



# Ecological enhancement of breakwater upgrades: size and type of rocks used influence benthic communities

Lea T. Mamo<sup>1,\*</sup>, Melinda A. Coleman<sup>1,2</sup>, Brendan P. Kelaher<sup>1</sup>

<sup>1</sup>National Marine Science Centre, Southern Cross University, Coffs Harbour, NSW 2450, Australia

<sup>2</sup>Department of Primary Industries, NSW Fisheries, Coffs Harbour, NSW 2450, Australia

**ABSTRACT:** Existing coastal breakwaters are ageing and will need to be upgraded to withstand additional forces associated with rising sea levels and storms. Structural upgrades can affect taxa living on or adjacent to breakwaters. These impacts can be mitigated by ecological engineering of breakwaters, which can enhance habitat quality without losing their primary purpose of protection. A recently upgraded breakwater at Coffs Harbour, NSW, Australia was eco-engineered to use boulder fields to mitigate impacts on a critically endangered alga (*Nereia lophocladia*) living on and adjacent to the infrastructure. Over a year, we assessed the effect of different rock sizes (small versus large), types (greywacke versus granite) and orientations (top versus bottom) on the composition and diversity of benthic taxa. *N. lophocladia* has yet to recruit to the eco-engineered habitat; however, we found rock size, type and orientation significantly influenced overall benthic assemblage composition, at least at one of the sites. Furthermore, the bottom of the rocks had a higher taxonomic diversity than the top side, and assemblages on native greywacke rocks were more diverse than those on granite, but only at one of the two sites. Overall, the magnitude of differences in benthic assemblage structure and diversity showed substantial temporal and spatial variation, with no clear temporal trends or successional patterns. Our results indicate that the ecological outcomes of coastal protection infrastructure upgrades could be improved by including native rocks of a range of different sizes in multiple patches and layers.

**KEY WORDS:** Coastal protection · Ecological engineering · Benthic · Coastal ecosystems · Habitat restoration · Boulder habitat

— Resale or republication not permitted without written consent of the publisher —

## 1. INTRODUCTION

Hard protection structures, such as seawalls and breakwaters, are one of the most frequently used adaption options to protect coastal areas from erosion and inundation (Nordstrom 2014). As a result, coastlines worldwide have been extensively armoured (Dugan et al. 2011), including over 50 % of Sydney Harbour in Australia (Chapman & Bulleri 2003), 10 to 40 % of shores in parts of the USA (Bilkovic & Mitchell 2013), over 80 % of Shanghai's coast (Wang et al.

2012) and approximately 3 % of the Chilean coast (Aguilera 2018). However, many coastal protection structures were constructed decades ago and are ageing, decayed or ineffective, necessitating their upgrading or rebuilding (Blacka et al. 2004). As opposed to frequently occurring minor maintenance interventions, upgrades usually include major rehabilitation or reshaping when a structure has lost its functionality (Colleter et al. 2011, Sherrard et al. 2016).

Similar to ecological impacts associated with existing and new protection structures (e.g. Chapman &

\*Corresponding author: lea.mamo@scu.edu.au

Bulleri 2003, Lam et al. 2009, Aguilera et al. 2014, Mayer-Pinto et al. 2018), major upgrades to such infrastructure can significantly alter benthic communities for years (Mamo et al. 2021). Such major upgrades act as a disturbance and, like maintenance and restoration measures, can attract opportunistic and invasive taxa and lead to a loss of habitat-forming species (Airoldi & Bulleri 2011, Suzuki et al. 2021). These ecological changes might affect the structure and function of species assemblages along urbanised coasts, with consequences for ecosystem services on which humans depend (Mayer-Pinto et al. 2018). As anthropogenic impacts increase, natural systems may no longer sustain these services without adequate mitigation. Consequently, coastal protection structure upgrades might perform better if they are implemented to be beneficial to natural ecosystems without compromising engineering standards (Naylor et al. 2017).

Ecological engineering techniques—the incorporation of ‘specific ecological design aspects into pieces of infrastructure to reduce environmental impacts’ (Perkins et al. 2015)—have been extensively studied in order to assess their ability to benefit ecological communities on existing infrastructure. Here, most attempts have focused on the manipulation of habitat structure (Strain et al. 2018), which is a critical driver for species diversity and abundance (Beck 2000, Kelaher 2003, Kovalenko et al. 2012). Indeed, the incorporation of complex and heterogenic biotopes can compensate potential negative impacts of construction works (Iannuzzi et al. 1996) and facilitate the development of rich and diverse marine flora and fauna (Firth et al. 2014, Ido & Shimrit 2015, Perkol-Finkel et al. 2018). However, while many eco-engineering techniques (e.g. complex tiles, rock pools, drilled holes) can be retrofitted to existing infrastructure (Margiotta et al. 2016, Bolton et al. 2018), this will mostly be practical in the intertidal (i.e. accessibility) and on relatively small scales to avoid compromising the integrity of the infrastructure. In contrast, simultaneous incorporation of eco-engineering during protective infrastructure upgrades enables the large-scale, real-world deployment of eco-engineered habitat in different zones (e.g. intertidal and subtidal), as well as cost reduction and enhanced resource management (Firth et al. 2014, Fredette et al. 2014).

Protection structure upgrades often involve the addition of berm to dissipate wave energy (Dengate et al. 2017), which creates the opportunity for alteration to serve as complex habitat, such as the use of different rock sizes. Unstable habitats made out of

small rocks, such as boulder, pebble or rubble patches, have been shown to support a large variety of additional species (Chapman 2002, Evans et al. 2018). These patches increase the surface area available for colonisation, provide sheltering crevices (Liversage et al. 2017), offer a broad array of illumination (Choi & Ginsburg 1983, Liversage 2016), and they roll about dislodging competitive dominant species (Sousa 1979, McGuinness 1987). Patches of boulders have been assessed for their suitability as a routine eco-engineering technique, with many showing that boulder fields can assist with the restoration of urbanised environments (Chapman 2012, 2013, Green et al. 2012). Notably, boulder material (Chase et al. 2016, Davis et al. 2017, Mos et al. 2019, Canessa et al. 2020b), shape (Liversage 2016), orientation (Chapman 2002, Hanlon et al. 2018) and origin (Aguilera et al. 2019) might affect species assemblages, highlighting the importance of assessing boulder choice for eco-engineering schemes.

A breakwater upgrade in Coffs Harbour, Australia was modified using eco-engineered boulder patches to mitigate impacts on a critically endangered seaweed, *Nereia lophocladia* (Main et al. 2016). A composite toe berm was the preferred upgrade design option; however, because *N. lophocladia* prefers habitat around the sand/rock interface, the small quarried rocks were added in between the large rocks to increase available habitat and scour while still maintaining engineering standards (~1% of total upgrade costs) (Mamo et al. 2018). Although the boulders look promising, *N. lophocladia* is yet to recruit to the eco-engineered habitats 3 yr after installation (Kelaher & Mamo 2020). However, ecological enhancements of coastal protection structures made for threatened species, such as *N. lophocladia*, can also create opportunities for other species, enhancing the diversity and abundance of flora and fauna. To evaluate how aspects of the ecological enhancements associated with upgrades to the Coffs Harbour breakwater influence benthic assemblage structure, we tested the hypotheses that assemblages would differ between (1) small and large rocks, (2) native greywacke and non-native granite boulders, and (3) the exposed (top) and sheltered (bottom) side of boulders. Here, we assume that species assemblage variability is an indicator of overall diversity, which can be an important driver of ecosystem function and resilience (Chapin et al. 1997). The outcomes of this study provide information that could be used to enhance the ecological outcomes of future upgrades of coastal breakwaters.

## 2. MATERIALS AND METHODS

### 2.1. Study area and design

The boulder fields for this study were established along the recently upgraded Coffs Harbour Northern Breakwater (NSW, Australia, 30 18.180° S, 153 8.807° E, Fig. 1). This breakwater was initially built in 1924 and is subject to considerable wave loading during large seas. Following damaging overtopping events, the breakwater was upgraded between 2016 and 2017 (Main et al. 2016). With the aim of improving the habitat available for diverse benthic assemblages, including the critically endangered alga *Nereia lophocladia*, the upgraded breakwater was built with a complex toe profile consisting of large, 5 to 8 t greywacke rocks (hereafter called 'large rocks'), as well as 2 areas with thick layers of small rocks comprised of small, 10 to 30 cm granite and greywacke boulders (hereafter called 'small rocks'; Fig. 1) (for more details see Mamo et al. 2018). Choice of rock types was based on greywacke being the dominant material from rocky reefs in the area (Smith & Simpson 1991) and granite being

one of the most commonly used building materials for coastal protection infrastructure (Davis et al. 2017). Greywacke and granite used in this study were quarried block-shaped rocks, characteristically hard and containing varying proportions of quartz, mica, feldspar and other minerals. However, they differ in their origin and colour, with greywacke being a brown to black sedimentary sandstone with a high clay content (Korsch 1981, Fergusson 1984), whereas granite is an igneous rock, which is light grey with dark sprinkles (Shaw & Flood 1981). The large rocks forming the composite toe were added along the entire breakwater. In contrast, the small rocks were deployed at 2 different sites that were approximately 400 m apart, filling in some voids between the large rocks (Kelaher 2017) (Fig. 1). The 'deep site' was approximately 4 to 7 m deep and the 'shallow site' was approximately 2 to 4 m deep (Kelaher 2017).

### 2.2. Data collection

To assess differences in benthic assemblages between rock sizes (large versus small), types (greywacke versus granite) and orientation (top versus bottom), photographic census on SCUBA was undertaken at each of the 2 sites along the breakwater at 5 times from August 2018 to October 2019. To minimise spatial bias, only large rocks amongst the boulder fields were sampled (see Fig. 1b). The first sampling took place 1 yr after the first small rocks were deployed to allow benthic assemblages to start developing and to ensure that large rocks had settled enough to be sampled safely by divers. At each site, underwater surveys were undertaken in a 2 m wide corridor from the sand/rock interface up the breakwater toe, using a digital camera (model Olympus TG-5, 16 megapixels).

#### 2.2.1. Rock size

To test the hypothesis that benthic assemblages differ between patches of small rocks and large rocks, benthic assemblages were sampled using randomly placed photo quadrats (50 × 50 cm) that were at least 50 cm apart to ensure independence. For large rocks, 60 quadrats were taken at the deep site and 45 at the shallow site, with the differences in sample size caused by surveys being aborted due to occasionally unsafe diving conditions. For small rocks, 60 photo quadrats were taken at each of the 2 boulder fields. To estimate the rugosity of the dif-

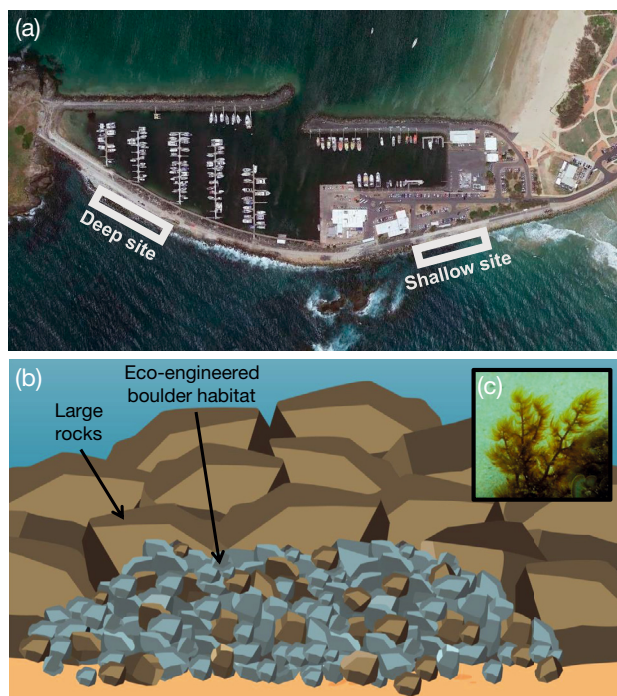


Fig. 1. (a) Location of study sites (white rectangles) along the breakwater, (b) the incorporated complex toe at each site, comprising 2 different rock sizes which include boulders (i.e. small rocks) made out of 2 rock types (i.e. greywacke and granite) and (c) the threatened alga *Nereia lophocladia* for which the eco-engineered habitat was used as a mitigation strategy. Map source: Google Earth

ferent size-patches, the 'chain-method' was used (Luckhurst & Luckhurst 1978). Here, a metal chain was laid across each 50 cm quadrat, following bottom topography, and a chain-tape index calculated.

### 2.2.2. Rock type and orientation

In each survey period and each boulder field, 2 different rock types (granite and greywacke) were sampled using 30 (15 small rocks, top and bottom) photo quadrats (10 × 10 cm) per rock type at each site. Here, each photo quadrat was of an individual small rock, and the individual rocks were at least 30 cm apart to ensure independence. The top of the rocks was defined as the side facing upwards, with the bottom being defined as the opposite side. To photograph the bottom, rocks were carefully turned upside down to prevent smothering or detachment of taxa and left in their initial state (i.e. facing up) after sampling was complete.

### 2.3. Photo analysis

The cover of benthic taxa was analysed using point-count methods in CoralNet (Beijbom et al. 2015). Each photo was cropped to the quadrat boundaries and, to account for any edge effects, 10 % of each side of the quadrat was excluded from analysis. Then, each photo was overlaid with 25 randomly generated points. The sum of points for each taxon was used to assess the total cover per photo. Taxa were identified to highest possible taxonomic resolution, with broader taxonomic groups being required for less conspicuous organisms (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m661p071\\_supp.pdf](http://www.int-res.com/articles/suppl/m661p071_supp.pdf) for list of taxa). It also has to be noted that dead and living structures could not be distinguished for sabellid worms; hence, these were grouped as 'sabellid worm tubes'.

### 2.4. Statistical analysis

To assess effects of rock size and type on benthic assemblages, non-parametric permutational analyses of variance (PERMANOVA, Anderson 2001) in PRIMER v. 7 + PERMANOVA add-on (PRIMER-e) were used. As preliminary analyses revealed significant differences between sites ( $p < 0.05$ ), likely due to depth differences, each site was analysed separately to avoid confounding. Analysis for the experi-

ment on rock size included 2 factors: Time of sampling ('Time', random, 5 levels) and rock size ('Size', fixed, 2 levels: small, large). Analysis for the experiment on rock type and top/bottom assemblages included 3 factors: Time of sampling ('Time', random, 5 levels), rock type ('Type', fixed, 2 levels: granite, greywacke) and orientation ('Orientation', fixed, 2 levels: top, bottom). Time was treated as a random factor to detect general patterns of temporal variability, rather than comparing single time points with each other. To account for the potential spatial dependence associated with the top and the bottom of individual boulders being sampled, the analysis was modified following the procedures for repeated measures PERMANOVA (i.e. excluding the highest-order interaction term; Anderson et al. 2008). As PERMANOVA can be sensitive to unbalanced designs with heteroscedasticity (Anderson & Walsh 2013), Type III sums of squares were chosen (Anderson et al. 2008) and tests of homogeneity of dispersions (PERMDISP; based on distance to centroids and 9999 permutations) were performed. If PERMDISP was significant, data were  $\log(x + 1)$  transformed to reduce heteroscedasticity and then re-tested. Significant PERMDISP results were carefully interpreted since effects may be a combination of average distance among centroids and dispersion (Anderson et al. 2008).

Multivariate analyses based on Bray-Curtis similarity matrices were used to compare dissimilarity of benthic assemblages among rock sizes and types. Data were fourth-root transformed to down-weight the influence of abundant taxa (Clarke & Green 1988). Differences between and within groups were visualised with metric multidimensional scaling (mMDS) plots. Taxa that corresponded most to the differences in benthic assemblages were identified using the similarity percentage (SIMPER) routine. Taxonomic richness (i.e. number of taxa) and diversity (calculated using the Shannon-Wiener index,  $H'$ ) of each photo were evaluated using the DIVERSE function. Univariate analyses, used to test hypotheses about differences in taxonomic richness and diversity among treatments, were based on Euclidean similarity matrices of untransformed data. Where tests indicated significant effects in PERMANOVA analyses, pairwise comparisons were used to test hypotheses where appropriate. To test the relationship between habitat rugosity (via chain length) and biological data, distance-based linear models (DistLM) with 9999 permutations were used (selection procedure: all specified; selection criterion:  $R^2$ ).

### 3. RESULTS

#### 3.1. Rock size

We found 24 taxa on large and small rocks along the breakwater, of which 3 algal taxa were unique to large rocks, and hydroids and gastropods were unique to small rocks (see Table S1 for taxa list). At each site, benthic assemblages differed significantly between large and small rocks, as well as among times of sampling (Table 1; see Fig. S1 in the Supplement for mMDS plot). While there was significant variation in benthic assemblages among times of sampling (Fig. 2), this could have been due to the combination of variation among centroids and dispersion (Table 1). Similar taxa contributed to the dissimi-

larly between rock sizes at each site. Small rocks were characterised by more bare substratum (contribution: 18.49% [deep site], 14.12% [shallow site]) and a higher cover of turf algae (13.18%, 16.70%) and crustose coralline algae ([CCA], 8.01%, 6.67%), whereas large rocks had a higher cover of *Sargassum* spp. (14.90%, 17.43%) and *Amphiroa anceps* (8.06%, 12.24%) (Table S2 in the Supplement).

The shallow and deep site showed similar taxonomic richness and diversity, with no significant differences between rock sizes (mean  $\pm$  SD diversity:  $0.90 \pm 0.37$  [large rocks],  $1.06 \pm 0.28$  [small rocks]). However, diversity varied significantly among times of sampling at the deep site, with September, March and July having significantly lower diversities than October (Table 1). At each site, rugosity (chain

Table 1. Results of PERMANOVA tests for comparison of (a) multivariate and (b) univariate measures of benthic community structure on small or large rocks ('Size') over time. Significant values ( $p < 0.05$ ) are given in **bold**. \*Significant PERMDISP results after log ( $x + 1$ ) transformation

		Deep site					Shallow site				
		df	SS	MS	Pseudo- <i>F</i>	<i>p</i>	df	SS	MS	Pseudo- <i>F</i>	<i>p</i>
<b>(a) Multivariate analysis</b>											
Assemblages	Time	4	12882.0	3220.5	5.639	<b>0.001*</b>	4	27656.0	6913.9	5.452	<b>0.001</b>
	Size	1	2311.6	2311.6	4.023	<b>0.033</b>	1	17226.0	17226.0	10.760	<b>0.016</b>
	Time $\times$ Size	4	2298.7	574.7	1.007	0.462	4	6554.9	1638.7	1.292	0.230
	Residuals	110	62829.0	571.2			95	120480.0	1268.2		
<b>(b) Univariate analysis</b>											
Species richness	Time	4	5.1	1.3	0.804	0.529	4	5.8	1.5	0.657	0.621
	Size	1	4.8	4.8	4.483	0.104	1	9.1	9.1	3.230	0.160
	Time $\times$ Size	4	4.3	1.1	0.682	0.598	4	11.5	2.9	1.295	0.275
	Residuals	110	172.7	1.6			95	210.4	2.2		
Species diversity	Time	4	1.0	0.3	2.494	<b>0.048</b>	4	1.0	0.3	1.517	0.203
	Size	1	0.7	0.7	6.892	0.067	1	1.1	1.1	6.949	0.068
	Time $\times$ Size	4	0.4	0.1	1.058	0.378	4	0.6	0.2	0.924	0.449
	Residuals	110	11.1	0.1			95	16.4	0.2		

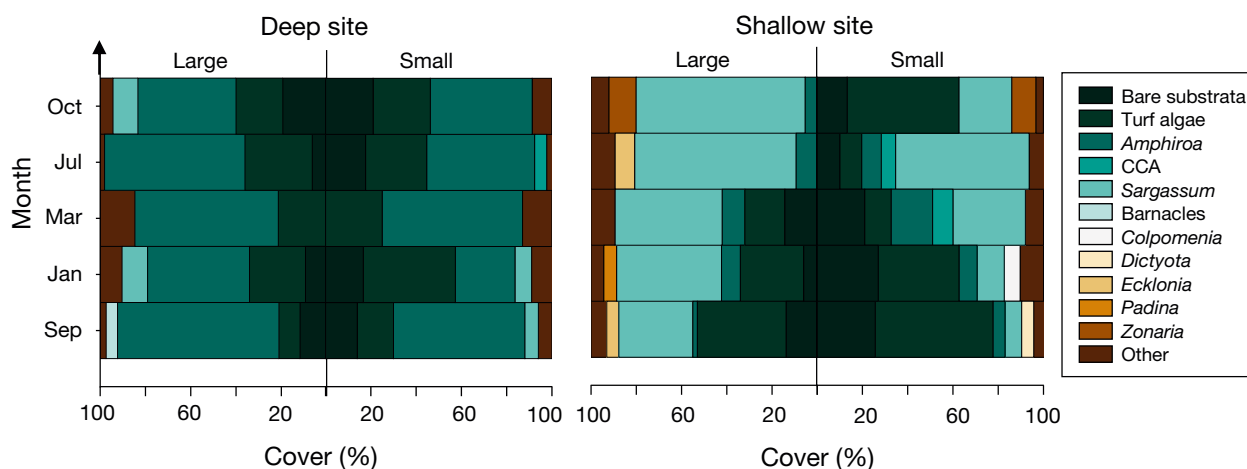


Fig. 2. Mean cover of benthic taxa on small and large rocks at the 2 sites over time. Taxa with a mean cover of  $<5\%$  are summed in 'Other'. CCA: crustose coralline algae. Full species names can be found in Table S1



length) differed significantly between small and large rocks ( $p < 0.001$  for both sites), with  $71.18 \pm 9.90$  (cumulative mean  $\pm$  SD) and  $57.39 \pm 4.37$  cm, respectively. Rugosity, however, only explained 2.24 and 4.85% of the total variation in assemblages at the deep and shallow site, respectively (DistLM,  $p < 0.05$  for both sites). Similarly, rugosity only explained <6% of the total variation of patterns in taxonomic richness and diversity at each site (DistLM,  $p < 0.05$  for both variables and sites).

### 3.2. Rock type and orientation

We found a total of 36 taxa on granite and greywacke rocks along the breakwater, of which 1 algal taxon was unique to granite and 3 algal taxa were unique to greywacke (Table S1). Furthermore, 5 algal taxa and erect sponges were unique to the top of the rocks, while 1 algal taxon, 2 mobile taxa (sea stars and gastropods), 2 sessile taxa (anemones and hard coral) and egg structures were unique to the bottom of the rocks (Table S1). At each site, benthic assemblages interacted between Time and Orientation (Table 2, see Fig. S2 in the Supplement for mMDS plot), with the top and bottom being different at each time of sur-

vey (see Table S3 in the Supplement for pairwise analysis). It must be noted that PERMDISP for the factor Time was significant (deep site:  $p < 0.001$ , shallow site:  $p = 0.02$ ) even after transformation. Generally, the top of rocks had a higher cover of *A. anceps* (contribution: 17.86% [deep site], 8.18% [shallow site]) and turf algae (12.63%, 22.08%), whereas the bottoms had more bare substrata (11.40%, 11.75%), sabellid worm tubes (15.82%, 15.07%), CCA (10.06%, 10.29%) and bryozoans (8.10%, 6.31%) (Fig. 3, Table S4 in the Supplement). At the deep boulder field, benthic assemblages differed significantly between granite and greywacke (Table 2), with the taxa contributing most to the difference being similar to those responsible for differences between top and bottom at each site. Here, granite rocks had a higher cover of *A. anceps* (contribution: 16.79%), sabellid worm tubes (12.53%) and CCA (10.92%), whereas greywacke rocks had a higher cover of bare substrata (12.60%) and bryozoans (7.55%).

Although there was significant variation in benthic assemblages among times of sampling, there were no clear temporal trends at the deep boulder field, with the top and bottom of rocks mostly covered in turf algae at the second time of sampling, whereas other taxa dominated in the rest of the surveys

Table 2. Results of PERMANOVA tests for comparison of (a) multivariate and (b) univariate measures of benthic community structure on the bottom or top ('Orientation') of greywacke or granite ('Type') boulders over time. Significant values ( $p < 0.05$ ) are given in **bold**. \*Significant PERMDISP results after log ( $x + 1$ ) transformation

		Deep site					Shallow site				
		df	SS	MS	Pseudo- <i>F</i>	<i>p</i>	df	SS	MS	Pseudo- <i>F</i>	<i>p</i>
<b>(a) Multivariate analysis</b>											
Assemblages	Time (Ti)	4	103680.0	25920.0	32.930	<b>0.001*</b>	4	83382.0	20846.0	27.072	<b>0.001*</b>
	Type (Tp)	1	4658.5	4658.5	14.795	<b>0.019</b>	1	1032.9	1032.9	0.864	0.512
	Orientation (Or)	1	93775.0	93775.0	26.360	<b>0.008</b>	1	84484.0	84484.0	9.502	<b>0.009</b>
	Ti $\times$ Tp	4	1259.2	314.8	0.400	0.945	4	4780.9	1195.2	1.552	0.078
	Ti $\times$ Or	4	14231.0	3557.9	4.520	<b>0.001</b>	4	35564.0	8890.9	11.547	<b>0.001</b>
	Tp $\times$ Or	1	1376.0	1376.0	1.748	0.163	1	1164.4	1164.4	1.512	0.208
	Residuals	282	221960.0	787.1			284	218680.0	770.0		
<b>(b) Univariate analysis</b>											
Species richness	Time (Ti)	4	275.8	69.0	38.955	<b>0.001</b>	4	233.9	58.5	37.275	<b>0.001</b>
	Type (Tp)	1	2.7	2.7	1.780	0.305	1	1.1	1.1	0.922	0.370
	Orientation (Or)	1	171.0	171.0	24.130	<b>0.011</b>	1	12.8	12.8	0.853	0.371
	Ti $\times$ Tp	4	6.1	1.5	0.862	0.484	4	4.7	1.2	0.748	0.562
	Ti $\times$ Or	4	28.3	7.1	4.004	<b>0.004</b>	4	60.1	15.0	9.575	<b>0.001</b>
	Tp $\times$ Or	1	0.7	0.7	0.405	0.526	1	0.2	0.2	0.136	0.713
	Residuals	282	499.2	1.8			284	445.6	1.6		
Species diversity	Time (Ti)	4	21.5	5.4	42.629	<b>0.001</b>	4	21.5	5.4	48.061	<b>0.001*</b>
	Type (Tp)	1	0.2	0.2	9.745	<b>0.044</b>	1	0.4	0.4	2.734	0.172
	Orientation (Or)	1	11.3	11.3	44.892	<b>0.007</b>	1	0.5	0.5	0.253	0.650
	Ti $\times$ Tp	4	0.1	0.0	0.146	0.965	4	0.5	0.1	1.192	0.316
	Ti $\times$ Or	4	1.0	0.3	1.990	0.100	4	8.6	2.2	19.254	<b>0.001</b>
	Tp $\times$ Or	1	0.2	0.2	1.270	0.259	1	0.0	0.0	0.348	0.560
	Residuals	282	35.6	0.1			284	31.8	0.1		

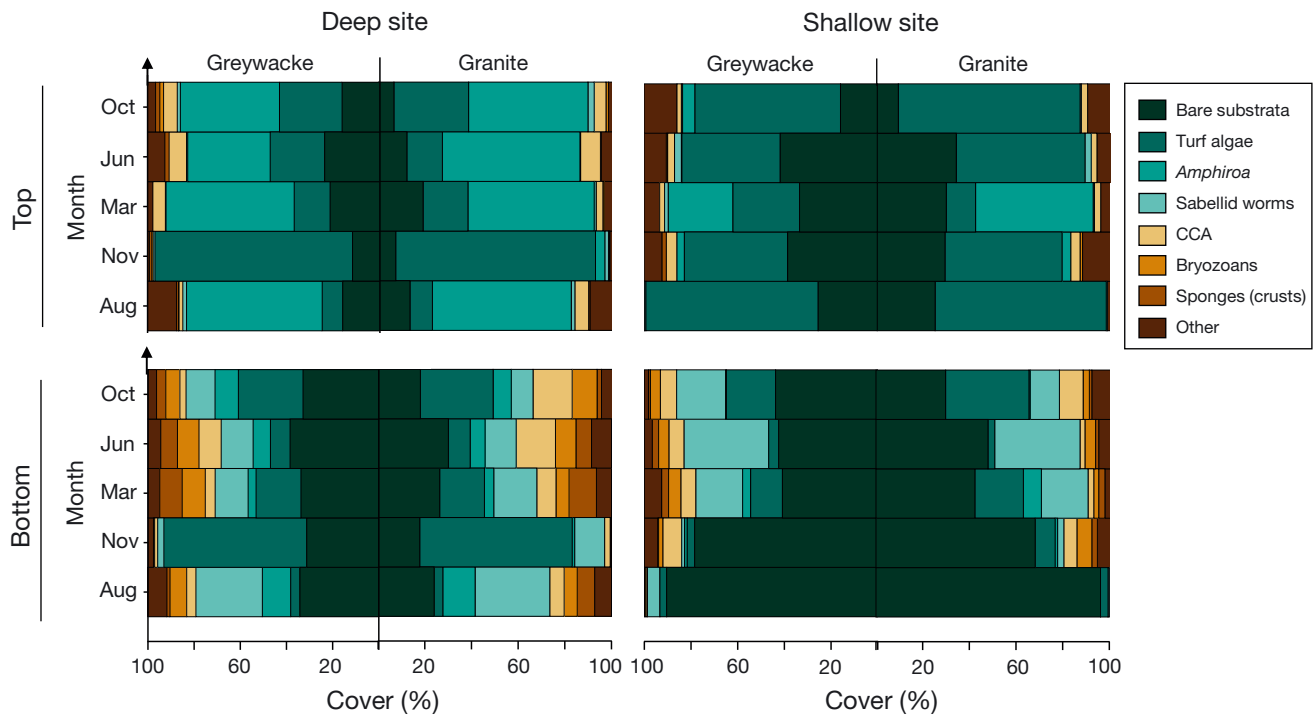


Fig. 3. Mean cover of benthic taxa on the top or bottom of small greywacke and granite rocks at the 2 sites over time. Taxa with a mean cover of <5% are summed in 'Other'. CCA: crustose coralline algae

(Fig. 3). In contrast, there was a decrease in bare substrata and an increase in CCA and invertebrates, such as sabellid worm tubes, bryozoans and encrusting sponges at the shallow boulder field over time (Fig. 3).

Similar to the benthic assemblage structure, taxonomic richness at each site and diversity at the shallow site showed a significant Time  $\times$  Orientation

interaction, and rock type had a significant influence on taxa diversity at the deep site (Table 2). In general, the bottom of the rocks had higher taxonomic richness and diversity than the top of rocks (Fig. 4). At the deep boulder field, diversity on the top and bottom decreased significantly at the second time of sampling and then increased again to a stable maximum after the third sampling time (Fig. 4). At the

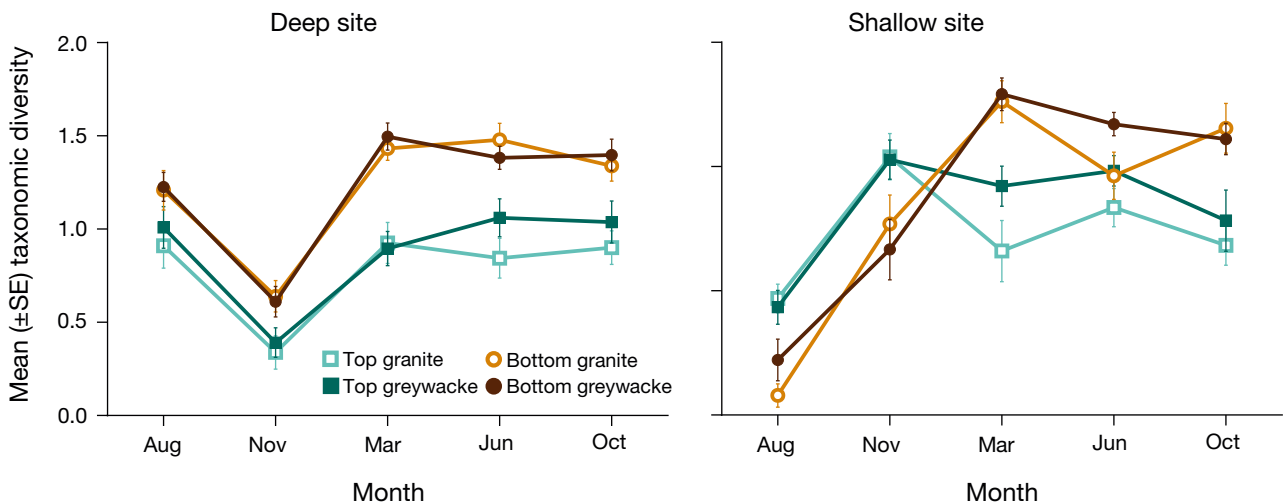


Fig. 4. Taxonomic diversity on the top or bottom of granite or greywacke boulders at the 2 sites over time. Calculations based on the Shannon-Wiener index

shallow boulder field, diversity started lower than at the deep boulder field and then increased to a stable maximum (Fig. 4).

#### 4. DISCUSSION

Our study showed that the composition and diversity of benthic taxa could, depending on the site, be influenced by rock size, type and/or orientation when boulder fields were used to improve the ecological outcomes of a breakwater upgrade. Generally, there was considerable temporal and spatial variation in assemblage structure on boulders, mostly due to differences in the cover of common taxa from boulder to boulder. This suggests that there are biodiversity benefits of installing boulder fields at the toes of breakwaters during structural upgrades. Understanding the value of these benefits to eco-engineered breakwaters in a broader ecological sense can help tailor mitigation strategies that achieve a prescribed conservation outcome, such as an increase in local biodiversity, an increase in fish important for recreational fishing, or the conservation of a threatened species.

The recruitment and establishment of benthic assemblages on the rocks were highly variable in time and within treatments, such that discerning underlying mechanisms and clear patterns is challenging (Hanlon et al. 2018). It could be argued that the taxonomic resolution used in our study may have limited the capacity to demonstrate clear patterns, as several taxa were grouped into broad groups due to the nature of the sampling technique (i.e. non-destructive photographic census) and associated taxonomic uncertainties. However, the majority of taxa observed were comprised of macroalgae, of which most were identified to species, suggesting that for this important group, species-level taxonomic resolution did not enhance the observation of clear patterns. While destructive sampling techniques would have allowed greater taxonomic certainty, we contend that our results, in combination with past studies (e.g. Chapman 2012, Green et al. 2012), provide a reasonable basis for evidence-based eco-engineering schemes involving boulders. However, future studies should consider including various scales of complexity, as well as an extended monitoring period (e.g. 5 yr) to establish temporal patterns of colonisation, which can help evaluate the right timing for rock deployments to prevent dominance of certain (e.g. invasive) taxa (Fletcher et al. 2018) and minimise recovery time (Airoldi & Bulleri 2011).

##### 4.1. Rock size

Rock size significantly influenced the structure of benthic assemblages, with more bare space, turf and CCA on patches of small rocks and more *Sargassum* spp. and *Amphiroa anceps* on large rocks. Different assemblage patterns between rock sizes might be due to the exposed orientation of the breakwater and the associated currents and wave loading. Small rocks can be more susceptible to disturbance through water movements because the frequency of overturning and movement-caused abrasion is inversely proportional to rock size (Davis & Wilce 1987, McGuinness 1987). Moreover, even stationary boulders can be indirectly subjected to disturbance if they are in close vicinity of moving boulders (Sousa 1979). Frequent disturbance events could constrain the time available for small rocks to develop mature communities dominated by slow-growing, large taxa, while more resilient taxa such as CCA can withstand these forces (Davis & Wilce 1987). Furthermore, disturbance creates new bare space, which can be quickly colonised by opportunistic taxa, such as tube-forming polychaetes (e.g. sabellid worms) and turf algae (Lieberman et al. 1979). Given enough time, these can then be partly replaced by more competitive and slow-growing taxa, creating successional sequences where different taxa can co-exist, eventually leading to highly diverse assemblages (described as the ‘intermediate disturbance hypothesis’, Connell 1978). However, in the present study, taxonomic diversity did not differ significantly between large and small rocks, whose disturbance frequencies likely differed (Davis & Wilce 1987, McGuinness 1987). Nevertheless, while temporal patterns of succession were not apparent at the deep site, both the large and small rocks at the shallow site showed an increase in canopy-forming *Sargassum* spp. over time, but, in Survey 5 (October 2019), turf algae had only increased significantly on the small rocks. This suggests that assemblage patterns could be driven by factors specific to rock size (e.g. disturbance frequency) but the influence of large-scale drivers, such as season, cannot be excluded, considering that some taxa (e.g. *Padina crassa*) showed similar cover patterns on small and large rocks.

Overall, there was high variability within treatments, and this seems common in boulder fields, as every rock is a discrete patch of habitat that is separated from others (e.g. Chapman 2002, Green et al. 2012). High within-treatment variability among benthic assemblages on boulders might also be the reason why significant differences in rugosity only explained



a small portion of the differences in assemblages. A high degree of habitat complexity, such as the presence of interstices and rough surfaces has been shown to enhance diversity (Loke et al. 2017, Hanlon et al. 2018). Thick layers of small rocky structures, such as in our study, can create shaded interstices, which can support a diverse community by providing favourable environmental conditions and shelter (Choi & Ginsburg 1983, Takada 1999, Liversage et al. 2017). However, large rocks had higher cover in canopy-forming seaweeds such as *Ecklonia radiata* and *Sargassum* spp., and big fish were often observed between large interstices, highlighting that rocks of varying sizes can attract diverse biota. This might be especially important for recreationally targeted fish and crustaceans, as breakwaters and adjacent natural reefs can be subject to considerable fishing pressure (Provost et al. 2020). Although not captured in our rugosity measure, additional habitat complexity was possibly provided by the mats of coralline algae (e.g. *A. anceps*) and *Sargassum* spp. These prevalent mat-forming organisms support diverse macrofaunal species (Kelaher 2005, Kelaher et al. 2007) and varied in cover between small and large boulders.

#### 4.2. Rock type and orientation

When upgrading breakwaters by adding boulders and larger rocks, we show that using a thick layer of small rocks can also create differently oriented habitats (i.e. top and bottom). Benthic assemblages, richness and diversity differed between the top and bottom of boulders, with more *A. anceps* and turf algae on the top and more bare space, sabellid worm tubes, CCA and bryozoans on the bottom of rocks. Unstable rocky habitats such as boulder fields with small rocks can be occupied almost entirely, because, as opposed to large rocks, they are not heavy enough to smother taxa living on the bottom (Davis & Wilce 1987). Nevertheless, we found more bare space on the bottom of boulders relative to the top, suggesting that free space takes longer to become occupied in an environment where continuous abrasive forces among rocks or between rocks and soft sediment disturb organisms (McGuinness 1987). This was most apparent at the shallow site, where the bottom of rocks was mostly bare at the beginning of the study and slowly became covered in taxa towards the end. Other temporal trends in assemblage development were generally lacking; however, the second survey at the deep site showed a significantly higher cover of turf algae and a drop in taxonomic diversity compared to other sampling times.

This could be due to seasonal effects, as the transition to Austral summer occurs in November. The absence of similar patterns at the shallow site suggests that site-specific drivers could have been at play, such as hydrodynamic or sedimentation processes.

The variation in microhabitats offered by small rocks is probably shaped through differences in exposure to biological and physical forces, and contact with other small rocks (Liversage 2016). The top side might be subjected to higher levels of water flow, illumination and higher temperatures, whereas the bottom is darker and might offer protection from currents and larger predators, such as fish (Takada 1999, Aguilera et al. 2019). Furthermore, the reduced light availability on the bottom of rocks decreases the competitive dominance of macroalgae, leaving more space for other taxa, such as anemones and hard coral, which were solely found underneath boulders. The top side of the rocks was dominated by a few taxa (*A. anceps* at the deep boulder field and turf algae at the shallow boulder field), whereas the dominance of single taxa was less pronounced on the bottom side. This was reflected in the species diversity and richness, which was generally higher on the bottom of rocks (as shown by McGuinness 1984) and included several sessile, low-growing taxa, such as sabellid worm tubes, bryozoans, encrusting sponges and barnacles. While bryozoans and sabellid worms have been shown to readily colonise underneath boulders (Chapman 2012), accurate population size estimates are challenging as some of the calcareous structures are post-mortem remnants, which tend to be less rapidly removed than on the exposed side of the boulders (Liversage et al. 2020). However, in many situations, dead structures can serve a similar ecological function to their living counterparts (Liversage 2020).

Similar to habitat orientation, rock type significantly influenced assemblages and diversity, but only at one of the sites. However, temporal trends did not differ between greywacke or granite, providing limited evidence that succession varies between rock types (Liversage et al. 2014). At the deep site, greywacke had a higher diversity and, overall, more taxa were unique to greywacke rocks than to granite. The influence of the rock type on patterns of colonisation can vary from species to species (Green et al. 2012, Liversage & Benkendorff 2013, Liversage et al. 2014) and can be driven by rock properties such as porosity, colour, chemical composition and heat retention (Liversage & Benkendorff 2013, Aguilera et al. 2019). Granite and greywacke differ in their origin (igneous versus sedimentary, respectively) and colour (light grey versus dark brown, respectively), possibly lead-

ing to differences in physical (e.g. thermal) properties that could affect larval settling (Bavestrello et al. 2018, Aguilera et al. 2019). Species-specific colonisation can, in turn, attract other settlers when certain taxa (e.g. algal crusts) act as secondary substrata and mask the influence of the primary substratum (i.e. bare rock) (Davis 2009, Canessa et al. 2020a). When deploying boulder fields, we suggest that the rocks mimic the naturally occurring rock in the particular area (here: greywacke) or, at least, be mineralogically similar and recycled rather than quarried or extracted from natural boulder fields to reduce the ecological footprint (Dahl et al. 2016).

## 5. CONCLUSION

Rising sea levels, increasing storm frequency and ageing coastal protection infrastructure will necessitate the upgrades of coastal breakwaters around the world, with possibly pervasive impacts on ecosystems (Mamo et al. 2021). While various eco-engineering techniques (e.g. complex tiles, rock pools) have been shown to enhance biodiversity when retrofitted to existing protective infrastructure (Strain et al. 2018), our results suggest that boulder fields located at the toe of a breakwater may be a useful and practical way of ecologically enhancing breakwaters during the upgrade process. Small rocks have been previously shown to be readily colonised by taxa from adjacent habitats (i.e. existing artificial and natural reefs), minimising the need for seeding or pre-conditioning (Chapman 2012, 2013). Furthermore, incorporation of eco-engineered habitat during major construction works is advantageous because it can be done on a larger scale and included in the design without risking the integrity of the infrastructure. Multiple disturbances can be avoided and costs can be reduced by utilising already present machinery, resources and expertise (Firth et al. 2014). Notably, upgrades often involve the addition of a rock berm (Burcharth et al. 2014, Dengate et al. 2017), which could be easily altered by adding varying rock sizes that support diverse assemblages different from those on the standard berm made out of large rocks. Increasing biodiversity can enhance ecosystem function and services, as well as resilience, which is especially important in a changing climate (Chapin et al. 1997). Using patches of smaller rock is not only promising in terms of ecological enhancement but also is straightforward in terms of deployment and can also contribute to further dissipation of wave energy (Komar & Allan 2010). Notably, the fact that the boulder patches

were intact at least 3 yr post deployment (Kelaher & Mamo 2020) suggests that this size boulder (i.e. 10 to 30 cm in diameter) is sufficient for medium-exposed structures. However, future studies assessing the interplay of exposure, depth, rock size and patch thickness on boulder movement could benefit the effective deployment of boulders in the future (Støttrup et al. 2017).

**Acknowledgements.** We thank S. Pryor, E. Provost, A. Tagliafico, B. Edgar, I. Shaw, D. Tardieu and S. Tschijevski for their support in the field and lab, as well as Southern Cross University for the supply of vessels and vehicles. We also thank the 3 anonymous reviewers who invested significant time and effort into improving the manuscript. This work was funded by the Postgraduate Student Grant from the School of Environment, Science and Engineering, Southern Cross University.

## LITERATURE CITED

- ✦ Aguilera MA (2018) Artificial defences in coastal marine ecosystems in Chile: opportunities for spatial planning to mitigate habitat loss and alteration of the marine community structure. *Ecol Eng* 120:601–610
- ✦ Aguilera MA, Broitman BR, Thiel M (2014) Spatial variability in community composition on a granite breakwater versus natural rocky shores: lack of microhabitats suppresses intertidal biodiversity. *Mar Pollut Bull* 87: 257–268
- ✦ Aguilera MA, Arias RM, Manzur T (2019) Mapping microhabitat thermal patterns in artificial breakwaters: alteration of intertidal biodiversity by higher rock temperature. *Ecol Evol* 9:12915–12927
- ✦ Airolidi L, Bulleri F (2011) Anthropogenic disturbance can determine the magnitude of opportunistic species responses on marine urban infrastructures. *PLOS ONE* 6: e22985
- Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecol* 26:32–46
- ✦ Anderson MJ, Walsh DCI (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? *Ecol Monogr* 83:557–574
- Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: Guide to software and statistical methods. PRIMER-e, Plymouth
- ✦ Bavestrello G, Bo M, Betti F, Canessa M, Gaggero L, Rindi F, Cattaneo-Vietti R (2018) Differences in composition of shallow-water marine benthic communities associated with two ophiolitic rock substrata. *Estuar Coast Shelf Sci* 200:71–80
- ✦ Beck MW (2000) Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. *J Exp Mar Biol Ecol* 249:29–49
- ✦ Beijbom O, Edmunds PJ, Roelfsema C, Smith J and others (2015) Towards automated annotation of benthic survey images: variability of human experts and operational modes of automation. *PLOS ONE* 10:e0130312
- ✦ Bilkovic DM, Mitchell MM (2013) Ecological tradeoffs of stabilized salt marshes as a shoreline protection strategy: effects of artificial structures on macrobenthic assemblages. *Ecol Eng* 61:469–481

- Blacka M, Carley J, Cox R (2004) Management and remedial options for historical seawalls. NSW Coastal Conference 2004, 13th Annual Coastal Conference, 9th to 12th November 2004, Lake Macquarie, NSW, p 204–210
- ✦ Bolton DK, Johnston EL, Coleman MA, Clark GF (2018) Caught between a rock and a hard place: fish predation interacts with crevice width and orientation to explain sessile assemblage structure. *Mar Environ Res* 140:31–40
- ✦ Burcharth HF, Lykke Andersen T, Lara JL (2014) Upgrade of coastal defence structures against increased loadings caused by climate change: a first methodological approach. *Coast Eng* 87:112–121
- ✦ Canessa M, Bavestrello G, Bo M, Trainito E and others (2020a) Coralligenous assemblages differ between limestone and granite: A case study at the Tavolara-Punta Coda Cavallo Marine Protected Area (NE Sardinia, Mediterranean Sea). *Reg Stud Mar Sci* 35:101159
- ✦ Canessa M, Bavestrello G, Trainito E, Navone A, Cattaneo-Vietti R (2020b) Lithology could affect benthic communities living below boulders. *J Mar Biol Assoc UK* 100:879–888
- ✦ Chapin FS III, Walker BH, Hobbs RJ, Hooper DU, Lawton JH, Sala OE, Tilman D (1997) Biotic control over the functioning of ecosystems. *Science* 277:500–504
- ✦ Chapman MG (2002) Patterns of spatial and temporal variation of macrofauna under boulders in a sheltered boulder field. *Austral Ecol* 27:211–228
- ✦ Chapman MG (2012) Restoring intertidal boulder-fields as habitat for 'specialist' and 'generalist' animals. *Restor Ecol* 20:277–285
- ✦ Chapman MG (2013) Constructing replacement habitat for specialist and generalist molluscs—the effect of patch size. *Mar Ecol Prog Ser* 473:201–214
- ✦ Chapman MG, Bulleri F (2003) Intertidal seawalls—new features of landscape in intertidal environments. *Landsc Urban Plan* 62:159–172
- ✦ Chase AL, Dijkstra JA, Harris LG (2016) The influence of substrate material on ascidian larval settlement. *Mar Pollut Bull* 106:35–42
- ✦ Choi DR, Ginsburg RN (1983) Distribution of coelobites (cavity-dwellers) in coral rubble across the Florida Reef Tract. *Coral Reefs* 2:165–172
- ✦ Clarke KR, Green RH (1988) Statistical design and analysis for a 'biological effects' study. *Mar Ecol Prog Ser* 46:213–226
- ✦ Colleter G, van Staden A, Blacka M, Louys J (2011) Mackay breakwater adaptability. Proc 20th Australasian Coastal and Ocean Engineering Conf and 13th Australasian Port and Harbour Conf, Coasts and Ports 2011: Diverse and Developing, 28th to 30th September 2011, Perth. Engineers Australia, Barton, Canberra, p 451–457
- ✦ Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- ✦ Dahl K, Støttrup JG, Stenberg C, Berggreen UC, Jensen JH (2016) Best practice for restoration of stone reefs in Denmark (codes of conduct). Technical Report from DCE—Danish Centre for Environment and Energy, No. 91, DCE, Aarhus University
- ✦ Davis A (2009) The role of mineral, living and artificial substrata in the development of subtidal assemblages. In: Wahl M (ed) *Marine hard bottom communities*. Springer-Verlag, Berlin, p 19–37
- ✦ Davis AN, Wilce RT (1987) Algal diversity in relation to physical disturbance: a mosaic of successional stages in a subtidal cobble habitat. *Mar Ecol Prog Ser* 37:229–237
- ✦ Davis KL, Coleman MA, Connell SD, Russell BD, Gillanders BM, Kelaher BP (2017) Ecological performance of construction materials subject to ocean climate change. *Mar Environ Res* 131:177–182
- ✦ Dengate C, Main R, Hartley A, Dwyer P (2017) Coffs Harbour Northern Breakwater upgrade—balancing technical and environmental outcomes. Proc 23rd Australasian Coastal and Ocean Engineering Conf and 16th Australasian Port and Harbour Conf, Coasts & Ports 2017: Working with Nature, 21st to 23rd June 2017, Cairns. Engineers Australia, Barton, Canberra, p 365–370
- ✦ Dugan JE, Airolidi L, Chapman MG, Walker S, Schlacher T (2011) Estuarine and coastal structures: environmental effects, a focus on shore and nearshore structures. In: Wolanski E, McLusky D (eds) *Treatise on estuarine and coastal science*, Vol 8. Academic Press, Waltham
- ✦ Evans J, Attrill MJ, Borg JA, Cotton PA, Schembri PJ (2018) Hidden in plain sight: species richness and habitat characterisation of sublittoral pebble beds. *Mar Biol* 165:35
- ✦ Fergusson CL (1984) Tectono-stratigraphy of a Palaeozoic subduction complex in the central Coffs Harbour Block of north-eastern New South Wales. *Aust J Earth Sci* 31: 217–236
- ✦ Firth LB, Thompson RC, Bohn K, Abbiati M and others (2014) Between a rock and a hard place: environmental and engineering considerations when designing coastal defence structures. *Coast Eng* 87:122–135
- ✦ Fletcher LM, Atalah J, Forrest BM (2018) Effect of substrate deployment timing and reproductive strategy on patterns in invasiveness of the colonial ascidian *Didemnum vexillum*. *Mar Environ Res* 141:109–118
- ✦ Fredette TJ, Suedel B, Banks CJ, Ruby RJ, Bijhouwer P, Friona AM (2014) Epifaunal community development on Great Lakes breakwaters: an Engineering With Nature demonstration project. Engineering with Nature ERDC TN-EWN-14-2, US Army Engineer Research and Development Center, Vicksburg, MS
- ✦ Green DS, Chapman MG, Blockley DJ (2012) Ecological consequences of the type of rock used in the construction of artificial boulder-fields. *Ecol Eng* 46:1–10
- ✦ Hanlon N, Firth LB, Knights AM (2018) Time-dependent effects of orientation, heterogeneity and composition determines benthic biological community recruitment patterns on subtidal artificial structures. *Ecol Eng* 122:219–228
- ✦ Iannuzzi TJ, Weinstein MP, Sellner KG, Barrett JC (1996) Habitat disturbance and marina development: an assessment of ecological effects. I. Changes in primary production due to dredging and marina construction. *Estuar Coasts* 19:257–271
- ✦ Ido S, Shimrit PF (2015) Blue is the new green—Ecological enhancement of concrete based coastal and marine infrastructure. *Ecol Eng* 84:260–272
- ✦ Kelaher BP (2003) Effects of frond length on diverse gastropod assemblages in coralline turf. *J Mar Biol Assoc UK* 83:159–163
- ✦ Kelaher BP (2005) Does colonization contribute to spatial patterns of common invertebrates in coralline algal turf? *Austral Ecol* 30:40–48
- ✦ Kelaher B (2017) Cobble scree deployment trials for the Coffs Harbour Northern Breakwater. Prepared for NSW Department of Industry Crown Lands and Water
- ✦ Kelaher B, Mamo LT (2020) Third post-upgrade survey for the critically endangered marine brown alga *Nereia lophocladia* on and near the Coffs Harbour Northern Breakwater. Prepared for NSW Department of Planning, Industry and Environment

- Kelagher B, Castilla J, Prado L (2007) Is there redundancy in bioengineering for molluscan assemblages on the rocky shores of central Chile? *Rev Chil Hist Nat* 80:173–186
- Komar PD, Allan JC (2010) 'Design with Nature' strategies for shore protection—the construction of a cobble berm and artificial dune in an Oregon State Park. In: Shipman H, Dethier MN, Gelfenbaum G, Fresh KL, Dinicola RS (eds) Puget sound shorelines and the impacts of armoring—Proceedings of a State of the Science Workshop, May 2009, US Geological Survey Scientific Investigations Report 2010-5254, p 117–126
- ✦ Korsch RJ (1981) Some tectonic implications of sandstone petrofacies in the Coffs Harbour Association, New England Orogen, New South Wales. *J Geol Soc Aust* 28:261–269
- ✦ Kovalenko KE, Thomaz SM, Warfe DM (2012) Habitat complexity: approaches and future directions. *Hydrobiologia* 685:1–17
- Lam NW, Huang R, Chan BK (2009) Variations in intertidal assemblages and zonation patterns between vertical artificial seawalls and natural rocky shores: a case study from Victoria Harbour, Hong Kong. *Zool Stud* 48:184–195
- ✦ Lieberman M, John DM, Lieberman D (1979) Ecology of subtidal algae on seasonally devastated cobble substrates off Ghana. *Ecology* 60:1151–1161
- ✦ Liversage K (2016) The influence of boulder shape on the spatial distribution of crustose coralline algae (Corallinales, Rhodophyta). *Mar Ecol* 37:459–462
- ✦ Liversage K (2020) An example of multi-habitat restoration: conceptual assessment of benefits from merging shellfish-reef and boulder-reef restorations. *Ecol Eng* 143: 105659
- ✦ Liversage K, Benkendorff K (2013) A preliminary investigation of diversity, abundance, and distributional patterns of chitons in intertidal boulder fields of differing rock type in South Australia. *Molluscan Res* 33:24–33
- ✦ Liversage K, Janetzki N, Benkendorff K (2014) Associations of benthic fauna with different rock types, and evidence of changing effects during succession. *Mar Ecol Prog Ser* 505:131–143
- ✦ Liversage K, Cole V, Coleman R, McQuaid C (2017) Availability of microhabitats explains a widespread pattern and informs theory on ecological engineering of boulder reefs. *J Exp Mar Biol Ecol* 489:36–42
- ✦ Liversage K, Kotta J, Fraser CML, Figueira WF, Coleman RA (2020) The overlooked role of taphonomy in ecology: post-mortem processes can outweigh recruitment effects on community functions. *Oikos* 129:420–432
- ✦ Loke LHL, Bouma TJ, Todd PA (2017) The effects of manipulating microhabitat size and variability on tropical seawall biodiversity: field and flume experiments. *J Exp Mar Biol Ecol* 492:113–120
- ✦ Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Mar Biol* 49:317–323
- Main R, Hartley A, Dengate C, Rowe E, Blacka M (2016) Coffs Harbour Northern Breakwater—not your average upgrade. *Proc 25th NSW Coastal Conference 2016*, 9th to 11th November 2016, Coffs Harbour, p 1–17
- ✦ Mamo LT, Kelagher BP, Coleman MA, Dwyer PG (2018) Protecting threatened species from coastal infrastructure upgrades: the importance of evidence-based conservation. *Ocean Coast Manage* 165:161–166
- Mamo LT, Porter AG, Tagliafico A, Coleman MA, Smith SDA, Figueira WF, Kelagher BP (2021) Upgrades of coastal protective infrastructure affect benthic communities. *J Appl Ecol* 58:295–303
- ✦ Margiotta AM, Shervette VR, Hadley NH, Plante CJ, Wilber DH (2016) Species-specific responses of resident crabs to vertical habitat complexity on intertidal oyster reefs. *J Exp Mar Biol Ecol* 477:7–13
- ✦ Mayer-Pinto M, Cole V, Johnston E, Bugnot A and others (2018) Functional and structural responses to marine urbanisation. *Environ Res Lett* 13:014009
- ✦ McGuinness KA (1984) Species-area relations of communities on intertidal boulders: testing the null hypothesis. *J Biogeogr* 11:439–456
- ✦ McGuinness KA (1987) Disturbance and organisms on boulders: I. Patterns in the environment and the community. *Oecologia* 71:409–419
- ✦ Mos B, Dworjanyn SA, Mamo LT, Kelagher BP (2019) Building global change resilience: Concrete has the potential to ameliorate the negative effects of climate-driven ocean change on a newly-settled calcifying invertebrate. *Sci Total Environ* 646:1349–1358
- ✦ Naylor LA, MacArthur M, Hampshire S, Bostock K and others (2017) Rock armour for birds and their prey: ecological enhancement of coastal engineering. *Proc Inst Civ Eng Marit Eng* 170:67–82
- ✦ Nordstrom KF (2014) Living with shore protection structures: a review. *Estuar Coast Shelf Sci* 150:11–23
- ✦ Perkins MJ, Ng TPT, Dudgeon D, Bonebrake TC, Leung KMY (2015) Conserving intertidal habitats: what is the potential of ecological engineering to mitigate impacts of coastal structures? *Estuar Coast Shelf Sci* 167:504–515
- ✦ Perkol-Finkel S, Hadary T, Rella A, Shirazi R, Sella I (2018) Seascape architecture—incorporating ecological considerations in design of coastal and marine infrastructure. *Ecol Eng* 120:645–654
- Provost EJ, Butcher PA, Coleman MA, Kelagher BP (2020) Assessing the viability of small aerial drones to quantify recreational fishers. *Fish Manag Ecol* 27:615–621
- ✦ Shaw SE, Flood RH (1981) The New England Batholith, eastern Australia: geochemical variations in time and space. *J Geophys Res Solid Earth* 86:10530–10544
- ✦ Sherrard TRW, Hawkins SJ, Barfield P, Kitou M, Bray S, Osborne PE (2016) Hidden biodiversity in cryptic habitats provided by porous coastal defence structures. *Coast Eng* 118:12–20
- Smith SDA, Simpson RD (1991) Nearshore corals of the Coffs Harbour region, mid north coast, New South Wales. *Wetlands Aust* 11:1–9
- ✦ Sousa W (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* 60:1225–1239
- ✦ Støttrup JG, Dahl K, Niemann S, Stenberg C and others (2017) Restoration of a boulder reef in temperate waters: strategy, methodology and lessons learnt. *Ecol Eng* 102:468–482
- ✦ Strain EMA, Olabarria C, Mayer-Pinto M, Cumbo V and others (2018) Eco-engineering urban infrastructure for marine and coastal biodiversity: which interventions have the greatest ecological benefit? *J Appl Ecol* 55:426–441
- ✦ Suzuki H, Aoki T, Inomata E, Agatsuma Y, Aoki MN (2021) Effect of breakwater restoration work following the subsidence caused by the 2011 Tohoku Earthquake on the subtidal kelp population. *Phycol Res* 69:3–11
- ✦ Takada Y (1999) Influence of shade and number of boulder layers on mobile organisms on a warm temperate boulder shore. *Mar Ecol Prog Ser* 189:171–179
- ✦ Wang J, Gao W, Xu S, Yu L (2012) Evaluation of the combined risk of sea level rise, land subsidence, and storm surges on the coastal areas of Shanghai, China. *Clim Change* 115:537–558