



# Ecosystem engineering kelp limits recruitment of mussels and microphytobenthic algae

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## Abstract

Ecosystem engineers often exert strong effects on the recruitment of other species through modification of the local abiotic and biotic environment. In 2015, artificial reefs in eastern Tasmania (− 42.64693, 148.01481) spanning seven different patch sizes (0.12–7.68 m<sup>2</sup>) and supporting four densities of transplanted kelp (*Ecklonia radiata* at 0, 4.1, 8.2 and 16.4 kelp m<sup>-2</sup>) were used to determine how the patch size and density of this ecosystem engineer influenced the recruitment of microphytobenthic (MPB) algae, and a secondary ecosystem engineer, the mussel *Mytilus galloprovincialis*. Increasing kelp density and patch size inhibited the establishment of subcanopy MPB algae on settlement slides and reduced the recruitment of mussels in standardised rope fibre habitats (RFHs). The productivity:biomass ratio (P:B) of mussel recruits tended to be lower on small reefs and reefs without kelp, relative to larger reefs with high densities of kelp. Canopy shading and reduced cover of turf algae appeared to negatively impact the recruitment of MPB algae and mussels, whilst reduced sediment accumulation on the reefs due to the kelp was also negatively associated with mussel recruitment. These findings highlight the role of ecosystem engineering by kelp in inhibiting the establishment of other species which may additionally impact community dynamics and primary and secondary productivity. The limited capacity of small kelp patches to inhibit the recruitment of other organisms supports the notion that fragmented patches of ecosystem engineers could be more susceptible to adverse outcomes from species interactions making them less resistant to shifts towards an alternative ecosystem state.

**Keywords** Artificial reef · Shellfish · Eco-engineering · Patch dynamics · Restoration · Fragmentation

## Introduction

Ecosystem engineers often exert strong effects on the recruitment of other species through their capacity to modify local abiotic and biotic environmental conditions (Lambrianos and Bando 2008; Wright et al. 2016). Understanding the consequences of variability in the structure of ecosystem engineers (i.e., their patch size and density) on the local environment and the establishment of associated species can help us anticipate the impacts of habitat degradation (i.e.,

habitat loss or fragmentation) or predict the benefits of ecological restoration (Crain and Bertness 2006).

Forests of canopy-forming kelp, which dominate rocky reefs in temperate and subpolar coastal waters around the world, face a barrage of stresses (e.g., ocean warming, range expanding herbivores, coastal development) which are causing precipitous declines in canopy cover in some locations (Steneck et al. 2002; Johnson et al. 2011; Wernberg et al. 2013; Krumhansl et al. 2016; Vergés et al. 2016). Restoring kelp forests, which in some instances requires use of artificial structures to provide substratum for the kelp to grow, provides an avenue to reverse these declines (Reed et al. 2006; Wood et al. 2019; Layton et al. 2020).

Kelp canopy cover substantially reduces the transmission of ambient light to the benthos whilst increasing rates of particle deposition to the substratum and baffling water flow beneath the canopy (Eckman et al. 1989; Wernberg et al. 2005; Layton et al. 2019b). The laminae of many smaller kelp species also sweep and scour the benthos

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which removes sediment and increases particle re-suspension (Toohey et al. 2004; Teagle et al. 2017). High kelp cover typically results in less understory algae and associated epifauna, whilst increasing the prevalence of sessile invertebrates (Arkema et al. 2009; Flukes et al. 2014; Miller et al. 2018; Shelamoff et al. 2019b, 2020a). The physical structure of the kelp itself can provide habitat complexity which supports some larger mobile species such as fishes and macroinvertebrates (Efrid and Konar 2014; Hinojosa et al. 2014; Bruno et al. 2018; Shelamoff et al. 2020b). Kelp additionally provides a range of physical and chemical cues which may enhance or discourage the recruitment of some organisms (Denley et al. 2014; Hinojosa et al. 2014). Furthermore, by directly influencing the abundance of various species, kelp also modify trophic and competitive interactions within the community, additionally affecting other species and community composition (Graham 2004; Arkema et al. 2009; Miller et al. 2018). In particular, canopy-shading and abrasion from kelp blades impedes the growth of understory turf algae which can otherwise outcompete more structurally diverse foliose algal species as well as filter feeding sessile invertebrates resulting in a less productive and diverse assemblage overall (Strain et al. 2014; Filbee-Dexter and Wernberg 2018). Highly persistent algal turfs are sometimes viewed as an alternative ecosystem state to kelp forests (Reeves et al. 2018). Turfs trap sediments and can modify chemical boundary layers (Layton et al. 2019a); however, some species thrive amongst the highly branched filamentous algae and the entrapped sediments that characterise these habitats (Connell et al. 2014; Fraser et al. 2020; Shelamoff et al. 2020a).

Abiotic and biotic ecosystem engineering by kelp is likely to have important implications for the recruitment of microphytobenthic (MPB) organisms (e.g., bacteria, cyanobacteria, benthic diatoms, other microalgae, and macroalgal spores), which are important primary producers beneath the kelp canopy. These organisms have a pivotal role at the base of coastal food webs in the cycling of carbon and nutrients, and additionally in stabilising sediments (Moncreiff and Sullivan 2001; Chang-Keun et al. 2006; Frankenbach et al. 2020; Hope et al. 2020). In kelp associated food webs, epilithic and epiphytic MPB species are a major food source for epifauna which then support the productivity of fishes and macroinvertebrates (Fraser et al. 2020; Shelamoff et al. 2020a). MPB organisms also facilitate the recruitment of many other species through the production of chemical cues which attract and induce settlement and metamorphosis of larvae, thus providing a further critical ecosystem function (Peteiro et al. 2007; Leise et al. 2009). Although spatially variable in composition, MPB organisms are highly abundant within sediments and on other benthic surfaces and are therefore likely to readily colonise available substratum from the immediate surrounds (Jackson et al. 2010).

On intertidal rocky shores, relatively small macroalgae such as *Pyropia* sp. and *Fucus* sp. positively influence the establishment of MPB algae by providing a refuge from the harsh physical environment (i.e., heat, desiccation, wave action, predation) and by helping to concentrate nutrients beneath their canopy (Sundbäck and McGlathery 2005; Umanzor et al. 2017, 2018). It is less clear whether MPB algae are influenced by the structure of canopy-forming kelp subtidally. Light limitation, especially beneath a dense kelp canopy, could impede the recruitment and growth of MPB algae through reducing photosynthesis. Turf algae beneath a more open canopy on the other hand, may allow for MPB organisms to flourish by providing a relatively light rich environment (i.e., no canopy shading), a high surface area on which to grow, and additional habitat in the form of sediments which co-occur with turf-algae (MacIntyre et al. 1996; Totti et al. 2009). There are however a range of additional factors such as surface stability, roughness, sediment characteristics, wave energy, and bulk water flow that vary depending on the amount of kelp or turf algae on reefs, and which could ultimately affect the establishment and composition of MPB organisms (Jantzen et al. 2013; Semcheski et al. 2016).

Kelp are also likely to influence the establishment of benthic macroinvertebrates including shellfish that can form extensive and complex three-dimensional reef structures and provide a range of additional ecosystem services including nutrient removal, microhabitat provision and modification, additional trophic interactions and pathways of energy flow, and fisheries enhancement (Nielsen et al. 2016; Fitzsimons et al. 2019; Rullens et al. 2019). Many shellfish reefs have been lost across the globe through over-exploitation, poor water quality, and other forms of habitat degradation which has prompted substantial efforts to restore these valuable ecosystems (Beck et al. 2011; Fitzsimons et al. 2019). Recruiting shellfish may respond either positively or negatively to macroalgal cover, which has implications for restoration practice (Witman 1987; Bulleri et al. 2006; Yang et al. 2007; Kochmann and Crowe 2014). The facilitatory effect of some macroalgae on shellfish recruitment may help to support the establishment of shellfish reefs whilst providing additional and complementary ecosystem services (Shelamoff et al. 2019b; McAfee et al. 2020; Reeves et al. 2020). Conversely, if macroalgae interact competitively with shellfish (Witman 1987; Chapman et al. 2005), this is likely to hinder shellfish restoration efforts. It is currently unclear how canopy-forming kelp will affect the establishment of many shellfish species.

Mussels are often a focal species in shellfish reef restoration efforts with a number of factors likely to influence their recruitment. Their larvae seek suitable habitats in which to settle and metamorphose. Choice of settlement location has been shown to be positively influenced by the presence and

abundance of MPB biofilms (Bao et al. 2007; Peteiro et al. 2007; Yang et al. 2017), but may be negatively affected by other factors such as the presence of conspecific settlers (von der Meden et al. 2010). Thin macroalgal filaments can also provide an initial attachment point for settling mussel larvae and rougher surface textures may additionally increase larval settlement (Petraitis 1990). Following initial settlement, mussel larvae may subsequently move location through gliding along the substratum or through substratum de-attachment and re-settlement prior to metamorphosis. After metamorphosis mussels may further re-locate through the detachment and reattachment of their byssal threads. For example, *Mytilus edulis* initially settles in areas of low flow, but can subsequently migrate to areas of high flow which better supports their filter feeding (Dobretsov and Wahl 2008). Small patches of reef and edge locations with higher water flow may offer improved environmental conditions for mussel growth and survival, however these locations may be more difficult to settle into and more exposed to predators (Svane and Ompi 1993). Despite the importance of filamentous algae for the settlement of some mussel species, it is unclear whether turf-dominated reefs (comprised mainly of highly branched and filamentous algae) that often occur in the absence of kelp enhance mussel settlement or improve survival prospects relative to the subcanopy environment of a kelp forest.

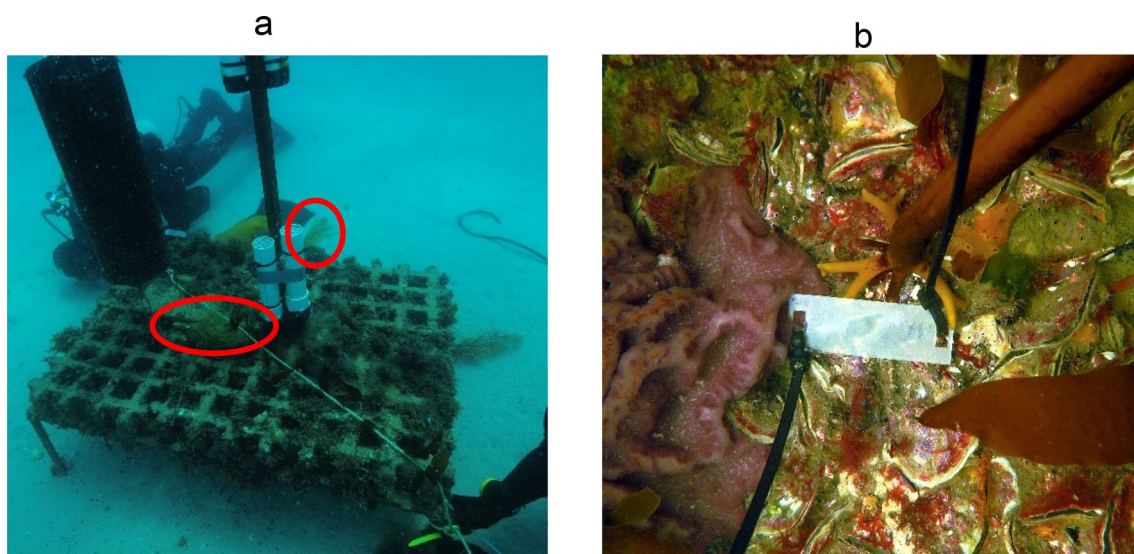
Here we aimed to determine the role of the patch size and density of Australasia's most widespread kelp species, *Ecklonia radiata*, on the recruitment of MPB algae and mussels. We then determined how these patch characteristics influenced the productivity to biomass ratio (P:B) of the mussels that recruited to the reefs. We also assessed how the

recruitment and P:B of mussels were affected by 'edge' vs. 'interior' patch positions. Finally, we explored the potential role of abiotic and biotic correlates (subcanopy: light, water flow, sediment deposition, the depth of accumulated sediments, and the percentage cover of turf algae) in explaining the abundance of MPB algae and mussel recruits (in the centre of patches). Overall, we predicted that increasing kelp patch size and canopy density would 1) reduce the development of MPB algae predominantly due to shading and 2) reduce recruitment of mussels as a result of water flow reductions and/or scour, but increase annual P:B of mussels. Mussels were also predicted to be less abundant and have a higher P:B, in central positions on the reefs compared to edge positions due to reduced adverse effects of kelp at the patch edge. Thus, small reefs and those without a sufficiently dense kelp canopy and which were dominated by turf algae (Shelamoff et al. 2019b), were expected to support relatively high abundances of MPB algae and mussels.

## Materials and methods

### Artificial reefs

This experiment used 28 artificial reefs supporting transplants of *Ecklonia radiata*, the dominant canopy-forming kelp across southern Australia, fully described in Layton et al. (2019b). To summarise, the experimental reefs were deployed in December 2014 and were constructed of concrete pavers supported on a steel frame elevated 30 cm above sandy substratum, spanning a range of sizes: 0.12, 0.24, 0.48, 1.08, 1.92, 4.32, and 7.68 m<sup>2</sup> (Fig. 1a). Adult *E. radiata*



**Fig. 1** Images of **a** an artificial reef without transplanted kelp highlighting the placement of the rope fibre habitats in the patch centre and edge, and **b** a polycarbonate slide used to assess recruitment of microphytobenthic algae

were transplanted to the pavers at four transplant densities (0, 4.1, 8.2, and 16.4 kelp  $\text{m}^{-2}$ ), hereafter referred to as: zero, low, medium and high densities, respectively. These densities were maintained for the duration of these experiments by replacing any losses with fresh transplant material at 6 week intervals. The medium density was the density of kelps on the natural reef where they were collected.

### MPB recruitment

We positioned a single settlement slide made of polycarbonate ( $25 \times 75 \times 3$  mm) near the mid-point of every experimental reef in October to November 2015 (we anticipated more rapid establishment of MPB algae for warmer/longer day length times of the year) to determine the effects of *E. radiata* structure on the abundance of MPB algae (Fig. 1b). Each slide was previously scraped using sandpaper (#550) to provide a rough surface to increase settlement. After 17 days on the reefs, slides were removed and individually placed into zip lock bags with ample seawater for transportation. Once in the laboratory, every slide was transferred to a plastic petri dish where they were preserved with Lugol's solution (1%). To quantify and identify MPB cells, slides were visually divided into ten equally sized sections. One haphazardly positioned photograph was taken from each of eight randomly chosen sections (avoiding the edges) under  $40\times$  magnification to yield eight images per slide and within each image cells were identified and quantified identified using Image J (Schneider 2012).

### Mussels

#### Recruitment

The recruitment of the mussel *Mytilus galloprovincialis* was assessed using standardised rope fibre habitats (RFHs) attached to the pavers in the centre and at the northern (light exposed) edge of each reef (to determine differences between an interior and a relatively consistent edge environment) between May 2015 and November 2015 (with high recruitment expected towards the end of this period) (Fig. 1a). A detailed description of the RFHs is given in Shelamoff et al. (2020a). After a 6-month deployment period, the RFHs were collected and brought to the lab for analysis. Mussels were enumerated after teasing the rope fibres apart using tweezers.

#### P:B

To understand variability in habitat quality across the different reefs in supporting a standing biomass of mussels, we assessed productivity to biomass ratio (P:B) by examining the size structure of mussels associated with the RFHs.

Here we used P:B ratios to indicate the quality of habitat for mussel growth, with low P:B values (a higher proportion of large individuals) indicating more beneficial habitats for mussel establishment relative to habitats with a higher P:B (a higher proportion of small individuals). We used the method outlined in Edgar (1990) based on size structure to estimate productivity and biomass and therefore P:B of the mussel recruits. This involved separating mussels into different size classes using a stacked series of sieves (1.0, 1.4, 2.0, 2.8, 4.0 mm aperture sizes) after their removal from the RFHs. We then used the abundance of mussels in each size class to estimate biomass (based on previously established relationships between size and biomass from the literature) (Edgar 1990). Productivity (P) was estimated as:  $P = 0.0049 \times \text{biomass}^{0.80} \times \text{temperature}^{0.89}$  and P:B determined accordingly (Edgar 1990) (water temperature at the time of collection was 14 °C).

### Environmental correlates

We used average annual data from Layton et al. (2019b) (light, water flow, sediment deposition, and sediment accumulation) and Shelamoff et al. (2019b) (percentage cover of turf algae) as quantitative descriptors of the abiotic and biotic environment for each experimental reefs beneath the canopy (on reefs where a canopy existed), and correlated these measures with recruitment of MPB algae (to polycarbonate slides) and mussels (to RFHs) in the centre of reefs only (as the abiotic and biotic measurements were indicative of the internal environment of the kelp patches, not the edge). Light was expressed as the percentage of above canopy light transmitted to the subcanopy (using a LI-COR LI-193 spherical sensor and logger). Flow was measured using plaster clod cards and expressed as the percentage of above canopy flow. Sediment deposition was the proportion of above canopy deposition that was measured at the benthos using sediment traps, and sediment accumulation was the depth of the algal-sediment matrix on the reef surface measured with a ruler. The percentage cover of turf algae was determined by analysing photo quadrats of the surface of each reef. Density of MPB algae on the settlement slides was also used as predictor of mussel recruitment to RFHs. Broadly speaking subcanopy light, water flow, sediment accumulation, and turf algae cover decreased with kelp patch size and density, and there was a simultaneous increase in the amount of sediment deposition (Layton et al. 2019b; Shelamoff et al. 2019b).

### Analyses and statistics

The effect of patch size (fixed effect covariate) and kelp density (fixed factor) on the number of MPB algal cells that recruited to the settlement slides was assessed using

an analysis of covariance (ANCOVA) conducted in R (ver. 3.2.4). ANCOVA was also used to assess the recruitment of mussels to RFHs and P:B, with the additional fixed factor of habitat position (reef edge vs. centre). Model assumptions were checked using diagnostic plots (for normality, linearity and homoscedascity) and model residuals (for linearity and homoscedascity). Data transformations were based on the maximum  $\lambda$  coefficient from the log-likelihood plots produced using the Box-Cox procedure. The covariate patch size was  $\log_2$  transformed to linearise the data (reflecting that patch size increased on a  $\log_2$  scale). Homogeneity of slopes was assessed by fitting the full model including the interaction term, and when the interaction term was non-significant ( $p > 0.25$ ), the unsaturated model without the interaction term was fitted. Significant kelp density effects ( $p < 0.05$ ) were further examined through pair-wise comparisons of covariate adjusted means with a Bonferroni adjustment of significance (to correct for multiple testing) (Quinn and Keough 2002). The potential influence of environmental correlates (light, flow, sediment accumulation, sediment deposition, and turf algae cover) on the abundance of MPB algal cells and mussels was assessed using multiple regression with the density of MPB algal cells also included as a predictor variable in assessing mussel recruitment. Normality, linearity and homogeneity of variance of the response variables was investigated through a scatterplot matrix and diagnostic plots (as outlined for ANCOVA). Multicollinearity of the predictors was satisfied through assessments of pairwise correlations and the variance inflation factor. Model selection was achieved by comparing the fit of all possible models for the two response variables (recruitment

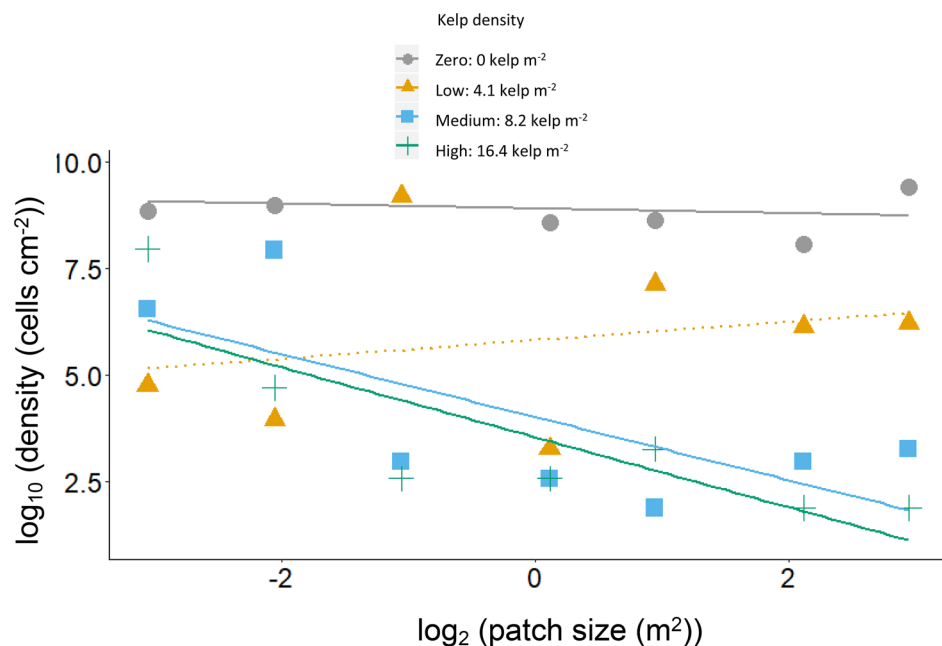
of MPB algae and recruitment of mussels) (Quinn and Keough 2002) using BIC (Bayesian information criterion) in the leaps package in R. We then used hierarchical partitioning to determine the independent contribution of all the predictor variables using the hier.part function. This allowed us to consider the relative independent effect of each of the predictors on the observed levels of recruitment. We then determined the likelihood that the independent contribution could be due to chance by performing a randomisation test and the assessing the significance of the Z scores to 95% confidence level.

## Results

### MPB algae

Overall, the benthic diatom *Amphora* spp. was the most abundant MPB organism recruiting beneath *Ecklonia radiata* canopies (68% of MPB cells) while other diatoms such as *Cylindrotheca* sp., *Melosira* sp., and *Navicula* sp and the dinoflagellate *Gynmodinium* sp. settled at much lower densities ( $< 1\%$ ) and only beneath lower-kelp-density treatments. There was an interactive effect of kelp density and patch size on the recruitment of MPB algae (Fig. 2, Table 1), reflecting that decline in MPB cell density with increasing reef size was only evident on reefs supporting medium to high kelp density. Omitting both the zero-density and the low-density kelp treatments indicated no significant differences in MPB cell density across medium- and high-density kelp treatments.

**Fig. 2** Log density of micro-phytobenthic algal cells that established on polycarbonate slides positioned on the benthos across artificial reefs of different sizes and supporting different densities of transplanted kelp



**Table 1** Results of ANCOVA testing for the effects of patch size (0.12–7.68 m<sup>2</sup>) and kelp density (zero: 0 kelp m<sup>-2</sup>; low: 4.1 kelp m<sup>-2</sup>; medium: 8.3 kelp m<sup>-2</sup>; high: 16.6 kelp m<sup>-2</sup>) on the abundance of microphytobenthic (MPB) algal cells recruiting to microscope slides,

and the abundance of mussels recruiting to rope fibre habitats positioned in two locations (reef centre or northern edge), across 28 artificial reefs

Model	Factor	SS (df)	F value	P value	Post-hoc
<b>MPB abundance</b>					
(Y) <sup>0.30</sup>	Log <sub>2</sub> (patch size) x kelp density	0.27 (3, 20)	4.02	0.02*	
Zero and low density omitted	Log <sub>2</sub> (patch size)	0.15 (1, 12)	15.89	0.002*	
(Y) <sup>0.70</sup>	Kelp density	0.006 (3, 12)	0.65	0.44	
<b>Mussel abundance</b>					
<b>Centre and edge</b>					
(Y) <sup>0.16</sup>	Log <sub>2</sub> (patch size) x kelp density x position	1.34 (3, 40)	2.88	0.02*	
<b>Centre</b>					
(Y) <sup>0.17</sup>	Log <sub>2</sub> (patch size) x kelp density	1.15 (3, 23)	4.62	0.01*	
Zero density omitted (Y) <sup>0.26</sup>	Log <sub>2</sub> (patch size)	46.79 (1, 23)	80.27	<0.001*	Low > medium, high
	Kelp density	9.56 (3, 23)	8.2	0.004*	
<b>Edge</b>					
(Y) <sup>0.43</sup>	Log <sub>2</sub> (patch size)	29.85 (1,23)	0.38	0.54	Zero > medium
	Kelp density	275.00 (3, 23)	3.5	0.03*	
<b>Mussel P:B</b>					
<b>Centre and edge</b>					
(Y) <sup>-1.61</sup>	Log <sub>2</sub> (patch size)	0.11 (1, 47)	46.62	<0.001 *	
	Kelp density	0.02 (3, 47)	3	0.04*	
	Position	2.1 e-5 (1, 47)	0.05	0.82	
<b>Centre</b>					
(Y) <sup>-0.30</sup>	Log <sub>2</sub> (patch size)	0.02 (1, 23)	28.2	<0.001*	
	Kelp density	0.004 (3, 23)	2.6	0.08	
<b>Edge</b>					
(Y) <sup>-5.65</sup>	Log <sub>2</sub> (patch size)	2.52e-6 (1, 23)	30.17	<0.001*	
	Kelp density	1.64e-7 (3, 23)	0.65	0.59	

Response variable transformations are shown in terms of the untransformed variable Y. The covariate (patch size) was log<sub>2</sub> transformed. Significant ( $p < 0.05$ ) effects are indicated by\*. Significant post hoc pairwise comparisons for density are shown in the post hoc column

## Mussels

### Recruitment

There was a significant interactive effect of patch size, kelp density, and habitat position on the recruitment of mussels to rope fibre habitats (RFHs) (Fig. 3a, b; Table 1). This reflects that declines in mussel density with increasing patch size was evident only on reefs supporting kelp cover, and in RFHs located in the centre of reef (i.e., not at the edge of the patch). There was no effect of patch size on the recruitment of mussels to RFHs located at the edge of reefs, however, recruitment to these edge positions was significantly elevated on reefs without kelp compared to reefs with kelp at the medium/natural density.

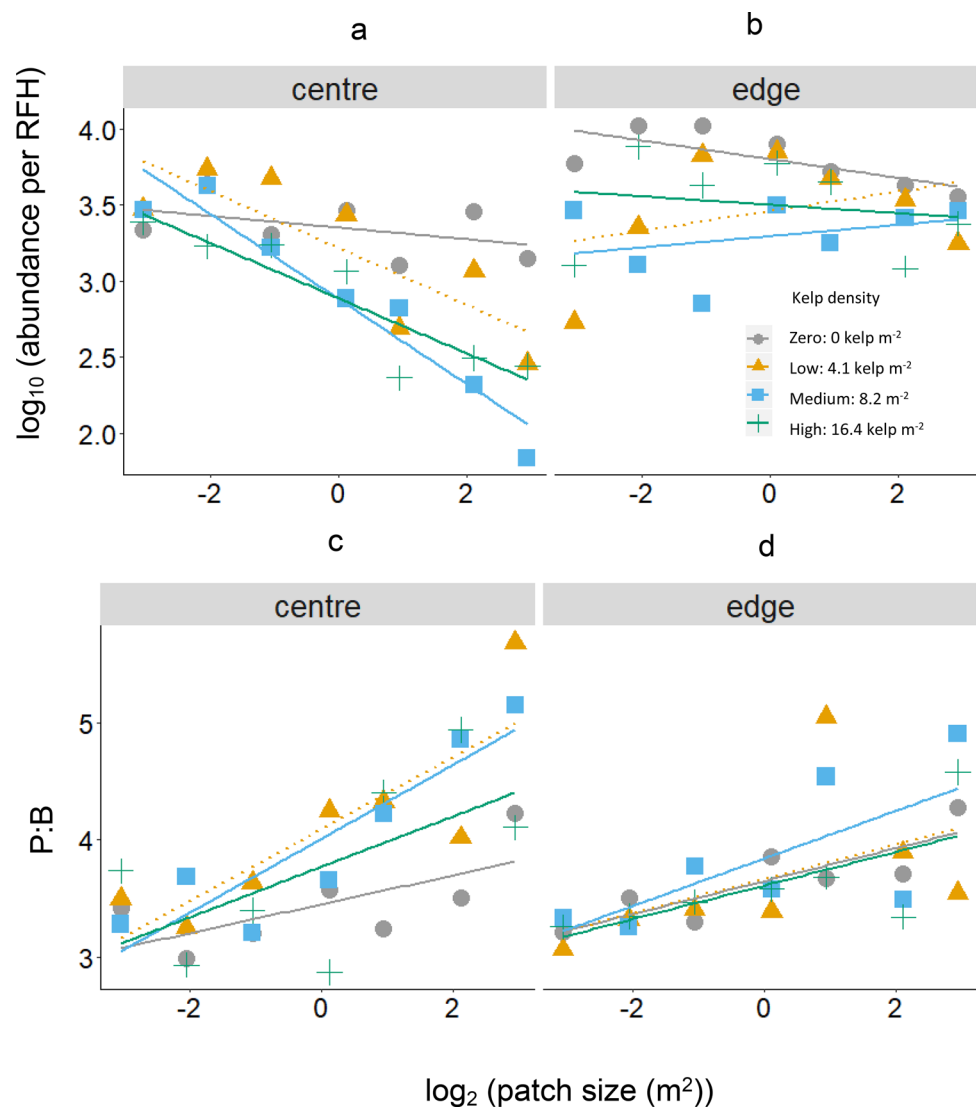
### P:B

Productivity to biomass ratio (P:B) of mussels was similar in RFHs located in both edge-of-patch and central position, and increased significantly with patch size (Fig. 3c, d; Table 1). Kelp density significantly affected P:B in the two-way ANCOVA although there were no significant differences in pairwise comparisons. Kelp density was not significant in either of the separate one-way ANCOVAs for each habitat position.

### Environmental covariates

The multiple regression indicated that light alone was the main factor correlated with the density of MPB algal cells, explaining around half of the variability (adjusted

**Fig. 3** Log abundance (a, b) and the productivity:biomass (c, d) of mussels that recruited to rope fibre habitats (RFHs) in two positions (centre and edge locations) on artificial reefs of different sizes and supporting different densities of transplanted kelp



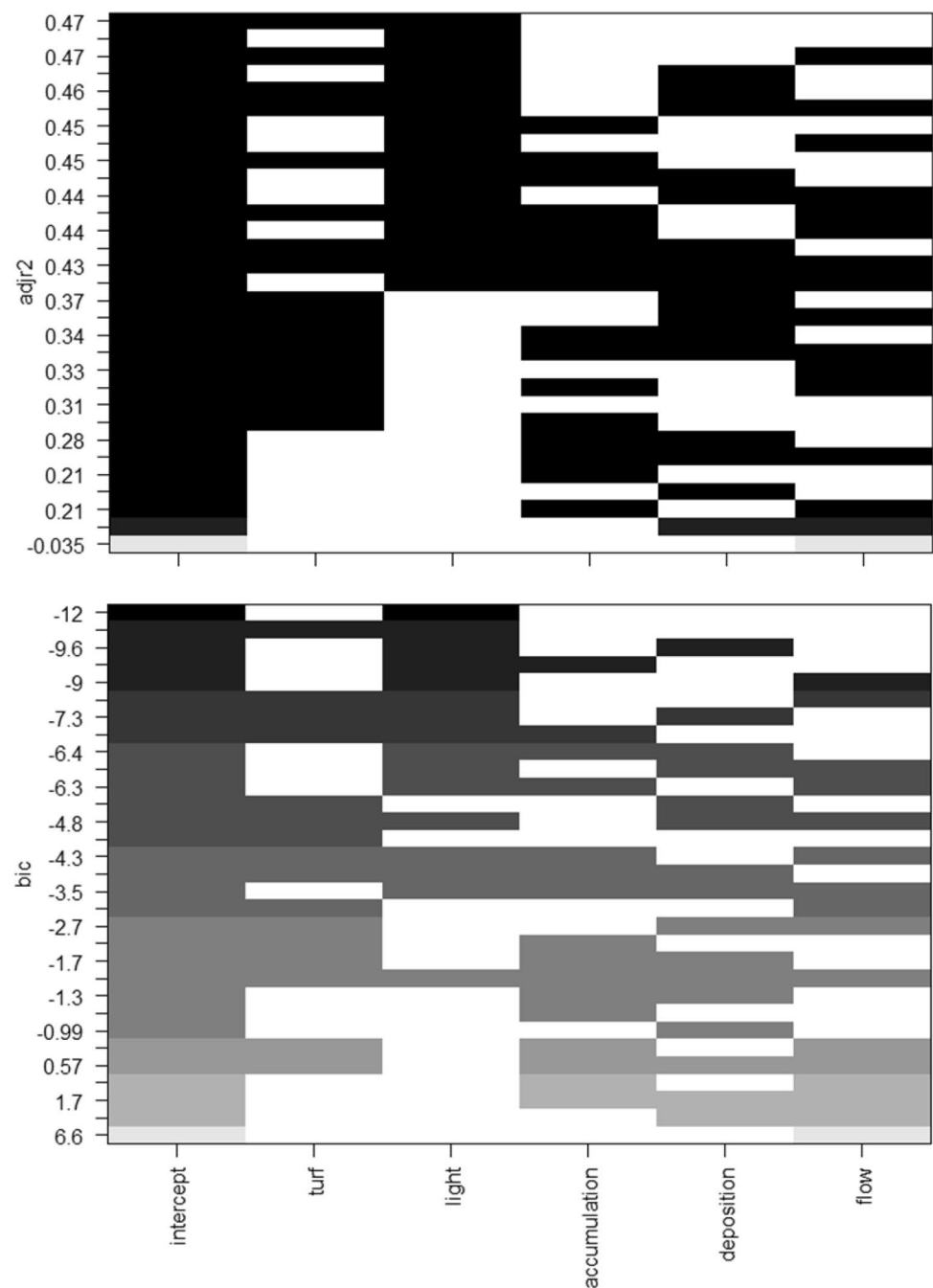
$r^2 = 0.47$ ,  $BIC = -12$ ). The more complex model including light and turf algae cover had the same explanatory power as the simpler model, but a higher BIC (adjusted  $r^2 = 0.47$ ,  $BIC = -9.8$ ) (Fig. 4). Subsequent hierarchical partitioning, however, supported the more complex model, showing that turf cover (24%) and light (44%) both had significant independent effects on MPB algae recruitment, whilst sediment accumulation (13%), water flow (3%), and sediment deposition (16%) had non-significant independent effects. The optimal multiple regression models explaining variability in the abundance of mussel recruits to centre RFHs in terms of the adjusted  $R^2$  value (0.76) all included turf algae cover, light, sediment accumulation, and sediment deposition, with water flow and MPB algae additionally being included in some of those models (Fig. 5). However, two simpler models, one including just turf algae cover, light, and sediment accumulation, and the other including just turf algae cover, sediment accumulation, and sediment deposition had the

lowest BIC value ( $-28$ ) albeit with slightly lower adjusted  $R^2$  values (0.75 and 0.74, respectively). Subsequent hierarchical partitioning supported the simpler model with turf algae cover (28%), light (21%) and sediment accumulation (24%) being the only factors having significant independent effects on mussel recruitment, whilst water flow (7%), sediment deposition (12%) and MPB algae (8%) had non-significant independent effects.

## Discussion

Increasing kelp cover in terms of both patch size and kelp density negatively affected the recruitment of microphytobenthic (MPB) algae and mussels. Densities of both declined with increasing patch size except on reefs where kelp was absent and for mussels on rope fibre habitats (RFHs) located at the reef edge. The adverse effect of kelp patch size on

**Fig. 4** Adjusted  $r^2$  and BIC (Bayesian information criteria) for multiple regression models explaining the density of microphytobenthic algal cell using five predictor variables (turf algae cover, light, sediment accumulation, sediment deposition, and water flow). The x-axis and the shaded blocks indicate the predictor term(s) included in the top performing multiple regression models, and the y-axis and the darkness of the shading indicate model performance



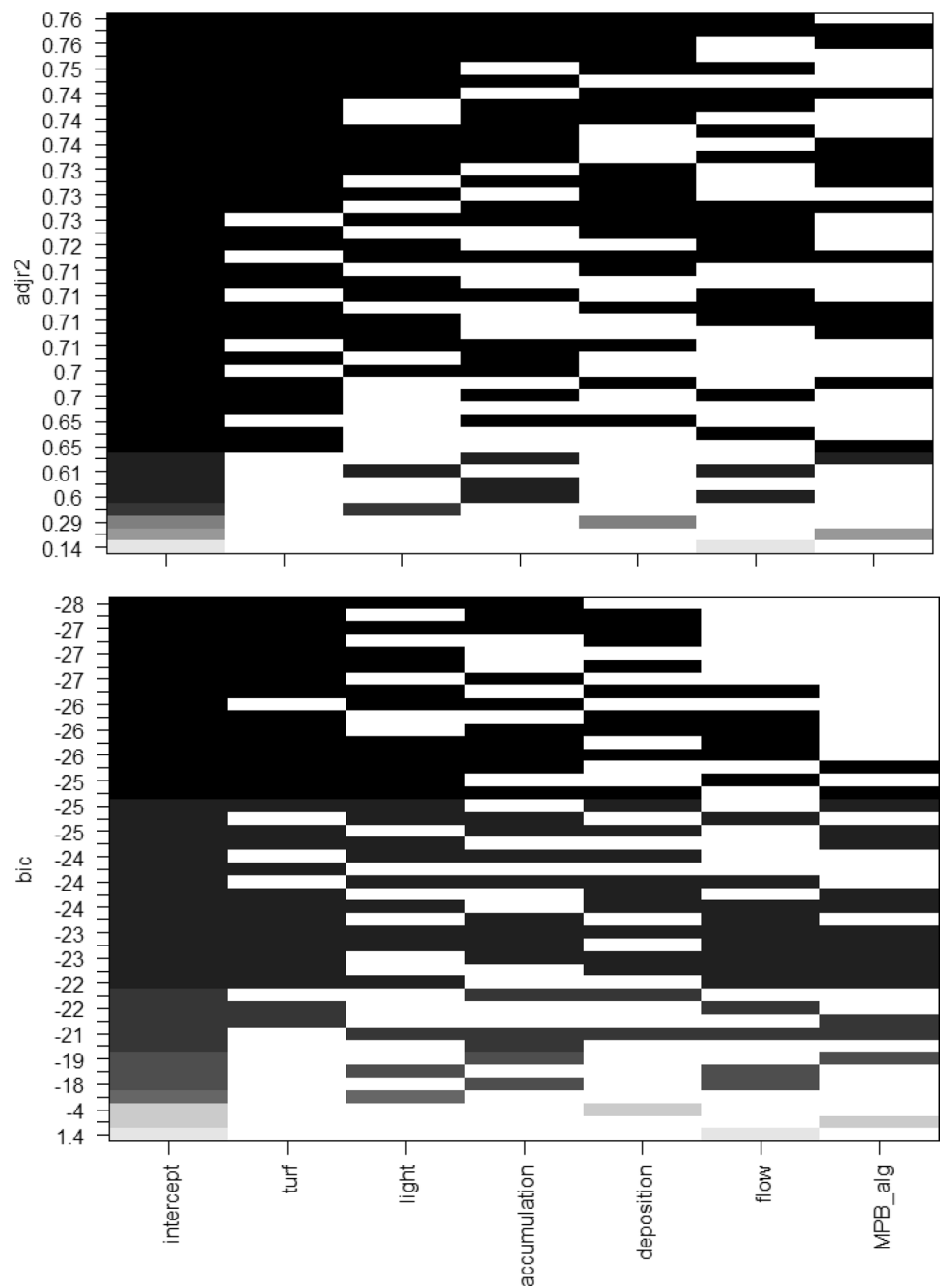
mussels also manifested in higher productivity:biomass (P:B) on larger reefs, indicating relatively few mussels reached the larger size classes on the larger reefs.

Low light and low cover of turf algae were identified as potential drivers limiting the abundance of MPB algae beneath kelp canopies, whilst low light, low turf cover, and low sediment accumulation appear to be drivers limiting mussel recruitment in the centre of reefs. Our results demonstrate that ecosystem engineers can generate an undesirable or hostile environment for other species to recruit

into. Recruitment inhibition of competitors provides a mechanism by which ecosystem engineers can support their own persistence. Contrary to the notion that reefs devoid of kelp and covered in turf algae present a harsh physical and chemical environment that adversely affects associated species (Filbee-Dexter and Wernberg 2018; Layton et al. 2019a), these types of reefs supported high establishment and persistence of MPB algae and mussels (Figs. 2, 3; Table 1), indicating that these ecosystems may yet support high productivity of certain species.



**Fig. 5** Adjusted  $r^2$  and BIC (Bayesian information criteria) for multiple regression models explaining the abundance of mussels recruiting to rope fibre habitats centrally positioned on artificial reefs using six predictor variables (turf algae cover, light, sediment accumulation, sediment deposition, water flow, and the log abundance of micro-phytobenthic algal cells). The x-axis and the shaded blocks indicate the predictor term(s) included in the top performing multiple regression models, and the y-axis and the darkness of the shading indicating model performance



### MPB algae

This adverse effect of *E. radiata* on MPB algae is in stark contrast to the beneficial effect intertidal macroalgae have on MPB settlement in providing shelter and helping to concentrate nutrients for benthic diatoms with low irradiance requirements (Sundbäck and McGlathery 2005; Umazor et al. 2018). Consistent with our prediction, the negative effect of shading appears to overcome any positive engineering effects from the kelp, presumably by limiting photosynthesis of MPB cells that typically have a relatively high

light optimum (Blanchard and Montagna 1992). Our results also suggest that turf algae which thrived on reefs with limited kelp cover, provided a beneficial environment for MPB algae. This beneficial effect may result from the high surface area of filamentous turf algae and/or the large amounts of entrapped sediments providing additional habitat. In contrast, larger foliose and corticated macroalgal species, which tended to dominate beneath a fuller canopy of *E. radiata* on our reefs (Shelamoff et al. 2019b), have a relatively low surface area, less associated sediments, and produce a secondary canopy which further limits light transmission to the

benthos (Tait and Schiel 2018). The highly variable effect of the low-density kelp treatment on MPB algal recruitment probably resulted from the specific placement of the settlement slides with respect to the patchy canopy cover (i.e., placement directly beneath the canopy resulted in low recruitment, whilst placement beneath a gap in the canopy resulted in high recruitment). Finally, MPB algae did not appear to influence the settlement of mussels, although other MPB organisms (e.g., bacteria, cyanobacteria), have been shown to enhance settlement of mussels and other marine organisms in studies elsewhere (Wang et al. 2012; Yang et al. 2017; Dobretsov and Rittschof 2020).

Reductions in the productivity of MPB algae through canopy shading could constrain levels of secondary productivity of epifaunal invertebrates (which often feed on the MPB algae) on kelp dominated reefs compared to turf-dominated reefs (Fraser et al. 2020; Shelamoff et al. 2020a). As these epifauna are a major food source for higher trophic level consumers, their diminished productivity could reduce the overall productivity of the associated food web. However, kelp also facilitate the export and deposition of resource subsidies through the erosion of their tissue, through increasing localised concentrations of holoplankton, and by elevating the deposition of detritus (Duggins et al. 1989; Miller and Page 2012). It is possible that these effects could counteract any reduction in food-web productivity triggered by canopy shading of the benthos. Nevertheless, it is clear that the productivity of benthic MPB algae is likely to increase in response to kelp loss and fragmentation and decrease in response to kelp forest restoration.

## Mussels

The observed negative effect of *E. radiata* on mussel recruitment is consistent with some other studies on subtidal bivalves (Witman 1987; Kochmann and Crowe 2014), but contrary to others where kelp has been shown to manifest a beneficial effect (Bulleri et al. 2006; Shelamoff et al. 2019a). In contrast to expectation and findings by Duggins et al. (1990) and Yang et al. (2017), our results do not support the notion that high water flow or MPB algal growth had major positive influences on mussel recruitment. Our results suggest *M. galloprovincialis* larvae are positively phototactic during settlement; however, this is in contrast to the negatively phototactic behaviour of *M. edulis* during settlement (Bayne 1964). The observed positive association with light is, however, consistent with observed reductions in recruitment of *M. galloprovincialis* with depth if driven by diminishing light levels with depth (Curiel-Ramirez and Caceres-Martinez 2010). This contrasts an increase in *M. galloprovincialis* recruitment with depth reported over a shallower depth range (Aghzar et al. 2012). We suspect that this apparent contradictory effect of depth may be explained

by the positive influence of light on recruitment being outweighed by other physical factors such as increased stress from water motion at shallower depths, whilst these additional factors diminish in importance with depth.

Turf algae cover may have positively influenced mussel recruitment through certain algal species providing positive chemical cues for settlement, through the fine algal filaments providing a beneficial surface for attachment, or through their suppression of other foliose or leathery algal species which could have negative effects on mussel recruitment (Eyster and Pechenik 1988; Dobretsov 1999). It is unclear why there was a positive correlation between the depth of sediments within the algal-sediment matrix on our reefs and the recruitment of mussels to RFHs. Potentially, this could be a result of the algal-sediment matrix providing additional settlement cues which attract settling larvae, or this matrix may have resulted in increased food availability for mussels through greater retention and resuspension of food particles close to the reef surface. Additionally, it is also possible that the *E. radiata* canopy provided a physical barrier to settling larvae or it may have provided negative settlement cues. Once settled, canopy sweeping and scouring of the benthos may have also dislodged vulnerable newly settled individuals (Connell 2003).

Abiotic engineering of water flow and scour by *E. radiata* may have also contributed to the high P:B of mussel recruits (through many of the same mechanisms described above) on the larger reefs with kelp. However, high P:B values may additionally result from size selective predation (Edgar and Aoki 1993). On our experimental reefs, the abundance of invertivorous fishes increased with kelp cover (Shelamoff et al. 2020b), and these fishes may have targeted larger sized prey invertebrates (i.e., mussels recruits). Although predation can affect the size structure of invertebrates and therefore P:B, predators do not necessarily affect the choice of initial settlement location for mussels (von der Meden et al. 2015). Turf algae which dominated in the absence of kelp, appeared to have a positive effect on recruiting mussels by increasing numbers and decreasing P:B. Whilst turfs are likely to negatively impact the recruitment of the native oyster *Ostrea angasi* (Shelamoff et al. 2019a; McAfee et al. 2020), filamentous turf algae could act as a conduit for mussel settlement (Yang et al. 2007; Fitzsimons et al. 2019).

The beneficial effects of small patch size, reef edges, and absence of kelp on mussel recruitment suggests that increasing fragmentation of kelp habitat is likely to provide more attractive and favourable conditions for *M. galloprovincialis* recruitment and establishment. It is also possible that the replacement of kelp forests by turf algae could positively affect mussels. Clearly then, restoration of *M. galloprovincialis* shellfish reefs is unlikely to be enhanced through a multi-species approach involving canopy-forming kelp (unlike the case for *O. angasi*). An

important caveat in interpreting these results and results from other studies that focus only on short-term recruitment of shellfish, is that initial recruitment patterns may not necessarily reflect long-term population establishment (Azpeitia et al. 2019) and that mussel populations are not necessarily stable over longer time periods (Ardizzone et al. 1996). At the end of the 2-year deployment of our reefs it was apparent that large-sized mussels (beyond the size of the recruits on the RFHs) were densely aggregated on the reef underside and to a lesser extent in the holes of the pavers. Potentially, strong competition with *O. angasi* on the upper surface of the reefs and increased refuge in the crevices influenced this distribution. These types of microhabitats may be required to support the longer-term persistence of mussels.

While canopy-forming kelp clearly have a facilitatory role in supporting the establishment and maintenance of species rich assemblages in some instances, these ecosystem engineers are also able to maintain dominance through creating an undesirable habitat for establishment of some species, thereby suppressing potential competitors (Falkenberg et al. 2012; Miller et al. 2018). Our study suggests that the ability of ecosystem engineers to facilitate or suppress other associated species can clearly depend on their patch size and their density.

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**Author contributions** VS, SU, CL, MT, MJC, JTW, CRJ conceived, designed, and performed the experiments; VS analysed the data and wrote the manuscript; SU, CL, JTW, CRJ edited the manuscript. We confirm this manuscript and data are original and have not been previously published or considered elsewhere.

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**Data availability** The full dataset associated with this research are available from IMAS Data Catalogue (Shelamoff et al. 2022).

## Declarations

**Conflict of interest** The authors have no conflicts of interest to declare.

**Ethical approval** All applicable international, national and/or institutional guidelines for sampling, care and experimental use of organisms for the study have been followed and all necessary approvals have been obtained. Work on invertebrates complied with ethical guidelines approved by the University of Tasmania's Animal Ethics Committee (Project no. A14511).

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## References

- Aghzar A, Talbaoui M, Benajiba MH, Presa P (2012) Influence of depth and diameter of rope collectors on settlement density of *Mytilus galloprovincialis* spat in Baie de M'diq (Alboran Sea). *Mar Freshw Behav Physiol* 45:51–61. <https://doi.org/10.1080/10236244.2012.678759>
- Ardizzone GD, Belluscio A, Gravina MF, Somaschini A (1996) Colonization and disappearance of *Mytilus galloprovincialis* Lam on an artificial habitat in the Mediterranean Sea. *Estuar Coast Shelf Sci* 43:665–676. <https://doi.org/10.1006/ecss.1996.0095>
- Arkema KK, Reed DC, Schroeter SC (2009) Direct and indirect effects of giant kelp determine benthic community structure and dynamics. *Ecology* 90:3126–3137. <https://doi.org/10.1890/08-1213.1>
- Azpeitia K, Rodriguez-Ezpeleta N, Mendiola D (2019) Settlement and recruitment pattern variability of the mussel *Mytilus galloprovincialis* Lmk from SE Bay of Biscay (Basque Country). *Reg Stud Marine Sci*. <https://doi.org/10.1016/j.risma.2019.100523>
- Bao WY, Satuito CG, Yang JL, Kitamura H (2007) Larval settlement and metamorphosis of the mussel *Mytilus galloprovincialis* in response to biofilms. *Mar Biol* 150:565–574. <https://doi.org/10.1007/s00227-006-0383-4>
- Bayne BL (1964) The responses of the larvae of *Mytilus edulis* L. to light and to gravity. *Oikos* 15:162–174. <https://doi.org/10.2307/3564753>
- Beck MW, Brumbaugh RD, Airoidi L, Carranza A, Coen LD, Crawford C, Defeo O, Edgar GJ, Hancock B, Kay MC, Lenihan HS, Luckenbach MW, Toropova CL, Zhang G, Guo X (2011) Oyster reefs at risk and recommendations for conservation, restoration, and management. *Bioscience* 61:107–116. <https://doi.org/10.1525/bio.2011.61.2.5>
- Blanchard GF, Montagna PA (1992) Photosynthetic response of natural assemblages of marine benthic microalgae to short- and long-term variations of incident irradiance in Baffin Bay Texas. *J Phycol* 28:7–14. <https://doi.org/10.1111/j.0022-3646.1992.00007.x>
- Bruno DO, Victorio MF, Acha EM, Fernández DA (2018) Fish early life stages associated with giant kelp forests in sub-Antarctic coastal waters (Beagle Channel, Argentina). *Polar Biol* 41:365–375. <https://doi.org/10.1007/s00300-017-2196-y>
- Bulleri F, Airoidi L, Branca GM, Abbiati M (2006) Positive effects of the introduced green alga, *Codium fragile* ssp *tomentosoides*, on recruitment and survival of mussels. *Mar Biol* 148:1213–1220. <https://doi.org/10.1007/s00227-005-0181-4>
- Chang-Keun K, Yong-Woo L, Eun Jung C, Jae-Ki S, In-Soo S, Jae-Sang H (2006) Microphytobenthos seasonality determines growth and reproduction in intertidal bivalves. *Mar Ecol Prog Ser* 315:113–127
- Chapman MG, People J, Blockley D. (2005) Intertidal assemblages associated with natural corallina turf and invasive mussel beds.

- Biodivers Conserv 14: 1761–1776 doi <https://doi.org/10.1007/s10531-004-0698-8>
- Connell SD (2003) Negative effects overpower the positive of kelp to exclude invertebrates from the understory community. *Oecologia* 137:97–103. <https://doi.org/10.1007/s00442-003-1312-6>
- Connell SD, Foster MS, Airoldi L (2014) What are algal turfs? Towards a better description of turfs. *Mar Ecol Prog Ser* 495:299–307
- Crain CM, Bertness MD (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. *Bioscience* 56:211–218. [https://doi.org/10.1641/0006-3568\(2006\)056\[0211:Eeaegi\]2.0.Co;2](https://doi.org/10.1641/0006-3568(2006)056[0211:Eeaegi]2.0.Co;2)
- Curriel-Ramirez S, Caceres-Martinez J (2010) Settlement of *Mytilus galloprovincialis* on collectors suspended at different depths in Bahía de Todos Santos B. C, Mexico. *Aquaculture* 300:102–106. <https://doi.org/10.1016/j.aquaculture.2009.12.019>
- Denley D, Metaxas A, Short J (2014) Selective settlement by larvae of *Membranipora membranacea* and *Electra pilosa* (Ectoprocta) along kelp blades in Nova Scotia, Canada. *Aquat Biol* 21:47–56
- Dobretsov SV (1999) Effects of macroalgae and biofilm on settlement of blue mussel (*Mytilus edulis* L.) larvae. *Biofouling* 14:153–165. <https://doi.org/10.1080/08927019909378406>
- Dobretsov S, Rittschof D (2020) Love at first taste: induction of larval settlement by marine microbes. *Int J Mol Sci* 21:731. <https://doi.org/10.3390/ijms21030731>
- Dobretsov S, Wahl M (2008) Larval recruitment of the blue mussel *Mytilus edulis*: the effect of flow and algae. *J Exp Mar Biol Ecol* 355:137–144. <https://doi.org/10.1016/j.jembe.2007.12.018>
- Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal ecosystems. *Science* 245:170–173. <https://doi.org/10.1126/science.245.4914.170>
- Duggins DO, Eckman JE, Sewell AT (1990) Ecology of understory kelp environments. II effects of kelps on recruitment of benthic invertebrates. *J Exp Mar Biol Ecol* 143:27–45. [https://doi.org/10.1016/0022-0981\(90\)90109-P](https://doi.org/10.1016/0022-0981(90)90109-P)
- Eckman JE, Duggins DO, Sewell AT (1989) Ecology of under story kelp environments. I effects of kelps on flow and particle transport near the bottom. *J Exp Mar Biol Ecol* 129:173–187. [https://doi.org/10.1016/0022-0981\(89\)90055-5](https://doi.org/10.1016/0022-0981(89)90055-5)
- Edgar GJ (1990) The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *J Exp Mar Biol Ecol* 137:195–214. [https://doi.org/10.1016/0022-0981\(90\)90185-F](https://doi.org/10.1016/0022-0981(90)90185-F)
- Edgar GJ, Aoki M (1993) Resource limitation and fish predation: their importance to mobile epifauna associated with JapaneseSargassum. *Oecologia* 95:122–133. <https://doi.org/10.1007/BF00649515>
- Efird TP, Konar B (2014) Habitat characteristics can influence fish assemblages in high latitude kelp forests. *Environ Biol Fishes* 97:1253–1263. <https://doi.org/10.1007/s10641-013-0211-x>
- Eyster LS, Pechenik JA (1988) Attachment of *Mytilus edulis* L. larvae on algal and byssal filaments is enhanced by water agitation. *J Exp Mar Biol Ecol* 114:99–110. [https://doi.org/10.1016/0022-0981\(88\)90131-1](https://doi.org/10.1016/0022-0981(88)90131-1)
- Falkenberg LJ, Russell BD, Connell SD (2012) Stability of strong species interactions resist the synergistic effects of local and global pollution in kelp forests. *PLoS One* 7:e33841. <https://doi.org/10.1371/journal.pone.0033841>
- Filbee-Dexter K, Wernberg T (2018) Rise of turfs: a new battlefield for globally declining kelp forests. *Bioscience* 68:64–76. <https://doi.org/10.1093/biosci/bix147>
- Fitzsimons J, Branigan S, Brumbaugh RD, McDonald T, zu Ermgassen PSE (2019) Restoration guidelines for shellfish reefs
- Flukes EB, Johnson CR, Wright JT (2014) Thinning of kelp canopy modifies understory assemblages: the importance of canopy density. *Mar Ecol Prog Ser* 514:57–70. <https://doi.org/10.3354/meps10964>
- Frankenbach S, Ezequiel J, Plecha S, Goessling JW, Vaz L, Kühl M, Dias JM, Vaz N, Seródio J (2020) Synoptic spatio-temporal variability of the photosynthetic productivity of microphytobenthos and phytoplankton in a tidal estuary. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2020.00170>
- Fraser KM, Lefcheck JS, Ling SD, Mellin C, Stuart-Smith RD, Edgar GJ (2020) Production of mobile invertebrate communities on shallow reefs from temperate to tropical seas. *Proc Royal Soc b: Biological Sci* 287:20201798. <https://doi.org/10.1098/rspb.2020.1798>
- Graham MH (2004) Effects of local deforestation on the diversity and structure of Southern California giant kelp forest food webs. *Ecosystems* 7:341–357. <https://doi.org/10.1007/s10021-003-0245-6>
- Hinojosa IA, Green BS, Gardner C, Jeffs A (2014) Settlement and early survival of southern rock lobster,  *Jasus edwardsii*, under climate-driven decline of kelp habitats. *ICES J Mar Sci* 72:i59–i68. <https://doi.org/10.1093/icesjms/fsu199>
- Hope JA, Paterson DM, Thrush SF (2020) The role of microphytobenthos in soft-sediment ecological networks and their contribution to the delivery of multiple ecosystem services. *J Ecol* 108:815–830. <https://doi.org/10.1111/1365-2745.13322>
- Jackson AC, Underwood AJ, Murphy RJ, Skilleter GA (2010) Latitudinal and environmental patterns in abundance and composition of epilithic microphytobenthos. *Mar Ecol Prog Ser* 417:27–38
- Jantzen C, Schmidt GM, Wild C, Roder C, Khokiattiwong S, Richter C (2013) Benthic reef primary production in response to large amplitude internal waves at the similan islands (Andaman Sea, Thailand). *PLoS One* 8:e81834. <https://doi.org/10.1371/journal.pone.0081834>
- Johnson CR, Banks SC, Barrett NS, Cazassus F, Dunstan PK, Edgar GJ, Frusher SD, Gardner C, Haddon M, Helidoniotis F, Hill KL, Holbrook NJ, Hosie GW, Last PR, Ling SD, Melbourne-Thomas J, Miller K, Pecl GT, Richardson AJ, Ridgway KR, Rintoul SR, Ritz DA, Ross DJ, Sanderson JC, Shepherd SA, Slotwinski A, Swadling KM, Taw N (2011) Climate change cascades: Shifts in oceanography, species' ranges and subtidal marine community dynamics in eastern Tasmania. *J Exp Mar Biol Ecol* 400:17–32. <https://doi.org/10.1016/j.jembe.2011.02.032>
- Kochmann J, Crowe TP (2014) Effects of native macroalgae and predators on survival, condition and growth of non-indigenous Pacific oysters (*Crassostrea gigas*). *J Exp Mar Biol Ecol* 451:122–129. <https://doi.org/10.1016/j.jembe.2013.11.007>
- Krumhansl KA, Okamoto DK, Rassweiler A, Novak M, Bolton JJ, Cavanaugh KC, Connell SD, Johnson CR, Konar B, Ling SD, Micheli F, Norderhaug KM, Pérez-Matus A, Sousa-Pinto I, Reed DC, Salomon AK, Shears NT, Wernberg T, Anderson RJ, Barrett NS, Buschmann AH, Carr MH, Caselle JE, Derrien-Courtlet S, Edgar GJ, Edwards M, Estes JA, Goodwin C, Kenner MC, Kushner DJ, Moy FE, Nunn J, Steneck RS, Vásquez J, Watson J, Witman JD, Byrnes JEK (2016) Global patterns of kelp forest change over the past half-century. *Proc Natl Acad Sci* 113:13785–13790. <https://doi.org/10.1073/pnas.1606102113>
- Lambrinos JG, Bando KJ (2008) Habitat modification inhibits conspecific seedling recruitment in populations of an invasive ecosystem engineer. *Biol Invasions* 10:729–741. <https://doi.org/10.1007/s10530-007-9165-2>
- Layton C, Cameron MJ, Shelamoff V, Fernández PA, Britton D, Hurd CL, Wright JT, Johnson CR (2019a) Chemical microenvironments within macroalgal assemblages: Implications for the inhibition of kelp recruitment by turf algae. *Limnol Oceanogr* 64:1600–1613. <https://doi.org/10.1002/lno.11138>
- Layton C, Shelamoff V, Cameron MJ, Tatsumi M, Wright JT, Johnson CR (2019b) Resilience and stability of kelp forests: the importance of patch dynamics and environment-engineer feedbacks. *PLoS One* 14:e0210220. <https://doi.org/10.1371/journal.pone.0210220>

- Layton C, Coleman MA, Marzinelli EM, Steinberg PD, Swearer SE, Vergés A, Wernberg T, Johnson CR (2020) Kelp Forest Restoration in Australia. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2020.00074>
- Leise EM, Froggett SJ, Nearhoof JE, Cahoon LB (2009) Diatom cultures exhibit differential effects on larval metamorphosis in the marine gastropod *Ilyanassa obsoleta* (Say). *J Exp Mar Biol Ecol* 379:51–59. <https://doi.org/10.1016/j.jembe.2009.08.007>
- MacIntyre HL, Geider RJ, Miller DC (1996) Microphytobenthos: the ecological role of the “secret garden” of unvegetated, shallow-water marine habitats. I distribution, abundance and primary production. *Estuaries* 19:186–201. <https://doi.org/10.2307/1352224>
- McAfee D, Larkin C, Connell SD (2020) Multi-species restoration accelerates recovery of extinguished oyster reefs. *J Appl Ecol* n/a. <https://doi.org/10.1111/1365-2664.13719>
- Miller RJ, Page HM (2012) Kelp as a trophic resource for marine suspension feeders: a review of isotope-based evidence. *Mar Biol* 159:1391–1402. <https://doi.org/10.1007/s00227-012-1929-2>
- Miller RJ, Lafferty KD, Lamy T, Kui L, Rassweiler A, Reed DC (2018) Giant kelp, *Macrocystis pyrifera*, increases faunal diversity through physical engineering. *Proc R Soc B-Biol Sci* 285:8. <https://doi.org/10.1098/rspb.2017.2571>
- Moncreiff CA, Sullivan MJ (2001) Trophic importance of epiphytic algae in subtropical seagrass beds: evidence from multiple stable isotope analyses. *Marine Ecol Prog Ser* 215:93–106
- Nielsen P, Cranford PJ, Maar M, Petersen JK (2016) Magnitude, spatial scale and optimization of ecosystem services from a nutrient extraction mussel farm in the eutrophic Skive Fjord, Denmark. *Aquac Environ Interact* 8:311–329
- Peteiro LG, Filgueira R, Labarta U, Fernández-Reiriz MJ (2007) Effect of submerged time of collector ropes on the settlement capacity of *Mytilus galloprovincialis* L. *Aquac Res* 38:1679–1681. <https://doi.org/10.1111/j.1365-2109.2007.01820.x>
- Petrattis PS (1990) Direct and indirect effects of predation, herbivory and surface rugosity on mussel recruitment. *Oecologia* 83:405–413. <https://doi.org/10.1007/BF00317568>
- Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, UK
- Reed DC, Schroeter SC, Huang D, Anderson TW, Ambrose RF (2006) Quantitative assessment of different artificial reef designs in mitigating losses to kelp forest fishes. *Bull Mar Sci* 78:133–150
- Reeves SE, Kriegisch N, Johnson CR, Ling SD (2018) Reduced resistance to sediment-trapping turfs with decline of native kelp and establishment of an exotic kelp. *Oecologia* 188:1239–1251. <https://doi.org/10.1007/s00442-018-4275-3>
- Reeves SE, Renzi JJ, Fobert EK, Silliman BR, Hancock B, Gillies CL (2020) Facilitating better outcomes: how positive species interactions can improve oyster reef restoration. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2020.00656>
- Rullens V, Lohrer AM, Townsend M, Pilditch CA (2019) Ecological mechanisms underpinning ecosystem service bundles in marine environments—a case study for shellfish. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2019.00409>
- Schneider CA, Rasband WS, Eliceiri KW (2012) NIH image to imageJ: 25 years of image analysis. *Nat Methods* 9:671–675. <https://doi.org/10.1038/nmeth.2089>
- Semcheski MR, Egerton TA, Marshall HG (2016) Composition and diversity of intertidal microphytobenthos and phytoplankton in Chesapeake Bay. *Wetlands* 36:483–496. <https://doi.org/10.1007/s13157-016-0756-5>
- Shelamoff V, Layton C, Tatsumi M, Cameron MJ, Wright JT, Johnson CR (2019a) Ecosystem engineering by a canopy-forming kelp facilitates the recruitment of native oysters. *Restor Ecol* 27:1442–1451. <https://doi.org/10.1111/rec.13019>
- Shelamoff V, Layton C, Tatsumi M, Cameron MJ, Wright JT, Johnson CR (2019b) Patch size and density of canopy-forming kelp modify influences of ecosystem engineering on understory algal and sessile invertebrate assemblages. *Mar Ecol Prog Ser* 632:59–79. <https://doi.org/10.3354/meps13155>
- Shelamoff V, Layton C, Tatsumi M, Cameron MJ, Edgar GJ, Wright JT, Johnson CR (2020a) Kelp patch size and density influence secondary productivity and diversity of epifauna. *Oikos* 129:331–345. <https://doi.org/10.1111/oik.06585>
- Shelamoff V, Layton C, Tatsumi M, Cameron MJ, Wright JT, Edgar GJ, Johnson CR (2020b) High kelp density attracts fishes except for recruiting cryptobenthic species. *Mar Environ Res* 161:105127. <https://doi.org/10.1016/j.marenvres.2020.105127>
- Shelamoff V, Layton C, Johnson C, Wright J (2022) Maria Island mussel and microphytobenthic algal data [Data set]. Institute for Marine and Antarctic Studies (IMAS), University of Tasmania (UTAS). <https://doi.org/10.25959/8GQV-PM83>
- Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MJ (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environ Conserv* 29:436–459. <https://doi.org/10.1017/s0376892902000322>
- Strain EMA, Thomson RJ, Micheli F, Mancuso FP, Airoidi L (2014) Identifying the interacting roles of stressors in driving the global loss of canopy-forming to mat-forming algae in marine ecosystems. *Glob Change Biol* 20:3300–3312. <https://doi.org/10.1111/gcb.12619>
- Sundbäck K, McGlathery K (2005) Interactions between benthic macroalgal and microalgal mats. In: Kristensen E, Haese RR, Kostka JE (eds) Interactions between macro- and microorganisms in marine sediments. <https://doi.org/10.1029/CE060p0007>
- Svane I, Ompi M (1993) Patch dynamics in beds of the blue mussel *Mytilus edulis* L.: effects of site, patch size, and position within a patch. *Ophelia* 37:187–202. <https://doi.org/10.1080/00785326.1993.10429917>
- Tait LW, Schiel DR (2018) Ecophysiology of layered macroalgal assemblages: importance of subcanopy species biodiversity in buffering primary production. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2018.00444>
- Teagle H, Hawkins SJ, Moore PJ, Smale DA (2017) The role of kelp species as biogenic habitat formers in coastal marine ecosystems. *J Exp Mar Biol Ecol* 492:81–98. <https://doi.org/10.1016/j.jembe.2017.01.017>
- Toohey B, Kendrick GA, Wernberg T, Phillips JC, Malkin S, Prince J (2004) The effects of light and thallus scour from *Ecklonia radiata* canopy on an associated foliose algal assemblage: the importance of photoacclimation. *Mar Biol* 144:1019–1027. <https://doi.org/10.1007/s00227-003-1267-5>
- Totti C, Poulin M, Romagnoli T, Perrone C, Pennesi C, De Stefano M (2009) Epiphytic diatom communities on intertidal seaweeds from Iceland. *Polar Biol* 32:1681–1691. <https://doi.org/10.1007/s00300-009-0668-4>
- Umanzor S, Ladah L, Zertuche-González JA (2017) The influence of species, density, and diversity of macroalgal aggregations on microphytobenthic settlement. *J Phycol* 53:1060–1071. <https://doi.org/10.1111/jpy.12565>
- Umanzor S, Ladah L, Zertuche-González JA (2018) Intertidal seaweeds modulate a contrasting response in understory seaweed and microphytobenthic early recruitment. *Front Mar Sci*. <https://doi.org/10.3389/fmars.2018.00296>
- Vergés A, Doropoulos C, Malcolm HA, Skye M, Garcia-Pizá M, Marzinelli EM, Campbell AH, Ballesteros E, Hoey AS, Vila-Concejo A, Bozec Y-M, Steinberg PD (2016) Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proc Natl Acad Sci* 113:13791–13796. <https://doi.org/10.1073/pnas.1610725113>

- von der Meden CEO, Porri F, McQuaid CD, Faulkner K, Robey J (2010) Fine-scale ontogenetic shifts in settlement behaviour of mussels: changing responses to biofilm and conspecific settler presence in *Mytilus galloprovincialis* and *Perna perna*. *Mar Ecol Prog Ser* 411:161–171. <https://doi.org/10.3354/meps08642>
- von der Meden CEO, Cole VJ, McQuaid CD (2015) Do the threats of predation and competition alter larval behaviour and selectivity at settlement under field conditions? *J Exp Mar Biol Ecol* 471:240–246. <https://doi.org/10.1016/j.jembe.2015.06.017>
- Wang C, Bao WY, Gu ZQ, Li YF, Liang X, Ling Y, Cai SL, Shen HD, Yang JL (2012) Larval settlement and metamorphosis of the mussel *Mytilus coruscus* in response to natural biofilms. *Biofouling* 28:249–256. <https://doi.org/10.1080/08927014.2012.671303>
- 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. <https://doi.org/10.1007/s10452-005-9009-z>
- Wernberg T, Smale DA, Tuya F, Thomsen MS, Langlois TJ, de Bettignies T, Bennett S, Rousseaux CS (2013) An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. *Nat Clim Chang* 3:78–82. <https://doi.org/10.1038/nclimate1627>
- Witman JD (1987) Subtidal coexistence: storms, grazing, mutualism, and the zonation of kelps and mussels. *Ecol Monogr* 57:167–187. <https://doi.org/10.2307/1942623>
- Wood G, Marzinelli EM, Coleman MA, Campbell AH, Santini NS, Kajlich L, Verdura J, Wodak J, Steinberg PD, Vergés A (2019) Restoring subtidal marine macrophytes in the Anthropocene: trajectories and future-proofing. *Mar Freshw Res* 70:936–951. <https://doi.org/10.1071/MF18226>
- Wright JT, Gribben PE, Latzel S (2016) Native ecosystem engineer facilitates recruitment of invasive crab and native invertebrates. *Biol Invasions* 18:3163–3173. <https://doi.org/10.1007/s10530-016-1206-2>
- Yang JL, Satuito CG, Bao WY, Kitamura H (2007) Larval settlement and metamorphosis of the mussel *Mytilus galloprovincialis* on different macroalgae. *Mar Biol* 152:1121–1132. <https://doi.org/10.1007/s00227-007-0759-0>
- Yang JL, Guo XP, Ding DW, Gao W, Huang DF, Chen YR, Liang X (2017) Interactions between natural biofilm, substratum surface wettability, and mussel plantigrade settlement. *Sci China-Earth Sci* 60:382–390. <https://doi.org/10.1007/s11430-016-0145-1>

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