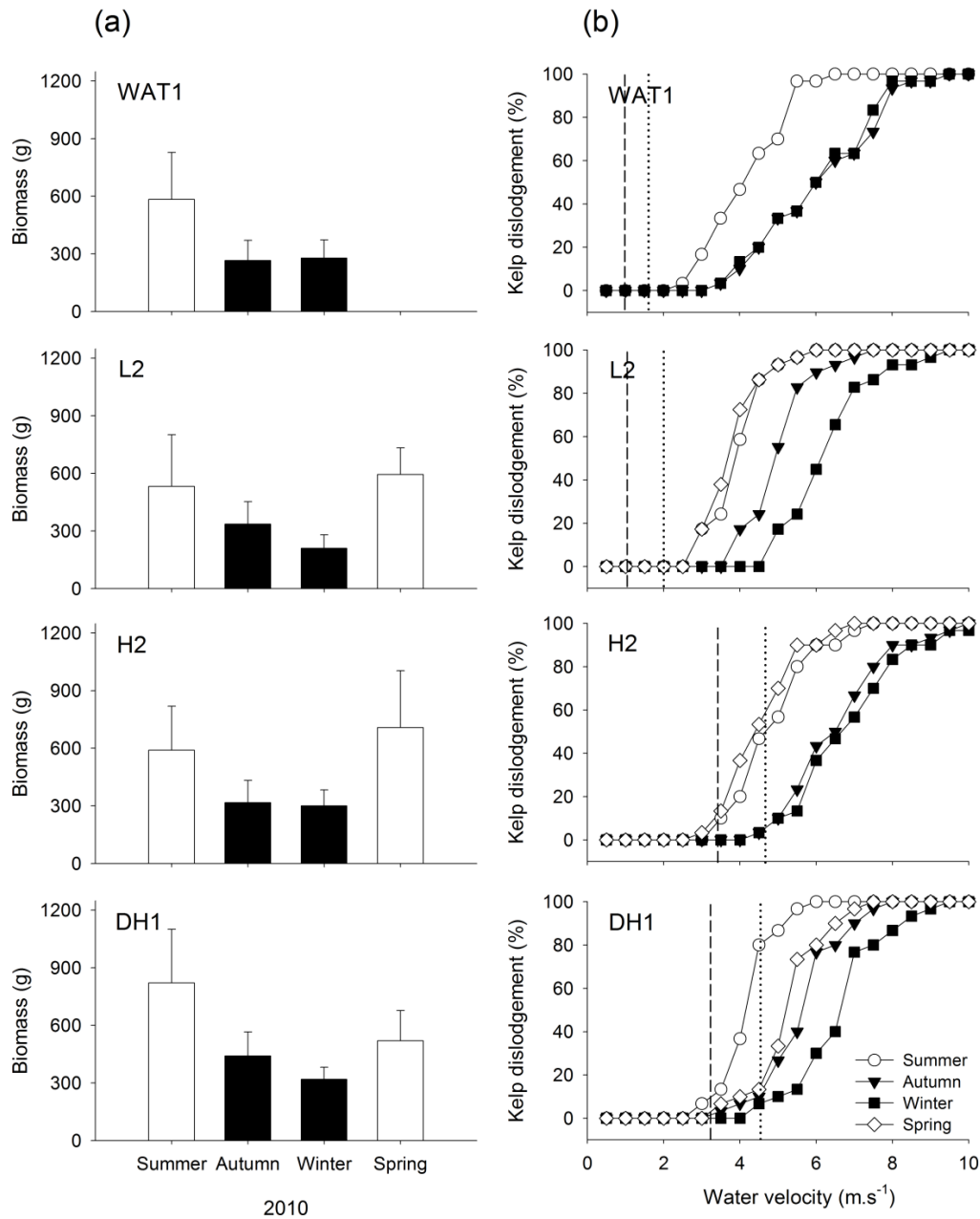


Figure 7 - (a) Mean individual kelp biomass for each season during the year 2010, and (b) the resulting dislodgement curves as a function of water velocity, kelp biomass (or thallus area) and attachment strength. The dashed vertical lines represent the maximum bottom water velocity according to the SWAN model and the dotted vertical lines represent the expected maximum water velocity *in-situ* (see Annexe 2) during the year 2010 at each site.

Modelling of the Environmental Stress Factor (ESF)

The most sheltered reef, L2, did not exhibit the same monthly variations in water velocities as the other sites (H2 and DH1) with values around 1 m s⁻¹ all year around

and only a small increase in winter (Fig. 8a). For all the three reefs, the changes in individual biomass were opposite to variation in water velocities with a maximum in late spring and summer and minimum in autumn and winter (Fig. 8b). Because the break force remained the same over time (Table 2) and the drag force is function of water velocity and kelp biomass (or thallus area), the opposite variation of both parameters resulted in a constant high ESF (ESF = break force/ drag force ≈ 10) for H2 and DH1 during the year (Fig. 8a,b,c). Due to the combination of minimum individual biomass in winter and a relatively constant water velocity over the year (Fig. 8a,b,c), the reef L2 had a higher ESF (> 10) in winter.

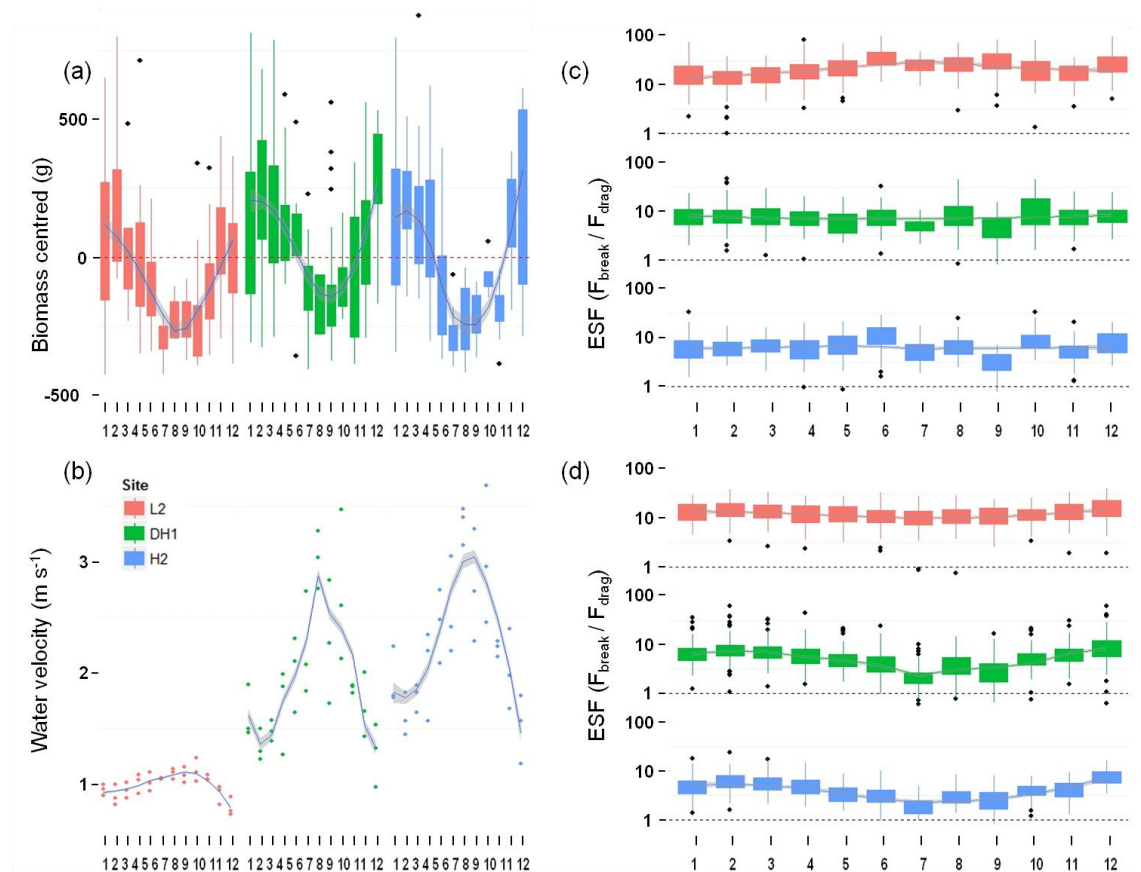


Figure 8 - 3-years modelling of the ESF for two scenarios (with and without biomass change) at 3 reefs. (a) Modelled monthly maximum water velocity for 3-years (2009 to 2011). (b) Monthly average of individual kelp biomass from the 3 years (c) Monthly ESF averaged across 3 years in natural conditions with (a) and (b) as inputs. (d) Monthly ESF with maximum individual biomass (February) applied to each month.

For the hypothetical scenario of no-biomass decrease in autumn-winter (maximum biomass maintained in the model), it resulted in lowering dramatically the ESF in winter (July-August) when the water velocities peaked, close to the limit ESF value of 1 when kelp get dislodged, for the most exposed reefs (H2 and DH1, Fig. 8d). For the most sheltered reef L2, the ESF remained high even in winter (ESF \approx 10, Fig. 8d).

4.5 Discussion

This study provides new insights on the relationship between peak water velocities and disturbance in kelp beds via dislodgement of individuals. Among the different scenarios of kelp dislodgement presented in the introduction (Fig. 1), our data support a model of constant dislodgement independent of the wave intensity (Fig. 1c); this model does not exclude a threshold “pulsed” response when the disturbance is extreme as indicated by results during the most severe storm (Fig. 1a). However, the seasonal kelp dislodgement is not greater in winter when storms are frequent. Therefore, winter-storms are probably driving mainly the transport of previous detached kelps to different habitats, instead of causing most of the kelp dislodgement. The biomechanical model showed how seasonal cycle of kelp biomass (thallus area) maintains a low and constant risk of dislodgement over the year and allow *E. radiata* to live in such harsh environment.

The biomechanical model outputs stressed the importance of seasonal variation in kelp individual biomass and provided a mechanistic explanation for the invariance in dislodgement observed among seasons. We demonstrated that seasonal variation in kelp individual biomass resulted in lower susceptibility to dislodgement during periods that coincided with peak water velocities, which in turn allows kelps to withstand storm velocities. This loss of biomass results from the combination of low kelp growth and high erosion of kelp tissue. Previous research in this region (Kirkman 1984; Wernberg and Vanderklift 2010; de Bettignies et al. 2012b) has found a low growth period in autumn and peak in distal tissue erosion in autumn-winter that leads to a decrease in the biomass of individual thalli from March to July (autumn-winter) from 800-700 g FW ind⁻¹ to 200-300 g Fresh wt ind⁻¹. This peak in erosion coincides with spore production and severe tissue wounding (de Bettignies et al. 2012b; de Bettignies et al. 2013). As a result, weakening of kelp tissue, combined with greater water motion likely facilitates pruning and erosion in autumn-winter (de Bettignies et al. 2012a; de Bettignies et al.

2012b). This in turn reduces drag and increased survival is therefore predicted by the biomechanical model. Similar thallus erosion and increase survival has been shown for intertidal algae (Blanchette 1997). Besides increasing survivorship, this process might be beneficial for spore release, as suggested by timing of reproduction (Blanchette 1997; de Bettignies et al. 2012b).

The difference in the pattern and magnitude of dislodgement of *Ecklonia radiata* to other studies can be explained by the intensity and regime of disturbance. Firstly, wave-driven mortalities of algae have been observed previously but particularly for intertidal seaweeds (Dudgeon and Johnson 1992; Pratt and Johnson 2002) and giant floating canopy kelps such as *Macrocystis pyrifera* (Dayton and Tegner 1984; Seymour et al. 1989; Reed et al. 2008). This difference in survival between these macroalgae and *Ecklonia radiata* can be explained by the extent of the hydrodynamic forces. Stipitate kelps (Steneck et al. 2002), such as *E. radiata*, do not experience breaking waves like other algae inhabiting intertidal rocky shores or the full force of surface waves like for floating canopy kelps. Maximum velocities generated by breaking waves on the shore can reach up to 15 - 25 m s⁻¹, a force equivalent to a wind more than 2000 km h⁻¹ (Denny 1988; Denny and Gaylord 2002), compared to *E. radiata* which experienced here maximum water velocities only of 1 to 4 m s⁻¹. Secondly, some of the most significant wave-driven mortalities recorded (Dayton and Tegner 1984; Seymour et al. 1989; Filbee-Dexter and Scheibling 2012) have been associated with ‘Large (i.e. severe) Infrequent Disturbance’ episodes, referred to as LIDs (Romme et al. 1998). The response of kelp canopy to these events can differ quantitatively and qualitatively (Romme et al. 1998). Pioneer work on disturbance pointed out already that distinction should be made between ‘catastrophe’ (~LID) and ‘disaster’ (more frequent, less severe) when evaluating the organism-environment relationship (Harper 1977; Paine 1979). This implies that species might have evolved to cope with, or even depend on disasters but are incapable of an adaptive response to catastrophes, which lead to severe ecological impact. LIDs can have long-lasting consequences for ecosystems and can be a dominant structuring force of the ecosystem (Turner and Dale 1998).

In conclusion, the dislodgement of *Ecklonia radiata* was independent of the wave forcing intensity in general, but can exhibit a relative pulsed response during the most

severe storms. We found that strong attachment strength to the reef and seasonal cycle in individual kelp biomass maintain the kelp at a low and constant dislodgement risk, offsetting the increase in water velocity in winter and minimizing storm-generated drag forces on kelp thalli. This temporal biomechanical modification to water flow can be compared to the spatial variation in shape and material properties for other kelp species, such as *Nereocystis luetkeana*, which have evolved a plastic phenotype to maintain a similar low risk to enable them to inhabit wave-exposed environments (Johnson and Koehl 1994). Our findings also suggested that a decoupling of the antagonistic parameters, kelp biomass and peak water velocity, might be critical for kelp survival. For example, the occurrence of severe storms in late spring and summer when kelp individual biomass is the greatest or an increase in storm intensity might affect kelp survival. For the last 23 years, the occurrence of extreme wave events (99th percentile significant wave height) has increased by ~1% per year along the south-western Australian coastline (Young et al. 2011), and this is likely to have implication for the loss of kelp habitats if the trend continues, particularly in warmer latitude where ecological performance of kelp recruits is reduced (Wernberg et al. 2010). Finally, results from previous research (de Bettignies et al. 2012a; de Bettignies et al. 2012b; de Bettignies et al. 2013) strongly suggest that *Ecklonia radiata* can survive in such hydrodynamic conditions thanks to its particular phenology (same timing of low growth, spore release, accumulation of wounds and severe thallus erosion) which results in large kelp tissue shedding (decrease of individual biomass by >50% in autumn-winter) and smaller pruned kelps with lower drag when storm-waves occur.

4. 6 Acknowledgements

TdB was funded through an ECU postgraduate award. Additional funding was obtained from the Western Australian Marine Science Institution (TdB) and The Australian Research Council (TW). We are grateful to M. Mohring, P. Bouvais, A. Turco, S. Bennett, P. Van Dyk and J. Godefroy for assistance with the diving and boating. Neil Collier (Research consultant Statistician at ECU) is acknowledged for providing help to model the environment stress factor (*R* software).

GENERAL DISCUSSION

This study of a dominant kelp species in temperate Australia, *Ecklonia radiata*, has significantly progressed our understanding of how kelp detritus is generated. Kelp detritus has repeatedly been demonstrated to be a key vector of trophic connectivity in temperate coastal ecosystems throughout the world (Bustamante et al. 1995; Colombini and Chelazzi 2003). Although there have been recent efforts to review the fate of kelp production (Krumhansl and Scheibling 2012), most studies of kelp detritus have ignored the mechanisms that generate kelp detritus. Understanding the supply of kelp detritus to recipient habitats and evaluating its broader impact, first requires an understanding of how this material is produced and exported from reefs. Such knowledge is also relevant to the dynamics of the kelp bed itself and the associated communities, which are strongly structured by the kelp as a foundation species (Dayton 1972; Dayton 1985). This research tested the hypothesis that storms are fundamentally important in detaching kelps and driving kelp detrital export of entire dislodged kelp. The findings did not support strongly this hypothesis. To the contrary, the results have led to the presentation of an alternative model that integrates kelp phenology, biomechanics and environmental forcing as important components driving the form and timing of detrital export, and which could have general applicability. The general discussion details (1) the key findings of each chapter, (2) the connection between different chapters through the relationship between erosion and dislodgement of kelp; and provides additional information on (3) the fate of kelp production and (4) kelp detritus and implications for spatial subsidies.

1 Key findings of the thesis

1.1 Understanding how kelp morphology affects drag force at peak velocity (Chapter 1)

The initial work in chapter 1 aimed to assess the influence of kelp morphology on hydrodynamic drag when subjected to storm-generated water velocities. Kelps of different morphologies were subjected to water velocities comparable to those generated in storms and the resultant drag was measured. The results revealed that only size (total area or biomass), not morphology, was important in determining the drag acting on

Ecklonia radiata at peak velocities. The drag coefficient converged to a constant value at increasing speed, suggesting that reconfiguration and streamlining of different thallus shapes caused a decoupling of drag and morphology at high flow. These results imply that the only way of minimizing drag forces at velocities experienced by *E. radiata* during storms would be a reduction of total thallus area (biomass as proxy) and not by modification of thallus shape. This chapter constituted the first step to build a mechanistic model of kelp dislodgement (Ch. 4).

1.2 The implication of wounds for kelp survival and detritus production (Chapter 2)

Previous work has shown that kelps can withstand severe wave action. However, if kelps are wounded, their biomechanical properties can be compromised, impacting on their survival. Wounds were found to be most abundant on kelps before peaks in winter storms. *Ecklonia radiata* carried up to 400 wounds per thallus, clearly documenting that kelps are generally not undamaged in nature. Simulated wounds caused significant loss of tissue integrity and strength. Together, these findings suggest that accumulation of wounds during summer mediates kelp pruning in early winter. Paradoxically, this may increase kelp survival during winter storms because the biomechanical drag is much lower on small, pruned kelps making them less likely to be torn off the reefs.

1.3 The relative contribution of dislodgement and erosion to kelp detritus production and drivers of kelp detrital production (Chapter 3)

In chapter 3, I investigated the relative importance of dislodgement and thallus erosion to the production of kelp detritus. Erosion of distal parts of kelp thalli accounted for the overwhelming proportion (~80%) of the annual detrital production, but occurred mainly in autumn (4 to 6 times greater than other times of the year) making a considerable, but pulsed contribution to the coastal system. In contrast, dislodgement was a minor and constant process throughout the year, with about ~13% of kelps dislodged each season. These findings challenge the common perception that wave-driven dislodgement is the predominant process for the production of kelp detritus. This phenomenon is conceptually comparable to the seasonal leaf fall from deciduous trees in autumn, which strongly affects temperate freshwater and terrestrial ecosystems. This erosion of *E. radiata* (loss of ~50% of individual biomass) was associated with the timing of kelp

reproduction (increasing numbers of zoospores released from kelp tissue) and not increased wave activity or temperature; spore release presumably causes a weakening of the tissue, making it more susceptible to erosion. The coincidence of a low growth rate and a high erosion rate in autumn led to a severe reduction in the biomass of individual kelps before winter, a decrease which resulted in lower drag forces acting on the thalli, likely reducing their susceptibility to dislodgement during peak wave action and highlights a possible relationship between dislodgement and erosion.

1.4 Relationship between kelp dislodgement and wave disturbance, using experimental and theoretical approaches (Chapter 4)

Until now, observations of kelp dislodgement have emphasized the dynamic nature of kelp beds that are constantly reshaped by wave disturbance with storm-generated waves frequently tearing kelp from the reef. In this chapter, direct measurement of kelp dislodgement was complemented by modelling which synthesised the biomass, drag, water velocity, attachment strength characteristics, modelled hydrodynamic forces acting on kelps and their susceptibility to dislodgement throughout the year. Contrary to expectation, there was a relatively low and constant dislodgement rate for all reefs despite strong temporal patterns of wave action and extreme water velocities. However, the most intense storm of the study period caused dislodgement pulse. The models indicated that the interaction between temporal patterns of wave-generated water velocity and change in thallus biomass is critical for dislodgement characteristics. The seasonal variation in individual biomass resulted in lower susceptibility to dislodgement (low biomass) coinciding with period of peak water velocities. The benefit of erosion in reducing drag forces on kelp thalli, as proposed in the previous chapter (Ch. 3), was demonstrated here it maintained dislodgement as low as possible. This provides a low steady supply of kelp detritus punctuated by smaller peaks during severe storms.

2 Relationship between Dislodgement and Erosion

Kelp beds have often been presented as highly dynamic systems affected by severe seasonal wave perturbation leading to local kelp mortality followed by rapid recovery (Kennelly 1987; Dayton et al. 1992; Graham et al. 1997). However, there are a broad range of different types of kelps, and they do not experience hydrodynamic forces in the same way. For example, giant kelp such as *Macrocystis pyrifera* (surface canopy kelp

up to 45m long) are structurally very different to small stipitate kelp (Steneck et al. 2002) such as *Laminaria sp.*, *Eisenia sp.* or *Ecklonia radiata* (less than 2 m long), the subject of this study. Even if *E. radiata* experiences extreme velocities of up to 3.5-4 m s⁻¹ (Ch. 1 & 4), it would never experience the full force of breaking waves that surface canopy kelps do and smaller kelp experiences less drag in general; and therefore its relationship with wave disturbance might be different. Synthesizing the findings of the four chapters presented in this dissertation, a new interaction between kelp dislodgement and wave disturbance is advanced (Fig. 1), which expands and refines the model of kelp dislodgement. Kelp adult biology, biomechanic characteristics and environmental forcing constitute the important components of this model, where their interplay promotes equilibrium in kelp beds with wave perturbation. This model (see details below) links the two main mechanisms that generate kelp detritus (erosion and dislodgement, Fig. 1).

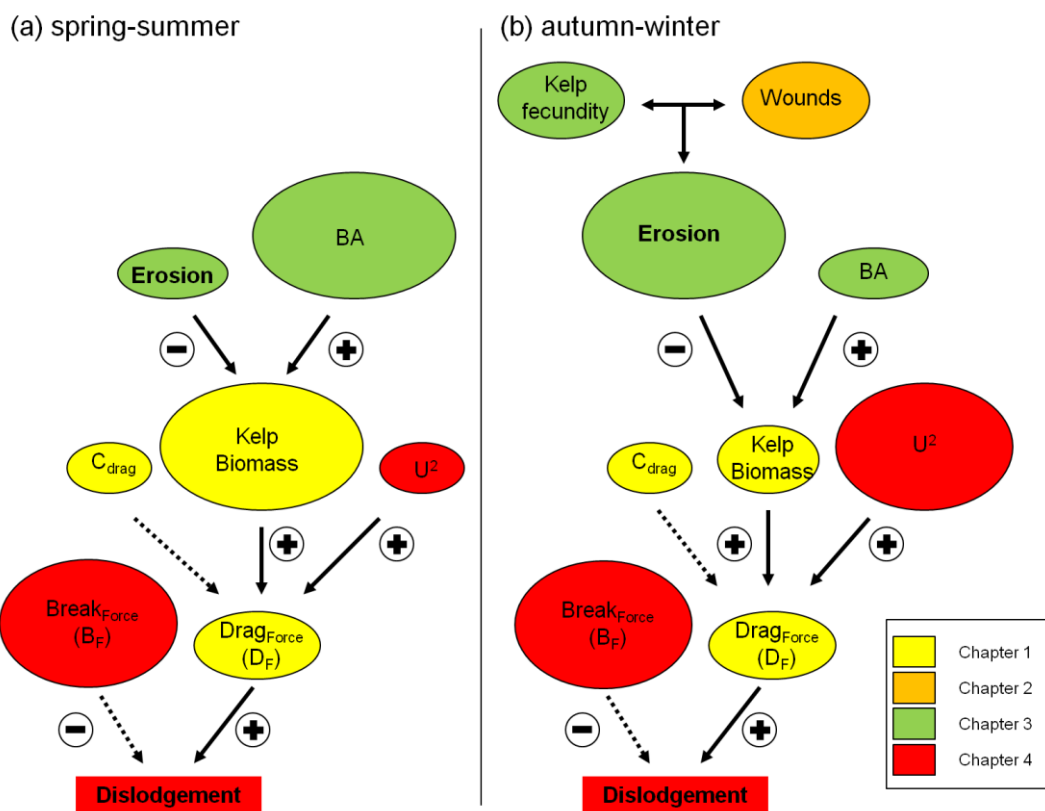


Figure 1 - Relationship between dislodgement and erosion for *Ecklonia radiata*. Sizes of the circles are proportional to the magnitude of importance of each variable. The arrows indicate the direction of the effect and the signs (+ or -) indicate whether it results in an increase (+) or decrease (-) of the target variable. BA and U^2 are the respective abbreviations for biomass accumulation and square of water velocity. Each

colour refers to the different thesis chapters (see legend) which provided knowledge to build this model. The dotted arrow means that the variable has the same importance throughout the year.

The dynamic of earlier life stages of *Ecklonia radiata* (stages 1 and 2) is likely to differ from the adult kelp population (stage 3). Contrary to the adult stage, stages 1 and 2 must exhibit less erosion than growth to reach the mature stage. Because the erosion peak was linked to kelp fecundity, it suggests that non-mature stages will not undergo such erosion and seasonal drop in thallus biomass. Furthermore, past studies found that stages 1 and 2 were more weakly attached (10 - 40 Newtons respectively) but the low drag associated with their small size/weight resulted in break velocities of 10 and 25 m s⁻¹ respectively (Thomsen et al. 2004). The adult stage had much lower break velocities between 3 and 6 m s⁻¹ (Thomsen et al. 2004) similar to the results presented (Chap. 4, Fig. 3 to 8 m s⁻¹). Also, the dense adult kelp canopy must buffer these earlier stages from extreme velocities and therefore combined with the high break velocities these stages should not be affected significantly by dislodgement except if they get entangled with previous mature dislodged kelp. Personal observations of kelp wrack predominantly composed of adult kelps confirmed it and highlight the minor role of the earlier stages 1 and 2 for kelp detrital production.

2.1 Spring-summer

Ecklonia radiata has a peak of growth in spring which causes large biomass accumulation along the thallus (Kirkman 1984; de Bettignies et al. 2012b; Bearham et al. 2013) (Fig. 1a). Combined with a low erosion rate during the same period, it results in a positive net productivity and a maximum in kelp biomass at the end of summer. The kelp individual biomass is one of the key parameters of the drag equation (Equation 2 in Ch. 1) together with the drag coefficient and water velocity on the reef, to predict the drag force acting on kelp thalli. In spring-summer, despite the large kelp biomass, the drag force remains relatively low compared to the opposing force that retains kelp on the reef (break force), because of the lack of storms and intense wave disturbance (i.e. low water velocity, Ch. 4). As a result, the susceptibility of kelp to dislodgement is very low (Fig. 1a, Ch. 4).

2.2 Autumn-winter

The very low biomass accumulation of *E. radiata* in autumn-winter, combined with a high erosion rate (peak in autumn), leads to a minimum in annual kelp biomass (>50% decrease in individual biomass, Ch. 3 & 4) (Fig. 1b). The compilation of monthly kelp biomass data over 3 years (subset of 3 reefs) has shown the same erosional process in late autumn (May-June, Ch. 4). This erosion peak is hypothesised to be the consequence of the production of sori and accumulation of wounds (Ch. 2 & 3), and the resulting mechanical weakening of kelp tissue (Ch. 2). Wounds are very common in kelp thalli in early winter (~300 wounds kelp⁻¹) and dramatically increase the susceptibility of kelp tissue to breakage (Ch. 2). During winter and its associated storms, the water velocity increases up to 3.5 - 4 m s⁻¹ but the low kelp biomass counteracts the severe wave action, minimizing drag force acting on kelp thalli. Once more, drag force is predicted to be lower than break force (Equation 2, Ch. 1) and no increased kelp dislodgement should be observed in autumn-winter due to this kelp defoliation and seasonal cycle of thallus biomass (Chapters 2, 3 and 4).

3 Fate of kelp production

Predictions can be made about the fate of kelp production and estimates of the annual balance between gross productivity and kelp loss. This was done for 8 of the 9 reefs surveyed over a year for the kelp population of stage 3 (predominant biomass on the reef). The gross productivity (P_G), total kelp loss (L_{kelp}) and net biomass accumulation (ΔB , g C m⁻² year⁻¹) of the adult kelp stand (stage 3) can be expressed as:

$$P_G = B_A + R_E \quad (\text{Equation 1})$$

where B_A is the biomass accumulation (Fairhead and Cheshire 2004) of the kelp stand (g C m⁻² year⁻¹) and R_E the recruitment of kelp individual into the Stage 3 cohort (g C m⁻² year⁻¹), and

$$L_{kelp} = E_r + D_i + G_r \quad (\text{Equation 2})$$

where E_r , D_i and G_r are the erosion, dislodgement and grazing of the adult kelp population (kelps of stage 3, g C m⁻² year⁻¹), respectively, and

$$\Delta B = P_G - L_{kelp} \quad (\text{Equation 3})$$

Because kelp dislodgement ($\sim 13\%$) and kelp density ($\sim 8 \text{ ind. m}^{-2}$) did not change significantly over the year, the recruitment of kelp individuals into the Stage 3 cohort must have balanced the dislodgement (Ch. 3). Thus the term R_E in Equation 1 should be the same as D_i in Equation 2, as suggested earlier by Kirkman (1981). This is consistent with the recruitment dynamic of *E. radiata*, which are mainly controlled by availability of gaps in the kelp canopy like most of kelp species, allowing light intrusion (Kirkman 1981; Reed and Foster 1984) and therefore, any free space will allow young kelp to grow and reach their mature stage (stage 3 for *E. radiata*). In south-western Australia, most of the grazing of kelp occurs on drift thalli or fragments, exclusively by sea-urchins (5 to 20% consumption of tethered pieces of kelp day^{-1}). In general, direct grazing on kelp by fishes (negligible in the canopy and $\sim 1\%$ of understorey kelp day^{-1}) and by sea-urchins ($\sim 1\%$ of understorey kelp day^{-1}) is a minor process (Vanderklift et al. 2009). However, grazing by fishes can be exceptionally high ($> 10\%$ of canopy kelp day^{-1}) when herbivorous fish density is high compared to the biomass of kelp (Wernberg et al. 2006; Vanderklift et al. 2009). Because most kelp beds in south-western Australia are dense (de Bettignies et al. in prep., Wernberg 2009) the overall direct grazing pressure on adult kelp remains very low and can be considered as negligible in Equation 2. Therefore, the net biomass accumulation of *E. radiata* beds (adult kelps only) in the study region can be simplified to the difference between biomass accumulation and erosion of the standing stock because the other processes are minor (grazing) or they offset each other (dislodgement vs. recruitment of stage 3 kelps). Thus, the net biomass accumulation (ΔB) can be approximated as:

$$\Delta B = B_A - E_r \quad (\text{Equation 4})$$

Then, the fate of kelp production can be estimated for 8 of the 9 reefs surveyed (Fig. 2). The dislodgement (and recruitment of stage 3 kelps), erosion and biomass accumulation of the kelp bed of *E. radiata* (averaged across the 8 sites for adult kelps) was respectively $110.1 (\pm 45.0)$, $390.1 (\pm 131.5)$ and $387.9 (\pm 140.0) \text{ g C m}^{-2} \text{ year}^{-1}$, which resulted in a net biomass accumulation of $-2.2 (\pm 8.5) \text{ g C m}^{-2} \text{ year}^{-1}$ (Fig. 2) with a standard deviation that overlaps 0.

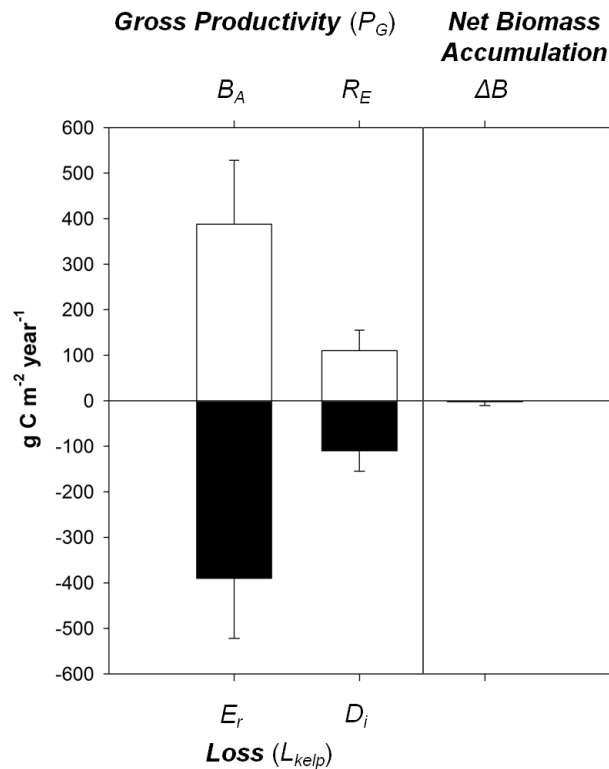


Figure 2 - Balance between kelp stand gross productivity (P_G) and kelp stand loss (L_{kelp} ; adult kelps, stage 3), with B_A the biomass accumulation, R_E the recruitment of kelp individual into the Stage 3 cohort, E_r the erosion of kelp, D_i the dislodgement of kelp and ΔB the net biomass accumulation of adult kelp stand averaged for 8 reefs (WAT1, L1, L2, H1, H2, DH1, DH2 and DH3).

This net biomass accumulation, close to 0 (Fig. 2), results in a large part from the opposing effect of large pulse of kelp erosion in autumn and peak kelp biomass accumulation in spring (Ch. 3). Erosion and biomass accumulation cancel each other out for the mature kelp of stage 3 on an annual basis. This must be different for younger plants (stages 1 & 2) that need to grow and develop to reach their mature stage, for which growth and productivity must overcome erosion, and therefore if added to Fig. 2 might result in an overall positive balance. Erosion rate was linked to kelp fecundity (Ch. 3) hypothesised to have weakened and wounded kelp resulting in high tissue fragmentation and erosion (Ch. 2 & 3). Also, it is possible that grazing and dislodgement of young kelp might differ from the adult population (Thomsen 2004), and we cannot apply the results from adult kelp to younger individuals.

In general, the observed dislodgement over the 2 years was independent of the wave energy on the reef and was rather constant over this period, except during the most severe storm. The increase of wave disturbance did not impact greatly kelp dislodgement rate (Ch. 3 & 4), and this was explained earlier by the autumn reduction in kelp biomass prior to peak flow velocities (see Fig. 1). Because of the temporal consistency of kelp dislodgement across a spatial continuum of wave disturbance, this ‘dislodgement’ might just reflect a constant mortality rate of the kelp adult population (Fig. 3). ‘Kelp survivorship’ can be estimated at each reef by subtracting to 100% (when kelps were first tagged) the cumulative dislodgement rate of each season and plot against the number of days of the corresponding season as followed (Fig. 3):

$$\begin{aligned} \text{For } x &= t_2 - t_1 \\ , y &= 100 - \sum_{t_1}^{t_2} Di_{1-2} \end{aligned} \quad (\text{Equation 5})$$

where x is the number of days, t_1 and t_2 the number of days at different time, y the kelp survivorship (% kelp dislodged) and Di_{1-2} the kelp dislodgement rate (%) between time 2 and 1. Figure 3 indicates that all reefs followed the same trend of constant decrease and the adult kelp population of *E. radiata* is renewed after 668 days on average (regression analysis with the 8 reefs: $y = -0.1446x + 96.563$, $P < 0.001$; $N = 72$).

To conclude this part, the kelp populations of the study region have similar stable characteristics with an annual net productivity almost null, driven by the balance between dislodgement vs. recruitment and erosion vs. gross productivity, which cancel each other out; and with near constant mortality rate which indicated that kelp adult populations are renewed every 2 years on average.

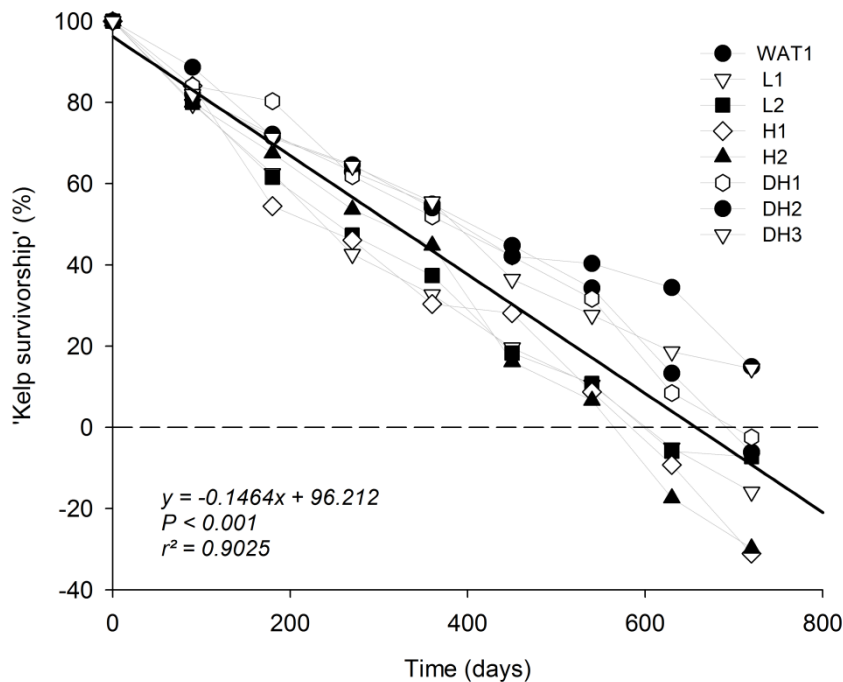


Figure 3 - Survivorship curves of adult kelp populations. The thicker black line represents the linear regression line of the 8 reefs together (with regression parameters).

4 Kelp detritus and implications for spatial subsidies

Erosion of distal parts accounted for nearly 80% of the annual kelp detritus production (Ch. 3) compared to a relatively lower and constant dislodgement process (Ch. 3 & 4). Unlike the unexpectedly large difference between these two mechanisms, the most significant finding was the strong temporal signal of erosion with a massive pulse in autumn: $\sim 40 \text{ g FW m}^{-2} \text{ day}^{-1}$ equivalent to $\sim 3.6 \text{ kg FW m}^{-2}$ for the 3 months autumn period (Ch. 3). Because the effect of kelp detritus as a subsidy depends largely of the ratio between the autochthonous and allochthonous resources (Marczak et al. 2007), the impact of this large pulse might be significant in habitats with otherwise low resource availability (Marczak et al. 2007).

The south-western Australian waters are known for their low nutrient concentrations (severely nitrogen limited) and low primary productivity because of a warm poleward current poor in nutrients (the Leeuwin current) and the absence of upwelling in the region (Johannes et al. 1994; Hanson et al. 2005). Despite these conditions, there is a seasonal increase in nitrates and chlorophyll *a* across the shelf in autumn-winter, decreasing further offshore (Lourey et al. 2006). River flow, drain run-off (Black et al.

1981) and groundwater discharge (Johannes 1980) are higher during this period and could potentially explain part of this seasonal peak of nitrates and phytoplankton productivity. However, these inputs are temporally and spatially restricted and by themselves cannot explain the extent of the phenomenon (Lourey et al. 2006; Lourey and Kirkman 2009). Instead, the cycling and remineralisation of abundant kelp tissue from erosion and to a lesser extent leaching from dislodged kelps may provide a more consistent contribution to this ‘unknown’ source of nutrients. According to data across the temperate coast of Australia, the peak in *E. radiata* erosion is a ubiquitous phenomenon (de Bettignies et al., *in prep.*). When considering the vast stretch of coastline in temperate Australia, the abundance of subtidal reefs, the dominance and abundance of *Ecklonia radiata*, and the magnitude of kelp erosion, it suggests that this kelp species is likely to be very important in the cycling of nutrients and functioning of the coastal ecosystem throughout temperate Australia.

5 Future directions of research

Given the importance of the erosion pathway to generate kelp detritus and the dominance of *Ecklonia radiata* across temperate Australia, further investigations are required to extricate the magnitude and its mechanism at larger spatial scales to implement these local findings. Furthermore, not only the quantity matter but also the quality of the kelp material exported for its likelihood to be assimilated by consumers. Kelp tissue have usually a C:N ratio over 20 (Atkinson and Smith 1983) whereas a C:N ratio of 17 is usually the limit to meet the nutritional requirement of a consumer (Russell-Hunter 1970). Mann (Mann 1972; Mann 1988) described the role of bacteria in kelp beds as “*making macrophyte energy stores available to animals*”. Future research on trophic subsidy should focus on this interaction between kelp and micro-organisms to comprehend the extent of kelp detritus impact on and assimilation in temperate coastal organisms and habitats.

The source of nutrients via kelp has been shown to play a key role in the dynamic of some submarine canyons (Vetter 1994; Vetter 1998). Submarine canyons are often referred as biological “hotspot” for diverse and abundant benthic communities (Vetter 1994; Vetter and Dayton 1998) because of their characteristic to trap and conduit sediments, nutrients and organic matter (Harrold et al. 1998; Vetter and Dayton 1999).

Canyons also concentrate phytoplankton productivity, constitute a feeding ground for fishes (Vetter and Dayton 1999) and nursery ground for whales (Hooker et al. 1999). More investigations are needed to look at the impact of the sinking and accumulation of this organic material in deeper waters and its trophic significance.

Additionally, distributions of large temperate algae in Australia have shifted and their abundance has decreased locally in response to global warming (Wernberg et al. 2011; Wernberg et al. 2013) and this has been recently accelerated by severe and sudden temperature warming (Smale and Wernberg 2013; Wernberg et al. 2013). This is likely to have important implications for the kelp-associated organisms and habitat which rely on kelp as source of nutrients. More research need to focus on the flow-on effect of kelp loss on the coastal trophic food web and how innovative reef-restoration procedures can be an alternative to mitigate this loss.

6 Conclusion

This study has provided a detailed investigation of the mechanisms that generate kelp detritus from *Ecklonia radiata* kelp beds. There is a high potential for the transferability of the findings to other systems because of the ecological and structural resemblance of *Ecklonia radiata* to abundant kelp species elsewhere in the world. *Ecklonia radiata* is very similar to *Ecklonia cava* (Japan), *Lessonia traberculata* (Peru and Chile), *Lessonia variegata* (New Zealand), *Undaria pinnatifida* (Northern and Southern Hemisphere), *Pterygophora californica* (Northwestern America) and some *Laminaria* species such as *Laminaria pallida* (South Africa) and *Laminaria digitata* (Europe and North-eastern America).

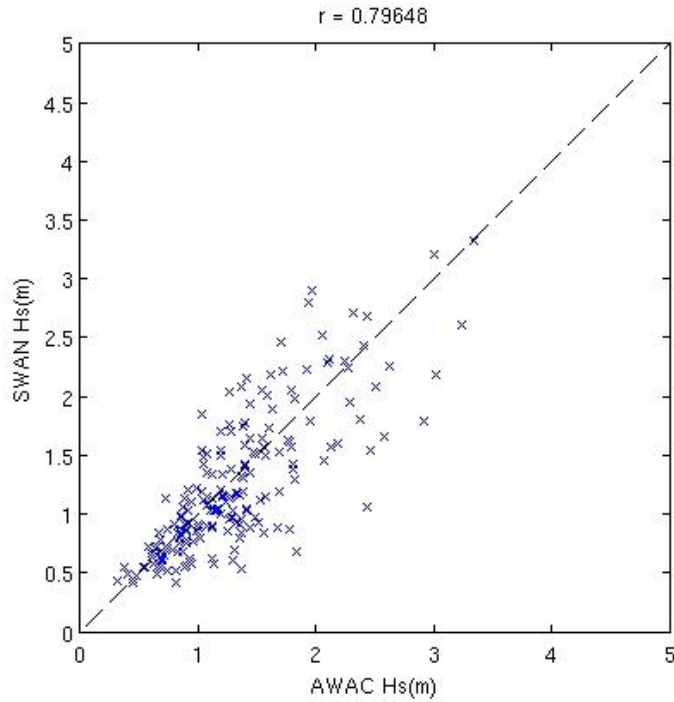
The key findings of the four chapters help refine the understanding of the origin of kelp detritus and to re-think assumptions about how these systems work. The results pointed out the dominance of kelp erosion and not kelp dislodgement as the main mechanism of kelp detrital production with a pulse of kelp material in autumn-early winter. The timing and extent of this mechanism in relation to the biology of kelps is analogous with terrestrial systems and the seasonal leaf fall, which strongly affects the dynamics of the surrounding habitats.

The magnitude of erosion was such that the drag acting on the kelps was altered via a severe decrease in kelp biomass coinciding with increasing water velocities. This resulted in minimizing kelp susceptibility to dislodgement via a drag-reducing form of the kelp when water velocities associated with winter storms increased. This crucial relationship between erosion and dislodgement explains the temporal consistency of kelp dislodgement over the year and refines the paradigm of wave-driven disturbance in kelp systems.

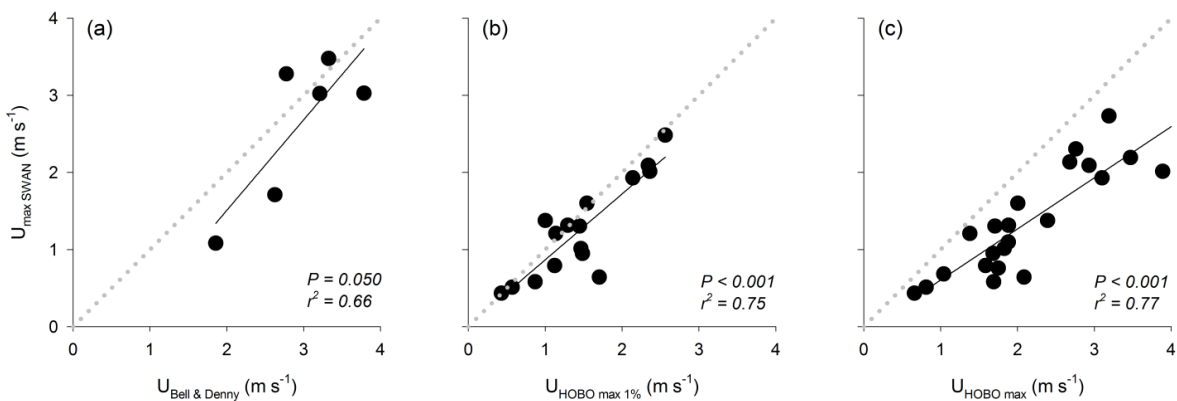
An alternative model was proposed, in which kelp beds are in balance with wave disturbance mediated by kelp biology, biomechanics and environmental forcing. This relationship between erosion in autumn and the susceptibility of *E. radiata* to dislodgement in winter demonstrates an adaptation of kelp population to their environment. Such timing of susceptibility to disturbance has to be considered carefully for adaption of kelp to changing climate, in regards to variations in storm intensity, frequency and timing. . Together with the findings on kelp erosion, these findings have implications for the understanding of the dynamics of coastal systems and the potential of kelp detritus as spatial subsidy.

ANNEXES

Annexe 1 - Validation of the SWAN model for the Marmion Lagoon region. Comparison of significant wave heights measured with an acoustic wave and current meter (AWAC) and significant wave heights outputs from the SWAN model.



Annexe 2 - Comparisons between the U_{\max} estimated from the SWAN model with the maximum water velocities given from the dynamometers, the 1% percentile of the maximum velocities from the gravitational loggers and the maximum water velocities from the gravitational loggers (HOBO).



APPENDICES

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de Bettignies T, Wernberg T, Lavery PS (2012b) Size, not morphology, determines hydrodynamic performance of a kelp during peak flow. Marine Biology doi: 10.1007/s00227-012-2138-8

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Volume: Reference Number: 12-444
Issue: Reference Number: 12-444
Chapter, article or figure name or title: Contrasting mechanisms of dislodgement and erosion contribute to production of kelp detritus Pages on which articles, data or figures appear: p 58-77 Special notes: Publication as a chapter of my PhD thesis.

2 PDF proofs of published work and manuscript in review

Mar Biol
DOI 10.1007/s00227-012-2138-8

ORIGINAL PAPER

Size, not morphology, determines hydrodynamic performance of a kelp during peak flow

Thibaut de Bettignies · Thomas Wernberg · Paul S. Lavery

Received: 6 June 2012 / Accepted: 23 November 2012
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Abstract The morphology and shape of algae can affect their survival in wave-swept environments because of the hydrodynamic drag created by water flow. Studies of morphology and drag are typically conducted at relatively low water velocities, and the influence of algal morphology on drag, over the range of water velocities algae must cope with in their natural environment, remains unclear. Here, we tested the link between morphological variation and hydrodynamic drag for a dominant kelp with complex morphology (*Ecklonia radiata*), over a range of water velocities representative of conditions on wave-swept reefs. Our results indicated that kelps on subtidal reefs must withstand maximal orbital water velocities in excess of $2\text{--}3\text{ m s}^{-1}$. Our measurements of drag, resulting from flows ranging from $1\text{ to }3\text{ m s}^{-1}$, revealed that shape- and width-related thallus and lamina characters were important to drag at low speed, but that total thallus area (or biomass) was the main determinant of drag at high flow. Drag

coefficients converged at increasing speed suggesting that, at high flow, significant thallus reconfiguration (more streamlined shape) decoupled drag from morphology. This implies that, at peak velocities, only size (total area), not morphology, is important to drag and the probability of dislodgment.

Introduction

Important questions in ecology and evolution centre on the relationship between an organism's morphology and its performance. Different morphological characters can lead to different performances, making a specific morphology more suitable to a given environment through enhanced survival and fitness (Koehl 1996; Wainwright 1996). For sessile marine organisms, morphology has critical implications for their likelihood of dislodgment or survival when experiencing intense hydrodynamic forces, driven by waves and currents (Denny 2006). Macroalgae such as kelps are found across different hydrodynamic environments and exhibit great intra- and inter-specific morphological variation (Johnson and Koehl 1994; Roberson and Coyer 2004; Wernberg and Vanderklift 2010). Consequently, they are good models for studying the ecological implications of morphology.

Differences in algal morphology are thought to be the consequence of a trade-off between limiting drag forces, which prevent breakage and dislodgement for wave exposed morphotypes (Kawamata 2001; Blanchette et al. 2002; Buck and Buchholz 2005) and maximizing light capture and transfer of gas and nutrients for photosynthesis and growth for sheltered morphotypes (Koehl and Alberte 1988; Stewart and Carpenter 2003; Haring and Carpenter 2007). Therefore, it is generally accepted that algae from

Communicated by K. Bischof.

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Published online: 15 December 2012

 Springer

Wounded kelps: patterns and susceptibility to breakage

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ABSTRACT: Kelps are highly productive seaweeds predominantly found in wave-exposed environments. Physical and biological processes such as sand abrasion, whiplash and grazing can wound kelp tissue, potentially weakening its ability to withstand wave forces. Despite the ecological importance of kelp tissue loss, few studies have quantified wounding patterns in kelps or how wounding might affect the biomechanical properties of kelps. We quantified the prevalence of wounds on 360 *Ecklonia radiata* kelps collected across 3 different reef lines (levels of wave exposure) in April (autumn), June (early winter), August (winter) and October (early spring) (i.e. before, during and after peak wave activity). Small holes in the centre of laterals dominated the wounds. Wounding pattern did not differ between reef lines but changed over time, with most in early winter and least in early spring (from 285 to 71 wounds kelp⁻¹). This pattern suggests that wounds accumulate over summer and that highly wounded parts of the frond (but not the entire kelp) break off when encountering the first storms. Biomechanical break-force tests assessed the effect of experimental wounds on the forces required to break kelp tissue. These tests showed that holes or horizontal cuts to the edge of the kelp frond dramatically reduced the strength, extensibility, toughness and stiffness of the tissue. We conclude that wounds are common in *E. radiata* and that the resulting loss of tissue integrity, caused by even small damages, can dramatically increase the susceptibility to breakage. Our findings may have important ecological implications; the peak in wounds in early winter is likely to increase fragmentation of the kelp, thereby reducing its size and hydrodynamic drag, and, paradoxically, reducing the risk of fatal dislodgment during severe winter storms.

KEY WORDS: Seaweed biomechanics · *Ecklonia radiata* · Wounds · Biomass loss · Pruning · Survival · Western Australia

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INTRODUCTION

Kelp forests are highly productive and ecologically important habitats along rocky coastlines in polar to warm temperate regions where they influence ecosystem dynamics (Mann 2000, Steneck et al. 2002). Kelps are common in wave-exposed environments, where they experience extreme forces (Denny 1994, Thomsen et al. 2004) that can cause loss of parts of

the thalli (pruning) and loss of the entire thalli (dislodgement) (Seymour et al. 1989, Dayton et al. 1992, Thomsen & Wernberg 2005), resulting in canopy loss on reefs and accumulation of drift kelp in adjacent habitats (Wernberg et al. 2006) and on the shore (Ince et al. 2007). Canopy loss and accumulation of drift kelp are important ecological processes that underpin much of the community dynamics on reefs (Dayton et al. 1992, Wernberg & Connell 2008) and in

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1 Running title: Detrital production from kelp beds

2

3 **Contrasting mechanisms of dislodgement and erosion contribute to**
4 **production of kelp detritus**

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6

7

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