2022

Patch dynamics driven by wave exposure in subtidal temperate seaweeds are exacerbated by warming oceans

Yannick Mulders

Lydiane Mattio

Julia C. Phillips

Paul S. Lavery
Edith Cowan University

Gary A. Kendrick

See next page for additional authors

Authors

Yannick Mulders, Lydiane Mattio, Julia C. Phillips, Paul S. Lavery, Gary A. Kendrick, and Thomas Wernberg

Patch dynamics driven by wave exposure in subtidal temperate seaweeds are exacerbated by warming oceans

Yannick Mulders[1,2,*], Lydiane Mattio[3,4], Julia C. Phillips[5], Paul S. Lavery[6], Gary A. Kendrick[1,2], Thomas Wernberg[1,2,7]

[1]UWA Oceans Institute, The University of Western Australia, 35 Stirling Hwy, Crawley, WA 6009, Australia
[2]School of Biological Sciences, The University of Western Australia, 35 Stirling Hwy, Crawley, WA 6009, Australia
[3]Department of Biological Sciences, University of Cape Town, Rondebosch 7701, South Africa
[4]blue[c]weed, 29200 Brest, France
[5]Water Corporation, Leederville, WA 6007, Australia
[6]Centre for Marine Ecosystem Research, Edith Cowan University, 270 Joondalup Drive, Joondalup, WA 6027, Australia
[7]Department of Science and Environment, Roskilde University, 4000 Roskilde, Denmark

ABSTRACT: Over the past decades, ocean temperatures have been steadily increasing and are projected to continue to do so, stressing many temperate marine organisms. Changing temperatures do not affect ecosystems in isolation, but interact with many other factors in shaping ecological communities. We investigated the changes over 2 decades in subtidal temperate seaweed communities over a wave exposure gradient in Western Australia, a global warming hotspot. We found higher diversity in the seaweed community and a higher proportion of biomass of species with a warm affinity (expressed as the tropicalization index: TI) over time. There was no decline in biomass of the dominant habitat-forming kelp *Ecklonia radiata* on low wave exposure reefs, while it was patchier and comprised a lower proportion of the total seaweed biomass on the medium and high wave exposure reefs. Furthermore, the presence of *E. radiata* was disproportionally associated with low abundances of seaweeds with warm affinity. The increasing patchiness of *E. radiata* likely provided a competitive release for other seaweeds, and the increase in abundance of *Scytothalia dorycarpa* likely provided a compensatory effect which resulted in a lower than expected TI. We found no indication of an ameliorating effect by wave exposure, and conclude that the patch dynamics driven by wave exposure are more likely exacerbated by increasing ocean temperatures on subtidal temperate reefs. If this continues, the reduction in *E. radiata* and increase in warm affiliated seaweeds will result in a more diverse seaweed community, but one with a lower standing biomass.

KEY WORDS: Ocean warming · Wave exposure · Rocky reefs · Kelp · *Ecklonia radiata*

1. INTRODUCTION

Ecological studies have long recognized abiotic environmental parameters as large spatial scale drivers of species distribution (Wiens & Donoghue 2004, Ashcroft et al. 2009). Multiple factors work simultaneously — potentially antagonistically or synergistically — on the tolerance of species to determine whether the environment is suitable (Menge & Olson 1990, Diez &

Pulliam 2007, Wiens 2011). As temperatures have been rising globally for decades, a trend which is projected to continue (IPCC 2018), the interactive effects with existing local-scale stressors are reshaping ecosystems. As a result, changes in species distributions are being reported worldwide (Russell & Connell 2012, García Molinos et al. 2016, Hastings et al. 2020).

Subtidal temperate reefs are home to some of the most productive ecosystems in the world: kelp forests

*Corresponding author:
yannick.mulders@research.uwa.edu.au

(Mann 1973, Wernberg et al. 2019b). They are defined by large habitat-forming seaweeds as foundation species that provide the physical structure and primary productivity which support a diverse community of associated flora and fauna (Wernberg & Filbee-Dexter 2019). As such, kelp forests are not only of immense ecological value but are also socio-economically important (Bennett et al. 2016, Smale et al. 2019), having been exploited by humans for millennia (Simenstad et al. 1978, Erlandson 2001). Temperate subtidal reefs in Australia stretch from the east coast to the west coast, encompassing the entire southern coast and Tasmania, collectively forming the Great Southern Reef (GSR) (Bennett et al. 2016). The most widespread and abundant kelp on the GSR is *Ecklonia radiata*, a relatively small kelp growing up to around 2 m in length (Wernberg et al. 2019a). Due to its lack of floating vesicles and rigid stipe in much of its distribution (Wernberg et al. 2003), it forms a prostrate canopy over the seafloor which shapes the physical environment of the benthos underneath (Wernberg et al. 2005).

As is seen for many other marine foundation species such as corals (Hughes et al. 2007) and sea-grasses (Thomson et al. 2015), kelps worldwide are under pressure (Krumhansl et al. 2016, Wernberg et al. 2019b) from a multitude of stressors such as temperature (Smale & Wernberg 2013, Wernberg et al. 2016a), herbivory (Vergés et al. 2014, Zarco-Perello et al. 2017), or competition with invasive species (Scheibling & Gagnon 2006). While any single source of stress can cause a decline in kelp, interacting stressors can compound their effects (Filbee-Dexter & Wernberg 2018). When stressors exceed the threshold of resilience, they can cause the total collapse of the kelp forest, leaving alternative steady states such as urchin barrens (Filbee-Dexter & Scheibling 2014) or macroalgal turfs (Filbee-Dexter & Wernberg 2018, Wernberg et al. 2019b).

In Western Australia, at the western edge of the GSR, temperate subtidal reefs are located in a global warming hotspot (Hobday & Pecl 2014), experiencing a gradual temperature increase of 0.013°C yr^{-1} since 1951 (Pearce & Feng 2007) and increasing frequency of short but severe heat events (marine heatwaves) which last days to weeks (Oliver et al. 2018, 2019). In a single marine heatwave in 2011, kelp cover was reduced by 43% along the west coast, going functionally extinct in an area of over 370 km^2 (Wernberg et al. 2016a). As a result, temperate communities have undergone changes, as incursions of warm-water-affiliated seaweeds (Wernberg et al. 2013, 2016b), invertebrates (Wernberg et al. 2016a,

Smale et al. 2017, Mulders & Wernberg 2020), and fishes (Wernberg et al. 2013, 2016a, Richards et al. 2016) have been recorded.

On a local scale, wave exposure affects the seaweed community, such as through the species-specific response in the abundance of seaweeds (Phillips et al. 1997), as well as plasticity in seaweed morphology in relation to wave exposure (Hurd 2000, Wernberg & Thomsen 2005). *Ecklonia radiata* exhibits morphological traits that aid in reducing drag or increasing strength (Wernberg & Thomsen 2005). It is possible that these morphological differences between levels of wave exposure covary with the vulnerability of *E. radiata* and other seaweeds to temperature stressors. Additionally, increased water motion improves the mixing of nutrients into the water column (Lourey et al. 2009) and increases the nutrient uptake by seaweeds (Hurd 2017). By ameliorating abiotic stressors, wave exposure has been shown to have positive effects on seaweeds in the intertidal zone (Starko et al. 2019), as well as in the shallow subtidal kelp *Nereocystis luetkeana* (Berry et al. 2021).

In this study, we tested the effect of the interaction between wave exposure and temperature on the seaweed communities of temperate subtidal reefs by investigating changes over a 20 yr period on reefs exposed to different levels of wave energy in a global warming hotspot. We hypothesized that if wave exposure is an ameliorating factor against temperature stress, the changes seen in the seaweed communities on the exposed reefs will be less pronounced than the changes on the sheltered reefs.

2. MATERIALS AND METHODS

2.1. Study site

Marmion Lagoon (31.852° S, 115.713° E, hereafter referred to as Marmion) is a shallow (<15 m deep) body of water situated 20 km north of Perth, Western Australia (Fig. 1). Oceanic swells from the west and south-west dominate the local wave climate year round (Searle & Semeniuk 1985). Locally generated wind waves, in addition to swell, have a significant influence close inshore and during storm events (Searle & Semeniuk 1985). Both types of waves are dampened, diffracted, and refracted as they approach the coast by a series of 3 parallel lines of limestone reefs. This dissipation of energy, as waves encounter each successive reef line, produces a gradient of physical disturbance ranging from high exposure reefs (offshore reefs) to reefs of low expo-
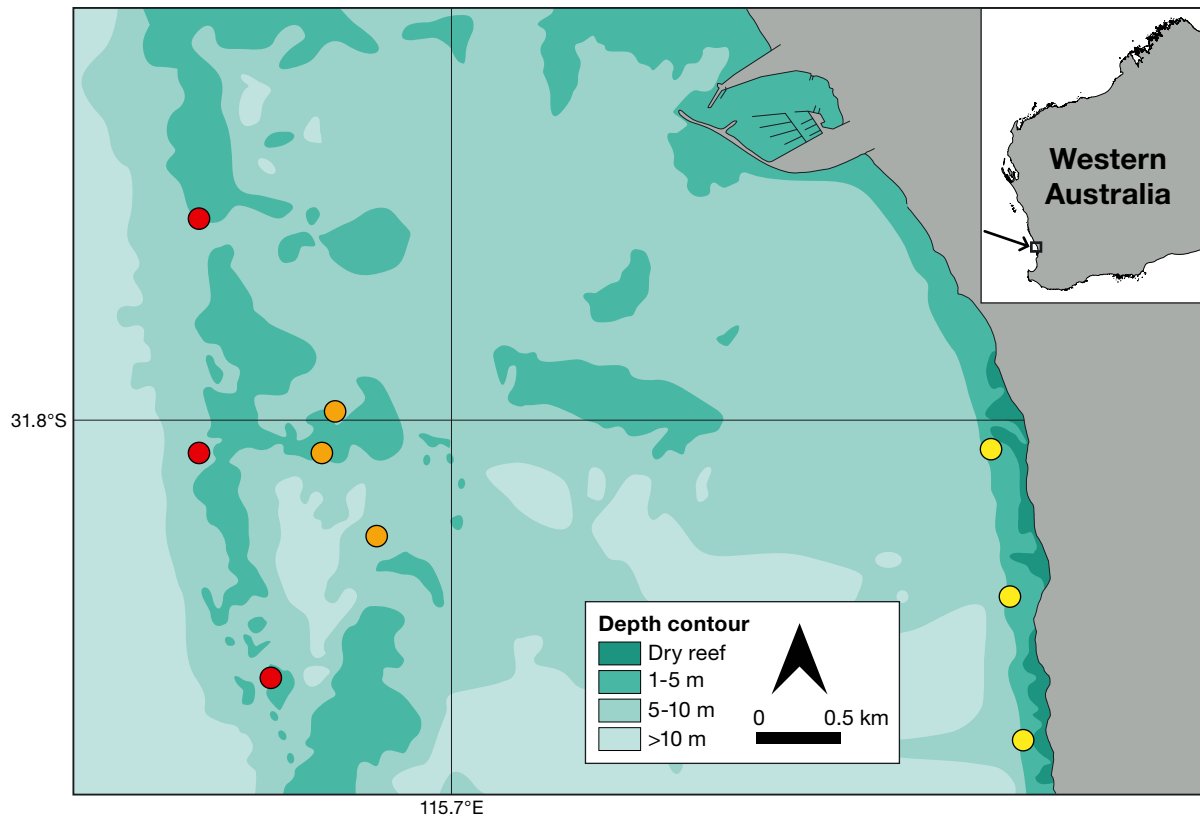
Fig. 1. Study sites were located on 3 main reef lines parallel to the coast in Marmion Lagoon, Western Australia. Wave energy dissipated towards nearshore, resulting in high exposure (red circles, 3.90 kJ m^{-2}), medium exposure (orange circles, 2.05 kJ m^{-2}), and low exposure sites (yellow circles, 0.91 kJ m^{-2})

sure (inshore reefs). Wave heights at each reef line, measured simultaneously for 2 h on 9 July 1996 using a Model 606 Submersible Data Logger (Yeo-Kal), were used to calculate the total energy per unit area of wave (Phillips et al. 1997). These measurements were intended to provide an indication of relative energy levels at the 3 reef lines, and not to describe temporal and spatial variation in absolute energy levels (Phillips et al. 1997, Smale et al. 2011). Wave energy at the offshore, midshore, and inshore reef lines was 3.90, 2.05, and 0.97 kJ m^{-2}, respectively. The existence of this wave exposure gradient has been independently confirmed in several other studies using a range of instruments (Smale et al. 2011, Symonds et al. 2011, de Bettignies et al. 2015).

A temperature profile was constructed for Marmion from January 1993 to December 2018 using sea surface temperature (SST) measured by satellite (IMOS 2019). The resolution of the satellite data did not allow for site-specific temperature profiles; however, studies deploying loggers over several years have demonstrated that within the depth range investigated here, site to site variation in temperature is negligible at these reefs (Smale & Wernberg 2009). The monthly SST anomaly (Fig. 2A) was calculated by subtracting the respective mean monthly SST from 1993 to 2018 from the mean SST for each individual month (Fig. 2B). The yearly mean SST showed an increase of 0.0118°C yr^{-1}, with high interannual variability ($R^2 = 0.036$, $p = 0.294$). Additionally, a long-term wave exposure profile was constructed using the significant wave height (SWH) from the closest waverider buoys: Rottnest Island (32.111° S, 115.402° E) and Cottesloe (31.978° S, 115.687° E) (IMOS 2021). The mean and maximum SWH (Fig. 2C) was determined for each month from 1999 to 2018, as no data were available before 1999. The mean SWH showed a decrease of 0.01 m ($R^2 = 0.112$, $p = 0.149$) and 0.007 m ($R^2 = 0.248$, $p = 0.03$) per year for Rottnest Island and Cottesloe, respectively.

2.2. Sample collection

For comparability between years, sites selected were the same as those used by Phillips et al. (1997),
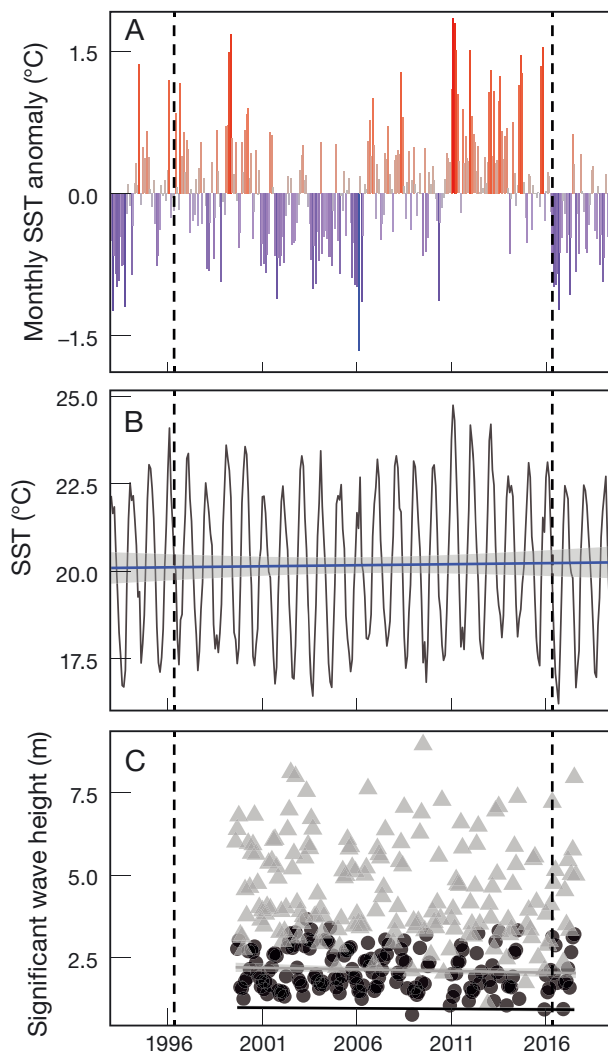
Fig. 2. (A) Monthly sea surface temperature (SST) anomaly (red: anomalous warming; blue: anomalous cooling) and (B) monthly mean SST (black line) and mean annual SST (blue line) with 95% CI from 1992 until 2018 in Marmion Lagoon, as well as (C) the mean (lines) and max (symbols) monthly significant wave height (SWH) at Rottnest Island (grey) and Cottesloe (black) from 1999 until 2017. Sampling times are indicated by the vertical black dashed lines. All SST and SWH data were sourced from the Integrated Marine Observing System (IMOS 2019, 2021)

i.e. 3 sites for each of the different exposure levels. Each site within an exposure level was separated hundreds of metres, and each quadrat within site was separated by metres. Collections were done during austral autumn (April–May) both in 1996 and 2016. At each site, 0.25 m^2 quadrats (n = 10) were placed haphazardly on the reef flat between 5 and 10 m of depth, and all seaweeds within the quadrat were collected by SCUBA divers. Special care was taken to remove seaweeds with or as close to the

holdfast as possible to help with identification purposes. All collected quadrats were kept frozen until sorting and identification. After sorting, identification was done to species level where possible, and each species per quadrat was dried separately at 60°C for 48 h to obtain dry weight. The ash weight was then determined by weighing each sample after combustion at 550°C for 2 h, and the ash-free dry weight (AFDW) by subtracting the ash weight from the dry weight. Due to the logistical constraints of a small combustion oven and large amounts of *E. radiata* biomass, the AFDW for *E. radiata* was determined by combusting 15 individuals (5 from each exposure level) and using the conversion ratio obtained through linear regression (r = 0.916) to convert *E. radiata* dry weight (DW) to AFDW according to the following formula:

$$AFWD = DW - (0.2816 \, DW + 4.6428) \tag{1}$$

2.3. Temperature affinity

Species' temperature affinities were determined based on records of their distributions and known thermal preferences (Huisman 2019). Any species that had no record of existing north of Geraldton (28.776° S, 114.611° E) was considered to be a cool-water species, whereas species that extended their distribution ranges (Western Australian Herbarium 1998, Guiry & Guiry 2020) further north were considered warm-water species. Cosmopolitan species that were documented to have higher abundances in warmer waters were also considered to be warm-water species. *Sargassum* was not identified to species level, and although there are *Sargassum* species that have a cool affinity, as a genus they were considered to have a predominantly warm affinity. A tropicalization index (TI) of the seaweed community was calculated for each quadrat by dividing the log-transformed sum of the biomass of species with warm affinity by the log-transformed sum of the biomass of species with cool affinity:

$$TI = \frac{\log(\text{Biomass}_{warm})}{\log(\text{Biomass}_{cool})} \tag{2}$$

2.4. Data analyses

Statistical tests were performed in R v.3.4 (R Core Team 2019). A principal coordinates analysis (PCoA) was made from the Bray-Curtis dissimilarity matrix of the presence/absence of seaweed species for each

exposure level. The difference over time was analysed using a permutational multivariate ANOVA (PERMANOVA) on the same dissimilarity matrix. A SIMPER analysis was then performed on the log-transformed biomass of the seaweeds to determine which species contributed most to the change in community biomass between years. The PCoA, PERMANOVA, and SIMPER analyses were done using the 'vegan' package in R (Oksanen et al. 2010). For comparing biomass, diversity, and the TI over time and exposure, nested linear mixed effects (LME) models using a restricted maximum likelihood approach were created using the 'nlme' package (Pinheiro et al. 2017). In these models, year (2 levels: 1996, 2016) was a fixed effect, exposure (3 levels: high, medium, low) was a fixed effect, site (n = 3) was a random effect, and quadrat (n = 10) was nested within site. The percent occurrence of *E. radiata* per site was calculated by the percentage of quadrats in which *E. radiata* was present. An LME model using year (2 levels: 1996, 2016) as a fixed effect, exposure (3 levels: high, medium, low) as a fixed effect, and site (n = 3) as a random effect was used to compare means. Post hoc comparisons of individual means within the LME models were done using a Tukey HSD test. Residuals in the LME models were visually inspected for normality. The homogeneity of variance was checked using Levene's test. Either a log or square root transformation was performed when needed. For comparing the fraction of *E. radiata* biomass in the total seaweed biomass, a PERMANOVA based on the Euclidean dissimilarity was performed, as none of the transformations of the LME passed Levene's test. For analysing the effect of the presence of *E. radiata* on biomass and TI in quadrats where *E. radiata* was present or absent, only quadrats from 2016 were used, as there was only 1 quadrat in 1996 without. Differences were tested using a 2-sample Student's *t*-test on the log transformed data in order to assure homogeneity of variance, which was confirmed with Levene's test. There is a potentially confounding effect of using *E. radiata* as a predictor variable when it also contributes to the response variable (Thomsen et al. 2016). We therefore calculated separate TIs with *E. radiata* biomass included and excluded when examining the effect of *E. radiata* biomass on the TI.

3. RESULTS

3.1. Seaweed community

A total of 98 seaweed species were identified, but over 90% of the Bray-Curtis dissimilarity of communities between years was accounted for by 30 species (Table S1 in the Supplement at www.int-res.com/articles/suppl/m685p085_supp.pdf). *Ecklonia radiata* accounted for the largest difference (15.7%) by a single species as the overall biomass decreased between 1996 and 2016. Two other common canopy formers, *Sargassum* spp. and *Scytothalia dorycarpa*, showed an increase in overall biomass. However, the total biomass of seaweeds did not change significantly between 1996 and 2016 (Table 1). While the low wave exposure reefs had significantly lower biomass than the other exposure levels (Tukey HSD, p = 0.012 and p = 0.012 compared to medium and high exposure, respectively) in 1996, in 2016 there was no significant difference of biomass over exposure levels (Fig. 3A). Species richness showed a significant increase from 1996 to 2016 ($F_{1,12}$ = 14.568, p = 0.002; Table 1, Fig. 3B), with the highest species richness found on the high exposure reefs.

Table 1. Nested linear mixed effects model comparing the seaweed biomass and richness, *Ecklonia radiata* biomass and presence, as well as the tropicalization index (TI) at Marmion Lagoon, Western Australia. Effects are measured over time (fixed factor, 2 levels: 1996, 2016), and exposure level (fixed factor, 3 levels: high, medium, low) with 3 sites (random effect) per exposure level, with 10 quadrats nested within site. **Bold** values indicate p < 0.05

Model	Transformation	df	MS	*F*	p
Seaweed biomass	None				
Year		1,12	24152.7	3.151	0.101
Exposure		2,12	44073.8	5.750	**0.018**
Year × Exposure		2,12	24509.0	3.198	0.077
Seaweed diversity	Log				
Year		1,12	2.474	19.042	**0.001**
Exposure		2,12	0.142	1.089	0.368
Year × Exposure		2,12	0.070	0.542	0.595
***E. radiata* biomass**	None				
Year		1,12	216.3	0.026	0.874
Exposure		2,12	38509.6	4.670	**0.032**
Year × Exposure		2,12	30622.2	3.714	0.056
***E. radiata* presence**	None				
Year		1,12	1088.9	13.067	**0.004**
Exposure		2,12	172.2	2.067	0.169
Year × Exposure		2,12	72.2	0.867	0.445
TI	Square root				
Year		1,12	0.689	12.495	**0.004**
Exposure		2,12	0.092	1.670	0.229
Year × Exposure		2,12	0.030	0.552	0.590

The increase in species richness was also seen in community composition (Fig. 4). There was a relatively low diversity in the seaweed community in 1996, and as a result, the quadrats clustered together at each exposure level. There was an increase in diversity from 1996 to 2016 at all exposure levels, and the difference in community composition over time was highest on the medium exposure reefs (PERMANOVA; pseudo-F = 15.187, p = 0.001), followed by the high exposure reefs (PERMANOVA; pseudo-F = 12.418, p = 0.001), and finally the low exposure reefs (PERMANOVA; pseudo-F = 11.13, p = 0.001).

The ratio of warm species to cool species biomass increased over time, as is reflected by the increased TI, but there was no significant trend over exposure (Table 1, Fig. 5). However, as with the PCoA, the biggest change over time was seen on the medium
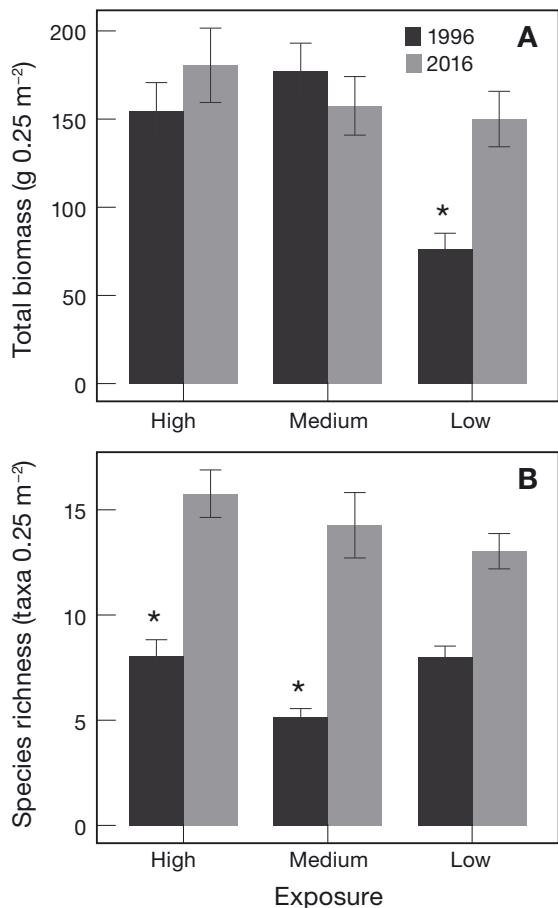

Fig. 3. (A) Total seaweed biomass and (B) seaweed species richness per quadrat across a wave exposure gradient at Marmion Lagoon. Ash-free dry weight biomass and species richness (mean ± SE) were determined for quadrats of 0.25 m² at each exposure level (n = 30 per level) in 1996 and 2016. Asterisks indicate significant differences between years (Tukey HSD, p < 0.05)
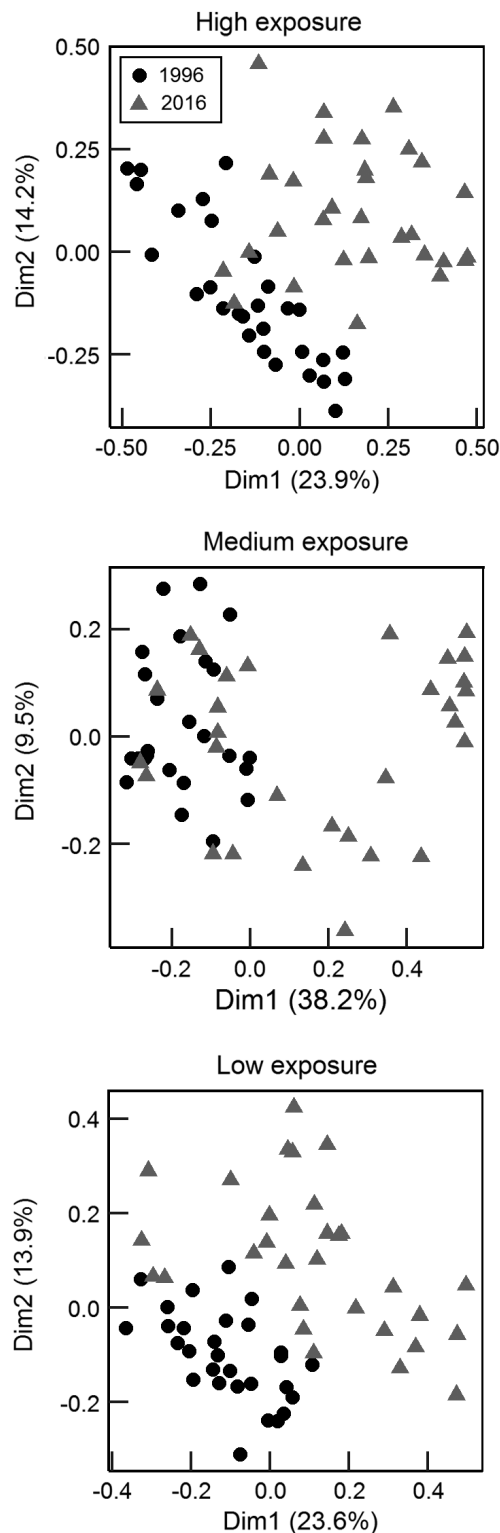

Fig. 4. Principal coordinates analysis of the Bray-Curtis dissimilarities of the presence/absence of seaweeds per quadrat on high (n = 60), medium (n = 60), and low exposure (n = 60) reefs at Marmion Lagoon over a 20 yr time interval
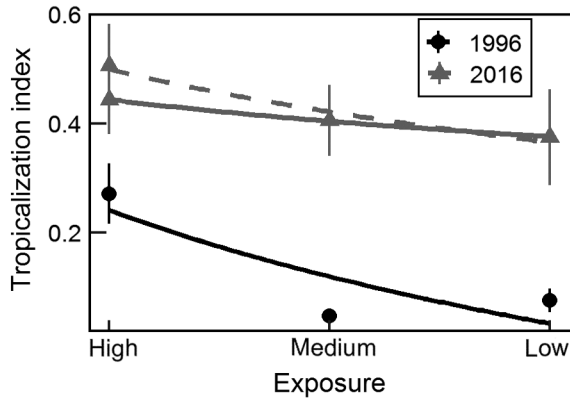
Fig. 5. The tropicalization index (TI): proportion of biomass of seaweed species with warm temperature affinity to seaweeds with a cool temperature affinity, over the exposure gradient at Marmion Lagoon in 1996 and 2016. The compensatory effect of competitive release is projected by removing *Scytothalia dorycarpa* from the equation (dashed grey line). Error bars indicate SE

exposed reef (Tukey HSD; p = 0.018), followed by the low (Tukey HSD, p = 0.055), and then the high exposure (Tukey HSD, p = 0.232) reefs. Both in 1996 and in 2016, the highest TI was found on the high exposed reefs. The increase in *S. dorycarpa* biomass over time limited the increase in the TI on the high exposed reef, compared to at the other exposure levels.

3.2. *E. radiata*

The reduction of *E. radiata* presence was the greatest individual contributor to the Bray-Curtis dissimilarity between years (see Table S1), while *E. radiata*

biomass did not show a significant change over time (LME; $F_{1,12} = 0.026$, p = 0.874; Fig. 6A). The roughly doubling of biomass seen on the low exposure reefs (Tukey HSD; p = 0.044) compensated the relatively small decreases on the high (Tukey HSD; p = 0.616) and medium exposed reefs (Tukey HSD; p = 0.171). However, there was a significant decrease in the fraction of *E. radiata* biomass of the total biomass, both on the high (PERMANOVA; pseudo-F = 9.866, p = 0.002) and medium (PERMANOVA; pseudo-F = 13.722, p = 0.001), but not on the low exposed reefs (PERMANOVA; pseudo-F = 0.512, p = 0.469; Fig. 6B). Combining all exposure levels, the fraction of *E. radiata* dropped from 85.2% in 1996 to 66.7% in 2016 (PERMANOVA; pseudo-F = 18.715, p = 0.001). Furthermore, the percentage of quadrats in which *E. radiata* was present was lower in 2016 than in 1996 (LME; $F_{1,12} = 13.067$, p = 0.004), with the reduction increasing with exposure (Fig. 6C).

There was a large discrepancy in multiple measures between quadrats in which *E. radiata* was present or absent in 2016. The TI was significantly higher in the absence of *E. radiata* (t-test; $t_{88} = 6.768$, p < 0.001; Fig. 7A), even when *E. radiata* was not included in the calculation of the TI (t-test; $t_{88} = 3.258$, p < 0.002). Indeed, there was an exponential increase in the TI as the *E. radiata* biomass decreased (Fig. 7B). While the total seaweed biomass was higher when *E. radiata* was present, this was mostly *E. radiata* biomass (t-test; $t_{88} = 7.320$, p < 0.001; Fig. 7C). When *E. radiata* was absent, the biomass of other seaweeds increased (t-test; $t_{88} = 3.079$, p = 0.003). Furthermore, as the TI of the seaweed community increased, there was a decrease in seaweed biomass (Fig. 7D).
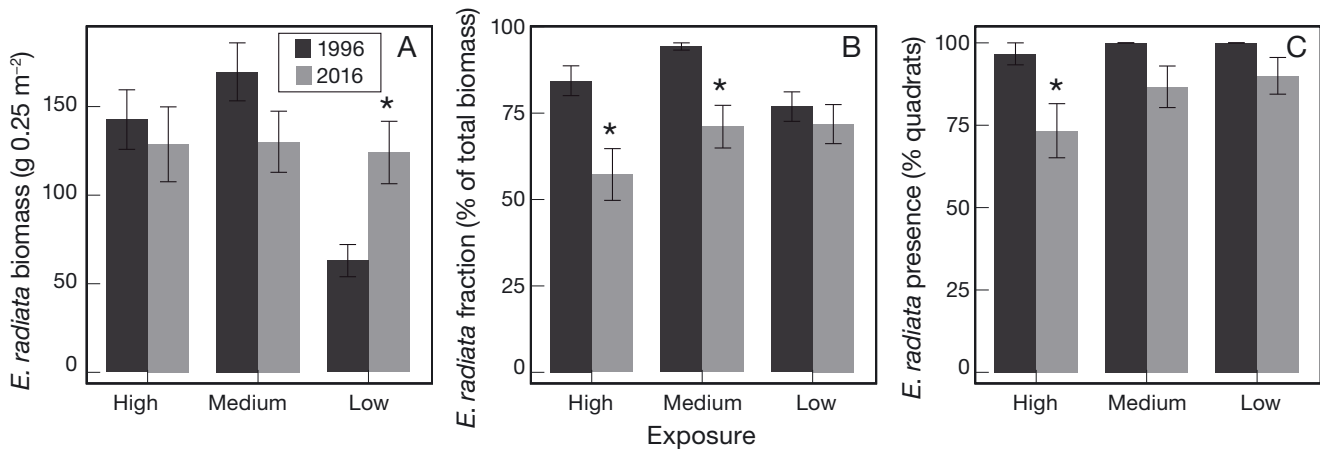

Fig. 6. (A) Ash-free dry weight biomass, (B) fraction of total biomass, and (C) presence in quadrats of *Ecklonia radiata* (mean ± SE) in 1996 and 2016 over the exposure levels (n = 30 per level) at Marmion Lagoon. Asterisks indicate significance differences (A,C; Tukey HSD test, p < 0.05) or individual mean comparison by PERMANOVA (B; p < 0.05)
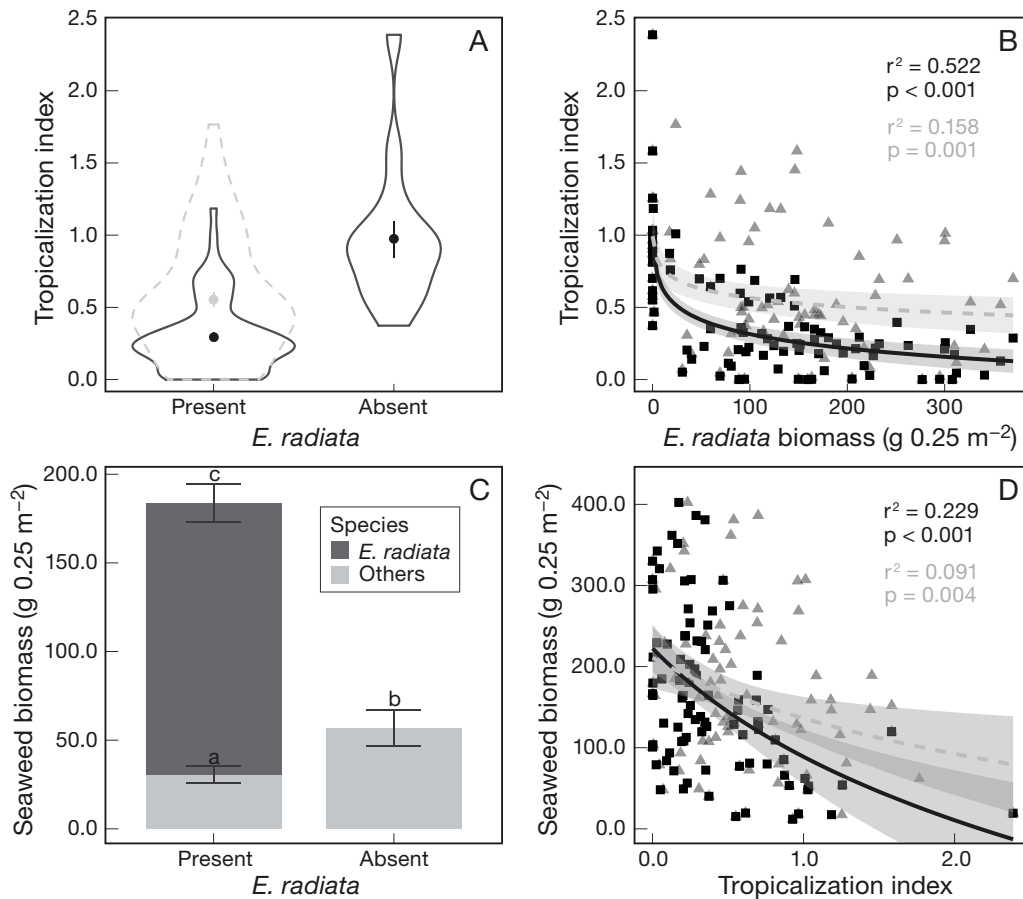
Fig. 7. Effect of *Ecklonia radiata* presence on (A) the tropicalization index (TI) of the seaweed community and (C) the seaweed ash-free dry weight biomass, and the effect of (B) *E. radiata* biomass on the TI and (D) the TI on the total seaweed biomass at Marmion Lagoon in 2016 (n = 90). TI values calculated including *E. radiata* biomass are indicated by black squares and solid lines, while TI values excluding *E. radiata* biomass are indicated by grey triangles and dashed lines. Error bars and shading indicate SE, and the letters in (C) indicate significance differences between means (*t*-test, p < 0.05)

4. DISCUSSION

The combined effects of increasing temperature over time and wave exposure resulted in different responses in the temperate subtidal seaweed community. The largest magnitude of changes to the community between sampling 2 decades apart was seen on the medium and high wave exposed reefs. Here, the reduction in the *Ecklonia radiata* fraction of the total biomass and percentage of quadrats in which it was present were largest. Additionally, there was a trend of increasing tropicalization (TI) values of the seaweed communities with increasing exposure. There was an increase in diversity of the seaweed communities seen over time, and a larger proportion of the seaweeds had an affinity to warmer temperatures. On the low exposure reefs, the diversity increase was smallest, and although the relative increase in TI was higher than on the high exposure reefs, the absolute

value remained lower. In addition to the percentage presence and the fraction of *E. radiata* of the total biomass remaining comparable, the total biomass of *E. radiata* increased on the low exposure reefs. These findings suggest that wave exposure exacerbated the effect of 2 decades of warming on subtidal seaweed communities, which contrasts what was reported for intertidal seaweed communities (Starko et al. 2019) and shallow subtidal kelp (Berry et al. 2021) in the North Pacific. It is possible that instead of ameliorating temperature stress as the previous studies described, over time *E. radiata* is being pushed out of the optimal temperature range, making it more vulnerable to wave exposure resulting in increased patchiness.

The snapshot resampling design that was employed for this study generally underperforms for detecting changes over longer time frames for single species abundance measures (Stuble et al. 2021), which might be contributing to the ambiguous trends

in *E. radiata* biomass over time and exposure. Additionally, other covariates that change over exposure need to be considered. For example, through infrastructure development, Marmion has seen increased storm water management, a decrease in homes with septic tanks, and the inception of ongoing water quality monitoring in 2002 (Marine Parks & Reserves Authority 2012) over the past decades. It is possible that water quality close to shore has improved as a result, which could be a contributing factor to the increase in *E. radiata* biomass found on the low exposure reefs close to shore either directly, or indirectly through increased light penetration.

A clearer trend was seen in the percentage of quadrats in which *E. radiata* was found in 2016 compared to 1996, which decreased on the high exposure reefs. Additionally, the fraction of *E. radiata* biomass of the total biomass has decreased more on the high and medium than the low exposed reefs. While the average size of individual *E. radiata* fronds was not measured, it could indicate that the *E. radiata* canopy has more gaps than before, even though the biomass of the individual might be slightly increasing. High wave energy has been shown to increase the dislodgement of kelps, including *E. radiata,* which results in canopy gaps (Graham et al. 1997, Thomsen et al. 2004). However, kelp recruits are generally abundant in the understorey, waiting for the right environmental conditions to rapidly grow (Toohey & Kendrick 2007). The absence of even *E. radiata* recruits in these gaps suggests they are not temporary post disturbance gaps, but potentially more permanent reductions in *E. radiata* canopy cover.

There is a strong competition for resources (e.g. light, substratum) among seaweeds (Carpenter 1990, Edwards & Connell 2012), and negative correlations between *E. radiata* biomass and species diversity have been shown before (Kendrick et al. 2004, Smale et al. 2011). Furthermore, there is evidence that the mixed canopies, which are more prevalent today, are relatively less abrasive on the understorey than monospecific stands of *E. radiata* (Irving & Connell 2006), which could contribute to increased diversity. Interestingly, the TI increased exponentially where *E. radiata* was absent from the reef. This suggests that *E. radiata* represses colonisation and growth of other algal species and favours those with an affinity for cooler water, presumably those species that co-evolved with *E. radiata*, as the TI was significantly lower in quadrats with *E. radiata* present, even when it was excluded from the calculation.

The reduction of *E. radiata* coincided with an increase in *Scytothalia dorycarpa*, another canopy-forming species that also has an affinity for cool water. This is counter-intuitive considering the decline of *S. dorycarpa* in lower latitudes during the 2011 marine heatwave (Smale & Wernberg 2013). Possibly, the competitive release from *E. radiata* is facilitating this increase, where a decrease was expected based on the thermal tolerance of *S. dorycarpa*. From a community perspective, this competitive release could serve as a short-term buffer against the tropicalization of the seaweeds, as is seen in the lower than expected TI value.

The effect of competitive release was also seen in the increase in biomass of other seaweeds with *E. radiata* decline. A similar effect happens over the annual cycle as *E. radiata* biomass waxes and wanes (Wernberg & Goldberg 2008), and it has been experimentally demonstrated in the competitive release resulting from *E. radiata* canopy loss in temperate seaweeds (Toohey & Kendrick 2008). While the increase in biomass in other seaweed species can compensate to some extent, the total seaweed biomass in the absence of *E. radiata* was over 3 times lower. As biomass is a strong determinant for net primary productivity (Reed et al. 2008), a significant reduction in standing seaweed biomass suggests that the productivity of the entire ecosystem will be reduced. While the overall seaweed biomass has not decreased over time, if the trend in reduction of *E. radiata*, and increase in TI, continues, this will likely be the case.

To conclude, while the absolute biomass of *E. radiata* remained relatively stable over the 20 yr time window, there were significant decreases in the contribution to the total biomass, and percentage of the reef surface that it occupied, particularly on high wave exposed reefs. The importance of *E. radiata* to the ecosystem cannot be overstated. Not only does it provide substantial amounts of biomass (and therefore net primary productivity) and habitat structure, but the competitive pressure also disproportionately limits intrusion of warm-water-affiliated species compared to temperate species. Although there was a significant increase in warm-water-affiliated species over time, there was a discrepancy between the calculated and the expected TI value based on the reduction of *E. radiata* at each exposure level. This suggests that other seaweeds could be providing compensatory effects due to competitive release, which limits the impact of the *E. radiata* reduction. Despite not finding significant trends over exposure within each time period, the low exposure reefs were most similar between sampling times and showed lower TI than the high and medium exposure reefs over time. This indicates that the patch dynamics driven by wave exposure are

exacerbated by the effect of warming on temperate subtidal reefs, and while the seaweed diversity is likely to increase if the current trends continue, the productivity of the ecosystem could decrease.

LITERATURE CITED

Ashcroft MB, Chisholm LA, French KO (2009) Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. Glob Change Biol 15:656–667

Bennett S, Wernberg T, Connell S, Hobday A, Johnson C, Poloczanska E (2016) The 'Great Southern Reef': social, ecological and economic value of Australia's neglected kelp forests. Mar Freshw Res 67:47–56

Berry HD, Mumford TF, Christiaen B, Dowty P and others (2021) Long-term changes in kelp forests in an inner basin of the Salish Sea. PLOS ONE 16:e0229703

Carpenter RC (1990) Competition among marine macroalgae: a physiological perspective. J Phycol 26:6–12

de Bettignies T, Wernberg T, Lavery PS, Vanderklift MA, Gunson JR, Symonds G, Collier N (2015) Phenological decoupling of mortality from wave forcing in kelp beds. Ecology 96:850–861

Diez JM, Pulliam HR (2007) Hierarchical analysis of species distributions and abundance across environmental gradients. Ecology 88:3144–3152

Edwards MS, Connell SD (2012) Competition, a major factor structuring seaweed communities. In: Wiencke C, Bischof K (eds) Seaweed biology. Ecological studies. Springer, Berlin, p 135–156

Erlandson JM (2001) Anatomically modern humans, maritime voyaging, and the Pleistocene colonization of the Americas. In: Jablonski NG (ed) The first Americans: the Pleistocene colonization of the New World. Mem Calif Acad Sci 27. California Academy of Science, San Francisco, CA, p 59–92

Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. Mar Ecol Prog Ser 495:1–25

Filbee-Dexter K, Wernberg T (2018) Rise of turfs: a new battlefront for globally declining kelp forests. Bioscience 68: 64–76

García Molinos J, Halpern BS, Schoeman DS, Brown CJ and others (2016) Climate velocity and the future global redistribution of marine biodiversity. Nat Clim Change 6: 83–88

Graham MH, Harrold C, Lisin S, Light K, Watanabe JM, Foster MS (1997) Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient. Mar Ecol Prog Ser 148:269–279

Guiry MD, Guiry GM (2020) AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. https://www.algaebase.org (accessed 14 May 2020)

Hastings RA, Rutterford LA, Freer JJ, Collins RA, Simpson SD, Genner MJ (2020) Climate change drives poleward increases and equatorward declines in marine species. Curr Biol 30:1572–1577.e2

Hobday AJ, Pecl GT (2014) Identification of global marine hotspots: sentinels for change and vanguards for adaptation action. Rev Fish Biol Fish 24:415–425

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D and others (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. Curr Biol 17:360–365

Huisman JM (2019) Marine plants of Australia. University of Western Australia Press in association with Australian Biological Resources Study, Nedlands

Hurd CL (2000) Water motion, marine macroalgal physiology, and production. J Phycol 36:453–472

Hurd CL (2017) Shaken and stirred: the fundamental role of water motion in resource acquisition and seaweed productivity. Perspect Phycol 4:73–81

IMOS (Integrated Marine Observing System) (2019) SRS – SST – L3S – Single Sensor – 6 day – day and night time – Australia. https://portal.aodn.org.au/search?uuid=023ae 12a-8c0c-4abc-997a-7884f9fec9cd (accessed 6 June 2019)

IMOS (2021) SRS-Surface-Waves_MW_SENTINEL – Australia. https://portal.aodn.org.au/search?uuid=91ae1b2f-39e4-4d30-a853-5deb774614ca (accessed 6 November 2021)

IPCC (2018) Global Warming of 1.5°C: an IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty. Intergovernmental Panel on Climate Change. https://www.ipcc.ch/sr15/

Irving AD, Connell SD (2006) Predicting understorey structure from the presence and composition of canopies: an assembly rule for marine algae. Oecologia 148:491–502

Kendrick GA, Harvey E, Wernberg T, Harman N, Goldberg N (2004) The role of disturbance in maintaining diversity of benthic macroalgal assemblages in southwestern Australia. Jpn J Phycol 52:5–9

Krumhansl KA, Okamoto DK, Rassweiler A, Novak M and others (2016) Global patterns of kelp forest change over the past half-century. Proc Natl Acad Sci USA 113: 13785–13790

Lourey MJ, Kirkman H, Lourey MJ, Kirkman H (2009) Short-lived dissolved nitrate pulses in a shallow Western Australian coastal lagoon. Mar Freshw Res 60:1068–1080

Mann KH (1973) Seaweeds: their productivity and strategy for growth. Science 182:975–981

Marine Parks & Reserves Authority (2012) Ten-year audit of the implementation of the Marmion Marine Park Management Plan 1992–2002. https://www.conservation.wa.gov.au/sites/default/files/4.3.8%20report%20on%20ten-year%20audit%20of%20marmion%20marine%20park%20management%20plan%20may%202012.pdf

Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. Trends Ecol Evol 5:52–57

Mulders YR, Wernberg T (2020) Fifteen years in a global warming hotspot: changes in subtidal mobile invertebrate communities. Mar Ecol Prog Ser 656:227–238

Oksanen J, Blanchet FG, Kindt R, Legendre P and others (2010) Vegan: community ecology package. R package version 1.17-4. https://CRAN.R-project.org/package=vegan

Oliver ECJ, Donat MG, Burrows MT, Moore PJ and others (2018) Longer and more frequent marine heatwaves over the past century. Nat Commun 9:1324

Oliver ECJ, Burrows MT, Donat MG, Sen Gupta A and others (2019) Projected marine heatwaves in the 21st cen-

tury and the potential for ecological impact. Front Mar Sci 6:734

Pearce A, Feng M (2007) Observations of warming on the Western Australian continental shelf. Mar Freshw Res 58:914−920

Phillips JC, Kendrick GA, Lavery PS (1997) A test of a functional group approach to detecting shifts in macroalgal communities along a disturbance gradient. Mar Ecol Prog Ser 153:125−138

Pinheiro J, Bates D, DebRoy S, Sarkar D, Heisterkamp S, Van Willigen B, R Core Team (2017) nlme: linear and nonlinear mixed effects models. R package version 3.1-131. https://CRAN.R-project.org/package=nlme

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reed DC, Rassweiler A, Arkema KK (2008) Biomass rather than growth rate determines variation in net primary production by giant kelp. Ecology 89:2493−2505

Richards Z, Kirkendale L, Moore G, Hosie A and others (2016) Marine biodiversity in temperate Western Australia: multi-taxon surveys of Minden and Roe Reefs. Diversity 8:7

Russell BD, Connell SD (2012) Origins and consequences of global and local stressors: incorporating climatic and non-climatic phenomena that buffer or accelerate ecological change. Mar Biol 159:2633−2639

Scheibling RE, Gagnon P (2006) Competitive interactions between the invasive green alga *Codium fragile* ssp. *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). Mar Ecol Prog Ser 325:1−14

Searle DJ, Semeniuk V (1985) Natural sectors of the inner Rottnest Shelf coast adjoining the Swan Coastal Plain. J R Soc West Aust 67:116−136

Simenstad CA, Estes JA, Kenyon KW (1978) Aleuts, sea otters, and alternate stable-state communities. Science 200:403−411

Smale DA, Wernberg T (2009) Satellite-derived SST data as a proxy for water temperature in nearshore benthic ecology. Mar Ecol Prog Ser 387:27−37

Smale DA, Wernberg T (2013) Extreme climatic event drives range contraction of a habitat-forming species. Proc R Soc B 280:20122829

Smale DA, Wernberg T, Vance T (2011) Community development on subtidal temperate reefs: the influences of wave energy and the stochastic recruitment of a dominant kelp. Mar Biol 158:1757−1766

Smale DA, Wernberg T, Vanderklift MA (2017) Regional-scale variability in the response of benthic macroinvertebrate assemblages to a marine heatwave. Mar Ecol Prog Ser 568:17−30

Smale DA, Wernberg T, Oliver ECJ, Thomsen M and others (2019) Marine heatwaves threaten global biodiversity and the provision of ecosystem services. Nat Clim Change 9:306−312

Starko S, Bailey LA, Creviston E, James KA and others (2019) Environmental heterogeneity mediates scale-dependent declines in kelp diversity on intertidal rocky shores. PLOS ONE 14:e0213191

Stuble KL, Bewick S, Fisher M, Forister ML and others (2021) The promise and the perils of resurveying to understand global change impacts. Ecol Monogr 91:e01435

Symonds G, Zhong L, Mortimer NA (2011) Effects of wave exposure on circulation in a temperate reef environment. J Geophys Res 116:C09010

Thomsen MS, Wernberg T, Kendrick GA (2004) The effect of thallus size, life stage, aggregation, wave exposure and substratum conditions on the forces required to break or dislodge the small kelp *Ecklonia radiata*. Bot Mar 47:454−460

Thomsen MS, Wernberg T, South PM, Schiel DR (2016) To include or not to include (the invader in community analyses)? That is the question. Biol Invasions 18:1515−1521

Thomson JA, Burkholder DA, Heithaus MRW, Fourqurean JW, Fraser MW, Statton J, Kendrick GA (2015) Extreme temperatures, foundation species, and abrupt ecosystem change: an example from an iconic seagrass ecosystem. Glob Change Biol 21:1463−1474

Toohey BD, Kendrick GA (2007) Survival of juvenile *Ecklonia radiata* sporophytes after canopy loss. J Exp Mar Biol Ecol 349:170−182

Toohey BD, Kendrick GA (2008) Canopy−understorey relationships are mediated by reef topography in *Ecklonia radiata* kelp beds. Eur J Phycol 43:133−142

Vergés A, Tomas F, Cebrian E, Ballesteros E and others (2014) Tropical rabbitfish and the deforestation of a warming temperate sea. J Ecol 102:1518−1527

Wernberg T, Filbee-Dexter K (2019) Missing the marine forest for the trees. Mar Ecol Prog Ser 612:209−215

Wernberg T, Goldberg N (2008) Short-term temporal dynamics of algal species in a subtidal kelp bed in relation to changes in environmental conditions and canopy biomass. Estuar Coast Shelf Sci 76:265−272

Wernberg T, Thomsen MS (2005) The effect of wave exposure on the morphology of *Ecklonia radiata*. Aquat Bot 83:61−70

Wernberg T, Coleman M, Fairhead A, Miller S, Thomsen M (2003) Morphology of *Ecklonia radiata* (Phaeophyta: Laminarales) along its geographic distribution in southwestern Australia and Australasia. Mar Biol 143:47−55

Wernberg T, Kendrick GA, Toohey BD (2005) Modification of the physical environment by an *Ecklonia radiata* (Laminariales) canopy and implications for associated foliose algae. Aquat Ecol 39:419−430

Wernberg T, Smale DA, Tuya F, Thomsen MS and others (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat Clim Change 3:78−82

Wernberg T, Bennett S, Babcock RC, de Bettignies T and others (2016a) Climate-driven regime shift of a temperate marine ecosystem. Science 353:169−172

Wernberg T, de Bettignies T, Joy BA, Finnegan PM (2016b) Physiological responses of habitat-forming seaweeds to increasing temperatures. Limnol Oceanogr 61:2180−2190

Wernberg T, Coleman MA, Babcock RC, Bell SY and others (2019a) Biology and ecology of the globally significant kelp *Ecklonia radiata*. Oceanogr Mar Biol Annu Rev 57: 265−323

Wernberg T, Krumhansl K, Filbee-Dexter K, Pedersen MF (2019b) Status and trends for the world's kelp forests. In: World seas: an environmental evaluation. Elsevier, London, p 57−78

Western Australian Herbarium (1998) Florabase—the Western Australian Flora. Department of Biodiversity, Conservation and Attractions. https://florabase.dpaw.wa.gov.au/ (accessed 6 June 2018)

Wiens JJ (2011) The niche, biogeography and species interactions. Philos Trans R Soc B 366:2336−2350

Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. Trends Ecol Evol 19: 639−644

Zarco-Perello S, Wernberg T, Langlois TJ, Vanderklift MA (2017) Tropicalization strengthens consumer pressure on habitat-forming seaweeds. Sci Rep 7:820