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Shield wall: Kelps are the last stand against corals in tropicalized reefs

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Abstract

1. Communities inhabiting biogeographic transition zones are shifting in composition as a result of progressive warming and heatwaves. In the marine environment, corals are expanding onto higher latitude reefs historically dominated by temperate kelp forests, initiating a shift towards warm affinity coral-dominated states.
2. Although these coral expansions are a global phenomenon, the mechanisms that are underpinning the expansion process remain poorly understood, which limits the projections of the rate and extent of ecosystem reconfiguration.
3. Here, we investigated the interaction between the kelp *Ecklonia radiata* and the high latitude scleractinian coral *Plesiastrea versipora* in several of Western Australia's temperate reefs, where coral colony abundance has increased by 50% in recent years. Combining field surveys with field and laboratory experiments, we test the importance of physical (abrasion and light reduction) and chemical (allelopathic) effects of kelp canopies on coral tissue cover, photosynthetic parameters and calcification rates.
4. In the field, kelp cover had a negative effect on coral density that was overwhelming in comparison to other dominant macroalgal taxa. Abrasion by kelp whiplash was the predominant mechanism by which kelp exerted a negative effect on *P. versipora* fitness, scraping up to 80% of live coenosarc from experimental colonies. In contrast, canopies had no effects on *P. versipora* photochemical efficiency and laboratory incubations showed that there were no allelochemical effects from kelp on *P. versipora*.
5. We conclude that *E. radiata* inhibits *P. versipora* establishment and development through abrasion, and the survey data confirmed that recent climate-driven kelp loss released corals from this effect, facilitating their expansion

[Correction added on 28-July-22, after first online publication: the surname of author Albert Pessarrodona, has been corrected.]

on high-latitude reefs in Western Australia. This shows how competitive interactions actively shield against species expansion in biogeographic transition zones and suggests a continued decline of kelp canopies will increase the permeability of temperate reefs to warm affinity species such as scleractinian corals.

KEYWORDS
competitive release, *Ecklonia radiata*, marine heatwaves, ocean warming, *Plesiastrea versipora*, tropicalization

1 | INTRODUCTION

Marine communities are experiencing acute changes in their structure and distribution in response to ongoing accelerated environmental changes (Beaugrand et al., 2019; Hyndes et al., 2016; Pecl et al., 2017; Vergés et al., 2014). In temperate regions, ocean warming and marine heatwaves have driven the poleward migration and establishment of warm affinity species, while dominant species locally declined and/or retracted towards cooler waters at higher latitudes (Vergés et al., 2014). The loss of dominant habitat-forming species directly affects the availability of food resources and spatial refuges, as well as local biogeochemical cycles and the reproductive output of the associated biodiversity (Vergés et al., 2019).

A striking example of climate-driven changes in habitat-forming species is the establishment of corals in temperate latitudes (Vergés et al., 2014). Novel coral-dominated ecosystems (Graham et al., 2014) are emerging and expanding in multiple temperate–subtropical biogeographic transition zones (Sommer et al., 2014) such as in Japan (Kumagai et al., 2018; Yamano et al., 2011), South Korea (Denis et al., 2014), Australia (Baird et al., 2012; Booth & Sear, 2018; Tuckett et al., 2017) and the Mediterranean Sea (Cutajar et al., 2020; Serrano et al., 2012; Serrano et al., 2013).

Despite the increase of corals in temperate regions, the processes and mechanisms enabling the expansions remain poorly resolved. Corals inhabiting higher latitudes face marginal conditions, yield less calcareous accretion due to low temperatures and low aragonite saturation, resulting in lower growth rates (Kleypas et al., 1999; Veron et al., 2015). Increases in temperature may remove some of these physiological limitations (McIlroy et al., 2019) and positively affect expanding species by promoting establishment in subtropical and temperate locations (Price et al., 2019). Dispersal potential, tolerance to environmental gradients such as the resilience to cold stress (Higuchi et al., 2020) and competitive ability are additional key features for overcoming biogeographic barriers (Keith et al., 2015; Sommer et al., 2014). Competitive interactions may also play a paramount role in the establishment of coral recruits in temperate areas, constraining expansions through competitive exclusion (Miller & Hay, 1996; Thomson et al., 2012).

In tropical reefs, macroalgae exert negative effects on corals by physical and chemical mechanisms (Fong et al., 2020; Jompa & McCook, 2003; Morrow et al., 2017). In temperate communities, it has been demonstrated that macroalgae such as kelps may damage corals by physical abrasion and overgrowth (Coyer et al., 1993; Miller & Hay, 1996). Abrasion takes place whenever the soft tissue of corals is exposed to brushing by kelp lamina (Coyer et al., 1993), and the removal of live coenosarc may impair several physiological functions such as growth, nutrition and excretion (Veron, 2000). Aside from the characterization of community patchiness (Thomson et al., 2012), interactions between kelp and corals have received little attention, and mechanisms of kelp-coral competition remain poorly resolved.

Declines of habitat-forming kelps due to warming have been proposed to provide a competitive release for corals, resulting in increased coral abundances (Tuckett et al., 2017). The observed concurrent decline in large habitat-forming kelps and increase in corals suggest a pathway to coral-dominated states in some regions (Kumagai et al., 2018), which can then promote the establishment of other tropical species (Yamano et al., 2011). Therefore, unravelling the driving mechanisms is central to understanding the dynamics of these regime shifts.

Across subtropical and temperate Australia, the laminarian kelp *Ecklonia radiata* is a major provider of habitat on reefs down to 40-m depth (Marzinelli et al., 2015; Wernberg et al., 2011; Wernberg et al., 2019). In recent decades, *Ecklonia* kelp forests in mid- and high-latitude regions in Australia have been losing ground to turf macroalgae and corals due to progressive warming, marine heatwaves and the migration of tropical grazers increasing consumer pressure on kelp biomass (Bennett, Wernberg, De Bettignies, et al., 2015; Connell et al., 2008; Vergés et al., 2016; Wernberg et al., 2016). The temperate coast of Western Australia (WA), where coastal and offshore reefs are particularly influenced by the southward-flowing Leeuwin Current, has experienced one of the most significant kelp losses recorded. Marine heatwaves, in combination with tropical herbivores facilitated by the warm waters of the Leeuwin Current (Feng et al., 2010; Wernberg et al., 2013), have caused kelp loss along the coast, at its extreme resulting in 90% loss of kelp forests over 100 km around 29°S

(Wernberg et al., 2016). Across this mid-west section of the WA coastline, coral counts more than doubled after an intense heatwave event in 2011 (Tuckett et al., 2017).

Here, we aim to investigate whether the trend of increasing coral abundance has continued in the years following the marine heatwave and unravel some of the mechanisms behind coral proliferation in temperate reefs. To do so, we resurvey sites from a longitudinal study on the abundance of seaweeds and corals along the mid-western WA coast, and measure the effects of physical (abrasion and shading) and chemical (allelopathy) interactions between kelps and corals through manipulative field and laboratory experiments. Specifically, we test the hypotheses that the abundance of corals in WA's mid-west coastal reefs (a) increased over time and (b) is negatively affected by macroalgal canopies.

2 | MATERIALS AND METHODS

2.1 | Coral survey

Data on the distribution and abundance of *P. versipora* populations were obtained by benthic surveys of 18 reefs spanning >130 km of the mid-west section of WA coastline. Sampled reefs and protocols are part of an ongoing monitoring programme (Fromont et al., 2006; Tuckett et al., 2017) and are located near the towns of Dongara (29°016′S, 114°055′E), Green Head (29°016′S, 114°055′E), Jurien Bay (29°016′S, 114°055′E) and Cervantes (29°016′S, 114°055′E; Figure 1). Benthic survey data were analysed along with data from Fromont et al. (2006) and Tuckett et al. (2017), which provided summed abundances for all the transects within one site. Coral and seaweed field collections were made under DPIRD #2971/2943 and DBCA REG17-08-001759-1/REG4-CE005649 permits.

Coral colonies were counted within three haphazardly placed transects of five 1-m^2 quadrats (i.e. plots). Once the quadrats were placed over the substrate, they were flipped four times in the same direction, according to the protocol used by Fromont et al. (2006) and Tuckett et al. (2017). Only coral colonies over 1-cm diameter were considered to enable identification in the field. A digital photograph of the entire plot was taken before screening each quadrat for at least 5 min. Coral colony sizes (cm^2) were calculated from the measurements of largest and smallest radius using the ellipse area formula. The cover of macroalgae was estimated for each plot (1 m^2) from the identification of species directly below random points (N = 30), overlaid in each image (CPCe, Kohler & Gill, 2006). Plots were then classified according to the dominant macroalgal taxa (>33% cover) by scoring abundances within broader functional form groups as follows: Red foliose (coarsely branched,

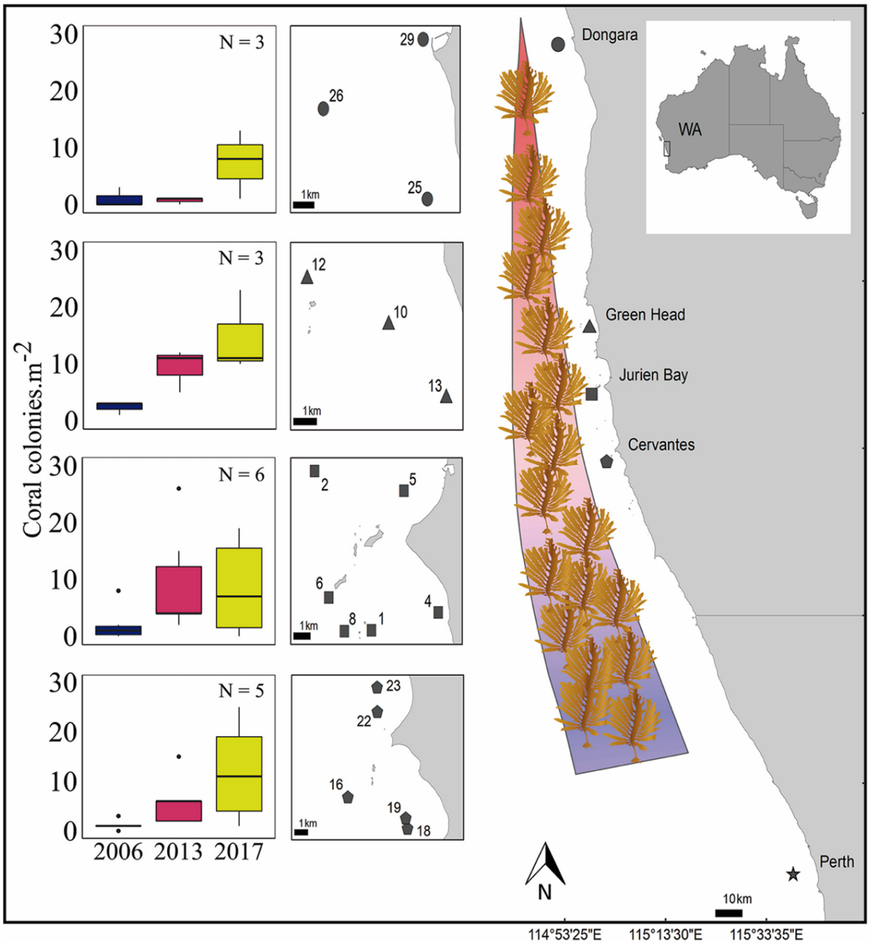

FIGURE 1 Density of *Plesiastrea versipora* colonies for each year and location in 2006 (Fromont et al., 2006), 2013 (Tuckett et al., 2017) and 2017 (present study) surveys, error bars = *SD*. Study area map (right), symbols = reefs location, numbers = sites, with 'wedge' illustration of kelp thinning northward following the 2011 marine heatwave (see Wernberg et al., 2016). Star indicates the field experiment site at Mindarie reef.

filamentous and corticated forms included, e.g. *Dictyomenia sonderi*, *Areschougia congesta*, *Callophycus oppositifolius*, *Hennedya crispa*, *Echinothamnion hystrix* and *Pterocladia lucida*); Red calcareous (e.g. *Amphiroa anceps*, *Metamastophora flabellata* and *Haliptilon roseum*); Prostrate (decumbent/flabellate, e.g. *Lobophora variegata* and *Padina elegans*); Kelp (*Ecklonia radiata*); Sargasso (*Sargassum* spp.); and Seagrass.

2.2 | Abrasion

To test the effect of abrasion from kelp on coral, we designed a field experiment in which colonies of *P. versipora* were deployed in the understorey of monospecific *E. radiata* canopies. Individual coral colonies (5–8 cm) were collected from Mindarie reef between 6 and 9 m of depth, kept in cooler tanks for transportation to the Indian Ocean Marine Research Centre at Watermans Bay and placed in aquaria. Specimens were left to acclimatize for 15 days in a flow-through system at a mean temperature of 21°C, 37 ppt salinity, 8:16 h light: dark cycle and a bottom irradiance at midday of 50 μmol m^{-2} s^{-1}.

Corals were then fixed to 20 cm^2 tiles and acclimatized for another 7 days. Each coral colony was photographed against a millimetre scale for baseline determination of tissue cover (CPCe, Kohler & Gill, 2006) and coral surface area (Image—J, Rasband, 2018). Calcification rates (mg day^{-1}) were obtained by calculating the dry weight using the buoyant weight technique (Jokiel et al., 1978), normalized to coral surface area. Half of the experimental coral tiles were then fenced with a plastic mesh to experimentally protect from kelp abrasion. A hole at the top minimized shading by the mesh, with its size being determined by measuring irradiance at the tile centre to match ambient levels.

The coral tiles were then deployed in kelp forests off Mindarie harbour (Perth; 32°S) for 40 days, being fixed to the substrate. We used a split-plot design with kelp presence as the whole-plot factor and tile fencing as the subplot factor. Circle plots of 4 m in diameter 5–10 m apart were set up at 6–9 m depth at two sites *c*. 1 km apart. Both sites were characterized by low relief reefs covered by extensive *E. radiata* kelp forests (~10 plants m^{-2}) and diverse brown and red foliose understorey macroalgae. Each site consisted of two canopy and two cleared plots. The control plots were cleared of all kelp by cutting the stipe near the holdfast and physically removing any understorey taxa over 5 cm. To prevent abrasion from edge plants, tiles were randomly distributed within a 2-m inner circle, leaving a 2-m buffer zone to the nearest kelp. To measure the amount of interference from *E. radiata* on the bottom, we deployed HOBO pendant sensors at one of the sites and recorded the amount of tilt over the sensors.

Additionally, a small experiment was set up to verify the effects observed in treatments. Fenced and unfenced tiles bearing agar-agar jelly mimics were deployed under an *E. radiata* canopy near Mindarie harbour and video recorded for 6 h. Each tile was photographed before and after deployment, and wet weight was determined to control for loss of agar mass.

2.3 | Allelopathic interactions

To test for possible mediation of coral–macroalgae interactions by allelochemicals in the absence of abrasion, a 21-day aquarium incubation experiment was set up in a flow-through system. Four treatments were applied: contact (kelp with no restraint), kelp mimic (baking paper), kelp restrained by a physical barrier and the no-kelp control ($N = 4$ per treatment). One coral was randomly assigned to 50 L aquaria on shelves under the same irradiance, temperature and salinity and an experimental treatment. A wave maker distributed evenly the exudates from kelp (when available) and coral within each aquarium. Coral tissue cover and calcification rates were measured to also allow comparisons with the results from the abrasion field experiment. Additionally, polyp activity was assessed every second day by scoring expansion states (Torrents et al., 2008), with stages 1—polyp totally expanded, 2—polyp emerging from gastric cavity, 3—fully retracted.

2.4 | Shading

To test for effects of kelp canopy shading over tiles deployed in the abrasion experiment, we used PAM fluorometry to measure the effective quantum yield (ΔF/Fm′) in actinic light derived from rapid light curves (Enríquez & Borowitzka, 2010), at the end of each experiment, using a Mini-PAM fluorometer, with settings: ML = 2, D = 2, G = 1, EF = 0.84, SW = 0.6, AF = 0.7, LW = 10 s. Curves were performed in nine steps between 0 and 550 μmol m^{-2} s^{-1}, with a saturating pulse intensity of 550 μmol m^{-2} s^{-1}. In addition, maximum quantum yield was obtained to assess whether photosystem II (PSII) was affected by kelp cover. Three replicates were excluded from photosynthetic data analysis due to shading artefacts following an episodic storm.

2.5 | Data analysis

To test for differences in *P. versipora* abundances over the years, we treated sampling year with three levels: 2006, 2013 and 2017; and location with four levels: Dongara, Green Head, Jurien Bay and Cervantes; as fixed factors, using the mean number of corals in each location (average across sites, all transects pooled), as response variable in a generalized linear model, fitted to a Poisson distribution, followed by a post hoc, Tukey HSD. The change in mean abundance over the years (across sites and locations) was verified with Wilcoxon rank-sum test, using robust analysis, followed by Tukey–Kramer pairwise comparison, with the RFIT package (Kloke & Mckean, 2012). The effect of the dominant macroalgal functional group (kelp and other taxa) on coral abundance was verified only in 2017 surveys. Due to the zero augmented dataset, earlier attempts to fit Poisson and quasi-Poisson models resulted in overdispersion, which was controlled by fitting a zero-inflated negative binomial model (ZINB; Zuur et al., 2009), using the pscl package (Zeileis et al., 2008). Models were simplified using a stepwise selection based on AIC starting on a full model (i.e. all factors and interactions) and sequentially dropping a given term from the model until a minimum AIC was achieved (Zuur et al., 2009). For the response variable percent cover of coral tissue from the abrasion experiment, we fitted beta distributions (Douma & Weedon, 2019), using the betareg package (Cribari-Neto & Zeileis, 2010). Calcification rate (mg day^{-1}) data from the latter experiment were analysed separately by fitting a linear mixed effect model with canopy and fencing as fixed factors nested within plot (Zuur et al., 2009). Photosynthetic parameters were analysed separately with Kruskal–Wallis non-parametric test. Data for the incubation experiment were analysed with a linear regression model, and analysis of variance (ANOVA), using treatment as a fixed factor with four levels: kelp with no restrain, kelp with restrain (barrier), shading mimic and control. Tilt data were analysed separately by fitting a linear mixed effect model with canopy as fixed factors and day as a random factor. Homoscedasticity and normality premises were verified using Shapiro–Wilk test and through visual inspection of residuals plots. All data analysis were performed in R environment, R Core Team (2018).

3 | RESULTS

3.1 | Coral survey

The field census indicated a marked expansion in *P. versipora* over the years, for three of four monitored locations (Figure 1; Table S1). Between 2006 and 2017, there was a tenfold increase in the southernmost location of Cervantes, and a fourfold increase in Jurien Bay. The northern sites of Green Head and Dongara had a sixfold increase each, although such differences in Dongara were not significant. Mean abundance between survey years (n = 17) was higher in 2017 (11.7 ± 9.6 colonies m^{-2}) in comparison to 2013 (6.8 ± 6.9 colonies m^{-2}) and 2006 (1.7 ± 2.0 colonies m^{-2}; Table S2). In the 2017 surveys, abundance was not explained by site or location, but by macroalgal canopy (Figure 2; Table S3), being significantly lower (0.1 ± 0.1 colonies m^{-2}) within kelp-dominated plots (>33% cover of *E. radiata*) than red-foliose (1.3 ± 0.2 colonies m^{-2}), prostrate (1.0 ± 0.6 colonies m^{-2}), sargasso (1.0 ± 0.2 colonies m^{-2}), red-calcareous (0.8 ± 0.3 colonies m^{-2}) and seagrass-dominated canopies (0.4 ± 0.2 colonies m^{-2}; Figure 2). It is worth noting that *P. versipora* colonies found in kelp-dominated plots were of small size (~1 cm^2), mostly occurring overhanging in vertical substrates or in cracks and crevices. The average size of colonies in plots with 10%–20% of kelp cover was slightly higher (3.4 ± 1.9 cm^2). Larger sizes (over 20 cm^2) were observed within non-kelp canopies and in plots with <10% kelp cover, with no significant differences between type of macroalgal canopy, or locations (Figure 2; Table S4).

3.2 | Abrasion

A total of 47 of 64 installed colonies (73%) were recovered from the field, the loss of tiles being due to a strong swell. Remaining replicates encompassed all plot and subplot factors. Unfenced tiles installed underneath *Ecklonia* canopy were considerably abraded, with the coenosarc being damaged or completely scoured down to bare skeleton (Figure S1). Percent cover of intact tissue was significantly lower in unfenced colonies from canopy treatments 22.4 ± 7.9% ($p < 0.001$, beta regression; Table S5), in comparison to other plot and subplot factor combinations. The amount of damaged tissue 39.6 ± 5.3% and exposed skeleton 38.0 ± 6.5% were also markedly higher compared to the other treatments. In contrast, there was no mechanical damage to fenced *P. versipora*

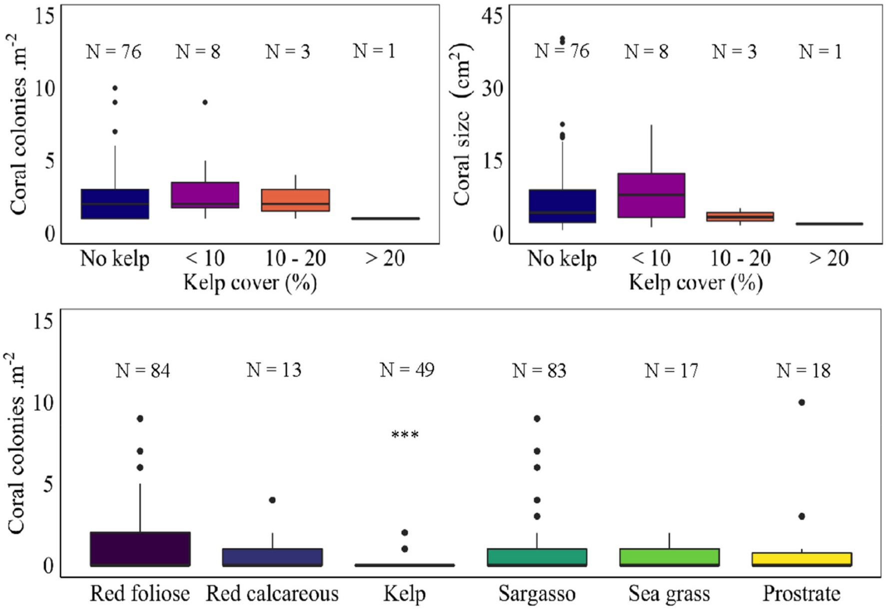

FIGURE 2 Density of *Plesiastrea versipora* colonies according to kelp cover (upper left) and different types of algal functional forms (bottom) and location (y-axis groups). Substrates under kelp were less colonized by *P. versipora* (***$p < 0.001$, ZINB model). Average size of colonies according to kelp cover (upper right). Colonies under 1 cm (max. Diameter) and colonizing crevices, cracks or under overhanging surfaces were excluded.

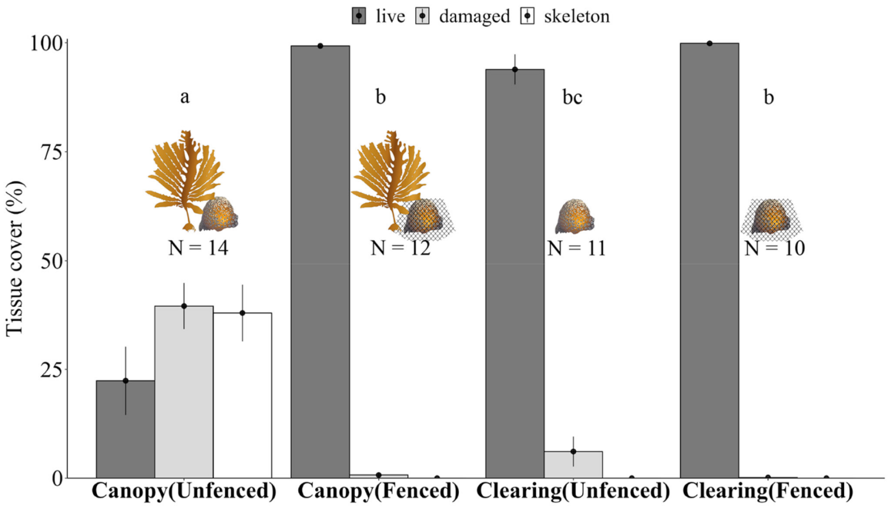

FIGURE 3 Tissue condition in *Plesiastrea versipora* colonies in different experimental conditions regarding exposure to abrasion from kelp in the field. Treatment labels (*x*-axis) refer to plot and sub-plot factor combination (see the analyses). Letters: Tukey HSD post-hoc tests. Error bars = *SD*.

colonies, regardless of kelp presence (Figure 3). There were no observable effects over calcification rates (Table S6). In the procedure control experiment, the jelly mimics from unfenced tiles were heavily scraped, with a mean percent variation in fresh weight of −13.1 ± 7.6% after 7 h under the kelp canopy, whereas fenced ones remained intact with negligible variation in fresh weight (Figure S1). Concordantly, the pendant sensors captured variation in tilting within the *Ecklonia* canopy in comparison to outside (Figure 4; Table S7).

3.3 | Shading

There was no significant effect of canopy or fencing on photosynthetic parameters (Figure 5). Still, all clearing tiles with one exception had a photochemical quenching around 70%, while corals from within *E. radiata* canopy had a lower yield. Additionally, tiles from within kelp canopies and from clearings had a similar response in effective quantum yield under actinic light, suggesting that photosynthetic machinery was not impaired by abrasion. Similar variation in F_v/F_m values indicates that photosystems experienced analogous light regimes across treatments, although the lowest values were observed in the abraded tiles.

3.4 | Allelopathic interactions

Coral colonies in the flow-through system maintained intact coenosarcs and visually healthy aspects (e.g. pigmentation), with no observable effect of treatments (Table 1). Polyp activity ranged from over 60% in kelp contact and kelp mimic treatments to >75% in control and barrier treatments, without swirling laminas over the colony, but there were no significant differences among treatments (ANOVA, $F_{1,3} = 0.9$, $p = 0.4$). Although mean calcification rates were higher in control tanks, there was no difference (ANOVA, $F_{1,3} = 0.6$, $p = 0.6$) in comparison to the contact and mimic tanks.

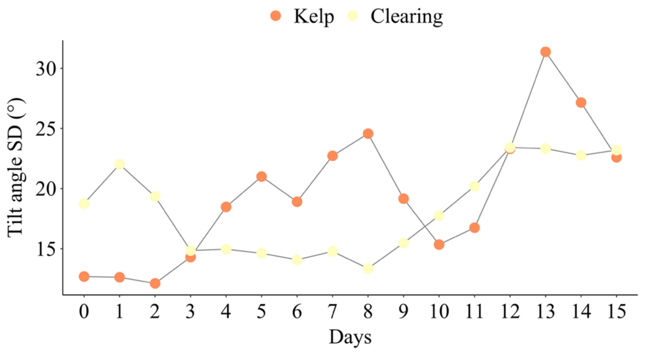

FIGURE 4 Variation in tilt angle of sensors within (orange circles) and outside (light yellow circles) the *Ecklonia radiata* canopy, plotted as standard deviation of tilt data for each day.

4 | DISCUSSION

The occurrence of the high-latitude coral *Plesiastrea versipora* in temperate macroalgal reefs of south-western Australia was negatively affected by the presence and dominance of the kelp *Ecklonia radiata* in the benthos. The mean abundance of *P. versipora* increased sixfold from 2006 to 2017 concurrent with observed declines in kelp, indicating that the *P. versipora* population has continued to expand. Surfaces exposed to kelp scour had virtually no corals, and kelp-dominated plots clearly constrained coral establishment. A similar pattern was previously reported by Coyer et al. (1993) in a long-term study of scleractinians and kelp forests in the eastern Pacific. In higher latitude locations, *P. versipora* is often seen in high numbers outside kelp forests (authors pers. obs.), also supporting the hypothesis that the understorey of *E. radiata* canopies inhibits coral development. Indeed, expansion of *P. versipora* appears to be associated with progressive poleward retraction of kelp forests following ocean warming and marine heat waves (Wernberg et al., 2016), combined with a tolerance to environmental gradients and temperature fluctuations (Higuchi et al., 2020).

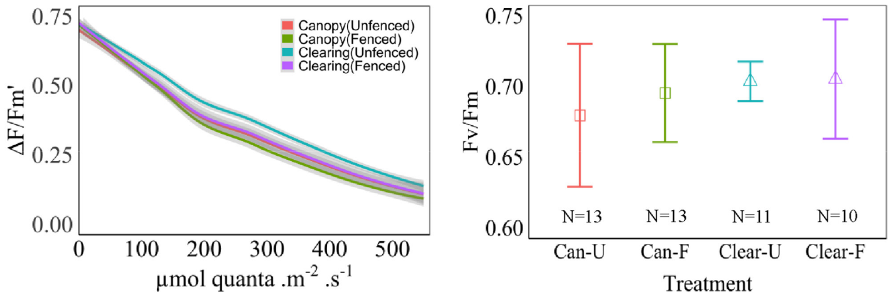

FIGURE 5 Photochemical efficiency of *Plesiastrea versipora* in experimental treatments. Effective quantum yield ($\Delta F/F_m'$) under actinic light (left) in each irradiance step. Maximum quantum yield (Fv/Fm, dark adapted) with no significant differences among treatments (Kruskal–Wallis: Chi = 2.8, *df* = 3, *p* = 0.4).

TABLE 1 Visual (tissue cover categories and polyp activity) and physiological parameters monitored in *Plesiastrea versipora* colonies during the 'allelopathic interactions' incubation experiment at flow-through system after 21 days. *N* = 4

	Treatment [mean (±*SD*)]			
Response variable	**Contact**	**Mimic**	**Barrier**	**Control**
Intact coenosarc (%)	100 (±0)	99.8 (±0.5)	100 (±0)	99.2 (±1.5)
Damaged coenosarc (%)	0 (±0)	0 (±0)	0 (±0)	0 (±0)
Exposed skeleton (%)	0 (±0)	0.3 (±0.5)	0 (±0)	0.8 (±1.5)
Calcification (mg day^{-1})	1.5 (±0.6)	1.9 (±0.6)	5.2 (±6.2)	4.3 (±4.1)
Polyp activity (%)	63.9 (±16)	69.4 (±23.4)	84.7 (±8.3)	77.8 (±23.6)

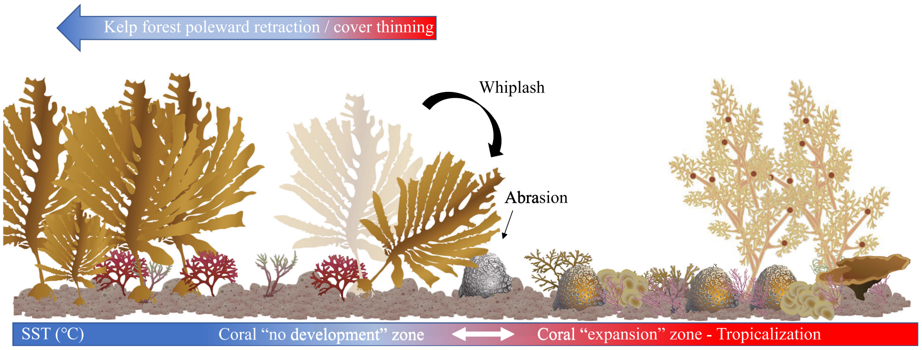

FIGURE 6 Conceptual model of benthic dynamics at mid-west biogeographic transition border in Western Australia coastal reefs.

To date, warming-mediated colonization and expansion of corals have been suspected to be mainly a consequence of increased ecophysiological coral performance, with little evidence for the mechanisms through which kelps and corals interact (e.g. Coyer et al., 1993; Thomson et al., 2012), and no characterization of ecological pathways leading to coral expansions (Kumagai et al., 2018). Our experiments demonstrate that *E. radiata* scours the bottom through a whiplash-like movement caused by waves, as previously observed (Layton et al., 2019; Toohey et al., 2004; Wernberg & Thomsen, 2005). This constant abrasion of the understorey community allows kelps to outcompete other habitat-forming species and limit growth and composition of macroalgal assemblages (Irving & Connell, 2006b; Toohey et al., 2004). Here, we found that whiplash is also particularly harmful to soft tissue organisms like scleractinian corals, with unfenced experimental corals deployed under kelp having up to 80% of the tissue either damaged or removed compared to no damage in other treatments. The similar abrasion effect of kelp whiplash on coral mimics, the amount of disturbance (tilt data) inside and outside kelp canopy, coupled with the near absence of damage in corals in cleared kelp areas, bring reinforcing evidence that the amount of continuous mechanical damage produced by kelps would impair coral development on their understory (Figure 6).

Macroalgae have been found to affect coral tissue and its microbiome through the release of allelochemicals and dissolved organic carbon (Morrow et al., 2017). However, our laboratory incubation results suggest that this effect is limited for the relationship between *E. radiata* and *P. versipora*, at least for short-term interactions (i.e. 3 weeks). Secondary metabolites within the *Ecklonia* genus are highly variable (Van Alstyne et al., 1999; Van Hees et al., 2017). Moreover, previous studies could not detect an effect of exuded phlorotannins neither as antifoulants (Jennings & Steinberg, 1997) nor as invertebrate settlement inducers (Steinberg & de Nys, 2002).

Kelp was the only macroalgal canopy capable of exerting a negative effect on the density of coral colonies. This agrees with low coral colony counts in kelp forests compared to *Sargassum* spp. beds found in this study and in a previous study by Mulders et al. (2022).

Interestingly, *P. versipora* also occurred in plots dominated by low-lying macroalgae like *Lobophora* sp., which is known to have negative effects on corals (Morrow et al., 2017). Colonies were also frequent among red foliose macroalgae outside the kelp canopy, a group which typically does not affect coral settlement (Speare et al., 2019). Our results suggest a remarkable plasticity of *P. versipora* to photoacclimate to low light environments, supported by frequent occurrences of *P. versipora* within plots under *Sargassum* spp. stands, which builds tall canopies and creates light gradients and a markedly shaded understorey (Britton-Simmons, 2004). Similarly, photochemical efficiency among corals from experimental plots within and outside kelp canopy suggests photoacclimatory mechanisms, given that *E. radiata* canopies affect light levels in their understory (Flukes et al., 2014; Wernberg et al., 2005).

While the value of coral reefs is well established, the value of healthy temperate reefs is often overlooked (Bennett, Wernberg, Connell, et al., 2015). The dense canopies of *E. radiata* can act as carbon sinks with a high net primary productivity (Filbee-Dexter & Wernberg, 2020), and exported detritus derived from particles of eroded sporophytes of *E. radiata* are significant sources of nutrients and allochthonous carbon for associated ecosystems (Ince et al., 2007; Wernberg et al., 2006). As foundation species, *E. radiata* also provides habitat complexity and modifies environmental conditions in their surroundings (Irving & Connell, 2006a; Wernberg et al., 2005), promoting epibionts diversity (Marzinelli et al., 2009; Russell et al., 2005) and mobile fauna (Tuya et al., 2009; Wernberg et al., 2008). Furthermore, the three dimensionality of their holdfast structures generates a variety of microhabitats and supports diverse communities (Coleman et al., 2007). The establishment of a coral-dominated steady state would limit kelp forest recovery and result in the loss of these specific ecological roles and associated ecosystem services.

This work indicates that kelp forests represent ecological bottlenecks for coral establishment in high latitudes, by slowing down the spread of corals in substrates exposed to abrasion. In this way, their climate-driven senescence will contribute to the emergence of transitory states in temperate ecosystems (Vergés et al., 2019). Lamina abrasion effects on corals seem to overwhelm other competitive mechanisms such as shading or chemical interactions. We demonstrate an ongoing competitive release process of corals following kelp die-off, which unveils an ecological pathway towards the tropicalization of high-latitude reefs. Altered dynamics due to the absence of substrate brushing by kelp may also promote novel interactions between stayers and new settlers. As kelps also constrain the distribution and composition of algae assemblages in temperate systems, their retraction may release both corals and algae species from competition and facilitate phase shifts.

AUTHORS' CONTRIBUTIONS

F.d.V.R., R.C.P. and T.W. conceived the ideas and designed methodology; F.d.V.R., Y.M., C.T. and A.P. collected the data; F.d.V.R. and A.P. analysed the data; F.d.V.R. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.fqz612jvs (Ribeiro et al., 2022).

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SUPPORTING INFORMATION

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