BIOLOGY AND ECOLOGY OF THE GLOBALLY SIGNIFICANT KELP *ECKLONIA RADIATA*

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Abstract

Ecklonia radiata is one of the most widespread kelps globally, dominating temperate reefs throughout much of Australasia and southeastern Africa. Throughout much of its range, it is the only laminarian kelp and hence plays a key role in facilitating biodiversity and driving food webs, and it underpins immense ecological and socioeconomic values. This review synthesises the growing literature on *E. radiata* from its phylogeny and distribution through to its biology, ecology and recent changes. It provides an assessment of the state of knowledge and identifies gaps in our understanding of this important species. Despite being tolerant of a wide range of abiotic conditions, recent environmental change has caused direct and indirect loss of *E. radiata* forests, with extensive areas transitioning to turf and urchin barrens. Ongoing climate change may require application of multifaceted and novel strategies to increase its resistance and resilience to future conditions. By integrating variation across space, time and environmental change, this review provides a description of the current status and possible future trajectories of *E. radiata* forests.

E. radiata: **A globally significant species**

One of the most widely distributed kelps globally is *Ecklonia radiata* (C. Agardh) J. Agardh (Figure 1). In contrast to many other kelp forest ecosystems, where multiple laminarian species coexist (Steneck & Johnson 2013, Wernberg et al. 2019), *E. radiata* often forms monospecific forests as it is the only laminarian kelp throughout much of its range (Figure 1). The ecological and socioeconomic importance of *E. radiata* has long been recognised (e.g. Bolton & Anderson 1994, Steinberg & Kendrick 1999). However, in contrast to other widespread and dominant kelp taxa such as *Macrocystis* (Graham et al. 2007) and *Laminaria* (Bartsch et al. 2008), there have not been any recent systematic assessments of our knowledge of the species. The only review of the species was 25 years ago by Bolton & Anderson (1994) as part of their review of the genus *Ecklonia*. Since then, significant work has been done on many aspects of the species. Indeed, a search for '*Ecklonia radiata*' in the core collection of the Web of Science (22 April 2018) revealed that 88% of 427 records have been published since 1994.

Figure 1 *Ecklonia radiata* forests support diverse ecological communities, economic values and cultural significance. It is the only laminarian kelp throughout much of its distribution, where it often forms dense monospecific forests. (All photos by the authors and Andrew Green).

This review synthesises the literature on the phylogeography (see the section entitled 'Phylogeny and distribution'), ecophysiology (see the section entitled 'Ecophysiology and environmental drivers') and population biology (see the section entitled 'Life history, dispersal and recruitment') of *E. radiata*, as well as the community ecology (see the section entitled 'Community ecology of *Ecklonia* forests') and recent changes in and future threats to *E. radiata* forests (see the section entitled 'Recent changes and future threats'). The synthesis concludes that although our current scientific understanding of the biology and ecology of *E. radiata* spans broad scales of space, time and scientific disciplines, common trajectories of ecological change warrant continued inquiry and integrated management interventions to ensure the long-term integrity and persistence of *E. radiata* kelp forests (see the section entitled 'Conclusion').

Background

Kelp forests: The foundation of temperate reef ecosystems

Ecologically dominant species play a critical role in creating and maintaining many ecosystems. Through their influence on the local abiotic environment and biotic interactions, organisms such as trees, marsh grasses, mangroves, corals and seaweeds drive the structure and function of associated communities. In addition to providing biogenic habitats and food, they support a range of other ecosystem services, such as influencing landscape-scale energy flows, biogeochemical cycles (including carbon and nitrogen) protection against severe weather (storms, floods, waves etc.) and provision of harvestable resources. Consequently, there is a keen interest in understanding the past, present and future trajectories of these important species.

Seaweeds (macroalgae) are dominant habitat-forming species across at least ~25% of the world's coasts, particularly at temperate and polar latitudes (Schiel & Foster 2006, Bolton 2010, Steneck & Johnson 2013, Filbee-Dexter et al. 2019). Seaweeds are among the fastest-growing plants on Earth, and they contribute substantially to the structure and energy that support the incredible biodiversity and production for which many marine ecosystems are renowned. Seaweed species within the order Laminariales (Ochrophyta; brown algae) are often referred to as *kelp,* although the term is sometimes used more broadly (Bolton 2010, Fraser 2012, Steneck & Johnson 2013, Bolton 2016, Wernberg et al. 2019). Kelps provide many of the same ecological functions underwater as trees on land, and like terrestrial forests, which are typically defined simply by the presence of trees, kelp ecosystems are best described as *kelp forests* (Wernberg & Filbee-Dexter 2019).

Kelp forests and humans

Temperate rocky coasts where kelp forests dominate play an important role for humans in both extant and historical contexts. There is a long history of use of kelp by indigenous people around the world, both as food and as tools (Kuhnlein & Turner 1991, Lightfoot & Parrish 2009, Clarke 2011). For example, along the rocky coasts of southern Africa, early humans relied on mussels, limpets and other marine organisms associated with kelp forests, providing necessary omega-3 fatty acids and trace elements required for brain function and development (Compton 2011). A tight relationship between humans and kelp ecosystems is also the basis of the *kelp highway theory,* which proposes that the colonisation of maritime peoples from Asia to the Americas during the end of the Pleistocene was strongly facilitated by making extensive use of the resource-rich kelp forests found around the Pacific Rim (Erlandson et al. 2007, 2015). Despite being comprised of different kelp taxa, these ecosystems shared the key property of supporting a wealth of coastal resources including seaweeds, shellfish, fish, marine mammals and seabirds, which required minimal adaptive adjustments for migrating coastal peoples. In

Australia, aboriginal people used kelp as food and to make water-carrying vessels and footwear (Akerman 2005, Clarke 2011) and as part of cultural and ceremonial activities (Thurstan et al. 2018). The stipe and fronds of *E. radiata* were roasted and eaten as food, and selected parts were also made into utensils (Wesson 2009).

Kelp forests contribute substantial ecosystem services to human populations representing large economic values (Smale et al. 2013, Vásquez et al. 2014, Bennett et al. 2016, Blamey & Bolton 2017). In contrast to other marine ecosystems such as coral reefs, however, there are surprisingly few studies quantifying these values (Bennett et al. 2016). Nevertheless, it has been estimated that *E. radiata* forests contribute more than $10 billion per year ($1400/ha/yr) to the gross domestic product (GDP) in Australia alone through direct values from activities such as recreational and commercial fishing and tourism (Bennett et al. 2016). The total value of kelp forests, however, far exceeds this if also considering indirect and less tangible values such as biodiversity, coastal protection, nutrient cycling, fisheries enhancement and carbon storage. Moreover, the bequest value of kelp forests to coastal communities (i.e. the value they have to people simply knowing that they are there for future generations) is immense but immeasurable (DPI 2014). Considering these indirect values, seaweed habitats are the third-most-valuable ecosystem globally (Costanza et al. 2014).

Phylogeny and distribution

Phylogeny and global distribution

Laminarian kelps (Order: Laminariales) are thought to have emerged in the Northern Hemisphere about 80 million years ago. In contrast, dominant groups, including *Ecklonia*, were derived more recently (ca. 25 Ma; Silberfeld et al. 2010). Colonisation of the Southern Hemisphere by kelp species, however, may be more recent (Silberfeld et al. 2010, Rothman et al. 2017). On the east coast of Australia, phylogeographic histories of species, including *E. radiata,* are shallow, suggestive of origins <3 Ma (Durrant et al. 2015). The genus *Ecklonia* has previously been placed in different families, including Laminariaceae, Alariaceae and Lessoniaceae. Although these families are still recognised, gene transcriptomics now place *Ecklonia* in a new family, Arthrothamnaceae (Jackson et al. 2016).

The relationships of species within the genus *Ecklonia* have only recently become clear with comprehensive molecular studies (Figure 2). A phylogenetic study concluded that Northern Hemisphere and Southern Hemisphere *Ecklonia* species form separate clades (Rothman et al. 2015). Moreover, all the Southern Hemisphere samples studied (including *Ecklonia brevipes* from Australia), with the exception of South African *E. maxima*, formed a single species: *E. radiata* (Rothman et al. 2015). In addition, the species of *Eisenia* and *Eckloniopsis* fell within the *Ecklonia* clade, and thus *Eisenia bicyclis* and *Eckloniopsis radicosa* were resurrected and the new combination *Ecklonia arborea* proposed (formerly *Eisenia arborea*).

These findings radically change the accepted global distribution of the genus *Ecklonia*. *Ecklonia sensu lato* is thus the most globally widespread kelp genus and grows in all oceans. It is also the most warm-tolerant genus of the Laminariales (tom Dieck 1993, Terada et al. 2016, as *E. radicosa*). The origins of the genus, however, are still not clear. Although the genus *Ecklonia* appears to be more speciose in the northwest Pacific suggestive of Northern Hemisphere origins, the species identities in this region have not been clearly defined using molecular methods.

Ecklonia radiata displays a great deal of morphological variation throughout its range, even on small spatial scales (e.g. Womersley 1987, Stegenga et al. 1997, Wernberg et al. 2003a), confusing species identity. A number of morphological variants have been subsumed into *E.*

radiata, including *E. biruncinata, E. exasperata* and *E. richardiana.* There have been historical records of *E. radiata* (or species currently considered synonymous with *E. radiata*) in a number of world regions. The type of *E. biruncinata* Bory was a specimen collected by D'Urville in Concepcion, Chile. This appears to be an error, as there is no other evidence that *E. radiata* (as *E. biruncinata*) is present in South America. Collections have been made of populations of *Ecklonia* in Northwest Africa (Mauritania, Senegal) and neighbouring islands (Canary Islands,
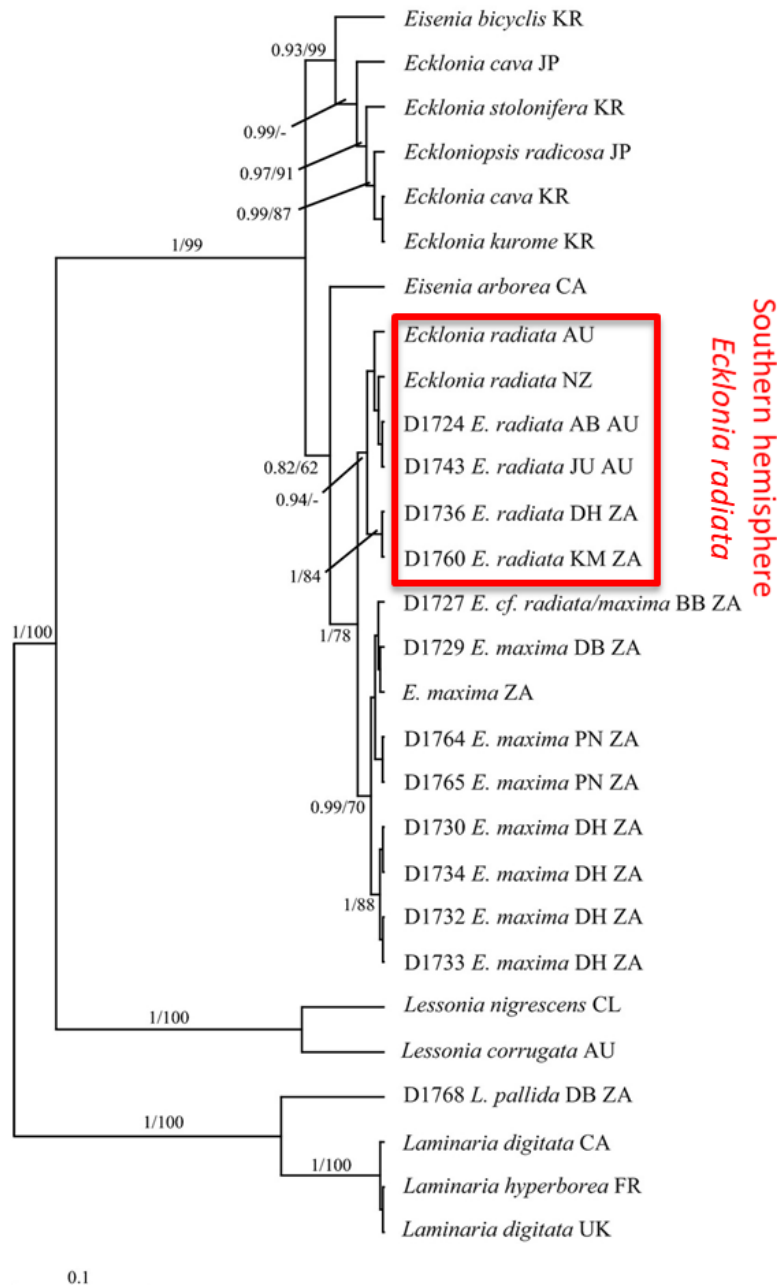

Figure 2 Phylogeny of *Ecklonia* and closely related species, showing all Southern Hemisphere *E. radiata* (Australia, New Zealand and South Africa) forming a distinct clade. Putative *E. radiata* specimens have been collected from Oman, Mauritania, Senegal and the Canary and Cape Verde Islands. However, molecular investigation is required to unequivocally confirm species identities. (Bayesian phylogeny based on concatenated rbcL/ITS alignment, from Rothman, M.D. et al.: A molecular investigation of the genus *Ecklonia* (Phaeophyceae, Laminariales) with special focus on the southern hemisphere. *Journal of Phycology.* 2015. **51**, 236–246. Copyright Wiley-VCH Verlag GmbH & Co. KGaA. Reproduced with permission).

Cape Verde Islands), particularly in upwelling and deeper sites. Some of these specimens were given the name *E. exasperate* (e.g. Kützing specimens in Leiden from Canaries and Cape Verde, Willem Prudhomme van Reine, pers. comm.). The *E. exasperata* type is from Tasmania, and this species is considered synonymous with *E. radiata*. The material from Mauritania was described as *E. muratii* by Feldmann (1937), and this name has been used more widely for the northeast Atlantic *Ecklonia* (Guiry & Guiry 2018). These putative *E. radiata* populations have not yet been sequenced, and their species identity and phylogenetic relationships remain unclear. Similarly, *Ecklonia* occurs in an upwelling zone on the northern Indian Ocean coast of Oman. These populations have always been described as *E. radiata*, also without molecular evidence on taxonomic relationships. It is clear that specimens of *E. radiata* collected outside the Southern Hemisphere require molecular investigation to confirm the species identity and ascertain the true distribution of this widespread kelp.

Continental distribution of E. radiata

As marine organisms, kelps are restricted upwards in the intertidal zone as they become increasingly limited by desiccation and other factors. In contrast to some other laminarian kelps, which can form extensive forests in the lower intertidal zone (e.g. species of *Undaria*, *Postelsia*, *Laminaria*), *Ecklonia radiata* is only occasionally found in the intertidal zone, suggesting that it is a true subtidal species with very low tolerances to desiccation (Larkum & Wood 1993). The exception is in South Africa, where *E. radiata* mostly inhabits the low intertidal/shallow subtidal (John Bolton, pers. obs.). However, the ecological performance of *E. radiata* has not been examined in a desiccation framework, implying that the mechanisms underpinning its absence from the intertidal zone remain speculative. Alternative, but less likely, models that need to be tested experimentally include competitive exclusion, grazer damage, light inhibition or ultraviolet (UV) damage.

Throughout its distribution in the Southern Hemisphere, *E. radiata* can be found on most subtidal rocky substrata from ~27°S to 48°S, except in South Africa where it is largely confined to the southeast coast, although deeper populations have recently been confirmed in Mozambique at 24°S (Figure 3). In Australia, *E. radiata* is found on temperate and subtropical rocky reefs along the entire continent and adjacent islands poleward of ~27°S (e.g. Houtman
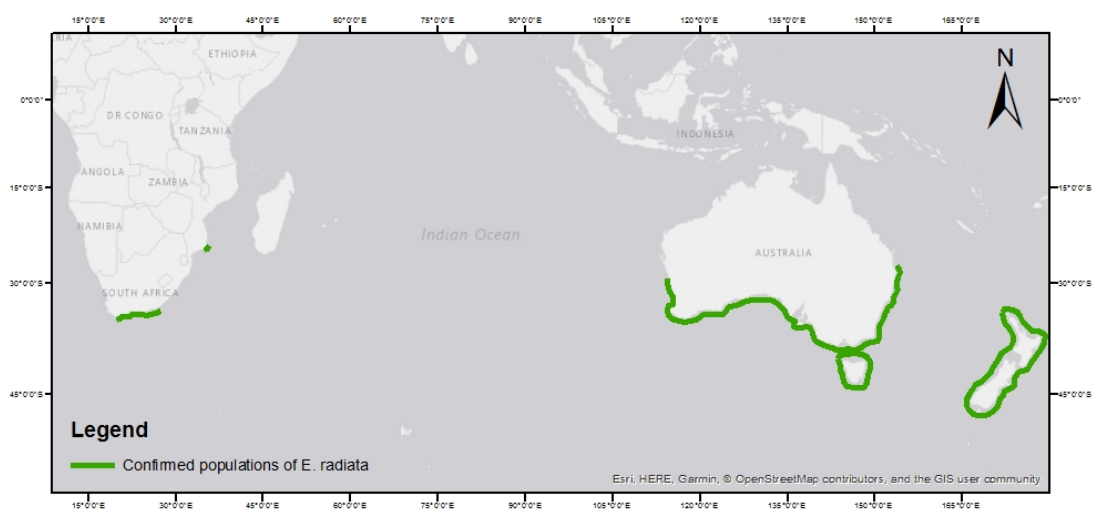

Figure 3 Distribution of *Ecklonia radiata* in the Southern Hemisphere. Putative *E. radiata* populations are also found in the Northern Hemisphere (Oman, Mauritania, Senegal and the Canary and Cape Verde Islands), although they remain to be confirmed using molecular methods and are not shown here.

Abrolhos, Western Australia; Tasmania; Moreton Island, Queensland) (Womersley 1987, Connell & Irving 2008, Wernberg et al. 2011c, Marzinelli et al. 2015b). This includes reefs on the open coast, as well as within estuaries such as Sydney Harbour (Coleman 2013, Johnston et al. 2015), where it is also found growing on artificial structures such as jetties (Marzinelli 2012). *E. radiata* occurs subtidally from the low tide mark to approximately 40-m depth, although large forests have been found at 60 m or more at the northern limit of its distribution on the Australian east coast (Marzinelli et al. 2015b), and to 80 m at its northern limit in New Zealand (about 30°S, Nelson et al. 2018). The vertical distribution and abundance of *E. radiata* varies with latitude and is related to physical factors such as light availability and water temperature, as well as biological processes such as grazing, resulting in marked biogeographical variation (Connell & Irving 2008, Marzinelli et al. 2015b).

On the east coast of Australia, *E. radiata* typically forms monospecific stands that are patchy (Underwood et al. 1991a, Connell & Irving 2008). In shallow waters (<~20 m), these patches can be driven by winter storm disturbances on small scales (Kennelly 1987a) and on larger scales, patches decrease in size and frequency south from around 32°S, representing a negative relationship to sizes and frequencies of sea urchin barrens formed by *Centrostephanus rodgersii* (Connell & Irving 2008). The range expansion of *C. rodgersii* to the northeast coast of Tasmania since about the 1950s has led to substantial changes from reefs dominated by dense forests of *E. radiata* and other seaweeds to sea urchin barrens (Johnson et al. 2005a, Johnson et al. 2011). In deeper waters (>about 30 m), the occurrence and abundance of kelp generally increase with latitude, despite some small-scale variability (Marzinelli et al. 2015b). Sea urchin barrens generally do not occur at these depths (but see Perkins et al. 2015); instead, reefs without kelp are dominated by sponges, solitary ascidians, byozoans and other encrusting invertebrates (Ferrari et al. 2018). At lower latitudes, the combination of high light availability and a significant decrease in water temperature at depths >30–40 m (<20°C in early summer) appears to maintain kelp forests at 30–60 m or more, with abundances that match dense forests at the highest latitudes (Marzinelli et al. 2015b). However, in shallower water at similar low latitudes, *E. radiata* stands become increasingly disjunct and rare (Vergés et al. 2016), presumably due to higher summer sea temperatures and greater herbivory, but also due to patchiness in availability of rocky reef habitat.

On the south and west coasts of Australia, *E. radiata* forests are much less patchy and typically occur in mosaics of mixed species with large canopy-forming fucoids (e.g. *Cystophora* spp., *Scytothalia dorycarpa*), covering most of the rocky reefs (Connell & Irving 2008, Wernberg & Connell 2008, Wernberg et al. 2011c, Coleman & Wernberg 2017). The distribution of *C. rodgersii* is limited to the east coast, and the absence of this herbivore from the continental south and west coasts may explain the marked differences in small-scale distribution patterns and patchiness of *E. radiata* compared with the east coast (Connell & Irving 2008). In shallow waters, the total extent of reef coverage by *E. radiata* and other fucoids does not change with latitude; however, the structure of the habitat does, with more monospecific stands of *E. radiata* at lower latitudes, presumably as cool-adapted fucoids disappear (Wernberg et al. 2003b, Wernberg et al. 2011c). Recent anomalies in water temperature during a strong marine heatwave caused significant reductions in the cover of fucoids at lower latitudes (Smale & Wernberg 2013), strengthening the latitudinal differences in heterogeneity, although these anomalies also led to strong declines of *E. radiata*, causing shifts from canopy-dominated to turf-dominated reefs at low latitudes (Wernberg et al. 2013a, Wernberg et al. 2016a). This pattern has also been observed along the east coast (Vergés et al. 2016; also see the section entitled 'Recent changes and future threats', later in this review).

Ecklonia radiata is the dominant laminarian kelp on rocky reefs throughout mainland New Zealand (Shears & Babcock 2007) but presumably due to the higher latitudes of the New

Zealand coasts, strong biogeographical patterns are not as evident as in Australia. On the northeast coast of the North Island, *E. radiata* forms extensive monospecific stands at depths >8 m (Schiel & Choat 1980, Schiel 1990, Shears & Babcock 2007) and can extend beyond 30 m in clear water (Grace 1983). It is found at lower densities at shallower depths, where it occurs in mixed stands with fucoids. *E. radiata* often has a bimodal distribution with depth in northern New Zealand due to the presence of sea urchin (*Evechinus chloroticus*) barrens, which can dominate between 3–17 m depths (Choat 1982, Shears & Babcock 2007). In southern New Zealand, *E. radiata* does not form extensive forests and is mostly restricted to shallower depths (<15 m) and usually occurs in mixed stands with several other species of seaweeds (Choat & Schiel 1982, Schiel 1990, Shears & Babcock 2007). *E. radiata* is notably rare in some regions, such as the west and southeastern coasts of the South Island (Shears & Babcock 2007). *E. radiata* has not been recorded in the Chatham Islands or in the sub-Antarctic Auckland Islands (Schiel 1990), except in the Snares Islands (Bolton & Anderson 1994). It occurs as far north as the Kermadec Islands (~29°S; Nelson et al. 2018).

In South Africa, *E. radiata* is mostly confined to the south and east coasts (Figure 3), where it forms a distinct subtidal fringe in sheltered habitats. It does not dominate the shallow subtidal, as it does in much of its Australasian distribution. The westernmost populations are around 60 km east of the southernmost point of Africa, the major biogeographical break of Cape Agulhas, and there is a single population further west at Bordjiesrif, on the Cape Peninsula (Rothman et al. 2015). There are also little-known subtidal populations on the Agulhas and Alphard Banks and at 25–30 m on Middle Bank (Tommy Bornmann, pers. comm.). At the eastern end of the distribution, *E. radiata* grows in the subtidal fringe only as far as the boundary between the Eastern Cape and KwaZulu-Natal provinces (Port Edward, De Clerck et al. 2005). The species occurs, however, in deeper subtidal populations, to at least 50 m and to the extreme northeast of South Africa (Sodwana), and specimens were recently collected from the subtidal in Mozambique (Kerry Sink, pers. comm.). The west coast kelp forests of the southwest coast of South Africa are dominated by the much larger *E. maxima*, which, until recently, was geographically separated from *E. radiata*. Around 2006, *E. maxima* extended its distribution approximately 70 km eastward, where the two species now grow on the same shores at De Hoop (Bolton et al. 2012) and may hybridise (Bolton & Anderson 1987, Rothman et al. 2015).

Ecophysiology and environmental drivers

Ecklonia radiata grows and reproduces across about 20° of latitude, from the shallow subtidal to a depth greater than 40 m (even as deep as 70–80 m in some places; Richmond & Stevens 2014, Nelson et al. 2018), and on reefs exposed to a wide range of hydrodynamic forces (Phillips et al. 1997, Goldberg & Kendrick 2004, Thomsen et al. 2004, Wernberg & Thomsen 2005, Wing et al. 2007, Connell et al. 2008a, Smale et al. 2011, de Bettignies et al. 2012). This wide distribution suggests that *E. radiata* has broad tolerance to many environmental conditions. A range of abiotic conditions, including both physical state factors (temperature, water motion, sediments, chemistry (salinity, pH and oxygen levels)) and resources (light, space/substratum and nutrients) may limit the performance and distribution of *E. radiata*. While individual conditions and resource levels have direct effects, they never affect *E. radiata* in isolation but rather interact in synergistic or antagonistic ways. This is particularly true for temperature, which affects all biological processes from subcellular enzyme kinetics to biogeographic distributions (Kordas et al. 2011). It is also important to note that performance responses may be different for gametophyte and sporophyte stages, as well as among different stages of sporophyte growth (juveniles versus adults) (Wood 1987, Thomsen et al. 2004, Franco et al. 2017), and knowledge about all life stages is required to fully understand what drives and limits population distribution (Russell et al. 2012).

Growth and primary production

The primary meristem of *E. radiata* is located just above the junction between the stipe and the primary blade. Consequently, growth and primary production can be quantified by punching a hole at the base of the central lamina above the meristem and measuring linear extension and biomass accumulation (BA) over time (Figure 4A, Mann & Kirkman 1981). These measurements have been done from the subtropical waters of the Houtman Abrolhos Islands (28°S) to the cooler waters of Doubtful Sound in New Zealand (45°S). Despite widely different environmental conditions, almost everywhere, individual kelps grow fastest in the austral spring (September–November) and slowest in late summer and autumn (February–April) (Table 1). These patterns tend to coincide with the periods when water temperatures are coolest and warmest, respectively, although the temperature maxima and minima differ. For example, the summer temperatures at the Houtman Abrolhos often exceed 24°C, while in Doubtful Sound, summer temperatures rarely exceed 20°C. For *E. radiata*, similar rates of primary blade growth have been recorded in New South Wales, South Australia and southern New Zealand ranging from 0.06 to 0.42 cm day^{-1}, and these are within the range recorded for other members of the order Laminariales (see Table 1 and Miller et al. 2011). Within this broad trend, growth is also positively correlated with the amount of light available (Fairhead & Cheshire 2004a, Bearham et al. 2013).

Table 1 Growth rates (linear blade extension using the hole punch method) and production in *E. radiata* over a range of studies, depths and locations.

Location	Extension (cm/ind/d)	Production (g/ind/d)	Depth (m)	Study
Western Australia: Abrolhos, 28°	0.03–0.2		2	Hatcher et al. (1987)
Western Australia: Jurien, 30°		0.7–6.3[w]	9–12	Bennett et al. (2015a)
Western Australia: Marmion, 32°	0.07–0.22	0.55–3.63[w]	2.5–17.3	Bearham et al. (2013)
Western Australia: Marmion, 32°	0.08–0.3		5–10	Hatcher et al. (1987)
Western Australia: Marmion, 32°		0.9–3.8[w]	8–11	de Bettignies et al. (2013b)
Western Australia: Marmion, 32°		0.4–4.6[w]	9–12	Bennett et al. (2015a)
New South Wales: Port Jackson, 33.8°	0.08–0.20	0.23–0.59[d]	1.5	Larkum (1986)
Western Australia: Hamelin, 34°		1.1–5.6[w]	9–12	Bennett et al. (2015a)
South Australia: West Island, 35°	0.08–0.22	0.16–0.79[d]	3–12	Fairhead & Cheshire (2004a)
New Zealand: Doubtful Sound, 45°	0.06–0.45	0.14–1.38[d]	15	Miller et al. (2011)

Note: w = wet weight and d = dry weight.

Figure 4 Measurements of *Ecklonia radiata* growth and productivity can be taken using methods including (A) tagging plants and 'hole-punching' to measure growth of the primary blade, which can be converted to biomass accumulation, (B) Pulse amplitude modulated (PAM) chlorophyll fluorescence to measure the rate of transport of electrons through photosystem II, which is increasingly used as a proxy for gross photosynthesis and (C) photorespirometry chambers to measure oxygen metabolism. (All photographs by the authors).

In a comprehensive study of *E. radiata* growth in southwestern New Zealand, growth rates were measured bimonthly for 15 months at two wave-exposed outer coast sites and one wave-sheltered fjord site (Miller et al. 2011), the seasonal patterns of growth were similar across all sites, with higher rates (0.4 cm/day) during spring (September–October) compared 0.1 cm/day in winter. However, growth rates were not correlated to a particular environmental parameter (light, inorganic nitrogen supply and water motion). However, while spring growth rates were higher than those of other seasons, those in spring 1999 (0.2 cm/day) were half those of spring 1998, illustrating variations that may be driven by differences in the environment between years.

Growth rate can also be expressed as biomass accumulation (BA, g dw/alga/day) if the dry mass is measured (Fairhead & Cheshire 2004a). BA of individuals for sites in Australia and New Zealand range from 0.12 to 0.98 g dw/alga/day (see Table 4 in Fairhead & Cheshire 2004a, Miller et al. 2011). In southern New Zealand, BA was similar for the wave-exposed and sheltered sites and (similar to linear growth) was maximal in spring. At West Island, South Australia, BA followed a similar seasonal pattern to that observed in New Zealand, with spring and summer rates being about 4 times greater than those in winter. Also, BA was lower at 3 m compared to 5, 10 and 12 m: this was because the tissue at 3 m was less dense; that is, it had less mass per unit area and was not related to linear growth rate, which was greater at 3 m compared to the other sites. In contrast, in northern New Zealand (Novaczek 1984a) and Perth, Australia (Kirkman 1989), BA was similar for samples taken at different depths. Light and temperature can have positive effects on BA, but the strength of these relationships vary with season, being stronger in spring and summer (Bearham et al. 2013).

Adding knowledge of population density (individuals per square meter) provides an estimate of primary production (g dw/m/day). BA primary production rates range from 0.43 to 12.1 g dw/ind/day (Miller et al. 2011) and again, are in the range of other Laminariales. In a New Zealand fjord, kelp density at outer-coast wave-exposed sites was much greater than that of the inner wave-sheltered site, resulting in a wave-exposed BA production rate that was five times greater than that of the wave-sheltered site, despite there being no difference in growth rates (Miller et al. 2011). Similarly, BA production rate was greater in deep (∼15 m) compared to shallow water, while growth rates were comparable (Novaczek 1984a, Kirkman 1989).

Measurements of net primary production (g C/m^2/day) for *E. radiata* are rare because carbon loss must be taken into account. Carbon loss due to tissue erosion can be measured using the hole-punch method (Mann & Kirkman 1981, de Bettignies et al. 2013b), and knowledge of tissue carbon content. However, the release of dissolved organic carbon (DOC) has not been measured for *E. radiata* or most other kelps, even though this can be a major carbon loss. For

example, 14% of *Macrocystis pyrifera* (Reed et al. 2015) and 26% of *Laminaria hyperborea* (Abdullah & Fredriksen 2004) production is released as DOC. To circumvent the limitations of *in situ* measurements, particularly relating to DOC, Rodgers & Shears (2016) used a physiological model to estimate primary production in relation to depth and season. The model showed that net primary production (NPP) was greater in shallow (6 m) compared to deep (14 m) water and was higher in summer (2.7–4.5 g C/m^2/day) compared to other seasons, with winter NPP close to zero at both depths. Of the few studies that have quantified erosion for *E. radiata* (Novaczek 1984a, Miller et al. 2011, de Bettignies et al. 2013b), results are difficult to compare because the methods used differ. However, one consistent finding is that erosion comprised a substantial proportion of the total biomass produced, a pattern consistent with kelps elsewhere (Krumhansl & Scheibling 2012). de Bettignies et al. (2013b) found that rates of erosion were highest during the austral autumn (when kelps grew slowly), and that this led to negative net production during this period. In contrast, in spring, kelps grew quickly and erosion was low, resulting in high net production. These patterns explained long-observed intra-annual trends in kelp biomass (e.g. Kirkman 1984, Wernberg & Vanderklift 2010). Whether via erosion or dislodgement, a high proportion of kelp production is exported beyond the kelp forest (see the section 'Community ecology of *Ecklonia* forests', later in this review, and Figure 8).

Photosynthesis and respiration

Photosynthesis and respiration have mainly been measured in the laboratory on small pieces of blade tissue (e.g. Stæhr & Wernberg 2009), and only rarely on whole individuals in the field (but see Fairhead & Cheshire 2004a, Rodgers et al. 2015, Figure 4C). Primary productivity of *Ecklonia radiata* is within the range of other Laminariales (Fairhead & Cheshire 2004a,b). At West Island, South Australia, primary productivity was five times greater, at 3 m (maximum about 2400 µmol O$_2$/m^2/day) than at 10 m (500 µmol O$_2$/m^2/day) throughout the year. Although there were some differences in rates of productivity in different months, there was no clear seasonal pattern at either depth (Fairhead & Cheshire 2004a).

Photosynthetic parameters, derived from photosynthesis (*P*) versus irradiance (*E*) curves, are a simple tool that has been used in conjunction with pigment content to examine how *E. radiata* acclimates (photoacclimation) to various irradiances. P_{max} is the maximum photosynthetic rate when light availability does not limit photosynthesis and the initial slope of the *P* versus *E* curve (α) is a measure of the light-harvesting ability at subsaturating irradiances. The compensation irradiance (*Ec*) is the irradiance at which net photosynthesis balances respiration, and E_k is the light saturation point. A strong gradient of light is found along Doubtful Sound, a fjord in southwestern New Zealand and provides a natural laboratory for studying mechanisms of photoacclimation in *E. radiata*, which grows at sites with maximum irradiances ranging from 650 to 1250 µmols photons/m^2/s^2 (measured at a 1-m depth in November 2000, Miller et al. 2006). P_{max} was similar at the five sites studied because the content of both chlorophyll *a* and accessory pigments was greater at low light compared to higher-light sites, which resulted in a greater ability to harvest light at low irradiances (i.e. increased α, Miller et al. 2006). Additionally, for the low-light sites, E_k was lower than at the high-light sites, as was E_c because of lower respiration rates. There was also a morphological acclimation, with blades being larger and thinner (i.e. greater surface area to volume ratio) at the low-light compared to high-light site, thought to reduce self-shading within the thallus.

Fairhead & Cheshire (2004b) studied photoacclimation of *E. radiata* in West Island, South Australia, at four depths during seven months of the annual cycle. The P_{max} tended to be greater in winter (May and June) compared to other times of year, for the four depths (3, 5, 10 and 12 m) studied. Alpha (α) was steeper and E_k lower in winter than summer, which is similar to the

New Zealand fjord study (Miller et al. 2006). However, at West Island, the differences observed in P_{max}, α and E_k were not explained by chlorophyll and accessory pigment content; although these parameters did vary with month, there were no clear patterns with season or depth.

Temperature affects all cellular processes, and therefore varying temperatures can influence photosynthetic and respiration rates. Respiration by *E. radiata* increases with increasing temperature, and adjustments of both E_c and E_k help maintain a positive carbon balance with increasing temperature (Stæhr & Wernberg 2009). The optimal temperature for net photosynthesis of *E. radiata* in Western Australia is 24°C, and rates decline at higher and lower temperatures, whereas respiration rates increase with increasing temperature between 0 and 30°C. The result is a thermal performance breadth ranging from 21.2°C to 26.5°C, and with relatively little variation across locations with different temperature regimes (Wernberg et al. 2016b). These tests, however, covered only a relatively narrow range of temperatures. In contrast to optimum temperatures, the temperature responsiveness differs between respiration and photosynthesis (Stæhr & Wernberg 2009, Wernberg et al. 2016b). Respiration rises faster than photosynthesis and peaks later, leading to a mismatch and inability to maintain positive carbon balance at higher temperatures. These differences likely have consequences for the capacity of these populations to respond to disturbances (Wernberg et al. 2010) and could be underpinned by genetic differences (Wernberg et al. 2018).

Carbon acquisition and pH

Based on widespread patterns in carbon-stable isotopes (i.e. typical ranges are between −24 and −14: Fenton & Ritz 1989, Vanderklift & Bearham 2014), *Ecklonia radiata* is a bicarbonate using seaweed that employs a carbon-concentrating mechanism or mechanisms (CCMs) to increase the supply of CO_2 to the enzyme Rubisco, which in turn fixes CO_2 into organic material (Beer et al. 2014). In an experiment in which the supply of CO_2 was increased, simulating the supply predicted for 2100 (i.e. ocean acidification), the $δ^{13}C$ of *E. radiata* became less negative (i.e. it increased), indicating greater uptake of CO_2 in the future (Britton et al. 2016). It has been hypothesised that greater CO_2 use in a future high-CO_2 ocean will enhance seaweed growth (Hepburn et al. 2011), but this may not be the case for *E. radiata,* as rates of photosynthesis and growth were unaffected by CO_2 supply in the laboratory (Britton et al. 2016) and in the field (Connell et al. 2018). This finding for *E. radiata* is similar to that of another Laminariales, *Macrocystis pyrifera*, which has at least two mechanisms for bicarbonate acquisition—an AE transporter plus external carbonic anhydrase (Fernández et al. 2014). However, for most seaweeds, including *E. radiata*, the types of CCM are unknown, but elucidating these mechanisms will be key to understanding responses to ongoing ocean acidification (Cornwall et al. 2017).

Numerous manipulative experiments that seek to examine the influence of pH on *E. radiata* have shown limited direct effects (Connell & Russell 2010, Connell et al. 2013, Provost et al. 2017, Connell et al. 2018). However, it may not be so much mean changes in pH that influence kelp, but rather normal diel fluctuations in pH that occur in supposedly healthy kelp forests (as a direct result of photosynthesis and respiration by the resident seaweeds), which benefit growth of juvenile sporophytes (Britton et al. 2016). In contrast, there is great potential for an increase in indirect effects of pH on *E. radiata* through competitive displacement (Connell et al. 2018), a result that appears commonly across widely different parts of the globe using contrasting methods (Connell et al. 2013). Carbon enrichment increases the growth of ephemeral algal species (turfs) which do not have CCMs but do have minor direct effects on *E. radiata* (Falkenberg et al. 2013a). This leads to a switch in competitive advantage, whereby turfs replace *E. radiata* (Connell et al. 2008b, Gorman et al. 2009). *E. radiata* forest collapse

is worsened when the increased production of turfs is exacerbated by reduction in its consumption by herbivores (Connell & Ghedini 2015). What this means is that small cumulative increases in carbon enrichment drives a much greater consequence than would be predicted from linear effects measured between competitors (e.g. *E. radiata* versus turfs) because these interactions are embedded within a broader network of change that propagates collapse.

Nitrogen uptake, C:N ratios and enrichment

Nitrogen is the nutrient that most commonly limits seaweed primary production. It is available in two dissolved inorganic forms, nitrate (NO_3^-) and ammonium (NH_4^+), the supply of which varies with season. Nitrate is available at higher concentrations in winter compared to summer, whereas ammonium is available at low concentrations year round (Hurd et al. 2014). *Ecklonia radiata* from Doubtful Sound, New Zealand, has nitrate uptake rates (at 10 µM) ranging from 0.13–1.6 µmol/gdw/s, compared to a slightly greater range for ammonium uptake of 0.07–3.0 µmol/gdw/s (Miller et al. 2006). In this system, nitrate and ammonium are available at similar concentrations (2–4 µM) for most of the year, and so make a similar contribution to primary production. However, this likely depends on the relative availability: *Ecklonia maxima* in South Africa takes up nitrate and ammonium simultaneously and at similar rates, but because the supply of nitrate in this upwelling system is much greater than that of ammonium, ammonium accounts for only 4% of total N acquired (Probyn 1985).

The ratio of tissue carbon to nitrogen (C:N) is a useful indicator of whether or not nitrogen is limiting primary production. Values of ~15–20 indicate nitrogen sufficiency for kelps, whereas those >20 indicate nitrogen limited growth. In southern New Zealand, C:N ratios of *E. radiata* range from 18 to 52 and are between 18 and 30 for most months, except between February and May when they can be >30 and >50 at wave-exposed and -sheltered sites, respectively (Miller 2004). In summer (i.e., December) in Western Australia, C:N ratios ranged from 25 to 44 and were positively correlated with temperature across a latitudinal gradient (Stæhr & Wernberg 2009). These results indicate that nitrogen may be limiting primary production throughout much of the year, with greater limitation during summer, at wave-sheltered and warm sites. Enrichment of nitrogen in South Australia caused the spring increase in biomass of *E. radiata* to triple (August–October), with a concomitant increase in $\delta^{13}C$ of tissue and decrease in the C:N ratio (Falkenberg et al. 2013b). These results are consistent with observations of the oligotrophic nature of the south coast (Connell 2007a), with high C:N ratios of kelp under ambient conditions indicating N-limitation, while the lower ratio under enrichment indicating lower N-limitation. Variation in such limitations among taxa have implications for the competitive balance of major ecosystem components under conditions of increased resource availability (Connell 2007b).

The transfer of nitrogen across ecosystem boundaries is considered one of the more important forms of natural resource subsidy, owing to its strong influence on both biological and abiotic characteristics of recipient systems (Polis et al. 1997). The degree to which nitrogen subsidies mediate kelp loss is contingent on both ambient and historical concentrations (Gorman et al. 2009) and the capacity of the system to assimilate additional nutrients (Marczak et al. 2007). Indeed, losses of *E. radiata* forests are greater where the difference in nitrogen availability between land and sea is larger (Gorman et al. 2009). The loss of *E. radiata* forests from nitrogen overloading represents the cumulative effect of failure of kelp to recover from pulse events (e.g. storms) that remove individuals or patches of individuals (Connell et al. 2008b). Eutrophication increases the accumulation of turfs and sediments following localised disturbances, preventing the recruitment of kelp (Gorman & Connell 2009). These localised impacts may be unconnected in time and space, but over many years, they coalesce and become

substantial across broader areas (Connell et al. 2008a). Consumption by herbivores may buffer the expansion of turfs during nutrient enrichment (McAllister & Bornman 1972, Sarnelle 1992, Russell & Connell 2005) and other resource perturbations (Ghedini et al. 2015, McSkimming et al. 2015). By keeping turf abundance in check and maintaining turf-free space, herbivores facilitate *E. radiata* recruitment and persistence (Gorman & Connell 2009).

Temperature

Laminarian kelps are generally considered cool-water organisms (see the section entitled 'Phylogeny and distribution', earlier in this review), but *Ecklonia* is the most temperature-tolerant genus in the order and many species are found in warm-temperate and subtropical waters. Biogeographically, *E. radiata* is found between about 8°C and 25°C (Bolton & Anderson 1994), and temperature is a significant determinant of the regional distribution of *E. radiata* (Wernberg et al. 2011a,b, Martinez et al. 2018) although physiological (adaptation) and biological (competition, herbivory) mechanisms can offset simple relationships between ocean temperature and local abundances (Connell & Irving 2008, Wernberg et al. 2010).

Metabolic processes such as photosynthesis and respiration show strong temperature dependency. In Western Australia, photosynthesis increases until about 24°C, after which it declines rapidly (Stæhr & Wernberg 2009, Wernberg et al. 2016a,b). Respiration, on the other hand, increases beyond about 24°C, driving a mismatch at high temperatures that implies that the seaweeds cannot maintain a positive carbon balance at high temperature (Stæhr & Wernberg 2009, Wernberg et al. 2016a,b). Physiological studies of sporophytes in Western Australia found only minor variation in optimum temperature across populations 6° latitude/4°C apart (Stæhr & Wernberg 2009, Wernberg et al. 2016a,b), suggesting little local adaptation in adult sporophytes. Nevertheless, the temperature dependency of both photosynthesis and respiration varied considerably depending on the local environment with lower Q10 values under warmer conditions (photosynthesis Q10: 3.35–1.45 and respiration Q10: 3.82–1.65), presumably an adaptation to keep metabolic rates under control in warm environments (Wernberg et al. 2010). Temperature can also act antagonistically with other stressors such as ultraviolet radiation B (UVB). For example, Xiao et al. (2015) demonstrated that negative effects of higher UVB on photosynthesis and growth were alleviated at warmer temperatures, possibly due to induction of photo-repair. At higher temperatures and UVB, *E. radiata* also decreased accessory pigments in the thallus (Xiao et al. 2015).

In Australia, *E. radiata* sporophytes are generally larger, have more reproductive tissue, grow faster and have lower mortality in cooler than in warmer waters (Hatcher et al. 1987, Mabin et al. 2013). Reduced growth and productivity have also been associated with seasonally warm water (Fairhead & Cheshire 2004a,b, Bearham et al. 2013). Temperature also affects reproduction and gametophyte development (Novaczek 1984a,b,c, Mohring et al. 2014). The optimum temperature for gametophyte development is broad, but shows regional differences consistent with thermal adaptation (12°C–20°C, New Zealand, Novaczek 1984a,b,c, 18°C–22°C, South Africa, Bolton & Anderson 1987, 18°C–23°C, Australia, Mohring et al. 2014). Still, lethal temperatures for gametophytes appear to be well above maximum temperatures experienced in the field (Novaczek 1984a,b,c, Mohring et al. 2014) suggesting that this life stage is not limited by high temperatures. It is, however, possible that minimum temperatures for gametophyte growth and reproduction set the cool limit for the species (Novaczek 1984a,b,c).

Temperature can alter interactions among *E. radiata* and its competitors, grazers and associated predators. Intraspecific competition is weaker where water temperatures are warmer, and canopy cover facilitates rather than competes with recruits (Wernberg et al. 2010,

Bennett et al. 2015b). Warming waters can also drive mismatches between consumption and predation, whereby urchin grazing on *E. radiata* increases but consumption pressure on urchins (by lobsters) decreases at higher temperatures, driving accelerated kelp loss (Provost et al. 2017). The interactive effects of temperature and CO_2 can indirectly affect *E. radiata* via positive effects on kelp competitors. For example, warmer temperatures increased the proliferation of turf competitors, particularly under elevated CO_2, which may inhibit kelp recruitment and recovery in future oceans (see the section entitled 'Recent changes and future threats', later in this review; also see Connell & Russell 2010). In conclusion, temperature affects all aspects of the biology of *E. radiata* from evolutionary scales and patterns of distribution through to contemporary impacts on physiology and biology. It interacts with other environmental and biological drivers through direct and indirect mechanisms to modify extant patterns and response to change.

Water motion: Waves

Water motion is a fundamental environmental state condition that affects all marine organisms. In marine systems, waters are never stagnant, and like other seaweeds (Hurd 2000), hydrodynamic forces affect the performance of *Ecklonia radiata*. Tidal currents play a relatively minor role in most places where *E. radiata* is found, and wave exposure is by far the dominant hydrodynamic force affecting the species. *E. radiata* is found across a wide range of wave exposures (Phillips et al. 1997, Turner & Cheshire 2003, Goldberg & Kendrick 2004, Thomsen et al. 2004, Fowler-Walker et al. 2005, Fowler-Walker et al. 2006, Wernberg & Thomsen 2005, Wing et al. 2007, Smale et al. 2011, de Bettignies et al. 2012), but typically it becomes increasingly replaced by other canopy-forming seaweeds (*Cystophora* spp., *Sargassum* spp.) and turf-forming species at low wave exposures and by other canopy-forming seaweeds (e.g. *Scytothalia* and *Phyllospora*) or sessile invertebrates at very high wave exposures (Turner & Cheshire 2003, Coleman et al. 2008, Wernberg & Connell 2008).

Wave forces are essential to break down boundary layers around the thallus, remove waste products and increase nutrient uptake rates (Hurd 2000). However, during storms, wave forces can result in pruning (removal of part of the frond) or dislodgment (removal of the entire kelp) from the substratum. Fully grown *E. radiata* can withstand water velocities of 2–5 m/s (Thomsen et al. 2004, de Bettignies et al. 2013b). *In situ* biomechanical pull-tests show that *E. radiata* often break above the meristem (pruning) at a force of 150–250 N, suggesting that recovery could be possible. This occurred more frequently on hard (igneous rock) compared to soft (sedimentary rock) substrata (Thomsen et al. 2004). On soft substrata, such as limestone rock, adult kelps typically break at the reef, often removing part of the rock and thereby resetting succession (Thomsen et al. 2004). Biomechanical measurements and calculations also suggest that *E. radiata* recruits are a lot less limited by wave forces than adults, as drag increases disproportionally with frond size compared to the attachment strength (Thomsen et al. 2004). Consequently, break velocities for adult *E. radiata* (2–5 m/s) are much lower than that for recruits (10–25 m/s). Moreover, *E. radiata* holdfasts are often found in fused aggregates, which appear to decrease dislodgment frequency through morphological changes and thallus compaction during the drag phase of the wave cycle (Wernberg 2005).

It is commonly observed that kelps have substantial morphological changes to reduce drag and increase attachment strength in response to wave exposure. Several studies suggest that *E. radiata* respond to wave forces by being smaller, having narrow laterals and blades, fewer spines, larger holdfasts and thicker blades and laminae (Fowler-Walker et al. 2005, Wing et al. 2007, Miller et al. 2011). Still, not all studies have reported consistent effects of wave exposure on specific morphological traits (Wernberg & Thomsen 2005). One reason could be that at peak flow velocities, *E. radiata* compacts (Wernberg 2005) such that only size (surface area),

not morphological traits, influences dislodgement and thereby survival (de Bettignies et al. 2013a). A tagging study of thousands of *E. radiata* from Western Australia found relatively low and constant dislodgement rates across seasons and wave exposures (de Bettignies et al. 2015), despite stronger wave action in winter and on exposed reefs. It was suggested that winter reduction in biomass through frond erosion, reduces kelp size (and hence drag) and thereby decouples the expected relationship between dislodgment, season and wave exposure (de Bettignies et al. 2013b, de Bettignies et al. 2015), as has also been indicated for other laminarian species (Johnson & Mann 1986).

While most biomechanical studies of *E. radiata* have focussed on 'healthy' kelps, small perforations are common in kelp thalli (cf. Figure 9). Tissue break-force tests show that holes and tears to the *E. radiata* thallus reduces the strength, extensibility, toughness and stiffness of the tissue by up to 82% and can dramatically increase susceptibility to breakage during storms (de Bettignies et al. 2012). These wounds can be found at all wave exposures, but they are most prevalent in early winter, suggesting that wounds accumulate over summer when waves are generally small (Lemm et al. 1999) and that wounded parts of the thallus break off as storms pick up in autumn and winter (de Bettignies et al. 2012). The ecological implication is that this pruning reduces kelp size and hydrodynamic drag and ultimately lowers the risk of fatal dislodgment during severe winter storms. Hence, where storms drive loss, they tend to sever individuals from above the holdfast rather than detaching the holdfast from rock (Goodsell & Connell 2005a).

Sediments and sedimentation

Sedimentation and turbidity are among a broad spectrum of land- and ocean-based activities, coupled with continued growth of the human population (Ruffin 1998, Airoldi 2003) and migration to coastal areas, that are driving unprecedented and complex changes in water chemistry (Boesch et al. 2001) and ecology of kelp forests (Connell 2007b, Filbee-Dexter & Wernberg 2018). *Ecklonia radiata* forests generally prevent the accumulation of sediment and turfs under their canopy (Melville & Connell 2001, Connell 2003a, Wernberg et al. 2005) and adult plants can survive and grow under a range of sediment loads. However, there appears to be a bottleneck at attachment and burial of microscopic stages (cf. the section entitled 'Ecophysiology and environmental drivers', earlier in this review) by sediment (Connell 2007b). Hence, *E. radiata* is rare or sparsely distributed in areas with extensive sedimentation, but variations in sedimentation with light and abrasion provide a strong set of physical conditions (Irving & Connell 2002, Connell 2005) that drive heterogeneity among various canopy types (Turner & Cheshire 2003, Connell 2007a).

Substratum and space

Hard substratum is of fundamental importance to kelp, providing space for settlement and growth of the holdfast structure. *Ecklonia radiata* can create extensive monospecific forests on a variety of rock types, including sandstone, limestone, granite and basalt (Underwood et al. 1991b, Wernberg et al. 2003b, Thomsen et al. 2004, Tuya et al. 2008, Tuya et al. 2009), with one study suggesting that densities are higher on limestone than granite reefs (Harman et al. 2003). *E. radiata* can be found on pebbles, boulders and large extensive reefs, where the minimal size of inhabitable rock can be predicted from the thallus size (which scale with attachment strength), its drag and wave exposure (the imposed force) (Thomsen et al. 2004, Thomsen & Wernberg 2005). *E. radiata* can also be dominant (with densities of >25 kelp/m^2) regardless of topographic complexity, ranging from simple to very complex reef topographies (Toohey 2007), although with higher density on low- compared to high-relief reefs (Harman et al. 2003). *E. radiata* readily settle on artificial substrates (e.g. Smale et al. 2011) and can often

be found on the vertical surfaces of coastal infrastructure, such as pier-pilings and seawalls (Marzinelli 2012, Marzinelli et al. 2018). No studies have looked at the importance of microtopography, such as cracks and crevices, although such features likely increase the settlement and attachment strength of gametophytes and provide a refuge from predators (Franco et al. 2015, Bolton et al. 2018).

Life history, dispersal and recruitment

Life cycle, reproduction and phenology

Ecklonia radiata has a typical laminarian life cycle, with alternations between a microscopic haploid gametophyte stage and macroscopic diploid sporophyte stage (Figure 5). *E. radiata* does not produce sporophylls. Instead, zoospores develop within the tissue of the main lamina and basal part of the laterals. When reproductively mature, sporogenic tissue becomes visible as slightly discoloured raised patches (Figure 5A). Zoospore production in *E. radiata* can be as high as ~1000–2000/mm^2 of lamina (Mohring et al. 2014) and seasonal timing of zoospore production appear to vary geographically. In Western Australia, peaks in both the presence of sori (Figure 5A) and zoospore (Figure 5B) release occur from mid-summer (January) to the end of autumn (May) and are positively correlated with seawater temperature and occur synchronously across the coast (Mohring et al. 2013a,b). It has been suggested that the timing of maximum zoospore production and release occurs when conditions are optimal for gametophyte germination, growth and subsequent sporophyte development, and this may be a strategy to increase success against competing algae (Mohring et al. 2013b). In contrast, in Tasmania, *E. radiata* has sori and produces zoospores throughout the year, but often with peaks in autumn and winter when seawater is coldest (Sanderson 1990, M. Tatsumi, unpbl. data). However, even though zoospores are produced throughout the year in Tasmania, they are not always viable—particularly during the summer (M. Tatsumi, unpbl. data). As well as external environmental factors, the amount of zoospores released per plant will reflect lamina morphology/size, with lamina length being a strong predictor of the amount of reproductive tissue (Mabin et al. 2013). The onset of sorus production appears to depend on thallus size and season, not age (Novaczek 1984a). In New Zealand, frond surface area needed to be at least 300 cm^2 and stipe diameter around 14 mm (Novaczek 1984a) for thalli to become reproductive. The fact that size (lamina length) is a strong predictor of the amount of reproductive tissue indicates that morphological changes in response to human impacts (e.g. warming) are likely influence the overall reproductive capacity in *E. radiata* (Mabin et al. 2013).

Once *E. radiata* zoospores are released, they have the ability to swim for at least 24 h (although they often do so for only 1–2 h), until they settle onto the substratum and germinate into male or female gametophytes (Figure 5C). Given the size of both zoospores (~5 µm) and gametophytes (~100–400 µm; Mabin et al. 2013, Mohring et al. 2014), the settlement of *E. radiata* is usually difficult to measure directly, and little is known about the processes that influence these very early life history stages in the field. The understanding of gametophytes is largely limited to laboratory studies. Gametophyte recruitment (i.e. densities) can be quantified in the laboratory at various times post-settlement up until the fertilisation of oogonia (Mabin et al. 2013, Mohring et al. 2013b, Mohring et al. 2014, Tatsumi & Wright 2016). After 12–15 days (by which time gametogenesis has typically occurred), successful recruitment of gametophytes (i.e. as a percentage of zoospores released) ranges between 0% and 50% (Mohring et al. 2013b). Gametophyte recruitment peaks between 16°C and 20°C and generally declines with increasing temperature (Mohring et al. 2013a, Mohring et al. 2014), increasing light (above 40–60 µmol photon/m^2/s) and decreasing zoospore density (Tatsumi & Wright 2016). Nonetheless, *E. radiata* gametophytes appear to be among the most temperature tolerant in the Laminariales, with an upper temperature tolerance of 26°C (New Zealand, Novaczek
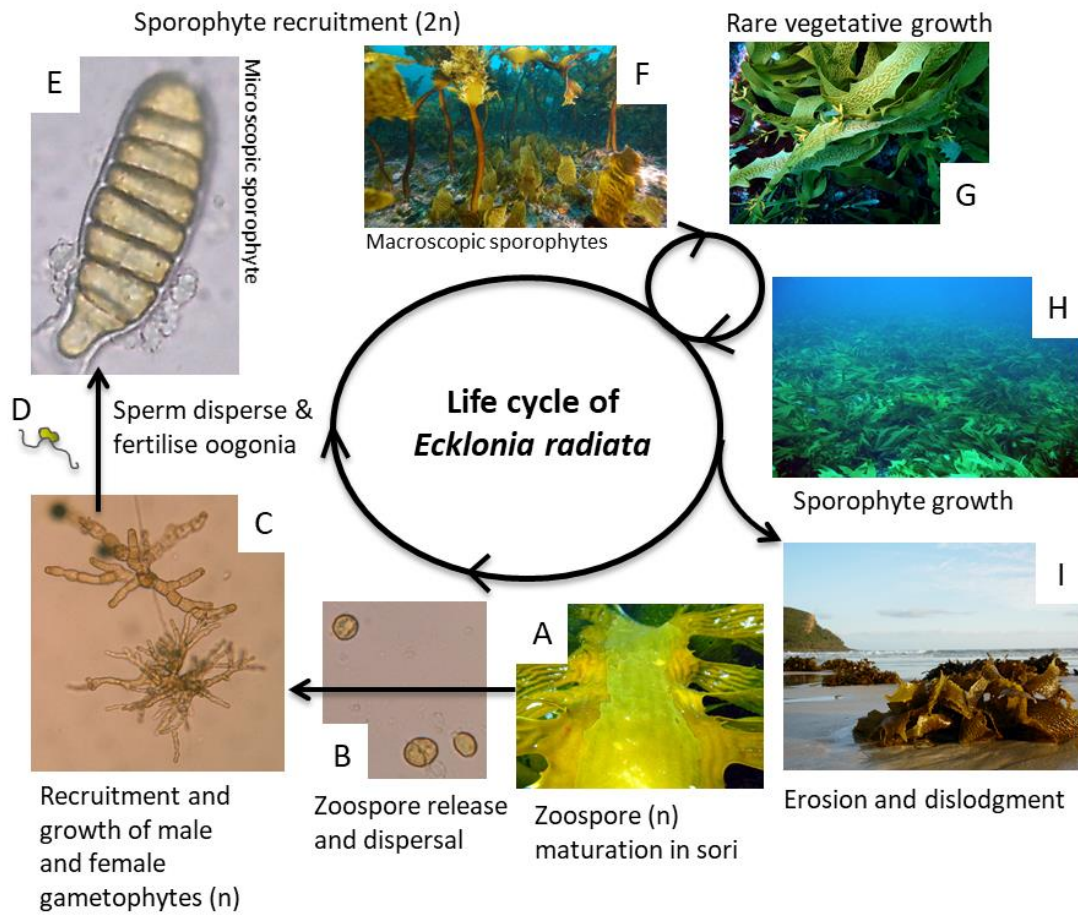
Figure 5 Life cycle of *Ecklonia radiata* from sorus tissue to kelp forest and detritus. (A) Macroscopic sporophytes become reproductive bearing sori (seen as slightly raised tissue) that release motile zoospores (B). Zoospores settle and grow into separate male and female gametophytes (C). (D) Sperm disperse and oogonia on female gametophytes are fertilised and juvenile (E) microscopic and (F) macroscopic sporophytes (in the understorey) develop. Sporophytes recruit and grow through stages 1, 2 and 3 (Kirkman 1981), often forming (H) dense, monospecific forests. (G) In some populations, known only in the Capes region in Western Australia, sporophytes can reproduce vegetatively. (I) Sporophytes are often dislodged or eroded during storms and detritus transported into other habitats where they provide important spatial subsidies (see the section entitled 'Community ecology of *Ecklonia* forests'). (All photos by the authors and Nahlah Abdullah Alsuwaiyan).

1984a; and South Africa, Bolton & Anderson 1987) to 28°C (Australia, tom Dieck 1993). The size of gametophytes varies between regions and is generally greatest at temperatures between 13°C and 15°C (New Zealand, Novaczek 1984a), 20°C–22°C (South Africa, Bolton & Anderson 1987; and Western Australia, Mohring et al. 2013b, 2014), 16.5°C–22°C (Tasmania, Mabin et al. 2013) and at higher light levels (Novaczek 1984b, Tatsumi & Wright 2016). Thus, it appears overall that gametophyte recruitment is susceptible to increasing temperatures and light, but those conditions result in better growth. In the field, low-light conditions that are best for gametophyte recruitment are found beneath the *E. radiata* canopy; light beneath the canopy varies as a function of season, time of day and canopy cover, but it is typically <100 µmol photon/m²/s and can be reduced by as much as 95% (<10 µmol photon/m²/s) compared to above the canopy (Wernberg et al. 2005, Tatsumi & Wright 2016). Temperature and light also influence egg production, with with most rapid egg production for South African *E. radiata* (as

E. biruncinata) in the range of about 15°C–19°C, but eventual maximum egg production per female at about 22°C (Bolton & Anderson 1987), a similar pattern is also seen for *E. radiata* in New Zealand (Novaczek 1984c). In addition, other factors including sedimentation, scour, grazing and pollutants are likely to affect these small gametophytes, but studies are scant.

Sporophytes are visible after 30–35 days (laboratory-grown microscopic sporophytes are clearly visible at this time, about 500 µm; Figure 5E). Recruitment appears to be negatively affected by high temperature (no sporophyte development at temperatures >22°C; Mabin et al. 2013) and low light (no sporophyte development <10 µmol photons/m²/s; Tatsumi & Wright 2016). Bolton & Anderson (1987) measured growth of 5 week-old sporophytes (c.1 mm in length) in South African *E. radiata* (as *E. biruncinata*) and found that they survived and grew over 2 weeks from 4°C to 26°C, with a broad optimal range for growth from 15°C to 22°C. Again, knowledge of processes affecting young sporophytes are biased towards laboratory studies due to the difficulties in finding and measuring microscopic states in the field. Although very small sporophytes have been measured in the field using an underwater microscope (Kennelly & Underwood 1984), recruitment in the field is usually measured when sporophytes are visible to the naked eye (i.e. stage 1 sporophytes, Kirkman 1981, Figure 5F) and have already undergone early post-recruitment mortality. Nevertheless, survivorship during the transition from microscopic to macroscopic recruitment in *E. radiata* has been estimated as ~0.6% (Tatsumi & Wright 2016), which is similar to other kelps for which this transition has been measured in the field (Schiel & Foster 2006).

Surviving *E. radiata* sporophytes are predominately perennial. The exception is at the Houtman Abrolhos Islands, off Western Australia, where plants could be annual (Hatcher et al. 1987). Stipe growth ring analyses suggests that individuals can be up to 10 years old in some places (Novaczek 1981), although in many other places, individuals are considerably younger, with maximum ages of 2–4 years (Larkum 1986, Andrew 1993, Wernberg 2005). Demographic modelling of tagged kelp populations from the same site studied by Novaczek indicate that while average age of mature plants in undisturbed deep water stands may reach 7 years (Haggitt 1999), disturbances such as dieback (Cole & Babcock 1996) shorten longevity to around 3 years and even as short as 1 year in shallow water stands (Haggitt 1999).

Although *E. radiata* generally exhibits a typical alternation of generations (haplodiplontic) life history strategy, vegetative reproduction from the thallus has been described in one population from Western Australia (Coleman & Wernberg 2018). Vegetatively reproducing sporophytes of *E. radiata* (Figure 5G) were formerly identified as a separate species, *E. brevipes*, first described from New Zealand (Huisman 2000), but recent genetic studies have revealed that Australian *E. radiata* and Australian *E. brevipes* are genetically similar and likely a single species (Rothman et al. 2015). Taxonomic relationships of the Western Australian 'brevipes' variant to the type locality of *E. brevipes* from New Zealand remains unknown. Despite strong morphological differences, *E. radiata* and *E. brevipes* are only weakly genetically differentiated where they co-occur in Western Australia, likely because *E. brevipes* can still undergo a haplodiplontic life cycle and interbreed with *E. radiata* (Coleman & Wernberg 2018). Hence, it is likely that *E. brevipes* is a vegetatively reproducing morph of *E. radiata* and it is treated as such here. The propensity for vegetative propagation of this morph is huge, with up to 20 small, club-like haptera (rudimentary holdfasts) produced on the margins of secondary laminae of each adult sporophyte (Coleman & Wernberg 2018). Although a similar form of vegetative reproduction has been described from drift *E. radiata* from New Zealand (Lindauer 1945), what is unique about Australian *E. radiata* is that vegetatively produced haptera eventually make contact with the substratum, attach to rocks by lodging in cracks and crevices and are subsequently torn off the parent plant, creating a new clonal individual (Lindauer 1945, Lindauer et al. 1961) and becoming a functional part of the local

kelp forest community. This mode of vegetative reproduction is unique among seaweeds and higher plants because it involves the reversal in polarity of growth and meristematic tissue, with the apex of the thallus becoming the holdfasts of new individuals (Lindauer 1945).

Dispersal and population connectivity

Dispersal and gene flow are critical ecological processes that connect populations and facilitate population recovery and persistence. Gene flow within and among populations ensures adequate genetic diversity to allow populations to respond to changing environmental conditions and stressors. *Ecklonia radiata* can disperse via three modes; zoospores, sperm and detached fertile drift material. There are few field studies on *E. radiata*. Studies on spore and sperm dispersal in other Laminariales suggest that sperm only disperse the small distances (centimetres) over which pheromones from the female gametophyte are effective (Reed 1990, Maier et al. 2001), and this is perhaps why self-fertilisation is common (Raimondi et al. 2004). Dispersal of zoospores (Reed et al. 1988) and detached fertile drift material (Hernández-Carmona et al. 2006) are the likely modes of longer distance dispersal. Zoospores may disperse widely within local populations (kilometres; Gaylord et al. 2002, Reed et al. 2004, Gaylord et al. 2006) but rapidly decline thereafter (among reefs). Similarly, fertile drift material of *E. radiata* is negatively buoyant and may disperse over long distances only via rafting with co-occurring buoyant species (e.g. *Sargassum* spp.).

Given the microscopic size of propagules, directly measuring dispersal is difficult. Dispersal measurements rely on direct observations of recruitment or indirect genetic methods. These latter techniques estimate gene flow and dispersal in sporophytes (microscopic gametophytes have never been observed in the field), so the relative contribution of dispersal modes is unknown, and each may play a key role in the population genetics of *E. radiata*. Population genetic studies on *E. radiata* using neutral microsatellite markers (Dolman & Coleman 2009) have identified that genetic structure around the Australian continent is weak, suggesting widespread gene flow that is mediated by the strength and direction of prevailing ocean boundary currents (Coleman et al. 2009, Coleman et al. 2011b, Figure 6) acting on shallow phylogeographic histories (Durrant et al. 2015). Strong relationships exist between the relative strength of each of Australia's boundary currents and overall genetic structure (F_{ST}) of *E. radiata* populations within those currents (Coleman et al. 2011b (Figure 6), Wernberg et al. 2018). Moreover, continental scale estimates of pairwise population genetic structure (F_{ST}) are positively correlated with oceanographic dispersal time (Coleman et al. 2013a, Figure 6).

On regional scales, dispersal and gene flow of *E. radiata* populations are also positively correlated with oceanographic dispersal time and the strength of prevailing currents, but the complexities of latitude and effective population size are apparent (Coleman et al. 2009). For example, populations of *E. radiata* at the low-latitude margins on both the east and west coasts of Australia have lower genetic diversity (expected heterozygosity and number of alleles), suggesting lower effective population size and limited dispersal (Coleman et al. 2011b, Wernberg et al. 2018). This is likely a result of limited connectivity from higher latitudes due the predominately poleward flow of boundary currents, as well as fragmentation of populations because rocky reef habitat is limited (New South Wales, Coleman et al. 2011a) or populations have undergone declines (Western Australia; Smale & Wernberg 2013, Wernberg et al. 2013a, 2016a, Provost et al. 2017, Vergés et al. 2016). Regardless, the erosion of genetic diversity within these populations combined with limited and declining connectivity (Coleman et al. 2017) confer on low-latitude *E. radiata* populations a limited ability to respond to climatic change and disturbance (Wernberg et al. 2010, Wernberg et al. 2018).
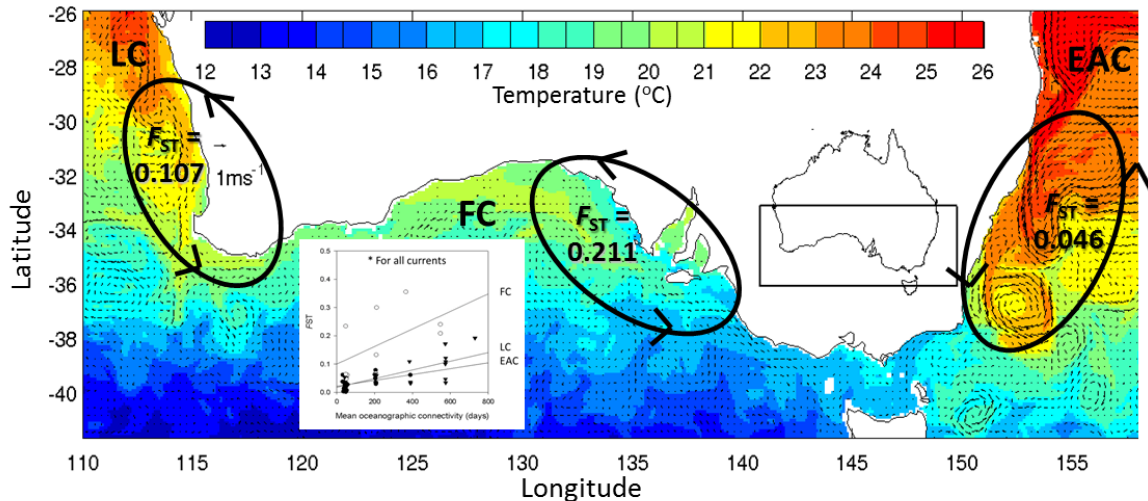
Figure 6 Genetic estimates of population connectivity (F_{ST}) of *E. radiata* within each of Australia's boundary currents: The East Australian Current (EAC), the Flinders Current (FC) and the Leeuwin Current (LC). Overlaid on an example of current strength, direction and temperature over a 6-day period in the austral autumn (Adapted from Coleman, M.A. et al. 2011b. *Journal of Ecology* **99**, 1026–1032). The inset graph shows positive correlations between mean oceanographic connectivity time and genetic structure (F_{ST}) within each boundary current. (Adapted from Coleman, M.A. et al. 2013a. Temperate shelf water dispersal by Australian boundary currents: implications for population connectivity. *Limnology and Oceanography: Fluids and Environments*, 2013. **3**, 295–309. Copyright Wiley-VCH Verlag GmbH & Co. KGaA. Reproduced with permission.).

Dispersal and gene flow in seaweeds are often determined by local factors, including coastal topography such as bays, beaches and river mouths (e.g. Faugeron et al. 2001, Billot et al. 2003, Coleman & Brawley 2005b, Coleman et al. 2011a, Muhlin et al. 2011, Coleman et al. 2019), position on the shore (Engel et al. 2003) and other barriers to dispersal (Coleman & Brawley 2005a, Durrant et al. 2015, Durrant et al. 2018). However, the role of these small-scale processes in influencing dispersal and connectivity in *E. radiata* are less well understood. Coastal topography (the presence of bays and estuaries) does not appear to limit dispersal in open coastal populations of *E. radiata* (Coleman 2013). However, prevailing patterns of water movement within estuaries (waves versus tides) may influence scales of dispersal (Coleman 2013, Coleman et al. 2019). A focus on small-scale studies and more powerful genetic markers (e.g. single-nucleotide polymorphisms) may be required to properly discern spatial patterns of genetic structure in *E. radiata*. Given its key role as a foundation species throughout its range, this information will be important to consider in marine protected area (MPA) planning (Coleman et al. 2011a, Durrant et al. 2014) and other conservation initiatives, such as rehabilitation (Campbell et al. 2014a, Wood et al. 2019).

Understanding patterns of dispersal and gene flow in *E. radiata* are in their infancy, and we know little from its range outside of Australia. Further, power to detect subtle genetic structure can now be greatly enhanced with advances in technology such as next-generation sequencing, which allows large sections of the genome to be interrogated via methods such as genotyping by sequencing (GBS; e.g. Elshire et al. 2011). These modern genetic techniques, which also examine functional areas of the genome potentially under selection, will pave the way for a more holistic understanding of *E. radiata* ecology and response to environmental change.

Settlement and recruitment

Settlement in benthic marine species is usually recognised as the termination of the pelagic phase (dispersal, as discussed previously) and the beginning of the benthic phase, while

recruitment involves the survival of settled individuals to a defined point in time, often when they can be seen in a population (Keough & Downes 1982, Rodriguez et al. 1993). Thus, for *Ecklonia radiata*, settlement can be defined as the attachment of planktonic zoospores to the benthos and their initial morphogenetic changes into male and female gametophytes, while recruitment includes the subsequent growth and survival of gametophytes and the development of the sporophyte (the latter grows from the oogonia on the female gametophyte after fertilisation of the oogonia by antherozoids). Given that little is known about the settlement of gametophytes, other than from laboratory studies (cf. the section entitled 'Ecophysiology and environmental drivers', earlier in this review), here, we focus on the recruitment of sporophytes into macroscopic *E. radiata* populations and the factors that influence them.

The ontogenetic development of the macroscopic sporophytes can be classed into three life stages based on thallus complexity and gross morphology; stage 1 (main thallus up to 15 cm), stage 2 (15–70 cm) and stage 3 (20–90 cm) (Kirkman 1981). Densities of macroscopic *E. radiata* recruits in the field vary markedly in space and time, with substantial small-scale spatial variation in recruit densities on scales of metres and kilometres (Wernberg 2009), indicating that a range of processes acting on those scales are likely to influence recruitment patterns. These processes include canopy loss (from storms) and increased light, temperature, scour, sedimentation, competition with understory algae and grazing. Recruitment in *E. radiata* has been described as seasonal, with high recruitment into clearings when gaps in the canopy form in winter (Kennelly 1987b) or spring (Schiel 1988), but slow recruitment when clearings are opened up at other times of the year. In some cases, if canopy removal occurs when spore production is low (e.g. late spring) and remaining sporophytes are sparse, then development of turf algae can minimise or prevent subsequent recruitment of *E. radiata* (Kriegisch et al. 2016). In Australia and New Zealand, stage 1 recruits appear in greatest abundance in October–November (early spring) and grow through stage 2 to stage 3 adults in 3–6 months depending on light levels (Kirkman 1981, Novaczek 1984a, Schiel 1988). The size and morphology of stage 3 kelps varies greatly from place to place (Wernberg et al. 2003a) but also exhibits seasonal variations as a consequence of growth in spring and summer and erosion in autumn and winter (Kirkman 1981, Kennelly 1987b, Wernberg & Vanderklift 2010, de Bettignies et al. 2015).

As in the laboratory for microscopic sporophytes, high light has positive effects on macroscopic sporophytes in the field. A number of studies have shown increased recruitment of *E. radiata* under increased light following the creation of experimental gaps in the canopy (Kirkman 1981, Kennelly 1987b, Goodsell & Connell 2002, Carnell & Keough 2014, Flukes et al. 2014). However, the scale of sporophyte removal is another important consideration because if the canopy becomes too sparse, light too high or both, then lack of spores and development of turf algae (in response to elevated light and absence of sporophyte blades sweeping the substratum) can lead to collapse of kelp recruitment (Kriegisch et al. 2016). Where the opening of gaps in the canopy results in elevated recruitment, it is not known whether these patterns are the result of zoospore settlement and subsequent sporophyte recruitment after gap creation or the post-recruitment growth of existing dormant microscopic gametophytes and sporophytes (Carney & Edwards 2006) that respond rapidly to the increased light. However, the effects of increased light appear to interact with temperature: On large scales in southwestern Australia, increased recruitment and post-recruitment growth occurred in zero canopy (high-light) environments at cooler sites, but the opposite result occurred at sites that were 2°C–4°C warmer (Wernberg et al. 2010). The changes to the subcanopy light environment can also have indirect negative effects on *E. radiata* recruits as higher light also increases the abundance of understory algae (Toohey et al. 2004, Flukes et al. 2014) which can inhibit *E. radiata* recruitment (Kennelly 1987a, Tatsumi & Wright 2016). This inhibition can

occur via competition for light, or when turf algae enhances sedimentation, which may further inhibit sporophyte recruitment (Kennelly 1987b, Connell 2003b, Connell 2005, Valentine & Johnson 2005a,b, Gorman & Connell 2009).

Determining post-recruitment mortality (stage 1, Kirkman 1981) requires tagging recruits in the field and following them through time. This has only been done a handful of times for *E. radiata*. Wood (1987) followed tagged recruits for 7 months in three experimental treatments and found that post-recruitment mortality ranged from 86% in an unmanipulated (full-canopy) treatment, 58% in a canopy-removal treatment to 24% in a canopy-removal treatment with shading. The post-recruitment mortality of tagged macroscopic recruits can be quite low. For example, survivorship of recruits to 30 days after canopy clearing was typically 70%–90%, being higher on topographically simple compared to complex reefs (Toohey & Kendrick 2007). After canopy removal, post-recruitment mortality does not appear to be due to physical removal of thalli from storms, but it has been attributed to photo-inhibition on exposure to high light (Wood 1987, Toohey & Kendrick 2007). In natural stands of *E. radiata* in northeastern New Zealand, the annual probability of survival for recruits was 17% based on 526 tagged recruits monitored quarterly (Haggitt 1999).

Community ecology of *Ecklonia* forests

Ecklonia radiata has a wide range of direct and indirect effects on other species by providing an arena where they can find resources and allies and avoid stress and enemies (Figure 7). Underpinning these ecological services are various forms of mutualism, habitat provision and modification and interaction chains such as trophic cascades, competition cascades and facilitation cascades (Thomsen et al. 2010).

Non-trophic ecological processes

Non-trophic direct and indirect facilitation processes associated with *Ecklonia radiata* have been documented from biogeographical and landscape scales (Fowler-Walker & Connell 2002, Anderson & Millar 2004, Irving et al. 2004b, Tuya et al. 2009, Vanderklift et al. 2009) to individuals and small patches (Taylor & Cole 1994, Taylor 1998) to smaller sub-individual scales such as holdfasts (Smith et al. 1996, Goodsell & Connell 2002, Anderson et al. 2005a, Anderson et al. 2005b, Coleman et al. 2007, Goodsell & Connell 2008, Smith et al. 2014).

Ecklonia radiata provides fundamental habitat space for many sessile and mobile species. For example, diverse microscopic bacterial films, protists and algae coat the thallus surface (Mazure & Field 1980, Russell et al. 2005, Marzinelli et al. 2015a) and macroscopic epiphytes and sessile animals are abundant especially on older parts of the thallus and the holdfast (Fletcher & Day 1983, Jennings & Steinberg 1997, Russell et al. 2005, Marzinelli et al. 2009). These communities of sessile epibionts are generally more abundant on *E. radiata* from areas of relatively low water motion or light levels, on artificial structures like pilings (Marzinelli et al. 2009, Marzinelli et al. 2011) and in areas with high nutrient levels (Russell et al. 2005). For example, epiphytes are typically less common under high-wave action, as fronds are abraded and cleaned by whiplash (Fletcher & Day 1983). Mobile epibionts on *E. radiata* are relatively sparse compared to canopy-forming fucoid seaweeds with finer branching structure (Taylor & Cole 1994, Taylor 1998, Tuya et al. 2008, Marzinelli et al. 2016), and epibiont diversity lower (Marzinelli et al. 2016, Coleman & Wernberg 2017). Nevertheless, the highly variable morphology of *E. radiata* (Wernberg et al. 2003a, Fowler-Walker et al. 2006, Wernberg & Vanderklift 2010) may increase the number of microhabitats and thereby allow for co-existence of more diverse communities of sessile and mobile species, as shown for crinkled *E. radiata*
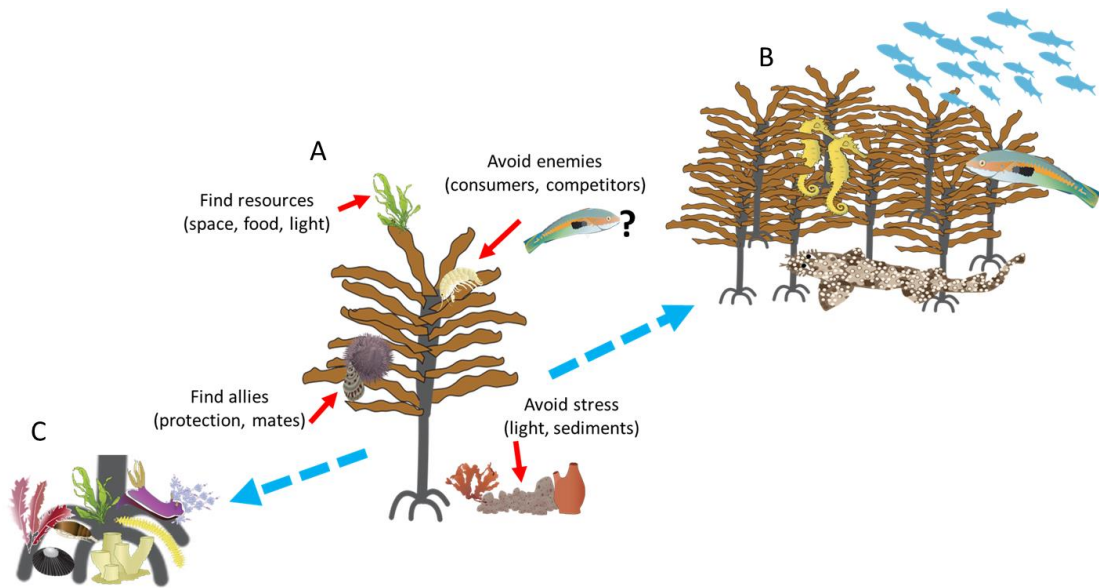
Figure 7 Mechanisms of non-trophic facilitation. (A) *Ecklonia radiata* provides ecological services to other species including stress and enemy avoidance and resource and ally provisioning. These services scale from (A) individuals up to (B) patch and landscape scales and (C) down to sub-individual structures of *E. radiata*. Symbols courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/).

fronds that were inhabited by more epibiota compared to smooth fronds (Fletcher & Day 1983, Jennings & Steinberg 1997, Fowler-Walker et al. 2005).

Epibiota on *E. radiata* also varies across space and time (Taylor 1998) with higher animal densities recorded at intermediate depths (6 m, with mean densities up to 200 animals per 100 g WW alga) (Table 2), perhaps because of variation in water motion and sedimentation with depth (Taylor & Cole 1994). Herbivorous gastropods can be highly abundant in *E. radiata* forests in northern New Zealand (Freeman & Creese 2011), but they tend to be rare at offshore islands (Choat & Schiel 1982, Shears & Babcock 2004). Similarly, gastropod assemblages are more abundant and species-rich in *E. radiata* forests on inshore than offshore reefs in Western Australia and vary across latitudes (Tuya et al. 2008, Wernberg et al. 2008).

Positive effects on epiphytes can lead to facilitation cascades becasue high *E. radiata* epiphyte loads can increase the abundance of mesofauna (Jennings & Steinberg 1997). However, once a sessile species has colonised *E. radiata*, increased competition may also occur, such as when epiphytic bryozoa outcompete epiphytic hydroids (Fletcher & Day 1983). Mobile species inhabiting *E. radiata* fronds are typically dominated by crustaceans, gastropods and polychaetes but most of them are generalists and can also be found in other habitats (Fletcher & Day 1983, Taylor & Cole 1994, Jennings & Steinberg 1997, Taylor 1998).

Table 2 Number of supported species/taxa associated with various structural components of *Ecklonia radiata*

Region	Location	Number of supported species/presence									Study
		Understory/Canopy	Holdfast	Epibiota	Microbial	Macroinverts	Sponges	Fish	Bryozoans	Annelids	
Australia	Continental	X			X						Connell & Irving (2008), Irving et al. (2004) , Marzinelli et al. (2015)
Australia	WA	82	160			X		X			Coleman et al. (2007), Crawley & Hyndes (2007), Harman et al. (2003), Toohey (2007), Toohey et al. (2004), Toohey & Kendrick (2008), Tuya et al. (2008, 2009), Wernberg et al. (2003, 2005), Kendrick et al. (1999)
Australia	SA	16				X		X			Baker & Edyvane (2003). Connell (2003), Daume et al. (1999), Fowler-Walker & Connell (2007), (2002, Goodsell & Connell (2005) Goodsell et al. (2004), Irving & Connell (2006a, b), Jenkins & Wheatley (1998), Melville & Connell (2001)
Australia	TAS	51				x	1	x	1		Edgar & (1999), Flukes et al. (2014)
Australia	VIC	9		37		5		X	1	1	Fletcher & Day (1983), Jones (1992), O'Hara (2001)
Australia	NSW	X	385	8 - 11	X	x	X	35			Andrew, N. L. (1993), Bell et al. (2014), Curley et al. (2002), Ettinger-Epstein & Kingsford (2008), Fulton et al. (2016), Marzinelli et al. (2009, 2011, 2012, 2014, 2016, 2018), Marzinelli (2012), Roberts & Scanes (1999), Smith (2000), Smith & Simpson (1992), Smith et al. (1996), Smith & Simpson (1993), Steinberg (1995), Wright et al. (1997), Zagal et al. (2003), Jenkins et al. (1993)
New Zealand	Northeast		351					42			Anderson et al. (2004, 2005a, b)

Kelp forests provide an arena to find intraspecific or interspecific allies, such as through facilitation cascades (Thomsen et al. 2010, Bell et al. 2014, Figure 7). In these cascades, *E. radiata* is the primary foundation species, facilitating intermediate species, through chemical (Steinberg 1984, 1985) or physical (Amsler et al. 1999) mechanisms, and thereby increasing the performance and survival of focal species (associational defences). For example, Bell et al. (2014) documented an intricate facilitation cascade whereby the sea urchin *Holopneustes purpurascens*, with its tube feet, rearranged the architecture of *E. radiata*'s fronds to create so-called 'safe houses' for the snail *Phasianotrochus eximius*, which thereby experienced less predation and dislodgement from waves. In addition, *E. radiata* can provide physical habitat where organisms find mating partners, such as weedy seadragons, *Phyllopteryx taeniolatus*, inhabiting *E. radiata* forests in New South Wales, Australia (Sanchez-Camara & Booth 2004).

Like other habitat-forming species, *E. radiata* can provide a space to avoid enemies (competitors and predators). Most enemy-avoidance mechanisms are direct, as small mobile animals can simply escape predation by hiding between blades and holdfasts (Smith et al. 1996, Goodsell & Connell 2002, Anderson et al. 2005b, Coleman et al. 2007). Because many of these small, mobile species are also herbivores, it can be difficult to separate whether the main facilitation mechanisms (in addition to direct feeding on *E. radiata*) are feeding on biofilms and epiphytes attached to *E. radiata*, or whether they are engaging in predator avoidance. Thus, similar to finding allies, proposed mechanisms for avoiding enemies have received little experimental research scrutiny. Further, some studies show that predation risk for some species is greater inside structurally complex *E. radiata* habitats than in nearby unvegetated habitats (Farina et al. 2014), suggesting that *E. radiata*'s role in mediating predator avoidance is highly species-specific.

Canopy-forming seaweeds, like *E. radiata*, may facilitate other species by reducing abiotic stress, in particular through frond abrasion and scouring, sedimentation, UV light and natural light—and possibly water motion and temperature as well (e.g. Bennett & Wernberg 2014, Bennett et al. 2015b). Light absorption by *E. radiata* results in a darker sub-canopy environment with less UV stress to provide a more benign habitat for light sensitive understory species (Kennelly 1989, Connell 2003a, Irving et al. 2004a, Wernberg et al. 2005, Marzinelli et al. 2011, Coleman & Kenelley 2019). For example, removal of *E. radiata* canopies results in rapid bleaching, reduced photosynthesis of both encrusting coralline algae (Irving et al. 2004a) and foliose red algae (Toohey et al. 2004, Wernberg et al. 2005) or both. Wave forces result in kelp blade whiplash and abrasion of the bottom, and thereby inhibit sediment accumulation (Kennelly 1989, Connell 2003a, Toohey et al. 2004, Wernberg et al. 2005, Irving & Connell 2006). There have been some discrepancies, however, in relation to whether understory species are predominantly facilitated by kelp through abiotic light and sediment reduction, or if abrasion has a more indirect effect because it can reduce recruitment and growth of fast-growing turfs, articulate calcifying algae or fucoids (Kennelly 1989, Melville & Connell 2001, Irving et al. 2004a, Toohey et al. 2004, Wernberg et al. 2005). Indeed, the latter example represents a novel competition cascade (Levine 1999, Thomsen et al. 2010), where *E. radiata*, through abrasion and light reduction, outcompetes strong competitors for light and space (e.g. fucoids) and thereby allows coexistence of weak (e.g. encrusting algae) competitors with various resource requirements.

Similar facilitation mechanisms scale up to larger *E. radiata* stands and down to specific structural components of an individual thallus (Figure 7). Upscaling of *E. radiata* individuals to stands of various landscape configurations, densities, and with mosaics of stands with interspersed gaps allows large species to find food and allies and avoid enemies (Andrew & Jones 1990, Jones 1992, Harman et al. 2003, Tuya et al. 2009, Vanderklift et al. 2009, Newcombe & Taylor 2010, Smith et al. 2014). Moreover, there is an emerging understanding

of *E. radiata* forest soundscapes that carry decision-making information needed for some species to locate resources and evaluate their quantity and quality. The presence of *E. radiata* forests produces distinct soundscapes, and loss of these forests causes a reduction in biological sound (Rossi et al. 2017).

Facilitation of communities associated with *E. radiata* holdfasts has been a frequent focus of study. Compared to *E. radiata* fronds, holdfasts provide a more stable habitat for attachment of sessile taxa such as barnacles, tube-forming polychaetes, hydroids, bryozoan, tunicates and sponges (Smith et al. 1996, Anderson et al. 2005b, Goodsell & Connell 2005b, Coleman et al. 2007). In addition, the interstitial spaces among the holdfast's haptera provide a unique 3-dimensional environment for mobile species, dominated by crustaceans and polychaetes (Smith & Simpson 1992, Smith et al. 1996, Anderson et al. 2005b, Goodsell & Connell 2005b, Coleman et al. 2007). These holdfast assemblages are highly diverse and contain many rare taxa (Goodsell & Connell 2005b, Coleman et al. 2007). For example, Smith et al. (1996) quantified 125,605 individuals representing 386 species (152 families and 10 phyla) from 258 holdfasts collected from northern New South Wales. Similar collections from northeastern New Zealand showed similarly high diversity, with 351 taxa (213 families and 15 phyla) associated with 80 holdfasts (Anderson et al. 2005a,b). Faunal communities associated with holdfasts differ with holdfast size and age (Anderson et al. 2005a) and depth (Goodsell & Connell 2002, Coleman et al. 2007).

Because of the insular structure and high biodiversity, holdfast communities have been used as a model system of island biogeography and landscape ecology to test hypotheses related to habitat size (Smith et al. 1996, Anderson et al. 2005b), isolation and edge effects (Goodsell & Connell 2002). Holdfast assemblages have also been used as a tool to detect impacts from anthropogenic stressors like sewerage discharge (Smith & Simpson 1992, Smith & Simpson 1993, Smith et al. 1996, Smith 2000). Artificial holdfasts can also be used as natural mimics (supporting up to 30 families; Magierowski 2006) and test hypotheses about community assembly and post-recruitment interactions (Magierowski & Johnson 2006).

Direct trophic interactions and food webs

Only a small number of invertebrate and fish species feed directly on adult *Ecklonia radiata*. The main consumers of kelp are sea urchins: in New Zealand, *E. chloroticus* (Choat & Schiel 1982), and in southeastern Australia, *C. rodgersii* (Andrew 1993, Andrew & Byrne 2001, Connell & Irving 2008). Also in southeastern Australia, in Port Phillip Bay (Kriegisch et al. 2016) and in Tasmania (Sanderson et al. 1996, Johnson et al. 2004, Pederson & Johnson 2007), *E. radiata* forests are subject to destructive grazing by the red sea urchin *Heliocidaris erythrogramma*. *H. erythrygramma* is also the main kelp-eating urchin throughout southern and western Australia, although the species here is mostly drift feeding (Vanderklift & Wernberg 2010). At high densities, these species are capable of removing entire kelp forests, grazing not only the blades and meristem, but also the base of stipes, a behaviour that results in accelerated canopy loss (Andrew & Jones 1990). If high densities of urchins are sustained, canopy loss can result in a shift towards urchin barrens, a system with no macroscopic foliose algae that is instead dominated by turf algae or crustose coralline algae (Choat & Schiel 1982, Fletcher 1987, Andrew & Underwood 1989, Underwood et al. 1991b, Andrew 1993, Andrew & O'Neill 2000, Johnson et al. 2004, Johnson et al. 2005a, Johnson et al. 2005b, Ling 2008, Johnson et al. 2011, Coleman & Kennelly 2019). Sea urchin overgrazing fundamentally transforms the ecosystem structure and dynamics of temperate reefs (Lawrence 1975, Filbee-Dexter & Scheibling 2014, Ling et al. 2015), leading to a loss of biodiversity and biomass in former *E. radiata* forests (Ayling 1981, Babcock et al. 1999, Ling 2008, Salomon et al. 2008) and declines of important commercial species (Johnson et al. 2005b, Johnson et al. 2011).

In contrast to sea urchins, gastropod grazing on *E. radiata* is relatively minor in terms of biomass consumed (Fletcher 1987). Small gastropods living on *E. radiata* seem mainly to graze either epiphytes or the old eroding end of the primary blade rather than live *E. radiata* tissue, though some (e.g. *Phasianotrochus eximius*) do directly consume *E. radiata*. Large turbinid gastropods readily consume *E. radiata* recruits in the laboratory (Wernberg et al. 2008, Miranda et al. 2019), and gastropod grazing may play an important role in supressing the recruitment of *E. radiata* and other algae in habitats where mature sporophytes have been removed (Ayling 1981, Choat & Andrew 1986, Fletcher 1987, Falkenberg et al. 2014, Ghedini et al. 2015, McSkimming et al. 2015). Smaller epifauna, such as amphipods and isopods, also graze on *E. radiata* (Taylor & Steinberg 2005). The lysianassid amphipod *Orchomenella aahu* has been associated with localised mass mortality of *E. radiata* in northeastern New Zealand (Haggitt & Babcock 2003), and Newcombe & Taylor (2010) found that amphipods not only grazed epiphytes on *E. radiata*, with some species grazing directly on its fronds.

Ecklonia radiata dominates the diet of only a handful of temperate fishes: *Olisthops cyanomelas* in eastern Australia (Jones 1992), several species of *Kyphosus* in Western Australia (Vanderklift et al. 2009, Bennett et al. 2015c) and *Odax pullus* and *Kyphosus sydneyanus* in New Zealand (Clements & Choat 1993, Moran & Clements 2002). At lower-latitude reefs, *E. radiata*is now also targeted by tropical and subtropical fishes, such as *Siganus fuscescens* and *Kyphosus* spp. (Bennett et al. 2015a,b, Vergés et al. 2016, Zarco-Perello et al. 2017), as these have moved poleward with ocean warming. Seasonal aggregations of *O. cyanomelas* can clear patches within *E. radiata* forests, but with little impact as they grow back annually (Andrew & Jones 1990). However, as is the case with grazing gastropods, the main ecological role of fish grazing may be in suppressing kelp recruitment, particularly following disturbance (Bennett et al. 2015c). Grazing by the temperate damselfish *Parma mccullochi* is hypothesised to maintain habitat heterogeneity on reefs in Western Australia by reducing or preventing the recruitment of large brown algae, including *E. radiata* within habitat patches (Saunders et al. 2015) or in larger spatial contexts following large-scale mortality of *E. radiata* (Bennett et al. 2015a,b).

Ecklonia radiata can be a high-preference food target, relative to other large, fleshy macrophytes, for important echinoid herbivores and some large gastropods in Australia and New Zealand (Schiel 1982, Andrew 1986, Steinberg & van Altena 1992, Cole 2001, Taylor & Steinberg 2005, Vanderklift & Wernberg 2008). It often supports high growth and reproduction for these herbivores (Andrew 1986, Steinberg & van Altena 1992). However, like many large, fleshy brown algae, it is often less frequently consumed than many other smaller, more delicate species, particularly by smaller gastropods or crustaceans (Taylor & Steinberg 2005, Wernberg & Goldberg 2008). There are exceptions to this trend (Williamson et al. 2004, Taylor & Steinberg 2005), including the arboreal sea urchin *Holopneustes purprascens* (Steinberg 1995a) and the amphipod *Allorchestes compressa*, which consumes detrital or detached *E. radiata* at higher rates than other less fleshy algae (Robertson & Lucas 1983).

Heliocidaris erythrygramma has also been observed to preferentially retain and consume detached *E. radiata* (Vanderklift & Wernberg 2008). In perhaps the most comprehensive analysis of consumption of temperate Australasian macroalgae including *E. radiata* by diverse herbivores, Taylor & Steinberg (2005) found that the feeding preferences of small mesograzers differed from that of larger grazers such as urchins. Much of the research on trying to understand the reasons for selectivity in feeding by herbivores for *E. radiata* in Australia and New Zealand, relative to other (brown) algae, has focussed on the effects on herbivores of the brown algal secondary metabolites known as *phlorotannins*. Phlorotannins are a mixture of complex polyphenols that are ubiquitous in brown seaweeds and have a role in both herbivore deterrence and cell wall formation (Schoenwaelder 2002).

Although levels of phlorotannins in temperate Australasian brown, including *E. radiata*, algae are typically very high (Steinberg 1989, van Hees et al. 2017), variation in levels among these different species do not affect herbivore selectivity for these seaweeds (Steinberg & van Altena 1992, Steinberg 1995a). Extracted, purified phlorotannin mixtures also do not generally deter feeding by Australasian herbivores, including dominant echinoid herbivores such as *E. chloroticus* or *C. rodgersii*, even at high levels, in contrast to their effects on North American (Steinberg & van Altena 1992, Steinberg 1995a) and European (Pavia et al. 1997) herbivores. Estes & Steinberg (1989) and Steinberg (1995b) proposed that these broad-scale biogeographic differences in algal chemical defences and herbivore response were a consequence of a trophic cascade in evolutionary time, driven by the absence of a key predator—sea otters—in Australasia. There is also no evidence for induction of higher levels of phlorotannins in *E. radiata* following simulated herbivory (Steinberg 1994), though induction of phlorotannins is known for other species of *Ecklonia* (Molis et al. 2006). Interestingly, some herbivorous fish such as *K. sydneyanus or O. pullus,* which consume *E. radiata* in Australia and New Zealand, have complex gut morphologies or high gut pH, which likely serve to deactivate phlorotannins.

Other factors affecting selectivity by herbivores for *E. radiata* are less well explored but may include thallus toughness and nutritional content (McShane et al. 1994) or possibly the production of other secondary metabolites (e.g. terpenoid, Hay & Fenical 1988) and secondary pigments (e.g. fucoxanthins). Finally, it should be emphasised that consumption and feeding selectivity are not the only factors that affect the impact of herbivores on *E. radiata* forests, with foraging behaviour (Andrew 1988), the physical environment (Shears et al. 2008), ecological context, particularly predators (Babcock et al. 1999, Shears & Babcock 2002, Spyksma et al. 2017a) and other aspects of the life history or habits of the herbivores (Steinberg 1995a) also playing key roles.

Indirect interactions and trophic cascades

Some of the first descriptions of subtidal coastal habitats in Australia and New Zealand were characterised by the juxtaposition of *Ecklonia radiata* forests and barrens habitat dominated by crustose coralline algae (Choat & Schiel 1982, Grace 1983, Underwood et al. 1991b). This configuration of habitats was generally considered to be the characteristic state of subtidal reefs. However, questions soon arose about whether this was in fact the case, or whether the barrens were created and maintained because of unnaturally high densities of sea urchins that resulted from other factors—principally reduced numbers of predators that allowed urchin populations to flourish. Such interactions, where impacts at higher trophic levels result in indirect effects at lower trophic levels, are known as *trophic cascades*. The existence of trophic cascades is difficult to demonstrate because experiments at realistically large spatial scales are problematic. However, a combination of factors has shown that trophic cascades do take place in *E. radiata* forests and suggest that extensive *E. radiata* canopies, rather than urchin barrens, are the more natural state of these subtidal reefs.

In New Zealand the creation of marine reserves allowed predator populations (mainly the lobster *Jasus edwardsii* and snapper *Pagrus auratus*) to recover to a point where they reduced the abundance of urchins (*E. chloroticus*) sufficiently to allow kelp forests to return to from formerly barrens habitat, while barrens outside the reserves persisted (Babcock et al. 1999, Shears & Babcock 2003, Spyksma et al. 2017b). On the coast of eastern Australia, especially south of Sydney, barrens maintained by *C. rodgersii* also exist over extensive areas (Andrew & O'Neill 2000, Connell & Irving 2008), but there is no evidence from relatively young reserves in this area, that predator populations have recovered enough to reverse the trophic cascade (Coleman et al. 2013b, Coleman et al. 2015). These heavily populated coastlines have historically been subject to intense fishing pressure, so barrens are likely maintained through a

combination of this harvesting legacy and ongoing climatic change that facilitates urchin transport (Coleman et al. 2017), recruitment and survival (Ling et al. 2009). Change in the ocean climate in southeast Australia as a result of increased eddy propagation of the East Australian Current (EAC; Ridgway 2007) has led to transport and establishment of *C. rodgersii* into Tasmania, precipitating large-scale transformation of kelp forests to barrens (see the section entitled 'Recent changes and future threats', later in this review).

In New Zealand, the transition from urchin barrens back to *E. radiata* forest has largely been attributed to the direct consumption of sea urchins by predators that result in an overall decline in sea urchin density (Babcock et al. 1999). However, sea urchins inside marine reserves exhibit a cryptic behaviour, occupying cracks and crevices (Shears & Babcock 2003, Spyksma et al. 2017b). This cryptic behaviour has been directly linked to increased predation risk (Spyksma et al. 2017b), suggesting that both density and behaviourally mediated interactions are important in the predator–sea urchin–kelp trophic cascade.

Indirect effects also structure maintenance of kelp-turf regime shifts, particularly in the context of resource enrichment. Consumption by herbivores may buffer the expansion of turfs during nutrient enrichment (McAllister & Bornman 1972, Sarnelle 1992, Russell & Connell 2005) and other resource perturbations (Ghedini et al. 2015, McSkimming et al. 2015). By keeping turf abundance in check and maintaining turf-free space, herbivores facilitate *E. radiata* recruitment and persistence (Gorman & Connell 2009). Increases in nutrient and sediment loads, which tend to go together, are likely to have detrimental effects on kelp forests, particularly in those regions where populations of herbivores are naturally ineffective, sparse or subject to decline (Ghedini et al. 2015). The aggregate of such changes in consumption can generate a mechanism of trophic compensation that stabilises community productivity in varying environments (Connell & Ghedini 2015). The reality is that alteration of both producers (e.g. nutrient-driven change) and consumers (e.g. extraction of consumers) require attention to the synergies they may create. In Port Phillip Bay, Australia, negative top-down effects of sea urchin grazers overwhelm positive bottom-up effects of enhanced nutrient loading on *E. radiata*, and local elevation of nutrients does not change the urchin density at which overgrazing or kelp recovery from overgrazing occurs (Kriegisch et al. 2016). Similarly, in South Australia, herbivory increases with nutrient enrichment so that the boosted effects of nutrients on turfs are negated (Falkenberg et al. 2014). By better recognising the environmental conditions which maintain or disrupt the balance between the processes of production and consumption (Ghedini & Connell 2016), it may be possible to improve forecasts regarding the probability of habitat stasis or shifts.

Context dependency and variation in the occurrence of trophic cascades

While regime shifts and trophic cascades provide graphic demonstrations of the importance of *Ecklonia radiata* within its ecosystem, it is important to note that throughout a lot of its range in New Zealand and Australia *E. radiata* is not subjected to high levels of grazing by fish or sea urchins and sea urchin barrens do not exist. Most commonly, *E. radiata* forests occur as near monospecific canopies or as mixed *E. radiata*/fucoid canopy (Schiel 1990, Fowler-Walker & Connell 2002, Shears & Babcock 2007, Connell & Irving 2008, Wernberg et al. 2011c). Urchin barrens are more prevalent in northern than in southern New Zealand (Shears & Babcock 2007, Schiel 2013), and in southern compared to northern New South Wales in eastern Australia (Glasby et al. 2017). Furthermore, within regions such as northern New Zealand, the extent of urchin barrens varies with depth and wave exposure. Consequently the effects of trophic cascades involving the indirect effects of predators on kelp forests is considered highly context dependent (Shears et al. 2008). To date, the cascading effects of fishing on kelp forests have been demonstrated only from northern New Zealand and Tasmanian reefs.

The reasons for the weak interaction between grazing echinoids and large brown algae across much of the range of *E. radiata* is not completely clear, but due to the widespread effects of fishing on top predators, such as lobster, it is unlikely that top-down impacts are limiting urchin populations across most of Australasia. Various lines of evidence suggest that lack of grazing pressure stems from bottom-up processes that control urchin recruitment. A case in point is the extension of the East Australia Current, which has resulted in not only the direct transport of *C. rodgersii's* larvae to Tasmania (Johnson et al. 2005a), but also the creation of oceanographic conditions suitable for *C. rodgersii* development at higher latitudes than previously (Ling et al. 2009). Across many parts of the New Zealand coastline, high levels of sedimentation inhibit the settlement and survival of *E. chloroticus* (Andrew & Choat 1985, Walker 2007), decreasing recruitment levels and resulting in low urchin population densities (Shears et al. 2008). The arid coastlines of southern and southwestern Australia are characterised by clear waters and are relatively free of fine sediment, but they also lack urchin barrens habitat. *Centrostephanus tenuispinus* is morphologically similar to *C. rodgersii* and is present on these coasts, but never highly abundant, possibly because of the relatively oligotrophic conditions that reduce the likelihood of dense recruitment. *C. rodgersii* larvae have been shown to have an extended larval phase of 3–5 months (Huggett et al. 2005), making them highly dependent on a consistent planktonic food supply. Understanding the drivers of variation in kelp forest structure and ecological processes at this scale remains a significant knowledge gap.

Ecosystem processes and trophic cascades

Ecosystem models focussed on reefs at Gisborne on the central eastern coast of New Zealand show that production by the seaweed canopy (mostly *Ecklonia radiata*) comprised almost an order of magnitude greater biomass than any other primary producer and contributed almost half of the total detrital budget to the system (Pinkerton et al. 2008). Seaweed (canopy) also make up a significant proportion of the diets of lobster, herbivorous invertebrates, phytal/infaunal invertebrates and herbivorous fish (16%, 30%, 39% and 23%, respectively (Pinkerton et al. 2008). *E. radiata* is estimated to be similarly important to food webs on the west coast of Australia, although there a higher proportion of primary production is consumed directly, and less than 25% goes through detrital food web pathways (Lozano-Montes et al. 2011). This model has been used to simulate and predict the ecosystem effects of recent loss in *E. radiata* canopy as a result of the 2011 heatwave (Wernberg et al. 2016a) on the central coast of Western Australia. A simulated persistent loss of 50% of the *E. radiata* canopy was projected forward for 33 years and showed declines in biomass at all levels of the food web, including key groups such as invertebrates (−38%), target fishes (−24%); rock lobster (−21%); herbivorous fish (−9%) (Hector Lozano-Montes, unpublished data). Also, the total biomass of the system declined (~10%), and an important loss in diversity (about 11%) measured by the Shannon Diversity Index was predicted by the model at the end of 2050. In addition, models have been used to identify thresholds and recommend management targets to avoid regime shifts from *E. radiata* forests to urchin barrens (Marzloff et al. 2016a).

Fate of production and trophic subsidies

Like most other kelps globally (Krumhansl & Scheibling 2012), *Ecklonia radiata* is not extensively consumed directly across much of its range. Instead, most biomass is lost through exudation of nutrients and polysaccharides, erosion of small fragments and dislodgment of entire individuals (Jennings & Steinberg 1994, Hyndes et al. 2012, de Bettignies et al. 2013b). Dislodged *E. radiata* material is often exported beyond the reef on which the kelp grows, providing spatial subsidies (*sensu* Polis et al. 1997) to organisms that live in distant habitats. Large fragments of *E. radiata* accumulate on beaches (Figure 8), in seagrass meadows and on

reefs, where they are eaten by numerous species of herbivores ranging from amphipods, sea urchins and fish to weevils (Wernberg et al. 2006, Vanderklift & Wernberg 2008, Crawley et al. 2009, Vanderklift & Wernberg 2010, Mellbrand et al. 2011). *E. radiata* is not the only macrophyte in such accumulations of wrack, but it tends to decompose faster (Gladstone-Gallagher et al. 2016) and be consumed at greater rates than most other macrophytes (Crawley & Hyndes 2007). The combination of the amount of material available and the relatively high rates of consumption means that *E. radiata* wrack is likely to be disproportionately more important than other species (Robertson & Lucas 1983, Vanderklift & Kendrick 2005). Experimental additions of kelp to beach sediments have sometimes (but not always) confirmed that such subsidies increase the abundance and richness of fauna (but see Bishop et al. 2010, Mellbrand et al. 2011, Bishop & Kelaher 2013). This in turn propagates to higher trophic levels, with evidence that detached macrophytes contribute to the nutrition of organisms from fish to spiders (Crawley et al. 2009), although no studies have unambiguously quantified the contribution of kelp alone.

Smaller particles of kelp suspended in the water are also likely to be an important food source for a diverse array of organisms, especially as they can travel orders of magnitude farther than large kelp detritus particles (Wernberg & Filbee-Dexter 2018). Experimental studies on the northeast coast of New Zealand have shown that organic carbon fixed by *E. radiata* is an important food source fuelling nearshore food webs, comprising 57% of the diet for mussels and 34% for oysters (Salomon et al. 2008). Plants may also benefit from kelp-derived resource subsidies as shown in Western Australia, where seagrasses and seagrass epiphytes take up nitrogen leaching from dislodged kelp exported to the seagrass meadows (Hyndes et al. 2012).

In addition to being a trophic subsidy to other ecosystems, *E. radiata* detritus can end up in habitats with capacity to sequester carbon, such as seagrass meadows, saltmarshes, mangroves or the continental shelf (Wernberg et al. 2006, Hill et al. 2015). Indeed, allochthonous carbon can contribute as much as 50% of the total organic carbon sequestered in seagrass meadows (Kennedy et al. 2010). Kelp also contain refractory compounds that are not fully broken down (Trevathan-Tackett et al. 2015), and the presence of seaweed derived carbon in deep sea sediments suggests that this could potentially be an important source of the carbon sequestered (Krause-Jensen & Duarte 2016). The large quantities of carbon stored in living kelp biomass have the potential to contribute significantly towards blue carbon sequestration. For *E. radiata*, however, future research is needed to quantify the ultimate fate of detached kelp wrack.
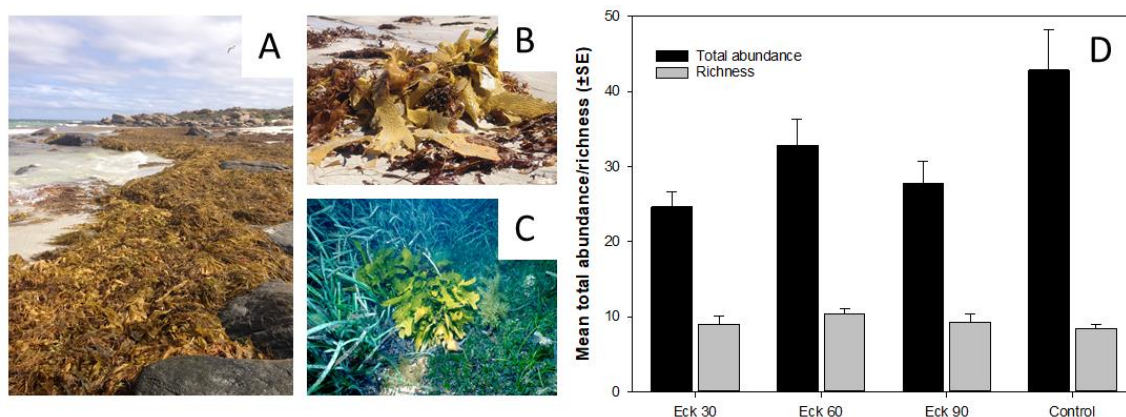

Figure 8 Detritus in the form of fragments and whole plants of *Ecklonia radiata* are transported into other habitats, including sandy beaches (A, B) and seagrass beds (C), where they break down and fuel marine food webs. (D) Relative to unenriched procedural controls, the total abundance was lower but richness greater of fauna in sediments enriched with 30, 60 or 90 grams of *E. radiata* detritus. (Data from Bishop et al. 2010. Photographs by the authors).

Microbial communities

Extensive microbial diversity is found within the microbiomes associated with marine organisms (Thompson et al. 2017), and these may be critical for the normal development and functioning of eukaryotic hosts (Egan et al. 2013, McFall-Ngai et al. 2013, Bourne et al. 2016). Kelps, and seaweeds more generally, are covered in microorganisms, and the importance of surface-associated microbes on the functioning of seaweeds is increasingly recognised (Egan et al. 2013). Changes in surface-associated microbial communities can have significant effects on host seaweeds, ranging from development and recruitment (Marshall et al. 2006, Morris et al. 2016), photosynthetic capacity (Marzinelli et al. 2015a), fecundity (Weinberger et al. 2007, Campbell et al. 2011) and survival (Egan et al. 2013, Peters 2015). Recently, there has been an increasing focus on understanding the interactions between microbiomes and large habitat-forming kelps because of their ecological importance (e.g. Bengtsson et al. 2010, Clasen & Shurin 2015, Marzinelli et al. 2015a, McKeown et al. 2017). Of these, *Ecklonia radiata* is probably the most studied kelp species (Thompson et al. 2017).

The microbiome of *E. radiata* is very diverse, and a large component of it is unique (Marzinelli et al. 2015a, Roth-Schulze et al. 2016, Beattie et al. 2018). A characterisation of microbial community structure from surfaces of *E. radiata* at multiple spatial scales spanning the entire latitudinal distribution along the east and west coasts of Australia and encompassing three biogeographic provinces (Waters et al. 2010) showed high bacterial and archaeal taxonomic diversity. Over 80% of the >8000 operational taxonomic units (OTUs, roughly equivalent to *species* for eukaryote ecologists) identified in this study had never previously been found elsewhere (Marzinelli et al. 2015a). The relatively small number of OTUs that could be classified belonged to ~230 families and 50 phyla (Marzinelli et al. 2015a).

Surface-associated viruses are another component of *E. radiata*'s microbiome that also appear to be extremely diverse. A recent study characterising the virome on the surfaces of *E. radiata* revealed a similar pattern to that observed for bacteria and archaea, with ~80,000 virus-like reads identified from metagenome sequencing, of which over 80% did not match any previously described viral sequences (Beattie et al. 2018). Preliminary analyses of fungal diversity on *E. radiata* targeting internal transcribed spacer (ITS) deoxyribonucleic acid (DNA) sequences are also showing striking patterns of diversity, with many of the ITS sequences previously unknown (Ezequiel Marzinelli & Peter Steinberg, unpublished data).

The structure (relative abundance of taxa) of *E. radiata*'s diverse microbial communities also differ significantly from those associated with other co-occurring seaweed species, seagrasses and inert surfaces (rocks) and are largely distinct from those in the water column (Roth-Schulze et al. 2016). Characteristics of the host, such as physio-chemical properties, rather than host phylogeny, appear to influence the type of taxa colonising the surfaces, leading to strong host specificity (Marzinelli et al. 2015a, Roth-Schulze et al. 2016).

There are strong spatial and temporal variation in *E. radiata*'s bacterial, archaeal (Marzinelli et al. 2015a) and fungal (Ezequiel Marzinelli & Peter Steinberg, unpublished data) surface-associated communities. This variation is related to temperature and light availability, and to a lesser extent to wave exposure (Marzinelli et al. 2015a). Interestingly, however, these patterns break down for microbiomes associated with stressed hosts. A putative disease of *E. radiata* characterised by tissue bleaching was consistently found in the large-scale continental surveys of Marzinelli et al. (2015b), with >50% of the individuals sampled in each population showing signs of bleaching at the end of summer, when the water is warmer (Marzinelli et al. 2015a). Bleaching affected kelp individuals by reducing their photosynthetic capacity (Marzinelli et al. 2015a). Host condition (healthy versus bleached) overrode effects of geographic location or

environmental variables on the structure of the kelp-associated microbiome (Marzinelli et al. 2015a).

These results suggest that environmental change may indirectly affect *E. radiata* via changes in the associated microbiome that can lead to disease. Indeed, a large-scale die-back of *E. radiata* in New Zealand was associated with high abundances of virus-like particles on the kelp blades, which showed signs of tissue decolouration, bleaching and degradation (Cole & Babcock 1996, Easton et al. 1997). Experiments provide further support for this idea, as warming and acidification mesocosm conditions mimicking future ocean conditions have been shown to cause changes in *E. radiata*'s microbial community structure, followed by tissue bleaching and subsequent degradation (see Figure 9; Qiu et al. 2019). Some of the bacteria that become abundant under such conditions are also abundant on bleached kelp in the field (Marzinelli et al. 2015a, Qiu et al. 2019) and on kelp growing on artificial structures such as pier-pilings (Marzinelli et al. 2018), which are typically in poor condition relative to kelp on adjacent natural rocky reefs (Marzinelli 2012, Marzinelli et al. 2012). Such changes in the microbiome can potentially mediate ecological interactions such as grazing and fouling (Marzinelli et al. 2011, Campbell et al. 2014b, Marzinelli et al. 2018), which can lead to strong detrimental effects on kelp populations and major declines.

Figure 9 Progression of tissue bleaching and degradation (Left to right) associated with temperature-mediated change in the microbiome of *Ecklonia radiata*. (From Qiu, Z. et al. *Proceedings of the Royal Society B-Biological Sciences* 2019. Photographs by the authors).

Two significant challenges for the study of the kelp holobiont are to understand functional interrelationships and to determine cause-and-effect relationships between hosts, microbiomes and environmental change. Analyses of functional genes via metagenomic sequencing on *E. radiata* and co-occurring macrophytes have found that abundances of genes related to enzymes involved in the breakdown of iduronate—a component of mucopolysaccharides, characteristic of brown seaweeds—were much higher on *E. radiata* than on other macrophytes or inert surfaces (Roth-Schulze et al. 2016). Thus, while *E. radiata*'s microbiome shares functional properties with microbes from other surface-associated habitats, it also hosts microbes that mediate host specificity (Roth-Schulze et al. 2016). Determining causation involves manipulating the microbiome, either via the addition or removal of specific taxa, or through changes in abundances of targeted taxa. Some of these approaches involve culturing and isolating the microorganisms associated with kelp, which can also allow identifying taxa that can potentially enhance host resilience to environmental stressors, providing new tools for management of these ecosystems (see the section entitled 'Recent changes and future threats', next).

Recent changes and future threats

Ecklonia radiata forests are dynamic ecosystems, responding to natural and human-driven changes in the environment. Across Australia, climate-induced changes to ocean boundary currents have underpinned recent marine heatwaves (e.g. Wernberg et al. 2013a, Oliver et al. 2017) and gradual warming (Johnson et al. 2011, Vergés et al. 2016), which have driven dramatic changes to *Ecklonia radiata* forests over contemporary time scales (Figure 10). At the same time, human-driven changes in resource (eutrophication, Connell 2007b) and consumer (fishing, Ling et al. 2009) levels have reinforced these changes (Wernberg et al. 2011a). A common result of these changes is the transition from complex kelp-dominated states towards more simplified turf and barrens states, a global phenomenon (Filbee-Dexter & Scheibling 2014, Filbee-Dexter & Wernberg 2018). Similar persistent losses of *E. radiata* forests have not been observed in New Zealand, likely due to the complexities of changing boundary currents and higher latitudes (Shears & Bowen 2017), or South Africa, where intensification of upwelling has caused localised cooling and expansion of some marginal kelp forests (Bolton et al. 2012).

Warming and marine heatwaves

Ecklonia radiata forests in eastern and western Australia and southeastern Africa are located in global warming hot spots, regions where the rate of warming over the past 50 years is in the top 10% globally (Hobday & Pecl 2014). This accelerated warming is driven by a strengthening of poleward flowing boundary currents (Wu et al. 2012), carrying warm, nutrient-poor water from low to high latitudes. Background warming has caused range shifts in seaweeds, invertebrates and fish inhabiting temperate reefs and *E. radiata* forests (Last et al. 2011,
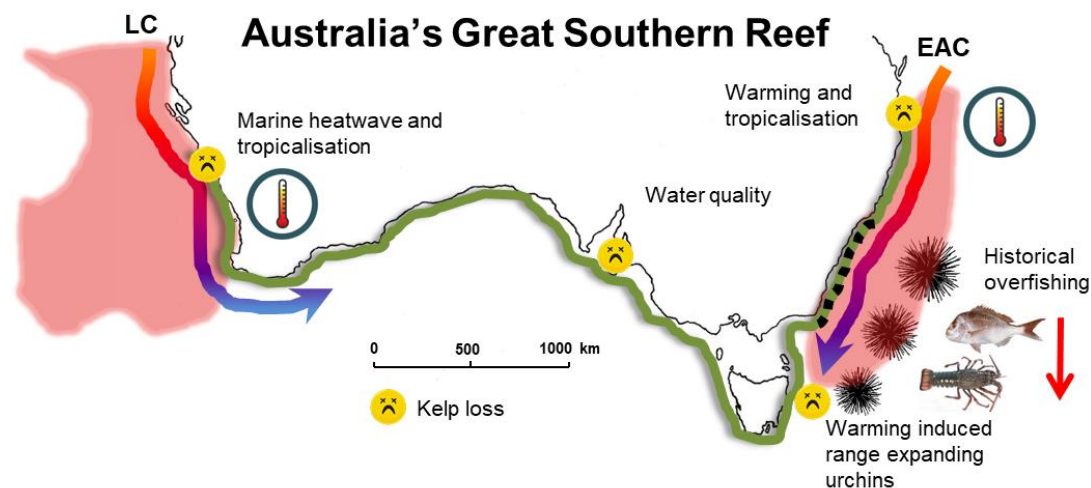

Figure 10 Overview of *Ecklonia radiata* loss across Australia, showing the various regional drivers. Both the East Australia Current (EAC) and Leeuwin Current (LC) transport warm water poleward (Wernberg et al. 2013b) with warming (east) and heatwaves (west) precipitating *E. radiata* loss at low latitudes. The red areas indicate warming hot spots, where the rate of warming is in the top 10% globally. *E. radiata* loss at higher latitudes on Australia's southeast coast (Tasmania) is an indirect result of the warming and strengthening flow of the EAC, facilitating the recent transport and survival of urchin larvae leading to transitions to barrens habitat. Barrens represent about 50% of the reef from about 33° latitude on the east coast. Historical overfishing of urchin predators along the east coast likely impedes *E. radiata* recovery. On the south coast, loss of *E. radiata* forests have been associated with declining water quality and the expansion of turfs.

Wernberg et al. 2011b, Poloczanska et al. 2013, Bennett et al. 2015c), leading to substantial changes in performance, composition and interactions within kelp forest communities (Vergés et al. 2014). To date, similar changes in species distributions or ecosystem states have not been observed in New Zealand kelp forests, where there has been minimal long-term warming (Shears & Bowen 2017).

There is a general consensus that ocean temperatures surrounding most *E. radiata* kelp forests will continue to increase (but see Bolton et al. 2012), although the pattern and magnitude of warming will depend on the trajectory of global CO_2 emissions. Warming could, at least initially, lead to localised expansion of *E. radiata* where more temperature-sensitive canopy-forming fucoids disappear (Wernberg et al. 2011c, Bennett et al. 2015a, Coleman & Wernberg 2017, Martinez et al. 2018). Nevertheless, species distribution models for Australia based on the RCP 2.6 (conservative) and RCP 6.0 (intermediate) CO_2 emission scenarios predict that a major poleward range contraction of *E. radiata* is likely within the coming 85 years (Martinez et al. 2018). Although *E. radiata* is currently found across the entire south coast and to about 27°S on the east and west coasts, it could become highly restricted to southeastern Australia and Tasmania (Figure 11), losing as much as 49% and 71% of its current distribution under the RCP 2.6 and RCP 6.0 CO_2 emission scenarios, respectively (Martinez et al. 2018). These projections do not consider additional effects of increasing frequency of marine heatwaves and tropical herbivores (as discussed next), synergies with other increasing human stressors such as eutrophication (Russell et al. 2009) or continued expansion of urchins into southern reefs (Coleman et al. 2017) that are predicted to be the only suitable habitat for *E. radiata* under future scenarios (Martinez et al. 2018).

As a consequence of the human-induced increase in mean ocean temperature, there has also been an increase in discrete extreme temperature events known as *marine heatwaves* (Hobday et al. 2016) an upwards trend that will likely continue (Oliver et al. 2017, Oliver et al. 2018). In 2011, Western Australia experienced the worst marine heatwave in recorded history, with
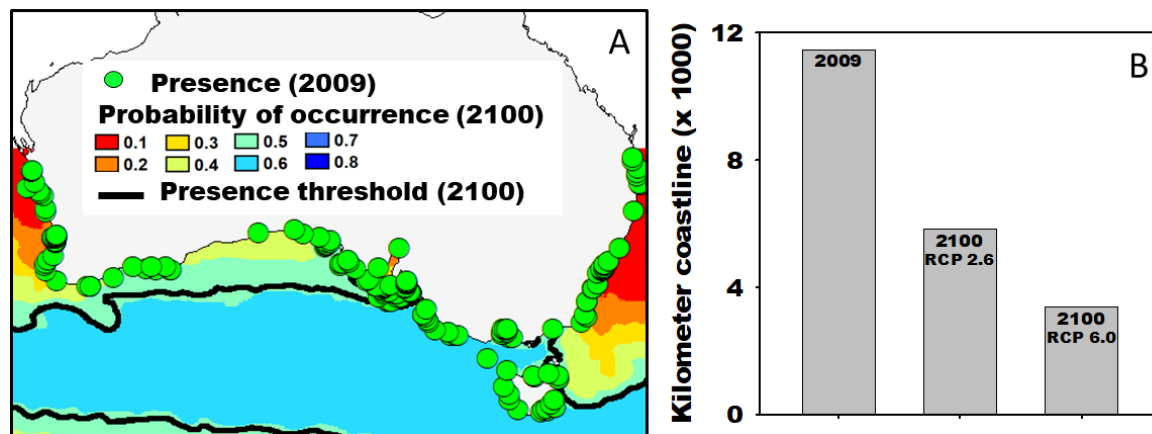

Figure 11 Distribution of *Ecklonia radiata* in Australia, now and projected into the future. Herbarium specimens lodged in the major Australian herbaria until 2009 (green dots) show *E. radiata* distributed all along the south coast and far up the east and west coasts of the continent (A). Species distribution models projecting the extent of suitable habitat (blue area between the black presence thresholds) for *E. radiata* in 2100 under the RCP 2.6 (conservative) (map not shown) and RCP 6.0 (intermediate) (B) scenarios of greenhouse gas emissions suggest there will be a major range contraction, isolating *E. radiata* to the southeastern corner of the continent and Tasmania, over the coming 85 years, even under optimistic emission projections. These estimates do not consider the additional impacts of increasingly severe marine heatwaves, range-shifting tropical herbivores or increased competition from turfs. (After Martinez, B. et al. 2018. *Diversity and Distributions* **24**, 1350–1366).

E. radiata forests experiencing temperature anomalies exceeding 4°C–5°C for several weeks. Over a few weeks, kelp forests collapsed entirely or were severely decimated across several hundred kilometres of coastline (Wernberg et al. 2016a), presumably as their lethal temperature threshold was exceeded (Smale & Wernberg 2013, Wernberg et al. 2016b, Figure 12). The magnitude of heatwave impact was negatively correlated with genetic diversity within *E. radiata* populations (low diversity populations were completely extirpated), suggesting that genetic diversity and population connectivity may underpin adaptive responses and resilience in these kelp forests (Wernberg et al. 2018). At their low-latitude distribution, kelp forests failed to recover due to increased fish grazing (Bennett et al. 2015a,b) and expansion of turf competitors (Wernberg et al. 2016a); 8 years later, these reefs remain dominated by turf (Figure 12; Thomas Wernberg, pers. obs.). Interestingly, a subsequent unprecedented marine heatwave in Tasmania did not cause a similarly catastrophic response in *E. radiata*, although several kelp associated taxa were negatively affected (Oliver et al. 2017). Differences in thermal tolerances as a consequence of relative position with the distributional range are the most likely explanation for the difference in impacts between Western Australia (warm range margin) and Tasmania (cool range centre) (Wernberg et al. 2013a, Bennett et al. 2015a).
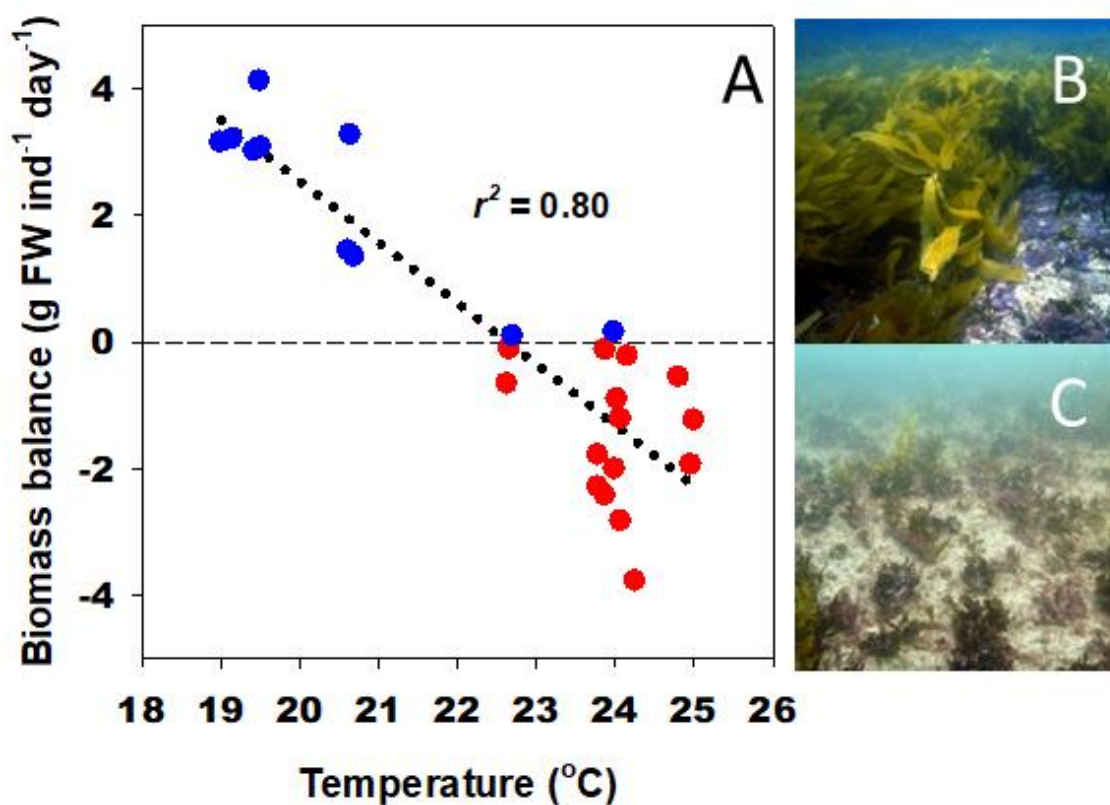

Figure 12 Along the west coast of Australia, the balance between *Ecklonia radiata* production and erosion becomes negative (i.e. the kelps shrink, red dots) when temperatures exceed about 23°C (each point represents the average of measurements on 15 kelp at a point in space and time, Wernberg unpublished data) (A). During the 2011 marine heatwave, temperatures exceeded this threshold across vast swathes of coastline for several weeks. Dense and healthy *E. radiata* kelp forests in Kalbarri (Western Australia) in 2005 prior to the heatwave subsequently collapsed (B), and the reef was colonised by sediment-laden algal turf (C). (Photographs by the authors).

Overgrazing: Tropicalisation and urchin incursion

One of the main impacts of climate change at the warm range edges of *E. radiata* forests is due to new species interactions emerging as a result of tropicalisation; that is, an increase in the proportion of tropical and warm-water species where temperate species previously dominated (Vergés et al. 2014). In particular, increases in the abundance of tropical and warm-temperate herbivores have been linked to declines of *E. radiata* in both eastern (Vergés et al. 2016) and western Australia (Wernberg et al. 2016a, Zarco-Perelló et al. 2017). Novel kelp-herbivore interactions are leading to the decline of *E. radiata* and the maintenance of alternative turf-dominated reefs via both direct consumption of macroscopic sporophytes and enhanced grazing on algal turfs, which prevents kelp re-establishment and provides high resilience to these novel ecosystems (Bennett et al. 2015c, Vergés et al. 2016). Although more than 90 herbivorous fish species have expanded their distribution into temperate reefs worldwide (Vergés et al. 2014), only a small number of species appear to be able to consume adult *E. radiata*. In particular, the rabbitfish *Siganus fuscescens* and sea chubs *Kyphosus* spp. have been implicated in the loss of *E. radiata* in both eastern and western Australia (Vergés et al. 2016, Zarco-Perelló et al. 2017) and also in Japan for *Ecklonia cava* (Yamaguchi 2010, Yamaguchi et al. 2010). In contrast, a much larger number of species appear to be implicated in enhanced turf grazing in tropicalised reefs, including multiple species of parrotfish (*Scarus* spp.) and surgeonfish *Acanthurus* spp. (Bennett et al. 2015c, Basford et al. 2016, Vergés et al. 2016).

Although low-latitude *E. radiata* populations are mostly being replaced by turf communities in Australia (Bennett et al. 2015c, Vergés et al. 2016), there is also evidence of some coral species expanding their distribution in eastern Australia (Baird et al. 2012) and other species expanding in cover in Western Australia (Tuckett et al. 2017). In southeastern Japan and southern Korea, some sites that used to be dominated by *E. cava* and other canopy formers have undergone a profound regime shift and are now dominated by fast-growing *Acropora* and other corals (Tribble & Randall 1986, Denis et al. 2013, Vieira et al. 2016).

In Tasmania, strengthening of the East Australia Current and incursion of warmer water into Tasmania have resulted in greater transport, survival and development of sea urchin (*C. rodgersii*) larvae and increased urchin reproduction (Ling et al. 2008), precipitating the formation of barrens and widespread loss of *E. radiata* and *M. pyrifera* kelp forests (Johnson et al. 2005b, Ling 2008, Johnson et al. 2011) and associated biodiversity (Ling 2008). Although barrens are now widespread in northeastern Tasmania, they remain incipient farther south, where urchins coexist with high-canopy cover of seaweeds (Johnson et al. 2011). The prevalence of urchin barrens is facilitated by a lack of predation pressure on *C. rodgersii* by large lobsters, which have been historically overfished (Ling et al. 2009). This may be further exacerbated in warmer oceans because of decreased predation pressure of lobsters on urchins and increased grazing of urchins on kelp, resulting in accelerated loss of *E. radiata* forests (Provost et al. 2017). It has been shown through large-scale experiments (Johnson et al. 2013) and modelling (Johnson et al. 2013, Marzloff et al. 2013, Marzloff et al. 2016b) that while large lobsters in largely intact *Ecklonia* forests are capable of preventing the ongoing spread of these barrens, rehabilitation of extensive urchin barrens by building lobster biomass is highly unlikely even if lobster fishing is ceased over many decades. This is because of the magnitude of the hysteresis in the lobster–urchin–kelp dynamic (Babcock et al. 2010, Johnson et al. 2013). Indeed, in New Zealand, such regime shifts took decades within MPAs once predators were protected (Shears & Babcock 2003, Marzloff et al. 2016b). In Tasmania, lobsters are also the principal predator of the urchin *H. erythrogramma* (Pederson & Johnson 2007), which also overgrazes *Ecklonia* to form urchin barrens, but only in relatively sheltered bays and at smaller scales. Densities of *H. erythrogramma* often appear to be only just sufficient to maintain barrens (Johnson et al. 2004), and anecdotal evidence suggests that persistence of *H.*

erythrogramma barrens is typically more ephemeral than extensive *C. rodgersii* barrens, which appear to persist indefinitely.

Predicted changes to dispersal and connectivity

Given that gene flow in *Ecklonia radiata* (and their competitors/herbivores) is largely dependent on passive dispersal (e.g. by currents, waves, tides), future changes to these vectors of dispersal will have important implications for population genetic parameters (Coleman et al. 2017), population demography and ability of *E. radiata* to respond to and recover from disturbances (Wernberg et al. 2018). Boundary currents globally are predicted to change under future scenarios of ocean change, with changes not only to temperature, but also hydrodynamics. In particular, in addition to warming, the strength of Australia's boundary currents are predicted to change in contrasting ways. The Leeuwin Current, in Western Australia, is predicted to weaken (Sun et al. 2012) and the East Australia Current is predicted to strengthen, separate at and penetrate into higher latitudes (Sun et al. 2012, Cetina-Heredia et al. 2014), with dispersal in eddies also predicted to increase (Matear et al. 2013, Cetina-Heredia et al. 2014, Oliver et al. 2015). Dispersal of *E. radiata* among populations may thus change in divergent ways, with a decrease on the west coast and an increase on the east coast.

Simulations of change in oceanographic connectivity along the east coast of Australia demonstrate that dispersal of organisms (including *E. radiata*) will be impacted, and this effect may be mediated by pelagic larval/propagule duration (Cetina-Heredia et al. 2015, Coleman et al. 2017). Specifically, under a future climatic scenario (A1B), dispersal in *E. radiata* shows a general trend of enhancement in a poleward direction and weakening in an equatorward direction (Coleman et al. 2017). This implies that already declining, low-latitude *E. radiata* forests will receive less gene flow and limited chance for genetic rescue under future scenarios of change. The intricacies of dispersal among populations along the coast are complex, however, and temporal variation within climatic scenarios is great (Coleman et al. 2017). To date, these projected changes to dispersal largely do not take into account the effects of temperature-mediated survival and performance of propagules (but see Cetina-Heredia et al. 2015) or adults (Figure 11, Martinez et al. 2018), which must be integrated to more accurately predict how dispersal and connectivity of *E. radiata* might change in the future.

Carbon and nitrogen emissions

Carbon and nitrogen are two of the most limiting resources on land and in the sea, and their increasing liberation through human activities within both realms is unprecedented (Vitousek 1994). Both affect water quality, and public concern over coastal water quality is renowned. Resource enrichment (e.g. nitrogen from terrestrial runoff or carbon from fossil fuel combustion) represents a persistent enigma for those who manage biogenic habitats, as enrichment often acts as a direct positive effect (i.e. resource, Connell & Russell 2010; also see the section entitled 'Life history, dispersal and recruitment', earlier in this review), but also as an indirect negative effect (i.e. stressor; Burkholder et al. 2007), where it favours faster-growing and opportunistic competitors such as turf-forming algae (Connell et al. 2013). Modern societies are dependent on the intensification of food production (nitrogen fertilisers), removal of human waste (nitrogen effluent) and supply of energy and goods to cities (carbon emissions). Kelp loss due to nutrient overenrichment is driven by the stimulation of seaweed turfs that typically trap sediment to form a semiconsolidated matrix that inhibits recruitment of *Ecklonia radiata* (Gorman & Connell 2009). This reversal of competitive dominance, whereby normally ephemeral turfs persist year round to displace kelps, is also enhanced by CO_2 enrichment (Connell et al. 2018). In locations where kelps have been lost to the indirect effects of nutrient pollution (e.g. Adelaide, South Australia), the public have valued the improvement

of water quality to be worth 100 s of millions of dollars that they would be prepared to pay (MacDonald et al. 2015). Nevertheless, researching the best ways to mitigate resource liberation is challenging, because of the complexity of understanding a complex system of buffering interactions (Goldenberg et al. 2018) that is prone to tipping points (non-linear cause effects; Connell et al. 2017b), that are lagged and not immediate (Connell et al. 2008a) and indirect rather than direct (Connell et al. 2013). What we do know is that co-limitations between nitrogen and carbon work in tandem to drive kelp loss in a high-CO_2 world (Falkenberg et al. 2013b). Whether together or separately, they provide the resources under which turfs expand and inhibit recruitment of *E. radiata* (Connell & Russell 2010).

Resource enrichment of algae can propagate into enhanced reproduction of herbivores that increase grazing intensity (Heldt et al. 2016, Connell et al. 2017a), but also create a mismatch between herbivore production and food demands of carnivores (Nagelkerken & Connell 2015). The effects of resource enhancement on kelp forests, therefore, are mediated by this shifting balance between the propagation of resource enrichment and its consumption across trophic levels. Top-down responses by herbivores and their predators can accelerate or reverse kelp loss (Goldenberg et al. 2018). When considered in conjunction with concomitant warming, herbivory has been observed to decline during warming events, which provides kelp-competitors (e.g. turfs) a refuge from herbivory (Mertens et al. 2015).

A key challenge for science and management of resource liberation is its duality; it can act as both a direct positive effect (i.e. resource, Connell & Russell 2010) and as an indirect negative effect (i.e. stressor; Connell et al. 2018). To date, research tended to focus on direct effects, reflecting the idea that the strongest drivers in ecosystems are direct. Yet, we increasingly recognise that indirect effects that affect production and consumption of habitats are often some of the strongest (Harley et al. 2017), and because they are often surprising (Hughes et al. 2013), they are underestimated in terms of their ubiquity and strength.

Mitigation and mechanisms that buffer change

Whilst the collapse of kelp systems highlights their susceptibility to local and global change (e.g. Wernberg et al. 2011a), it also emphasises a need to explore mechanisms that can buffer, reduce or reverse the extent of change (Connell & Ghedini 2015). Hence, understanding the range of mechanisms that can enhance community persistence in the face of rapid environmental change is a central theme of current ecological research. These could include active mitigation through intervention, genetic/genomic manipulation or increasing resilience through protected areas or better understanding of ecological interactions and compensatory dynamics.

Restorative actions can enable recovery to the defined historical habitats in some degraded systems. Others are resilient to restoration efforts as they have either undergone a shift to an alternative persistent state with a strong basin of attraction or the dynamic equilibrium between alternative states has shifted (Suding et al. 2004, Johnson et al. 2011, Lotze et al. 2011). It is the existence of these alternative stable states and their resilience to restorative actions (i.e. the magnitude of hysteresis) that underlie many of the difficulties in anticipating the potential for re-establishment of historical habitats (Beisner et al. 2003). Restorative actions in which loss of *Ecklonia radiata* forests has been a direct result of climatic changes (particularly at low-latitude margins) are unlikely to be successful, given that predicted ongoing and increasing change are exceeding the thresholds of *E. radiata* to survive (Wernberg et al. 2013a). Restoration of trophic structures via the designation of MPAs (Babcock et al. 2010) and/or urchin culling (Andrew & Underwood 1993) may be successful, particularly when done together. Urchin culling alone, however, is not a long-term solution to *E. radiata* loss. Not only

is it extremely resource and cost intensive (Sanderson et al. 2016), but culling by divers cannot tackle the scale of barrens and the depths to which they occur (Johnson et al. 2011). Moreover, slow incursion of adult urchins and continued recruitment of larvae back into newly established forests prevent long-term success without ongoing intervention (Tracey et al. 2015) such as to rebuild populations of urchin predators (Marzloff et al. 2013, Marzloff et al. 2016b).

In the case of urchin barrens formation, in which both the magnitude of hysteresis and the spatial extent of the problem is large, it has been suggested that the best use of limited resources is to attempt to prevent further barrens formation but not to attempt restoration of extensive barrens back to kelp forest (Johnson et al. 2017). In Tasmania, it is clear that rebuilding populations of large, predation-capable lobsters can be effective in arresting ongoing barrens formation in kelp forests and incipient barrens, but it is unlikely to have any effect in restoring kelp forests on extensive urchin barrens (Johnson et al. 2013, Marzloff et al. 2013, Marzloff et al. 2016b). The extensive urchin barrens in Tasmania are likely to be an enduring feature of the coastline unless innovative approaches currently under trial (e.g. development of smart automated robotics to locate and remove urchins) meet with success. Manipulative experiments have shown that restorative actions to reverse shifts from algal turfs back to barrens require transplantation of adult kelps to reinstate environmental conditions (high scour and low light) that inhibit turf growth and sediment accumulation, as well as provide a source of spore supply. However, all forms of intervention and restorative actions that seek to reverse regime shifts are unlikely to be successful in the long term unless conditions that precipitated shifts (e.g. poor water quality) are also improved.

MPAs may play a role in increasing resilience of *E. radiata* forests to climate stress or providing sources for reseeding or recolonisation in landscapes of increasing degradation. Many MPAs globally limit not only extractive activities, but also are protected by legislation that limits other activities that may affect marine biota. As such, MPAs may indirectly increase resilience of *E. radiata* to climate change by reducing interacting stressors such as coastal development and pollution. In addition, if MPAs can protect existing *E. radiata* forests in general landscapes of degradation, then these areas will be important sources of dispersal for recovery of denuded areas or donor populations for restoration efforts (Coleman et al. 2011a, 2017). However, to date, there is no empirical evidence that MPAs have played either of these roles for *E. radiata*. Certainly, MPAs have played a significant indirect role in recovery of *E. radiata* forests in New Zealand following historical fishing (Babcock et al. 2010). However, where urchin barrens are pervasive and widespread and climate-mediated dispersal of urchin larvae continues, such trophic cascades are unlikely to be realised even with significant restoration of predator populations (see above).

An emerging and topical component of future conservation and management of marine habitats, including *E. radiata* forests, centres on the concepts of enhancing resilience through genetic or genomic manipulation (Coleman & Goold 2019). Termed *assisted adaptation* or *assisted gene flow*, the general concept is that by introducing better-adapted (to a particular stressor of interest) genotypes into populations, it may be possible to boost the resilience of those populations to future stress (Aitken & Whitlock 2013). A similar concept is *genetic rescue,* whereby the fitness of small or genetically depauperate populations is enhanced through assisted immigration (Whiteley et al. 2015). Although such ideas have been employed in terrestrial systems and aquaculture for centuries (such as selective breeding), the advent of sequencing technologies and the ability to identify loci (and genotypes) that are selected for under certain environmental conditions now makes this a reality for natural marine systems. Indeed, such technology opens the possibility to design bespoke assisted adaptation strategies to boost resilience against a variety of stressors, if loci under selection can be linked to certain stressors of interest (e.g. temperature, pollution, nutrient input, grazing tolerance).Despite its

promise, caution must be taken to avoid outbreeding depression or disrupting adaptation to additional (non-target) stressors (Aitken & Whitlock 2013). In addition, unintended ecological surprises may arise when a change in one species resilience results in alteration to interactions among species (e.g. competition). Gene-editing technologies are an additional emerging area that could transform the resilience of organisms to stress some day (Coleman and Goold 2019). This could be coupled with manipulations of the associated microbiome to enhance resilience (see the section entitled 'Community ecology of *Ecklonia*forests', earlier in this review). Despite the fact that both these concepts present ethical challenges and debate, they should remain within discussions about conservation tools for the future (Filbee-Dexter & Smajdor 2019).

Future generations may also place greater value on research that seeks to understand the circumstances in which environmental change is resisted. Critically, knowledge of stabilising processes may be useful to managers in circumstances where kelp loss is undesirable and preventable. The erosion of stabilising processes releases the culminated potential of change (Ghedini et al. 2015), such that stability was, actually, long undermined before collapse. Such lagged responses have been considered as 'living dangerously on borrowed time during slow, unrecognised regime shifts' (Hughes et al. 2013). Whilst system collapse and its drivers are, in fact, readily observable, stability and its drivers remain among the least-studied processes in ecology (Connell & Ghedini 2015).

By bolstering the processes that compensate for change and thereby stabilise kelp forests, we may enable them to resist future shocks. A key symptom of systems undergoing negative change is loss of biodiversity, the very factor that appears to buffer the direct, negative effects of human activities (Hautier et al. 2015). Where communities are more complex, they tend to be more stable because of the inherent capacity for compensatory dynamics among the web of species interactions (Goldenberg et al. 2018). Hence, the relatively simple rule of thumb of conserving diversity may actually be one of the more tractable levers of management. In this regard, given the diversity of fucoids and range of environments they occupy, they may replace *E. radiata* as habitat-forming kelps for habitat and energy provision.

The cover of fucoids on many shallow reefs across southern Australia exceeds that of *E. radiata* (Cresswell et al. 2017). *E. radiata* and fucoids, however, support different communities and abundance of economically important species (e.g. Marzinelli et al. 2014) and are not entirely functionally equivalent (see review by Coleman & Wernberg 2017). Moreover, with the possible exception of some species of tropical *Sargassum*, the potential for fucoids to replace *E. radiata* as the dominant habitat formers on temperate reefs is less likely at lower latitudes on Australia's east coast, where fucoids are generally lacking and *E. radiata* forms monospecific forests.

Conclusion

Over evolutionary and contemporary scales, *Ecklonia radiata* has adapted to a wide range of environmental conditions; from about 27°S to 48°S throughout Australasia and southeastern Africa, it occurs on hard substrates from the shallow subtidal down to mesophotic reefs at about an 80-m depth. Such extreme variations in environmental conditions appears to drive great morphological plasticity, which has confused the species' identity. As such, identifying the true distribution of *E. radiata* requires molecular confirmation, particularly of putative Northern Hemisphere populations. There has been an enormous growth in our understanding of *E. radiata*and the ecosystems that it supports over the past 25 years, especially in Australasia, while gaps exist for other parts of its range. Wherever *E. radiata* occurs, however, it plays a major role in determining patterns of subtidal biodiversity and ecosystem structure. From

individual holdfasts to entire forests, *E. radiata* supports thousands of species, underpins food webs and represents immense scientific, economic and social values.

Of concern is that climate change, especially warming and other anthropogenic stressors are driving the loss of *E. radiata* forests, and while there are regional differences in the drivers of this loss, there is ubiquity in patterns of change. Regime shifts to undesirable states (algal turfs or urchin barrens) are a common consequence of *E. radiata* loss and are accompanied by strong hysteresis making restoration difficult. Restorative activities will need to move beyond simply abating stressors and incorporate multifaceted intervention strategies that could include combinations of removing competitors and grazers, restoring the trophic structure of *E. radiata* forests and emerging interventions such as genetic rescue, assisted gene flow and adaptation (Coleman & Goold 2019). Despite a general landscape of contemporary loss, the evolutionary history of *E. radiata* has shaped a temperature-tolerant, plastic and widely distributed species that may be among the best-placed kelps to adapt or tolerate future oceans. Simultaneously, science must continue to generate understanding and discover novel solutions to ensure that these underwater forests survive and flourish in a future of increasing change.

Acknowledgments

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