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Restored kelp facilitates lobster recruitment but not other mid-trophic macroinvertebrates

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Abstract

1. The patch dynamics of foundation species profoundly affects community assembly and thus has important implications for ecosystem restoration. However, it is unclear how restored kelp patches that vary in size and density will influence the establishment of mid-trophic level (MTL) macroinvertebrates, a key functional group in coastal ecosystems.

2. Artificial reefs with transplants of the canopy-forming kelp, *Ecklonia radiata*, were used to quantify the effect of patch size and kelp density on the densities of MTL macroinvertebrates (primarily decapod crustaceans) and on the recruitment of an ecologically important and commercially valuable lobster species.

3. Densities of MTL macroinvertebrates, which were dominated by hermit crabs, decreased with increasing patch size but responded inconsistently to kelp density. There was, however, an overall positive relationship between MTL macroinvertebrates and the density of small epifaunal grazers (a potential food source), along with a negative association with cover of understorey foliose algae.

4. In contrast, the total abundance and density of lobster recruits was higher on larger reefs, and reefs with kelp had up to double the number of recruits relative to reefs with no kelp. After 12 months, most of the surviving lobster recruits occurred on reefs supporting low and medium densities of kelp.

5. These results show that patchy reef substratum is effective in supporting high densities of some MTL macroinvertebrates, irrespective of kelp presence. Although conversely, larger reefs with restored kelp at natural – or even relatively low – densities appear critical to the recruitment of lobsters, which could motivate and provide positive feedback for kelp restoration projects in some locations.

6. Patch dynamics may be used to support restoration efforts by helping to accelerate the recovery of key species and ecosystem services; however, trade-offs will exist through different taxa responding to patch characteristics in different ways, some positive and some negative.

1 | INTRODUCTION

Habitat patch characteristics (i.e. size, shape, position relative to other habitat, and structural complexity) influence the recruitment of associated species and the carrying capacity of individual patches, which has important implications for ecosystem restoration. However, it is often unclear how the structure of newly restored patches of marine habitat-formers (e.g. corals, seagrass, kelp, and mangroves) are likely to influence the assembly of the associated species, including those that provide valuable ecosystem services and are likely to improve the trajectory of ecosystem recovery. Canopy-forming kelp are foundation species that provide habitat for productive and diverse food webs in temperate and subpolar waters globally (Dayton, 1985; Steneck et al., 2002; Krumhansl et al., 2016). Kelp beds facilitate community establishment through providing physical and chemical cues that attract larval, juvenile, and mature individuals from the water column and surrounding benthos (Rossi, Connell & Nagelkerken, 2017; Hinojosa et al., 2018). They support associated communities by providing complex physical structure, which moderates the abiotic environment and augments the supply of food and shelter (Teagle et al., 2017; Layton et al., 2019). The kelp bed structure additionally influences trophic and competitive interactions among species, which further affects community dynamics (Graham, 2004). However, in many areas kelp structure is being increasingly modified through escalating environmental stressors, such as ocean warming, coastal development, overfishing, and an increasing abundance of grazers, and this is manifesting in kelp loss and the degradation of kelp forests in some locations (Ling et al., 2009; Johnson et al., 2011; Krumhansl et al., 2016; Wernberg et al., 2016; Smale, 2020).

To mitigate the decline of these systems and the impact on associated communities, there is increasing interest in restoring kelp ecosystems and in providing supplementary kelp habitat through restoration or coastal 'greening' (Wood et al., 2019; Layton et al., 2020; Morris et al., 2020). In highly modified systems, artificial reefs and other coastal infrastructure may be required to provide a suitable substratum onto which kelp can be grown (Carter et al., 1985; Reed et al., 2006; Campos et al., 2020; Fredriksen et al., 2020). Despite increased recognition of the benefits of creating kelp habitat in attracting many of the associated species that provide valuable ecosystem services, there is relatively scant experimental work investigating how the structure of restored kelp habitat influences mid-trophic level macroinvertebrate assemblages (referring to predominantly carnivorous species, including scavengers), a key functional group in coastal ecosystems. In contrast, there is a growing body of research that has focused on kelp demography (Deysher et al., 2002; Layton et al., 2019), algal and sessile invertebrates (Schroeter, Reed & Raimondi, 2015; Shelamoff et al., 2019b; Campos et al., 2020), epifauna (Shelamoff et al., 2020a), and fishes (DeMartini, Roberts & Anderson, 1989; Campos et al., 2020; Shelamoff et al., 2020b) associated with restored kelp patches.

Mid-trophic level (MTL) macroinvertebrates are highly abundant in kelp forests globally, and include many species of high social, ecological, and economic importance (Boudreau & Worm, 2012; Hermosillo-Núñez, 2020). These macroinvertebrates often exert top-down influences on food webs, but are also a key food source for other invertebrates, fishes, and marine mammals (Pauly et al., 1998; Menge et al., 1999; Ling et al., 2009). The southern rock lobster *Jasus edwardsii* supports one of Australia's most valuable fisheries, worth >AU$250 million per year. In Tasmania, large rock lobsters are the only predator able to reduce the number of adults of the destructive long-spined sea urchin *Centrostephanus rogersii* (Ling et al., 2009), which contributes to the widespread loss of kelp forest ecosystems along the east coast of Tasmania and their replacement with barren habitat (Johnson et al., 2011; Ling & Keane, 2018). Kelp presence is beneficial to the settlement and subsequent survival of rock lobsters (Hinojosa et al., 2014), and thus the loss of kelp forest habitat is likely to compound the declines in lobster numbers caused by overfishing (Ling et al., 2009).

The effects of macrophyte patch size and structural complexity within patches (i.e. density of habitat-formers) on marine macroinvertebrates has been examined most extensively for seagrass ecosystems (Robbins & Bell, 1994; Eggleston et al., 1999; Attrill, Strong & Rowden, 2000; Hovel & Lipcius, 2001), with similar effects of patch characteristics likely to be broadly applicable across a variety of ecosystems (Levin & Paine, 1974; Sousa, 1984; Wright & Jones, 2004). Habitat patch size influences the patch edge-to-interior ratio, with small patches having a higher ratio than larger patches of an equivalent shape. The proportionally higher edge-to-area ratio of smaller patches is likely to increase the encounter rates between recruiting organisms and the patch (with organisms typically recruiting into patches from the edge), potentially leading to higher initial densities of some macroinvertebrates (Eggleston et al., 1999; Fahrig, 2020). Furthermore, large predatory species often require increased areas of habitat to meet their resource demands, and thus small patches could provide a refuge from these predators (Hovel & Lipcius, 2001). However, despite some species benefitting form a small patch size, resource constraints may ultimately limit the ability of these patches to sustain high population densities (Sweatman, Layman & Fourqurean, 2017). Increased structural complexity resulting from higher densities of foundation species is likely to increase the provisioning of refuge and food and could provide stronger cues to attract recruiting organisms (Attrill, Strong & Rowden, 2000; Mills & Berkenbusch, 2009). It is therefore possible that the density of MTL macroinvertebrates will decrease with increasing kelp patch size but increase with increasing

density of kelp, with both relationships potentially reaching a threshold point before possibly changing direction. Conversely, more rock lobsters may recruit into larger and denser kelp patches through increased settlement cues and the greater provisioning of refuge (Hinojosa et al., 2015).

Kelp patch size and density exert a complex array of separate and interactive effects on the local abiotic and biotic environment, which are likely to have ramifications for the establishment of MTL macroinvertebrate assemblages (Dayton et al., 1984; Flukes, Johnson & Wright, 2014; Layton et al., 2019; Shelamoff et al., 2019b; Shelamoff et al., 2020a). Water flow and penetration of light to the benthos decrease with kelp patch size and density (Layton et al., 2019), which can reduce the secondary productivity of small grazing epifauna on a per unit area basis (Shelamoff et al., 2020a). A reduction in such a major food source could reduce the carrying capacity of the patch and limit the populations of MTL consumers. Larger patches of dense kelp can also provide more stable environmental conditions and reduced edge effects, compared with smaller patches (Harris., 1988; Layton et al., 2019). However, they also tend to support a greater abundance of predatory fishes that can potentially exert top-down effects on macroinvertebrates (Jane, Pauline & Rod, 2006; Shelamoff et al., 2020b). An additional consideration is that, above a threshold density, the capacity of predators to consume prey is likely to decrease with kelp structural complexity, as a result of the increased benefits of habitat refuge and restricted predator manoeuvrability (Hovel & Lipcius, 2001; Warfe & Barmuta, 2004; Hinojosa et al., 2014). For the same reason, subcanopy foliose algae may also lead to reduced densities of carnivorous species (Bué et al., 2020), with these algal species being more prevalent on larger patches supporting intermediate kelp densities (Flukes, Johnson & Wright, 2014; Shelamoff et al., 2019b).

Here, the aim was to determine the role of kelp density and patch size in influencing densities of MTL macroinvertebrates and the recruitment of an ecologically and economically valuable lobster species (*J. edwardsii*). Artificial reefs of different sizes and supporting different densities of the dominant Australasian kelp species *Ecklonia radiata* were established to test two main hypotheses: H1, densities of MTL macroinvertebrates will decrease with increasing patch size but will increase with increasing kelp density; and H2, the recruitment (density and absolute abundance) of *J. edwardsii*, as a species that is likely to depend on kelp for recruitment, will increase with kelp patch size and density. The importance of: (i) the biomass of small epifauna (a potential food resource) and (ii) subcanopy foliose algal structure (possible refuge) were also explored as possible correlates, additionally driving densities of MTL macroinvertebrates.

2 | METHODS

2.1 | Experimental reefs

This experiment utilized an array of 28 artificial reefs populated with *E. radiata* transplants of uniform size and morphology, collected from

a nearby reef (Layton et al., 2019; Layton et al., 2021). *Ecklonia radiata* typically grows to approximately 1.5 m in length and is the dominant canopy-forming macroalgal species across temperate Australasia, where it forms subtidal forests down to depths of approximately 60 m (Bennett et al., 2016). The 28 reefs were installed on the western side of Maria Island on Tasmania's east coast, comprising seven different patch sizes (0.12, 0.24, 0.48, 1.08, 1.92, 4.32, and 7.68 m^2) crossed with four kelp density treatments (zero, low, medium, and high, defined as 0, 4.1, 8.3, and 16.6 kelp m^{-2}, respectively), as described by Layton et al. (2019). Note that 'medium' density was the mean density encountered on natural reefs in the area, and thus 'low' and 'high' densities were half and double the natural kelp density. Each of the experimental reefs was constructed from concrete pavers elevated 0.3 m above sandy substratum on a steel frame, the array of reefs was >1.5 km from the nearest natural rocky reefs, and the reefs were positioned in a grid formation separated by 25 m, covering approximately 1.6 ha in total. The array of reefs was installed in December 2014 and kelp was first transplanted to the reefs in January and February 2015. Sampling of the associated macroinvertebrate assemblages took place from November 2015 to December 2016. Throughout the deployment of the reefs, kelp densities were maintained by replacing any losses at regular intervals (approximately every 6 weeks), whereas communities of other algae, invertebrates, and fishes established themselves naturally on the reefs (i.e. the addition of kelp was the only manipulation that took place).

2.2 | Macroinvertebrate surveys

Macroinvertebrates were assessed by diver-based visual surveys conducted at three stages of the experiment: early (spring, November 2015), middle (autumn, March–April 2016), and late (spring, November–December 2016), approximately 11, 16, and 23 months, respectively, after the reefs were deployed. At each of these stages, two separate surveys were conducted (4–6 weeks apart) and the results were averaged. All surveys were conducted by the same observer (VS), who systematically examined each paver and the associated algae in turn and then examined the underside surface of the elevated reef platforms. All mobile macroinvertebrates >50 mm on each reef were recorded. The total time needed to survey each reef differed depending on the reef area and kelp density, but an approximately equivalent search effort per paver was devoted across the reefs supporting a given kelp density. Lobster (*J. edwardsii*) recruits were counted concurrently, although additional surveys focused solely on lobsters also took place in January and August 2016. To assess the retention/survival of lobsters on the reefs, only lobsters with a total length of >100 mm (carapace length of >40 mm) were included in surveys after January 2016, whereas small individuals (50–100 mm) were still counted as part of the macroinvertebrate assemblage. Lobsters of >100 mm were thought to have made the ontogenetic transition from the 'early juvenile stage' of their life to the 'juvenile stage' (Linnane et al., 2012). Following the macroinvertebrate surveys, species identified as herbivores were

separated from MTL macroinvertebrates and were excluded from the analyses (Appendix S1). The work on invertebrates complied with the ethical guidelines approved by the University of Tasmania's Animal Ethics Committee (project no. A14511).

2.3 | Environmental correlates

Data quantifying the composition of understorey algae (Shelamoff et al., 2019b), and the biomass density of small grazing epifaunal invertebrates (Shelamoff et al., 2020a), across the experimental reefs were utilized to investigate the potential role of subcanopy foliose algal species, and epifaunal biomass as a food resource, in influencing the abundance of MTL macroinvertebrates. In those studies, the abundance of foliose algae on each of the reefs was determined by photo quadrats conducted at the same time of year as the macroinvertebrate surveys (Shelamoff et al., 2019b), whereas the biomass density of epifauna was estimated by examining the size structure of epifauna associated with standardized rope fibre habitats collected from the centre of each reef in November 2015 (Shelamoff et al., 2020a).

2.4 | Analyses and statistics

Analysis of covariance (ANCOVA) was used to determine the effects of kelp density (fixed factor) and patch size (covariate) on the density of MTL macroinvertebrates (including lobsters) (abundance/reef area) at each of the three stages of the experiment using R 3.2.4. ANCOVA was also used to determine the effects of patch size and kelp density on the maximum number of lobster recruits (observed on the reefs at any time) and the number observed on reefs in the January 2016 survey (the survey with the highest total number of recruits). Other time periods were not analysed as a result of multiple reefs having zero lobsters, which limited the power of any analyses. Robust analyses of the density of lobster recruits could not be performed because of high variability in this response. In part this variability was linked to very small patch sizes supporting any animals (i.e. very low absolute numbers) that yielded a high density. Model assumptions were checked using diagnostic plots (for normality, linearity, and homoscedascity), the structure of model residuals (for linearity and homoscedascity), and the Shapiro–Wilks normality test. Data transformations were based on the maximum λ coefficient from log-likelihood plots produced using the Box–Cox procedure. The covariate patch size was $\log_2$ transformed to linearize the data (reflecting that the patch size increased on a $\log_2$ scale). The homogeneity of slopes was assessed by fitting the full model including the interaction term, and when the interaction term was highly non-significant ($P > 0.25$), the unsaturated model was fitted (i.e. with the interaction term pooled with the within-cells error to provide a better estimate of the error). Significant effects of kelp density were investigated further through pairwise comparisons of covariate adjusted means with a Bonferroni adjustment of significance

(to correct for multiple testing) (Quinn & Keough, 2002) using the LSMEANS and MULTCOMP packages.

Multiple regression was used to determine the influence of patch size, kelp density, percentage cover of foliose algae, and the biomass of epifaunal invertebrates on the density of macroinvertebrates averaged across two time periods: (i) early to middle experimental stages; and (ii) middle to late experimental stages. For these analyses, average values across consecutive time periods were used because MTL macroinvertebrate densities were not expected to respond concurrently with the predictor variables (especially subcanopy algal cover), whereas they might show an incremental response over several months. Normality, linearity, and homogeneity in variance of response variables were investigated with a scatter plot matrix and diagnostic plots (as outlined for ANCOVA). Multicollinearity was investigated through pairwise correlations and the variance inflation factor of predictor variables. Model selection was achieved by comparing the fit of all possible models for each response variable (Quinn & Keough, 2002) using adjusted R^2 values and Bayesian information criterion (BIC), obtained using the LEAPS package. The importance of the different predictor variables (patch size, kelp density, foliose algal cover, and epifaunal secondary productivity) was also investigated using hierarchical partitioning (the *hier.part* function) to determine the independent contribution of each of the predictors in the multiple regression model. Afterwards, the likelihood that the independent contribution could result from chance was determined by performing a randomization test and assessing the significance of the Z-scores at the 95% confidence level.

3 | RESULTS

3.1 | Macroinvertebrate density

Mid-trophic level (MTL) macroinvertebrates accounted for 87% of all macroinvertebrates recorded in the surveys (the remainder was almost entirely the herbivorous swimmer crab *Nectocarcinus integrifrons*, 12%), with decapod crustaceans comprising 96% of these invertebrates. The scavenging hermit crab *Paguristes frontalis* (62%) was the most dominant species, followed by the lobster *J. edwardsii* (16%) (Figure 1; Appendix S1). Similar total numbers of macroinvertebrates across all reefs were recorded during the early and late stages of the experiment (326 and 363, respectively), but almost double that number (637) was recorded in the middle stage of the experiment. The density of MTL macroinvertebrates was affected by a three-way interaction between survey time, patch size, and kelp density (Figure 2; Table 1). Patch size did not affect macroinvertebrates at the early stage of the experiment, whereas densities declined significantly with patch size during the middle and late stages, when densities were approximately four times greater on the two smallest reefs compared with the two largest reefs. Kelp density was only significant during the middle stage of the experiment, when reefs with zero kelp and kelp at the highest density supported >50% higher densities of macroinvertebrates than reefs with the medium (i.e. natural) density of kelp on average.
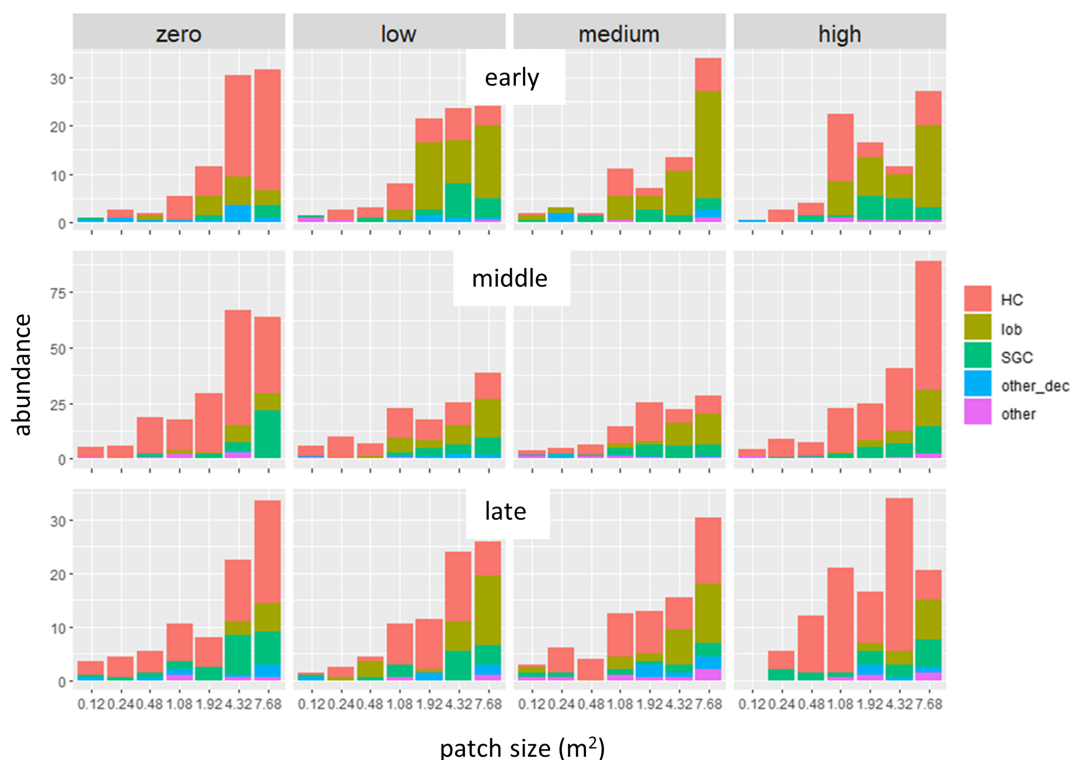
FIGURE 1 Abundance of MTL macroinvertebrates on artificial reefs of different sizes (0.12–7.68 m²), supporting different densities of transplanted *Ecklonia radiata* (zero, 0 kelp m⁻²; low, 4.1 kelp m⁻²; medium, 8.3 kelp m⁻²; high, 16.6 kelp m⁻²) at three stages of the experiment (early: spring, November 2015; middle: autumn, March–April 2016; late: spring, November–December 2016). HC = southern hermit crab (*Paguristes frontalis*), lob = lobster (*Jasus edwardsii*), SGC = seagrass crab (*Nectocarcinus integrifrons*), other_dec = other decapods, other = all remaining macroinvertebrates. *X*-axis values (not shown) for each panel are: 0.12, 0.24, 0.48, 1.08, 1.92, 4. 32, 7.68

FIGURE 2 Density of MTL macroinvertebrates across artificial reefs of different sizes, supporting different densities of transplanted kelp, at three stages of the experiment (early: spring, November 2015; middle: autumn, March–April 2016; late: spring, November–December 2016)
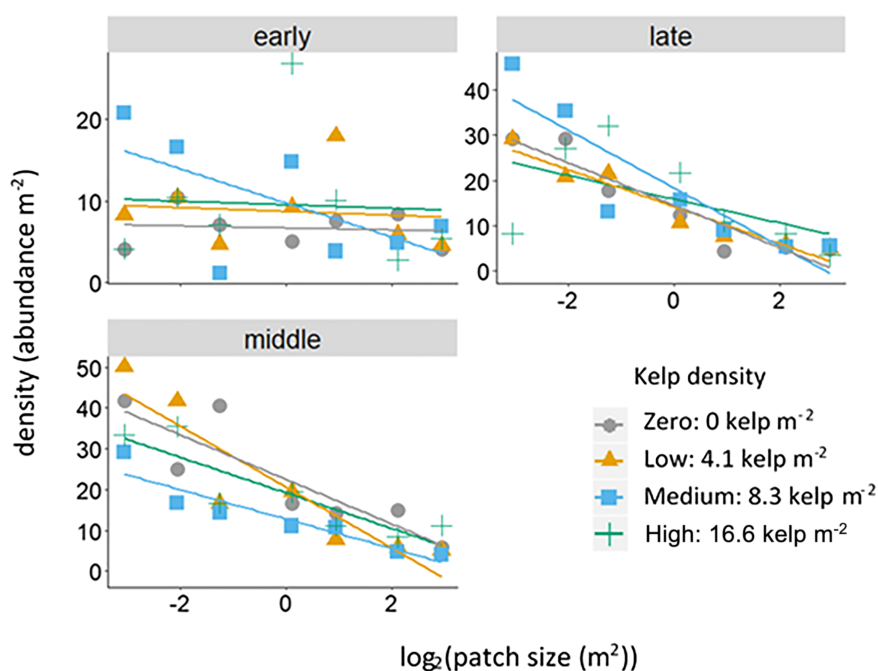
TABLE 1 Results of ANCOVA testing for the effects of patch size (0.12–7.68 m^2) and kelp density (zero, 0 kelp m^{-2}; low, 4.1 kelp m^{-2}; medium, 8.3 kelp m^{-2}; high, 16.6 kelp m^{-2}) at three stages of the experiment (early: spring, November 2015; middle: autumn, March–April 2016; and late: spring, November–December 2016) on the density of MTL macroinvertebrates and the abundance of lobsters. Response variable transformations are shown in terms of the untransformed variable Y. The covariate (patch size) was log$_2$ transformed. *Significant effects ($P < 0.05$). Significant post-hoc pairwise comparisons are indicated in the post-hoc column

Model	Factor	SS (df)	F-value	P-value	Post-hoc
MTL macroinvertebrates: all times					
Density	log$_2$(patch size)*	0.55 (6, 47)	0.67	0.004 *	
$(Y)^{0.34}$	kelp density* time				
MTL macroinvertebrates: early					
Density	log$_2$(patch size)	0.066 (1,23)	51.22	0.28	
Log$_{10}(Y)$	kelp density	0.025 (3,23)	3.12	0.93	
MTL macroinvertebrates: middle					
Density	log$_2$(patch size)	1.34 (1,23)	131.44	<0.001*	high, zero > medium
Log$_{10}(Y)^{0.83}$	kelp density	0.17 (3,23)	5.43	0.006*	
MTL macroinvertebrates: late					
Density	log$_2$(patch size)	3.15 (1,22)	196.15	<0.001*	
Log$_{10}(Y)^{1.12}$	kelp density	0.13 (3,22)	2.69	0.07	
Lobsters: January					
Abundance	log$_2$(patch size)	10.41 (1,23)	124.95	<0.001*	
$(Y)^{0.26}$	kelp density	0.73 (3,23)	2.92	0.06	
Lobsters: maximum					
Abundance	log$_2$(patch size)	21.53 (1,23)	145.37	<0.001*	zero > low
$(Y)^{0.37}$	kelp density	1.48 (3,23)	3.34	0.04*	

3.2 | Lobster recruitment

A peak of 220 lobsters was recorded on all reefs in January 2016 and that number declined by nearly 80% by the end of the experiment, when the remaining 48 juvenile lobsters (>100 mm) were predominantly found on the larger reefs that supported low and medium densities of kelp (Figure 3a). In January, when numbers were high, the absolute abundance of lobster increased significantly with patch size, with only seven lobsters observed across the three smallest patch sizes (reefs of <1 m^2), whereas at this time any effect of kelp density on lobster density was not significant (Figure 3a; Table 1). Kelp density did, however, affect the maximum number of lobsters recorded on each reef across the entire sampling period (usually in January 2016), where reefs with kelp at low densities supported twice as many lobsters on average than reefs with zero kelp (Figure 3a; Table 1). The densities of lobsters also appeared to increase with patch size (Figure 3b); however, the highly variable densities obscured any possible effect of the treatment.

3.3 | Environmental correlates

The optimal multiple regression models explaining the density of macroinvertebrates for the two time periods (early–middle and middle–late) in terms of the adjusted R^2 value and BIC always included patch size and epifaunal biomass as predictor variables, whereas in one instance (adjusted R^2 for the middle–late period) kelp density was also included (Appendix S2). The explanatory power of these models (adjusted $R^2 = 0.77$ for early–middle and 0.89 for middle–late; BIC $= -33$ for early–middle and -54 for middle–late) provided only a slight improvement on the simpler model using patch size as the only predictor variable (adjusted $R^2 = 0.75$ and 0.87, respectively; BIC $= -33$ and -52, respectively). The results of the hierarchical partitioning differed slightly from the multiple regression: it similarly revealed important effects of patch size and epifaunal biomass, but additionally indicated significant effects of foliose algae and a non-significant and negligible effect of kelp density (Appendix S3). Independent effects of patch size explained 43–48% of variability in macroinvertebrate density, with epifaunal biomass explaining a further 32% of variability, and cover of foliose algae providing an additional 17–22%.

4 | DISCUSSION

All artificial reefs attracted and sustained high densities of MTL macroinvertebrates, with the reef patch characteristics (i.e. patch size and kelp density) affecting these assemblages at various stages. Consistent with our hypothesis, the densities of all MTL

FIGURE 3 (a) Abundance and (b) density of lobsters on reefs of different sizes, supporting different densities of transplanted kelp at four times (jan, January 2016; apr, April 2016; aug, August 2016; dec, December 2016)
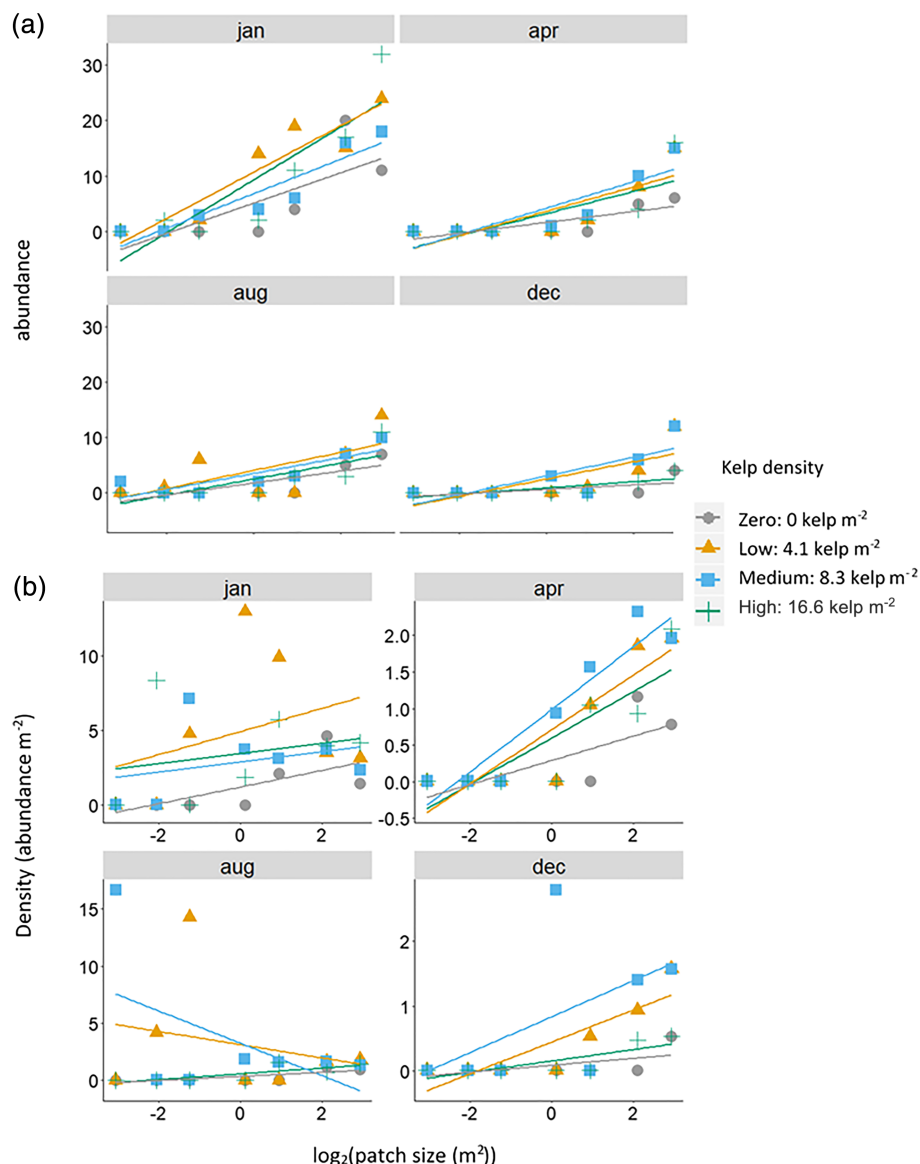
macroinvertebrates generally declined with increasing patch size, whereas the density and absolute total abundance of recruiting lobsters seemed to increase with patch size. However, contrary to expectation, neither the density of MTL macroinvertebrates nor the abundance of lobsters increased with kelp density. Kelp density only had a significant effect on MTL macroinvertebrate densities during the middle stage of the experiment (zero, high > medium) when macroinvertebrate densities were highest. Meanwhile, the presence of kelp, especially at low and medium (i.e. natural) densities, was associated with an increased recruitment of lobsters. The biomass density of epifaunal invertebrates (positive effect) and the percentage cover of subcanopy foliose algae (negative effect) appeared to be key factors associated with the densities of MTL macroinvertebrates, but not the kelp density per se. These results indicate that some MTL macroinvertebrates, e.g. hermit crabs, are likely to be robust to kelp loss, with high numbers likely to establish rapidly in response to additional provisioning of patchy hard substratum. On the other hand,

the abundance of lobsters would be expected to decline with the degradation and fragmentation of kelp habitat, whereas the restoration of relatively continuous kelp patches at natural densities – or even at lower than typical natural densities – is likely to benefit the (re-)establishment of these populations.

4.1 | Macroinvertebrate density

Even with the considerable temporal variability observed, the density of MTL macroinvertebrates on the artificial reefs appeared to be several times higher than those on nearby natural reefs, although the overall species richness was lower (Alexander et al., 2009). Similar increases in faunal abundance have also been observed with fish assemblages associated with artificial reefs (Bohnsack, 1989; Reed et al., 2006; Shelamoff et al., 2020b). However, many of these fishes are likely to be highly vagile and thus have low reliance on the

resources provided by the reef. Conversely, many of the macroinvertebrates observed appeared to be residents of the reefs, and because of their limited mobility are likely to be highly dependent on the reef resources. High densities of these macroinvertebrates may indicate that artificial reefs provided higher quality habitat compared with natural reefs, e.g. the crevices in the pavers appeared to provide refuge. High densities of MTL macroinvertebrates could also result from relatively low numbers of predators and competitors associated with the artificial reefs. Although the reefs attracted elevated densities of invertivorous fishes (possible predators) compared with natural reefs (Shelamoff et al., 2020b), the majority of these are thought to prey mostly on smaller epifauna (Edgar & Shaw, 1995). The observed MTL macroinvertebrate assemblages could conceivably constitute an early stage of community succession that could substantively shift through longer deployment of the reefs. Nonetheless, there was a consistent effect of kelp patch size for the duration of the experiment, and temporal fluctuations in the densities of MTL macroinvertebrates (with higher densities during the middle stage of the experiment) reflected seasonal shifts in productivity related to water temperature. Therefore, although the effects of recruitment limitation on the densities of MTL macroinvertebrates cannot be ruled out, it appears more likely that the observed densities of macroinvertebrates were indicative of the carrying capacity of the different reefs. Top-down predation effects, which could be higher on smaller reefs, compared with larger reefs, through increased predator foraging efficiency, may have been less important in this study because of the dominance of well-protected hermit crabs, the high level of refuge provided by the reef structure, and/or an apparent lack of predators that consume larger-sized macroinvertebrates.

4.2 | Environmental correlates

The positive correlation between epifaunal biomass density (a potential food source) and macroinvertebrate densities supports the notion that 'bottom-up' processes driven by water temperature and changes in production, but ultimately mediated by kelp patch size and density, limited the densities of MTL macroinvertebrates. The influence of patch size and kelp density on subcanopy light levels, water flow, and the prevalence of the foliose algae *Ulva* spp. were previously identified as likely drivers affecting the prevalence of epifaunal invertebrates across the reefs (Shelamoff et al., 2020a). The strong independent effect of epifauna on densities of MTL macroinvertebrates indicates that productivity associated with small grazers could transfer through the food web to affect the abundance of higher trophic-level consumers. Although additional (net) primary production sometimes associated with artificial reefs would theoretically increase the overall secondary productivity associated with the reef, this association is yet to be clearly demonstrated (Layman & Allgeier, 2020). The structure of food webs associated with the experimental reefs was not examined. However, the primary productivity of *E. radiata* and other macroalgae (which presumably

increases with algal biomass) does not appear to increase the secondary productivity of the reef micro- and meso-epifauna per unit area (which are likely to feed predominantly on microphytobenthic algae and detrital resource subsidies) (Shelamoff et al., 2020a), and also does not appear to relate to the density of MTL macroinvertebrates.

The elevated density of MTL macroinvertebrates on small reefs and the absence of a positive response to kelp density potentially indicates that those assemblages favoured the reef-edge microhabitat and were not dependent on kelp as a habitat. Increased densities of macroinvertebrates associated with small patches is consistent with other studies on marine macrophytes (Robbins & Bell, 1994; Eggleston et al., 1999; Hovel & Lipcius, 2001), but is contrary to the trend in density of fishes associated with the same experimental reefs (Shelamoff et al., 2020b). The multiple regression and hierarchical partitioning analyses indicated that the high densities of MTL macroinvertebrates on small reefs was likely to be influenced by the high abundance of epifauna and the reduced coverage of foliose algae on these reefs, although there was still additional unexplained variability related to patch size. Potentially, the high edge-to-area ratio of small reefs may have increased encounter rates between recruiting macroinvertebrates and the reef edge, leading to higher establishment rates. There may also have been reduced numbers of macroinvertebrate predators and competitors, such as fishes, on the smaller reefs, compared with the larger reefs, although their foraging efficiency is likely to be higher on smaller reefs compared with larger reefs (Hovel & Lipcius, 2001; Shelamoff et al., 2020b). It is unclear why MTL macroinvertebrates were negatively associated with foliose algae, although it is possible that foliose algae inhibited the foraging efficiency of these macroinvertebrates, resulting in fewer individuals (Bué et al., 2020).

4.3 | Lobster recruitment

Large reefs with kelp at low and medium densities that supported the greatest retention of lobster recruits also tended to support the lowest total density of MTL macroinvertebrates. It is therefore possible that adverse species interactions with other MTL macroinvertebrates (e.g. predation or competition) impacted lobster survivorship (or lobsters may have negatively affected other MTL macroinvertebrates). Alternatively, the reefs preferred by lobsters (larger reefs with low and medium densities of kelp), which supported a dense cover of oysters and foliose algae, may have provided increased settlement cues, refuge, food, and better survival prospects for lobsters (Hinojosa et al., 2014; Shelamoff et al., 2019a; Shelamoff et al., 2019b). Consistent with the findings of Hinojosa et al. (2014), the presence of kelp is likely to have increased both the settlement and the subsequent survival of lobsters. Additionally, a patch size greater than approximately 2 m^2 was required to sustain lobsters for the duration of the experiment. It is possible that the lack of foliose algae on small reefs meant that there wasn't suitable nursery habitat for recruiting lobsters, making them vulnerable to predation. Our

results also suggest that artificial reefs supporting kelp, as well as kelp restoration efforts on natural reefs, could potentially be used to assist the management of commercially important species, such as lobsters. Although kelp was critical for lobsters, it only appeared to indirectly influence other MTL macroinvertebrates. This could lead to highly variable and context-specific effects of kelp addition on MTL macroinvertebrate assemblages.

4.4 | Implications for conservation

There is increasing interest in using artificial structures and habitat restoration to mitigate the degradation of coastal ecosystems (Carter et al., 1985; Wood et al., 2019; Layton et al., 2020; Morris et al., 2020). The high commercial and ecological value of lobsters in Australia (and the likelihood that similar associations between lobsters and kelp exist elsewhere), could motivate funding for these projects in some locations. Also, although the addition of kelp to the study reefs did not increase the total abundance or diversity of MTL macroinvertebrates, it did increase the diversity of other macroalgae, epifauna, and fishes associated with the reefs (Shelamoff et al., 2019b; Shelamoff et al., 2020a; Shelamoff et al., 2020b). Kelp also helped facilitate the recruitment of *Ostrea angasi*, a critically depleted reef-forming oyster (Shelamoff et al., 2019a). Moreover, these positive community responses further improved with increasing kelp patch size, highlighting a potential upside of upscaling the 'greening' of marine infrastructure. Although there is a need to develop cost-effective strategies to support kelp restoration at spatial scales of hundreds to thousands of square metres (Layton et al., 2020; Morris et al., 2020), there are still likely to be localized benefits for the ecosystem of smaller-scale (1–10 m^2) projects. Knowledge of patch dynamics will help management efforts to expedite the recovery of marine ecosystems.

CONFLICT OF INTEREST
None.

DATA AVAILIABILITY STATEMENT
The full dataset associated with this research are available from IMAS Data Catalogue (Shelamoff et al., 2022).

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