

Impacts of coastal armouring on rubble mobile cryptofauna at shallow coral reefs in Okinawa, Japan

GIOVANNI D MASUCCI^{1,2,†,*}, PIERA BIONDI^{1,2} & JAMES D REIMER^{1,3}

¹*Molecular Invertebrate Systematics and Ecology Laboratory, Graduate School of Engineering and Science, University of the Ryukyus, Nishihara, Okinawa 903–0129, Japan*

²*The Oceancy MTÜ, Männimäe/1, Pudiõoo küla, Kuusalu vald, Harju maakond, 74626, Estonia*

³*Tropical Biosphere Research Center, University of the Ryukyus, Nishihara, Okinawa 903–0129, Japan*

[†]*Present address: Physics and Biology Unit, Okinawa Institute of Science and Technology Graduate University (OIST), 1919–1 Tancha, Onna-son, Okinawa 904–0945, Japan*

Received 14 December 2020; Accepted 7 May 2021 Responsible Editor: Kensuke Yanagi

doi: 10.3800/pbr.16.237

Abstract: Shoreline armouring has progressively affected the coastal landscapes of countries all over the world, and armouring construction will increase in coming years as a consequence of climate change. Armouring has the potential to affect coastal environments and induce changes in the abundance and diversity of marine communities, and its effects might be increased by wide adoption. Moreover, compared with temperate locations, the effects of armouring have been less studied in tropical and subtropical areas. Okinawa Island, the largest and most populated island of the Ryukyu Archipelago in southern Japan, has been affected by numerous civil and military engineering works. After decades of development, less than 40% of its coastline remains natural, and yet impacts from armouring on local marine communities have been overlooked until recent years. The aim of this research was to evaluate effects of near-shore armouring on the surrounding environment by comparing diversity and abundance of coral rubble mobile cryptofauna benthic communities between armoured and control sites. Across six different geographic locations, coral rubble was sampled in front of subtidal breakwaters and at nearby control sites. Armoured sites were associated with lower cryptofauna abundances and reduced richness and diversity at higher taxonomic levels (phylum and class). Reduction in spatial complexity could be a plausible reason for the observed patterns. Impacts could be mitigated by combining technical innovations, habitat restoration, and use of natural spaces as buffers for coastal protection. Since less than half of Okinawa Island's coastline remains in a natural state, environmental conservation should be prioritized.

Key words: coastal armouring, coastal development, conservation, coral reefs, cryptic diversity

Introduction

Coastal armouring is the deployment of human-made barriers for coastal defence to protect infrastructures from storms and erosion (Kraus 1988). Artificial barriers, which include seawalls, breakwaters, revetments, and groynes, have been utilised over the coastlines of numerous countries all over the world, such as in Australia (Chapman & Underwood 2011), China (Luo et al. 2015), Italy (Airoldi et al. 2005), Singapore (Heery et al. 2018), the United King-

dom (Firth et al. 2014, Hall et al. 2018), and the United States (Gittman et al. 2015). Their deployment has been expanding to an increasing number of countries (Aguilera 2017) and is expected to further increase in the coming years in response to the effect of climate change, particularly the rise of sea levels (King et al. 2016) and the intensification of storm events (Lucrezi et al. 2010).

Despite their increasing adoption and a certain popularity among the general public in some countries (Hesse 2007), the deployment of hard defence structures needs to be carefully evaluated as coastal armouring can potentially lead to detrimental environmental effects as a consequence of physical alterations of the intertidal and subtidal ecosystems (Oricchio et al. 2016). Consequences can range from

*Corresponding author: Giovanni D Masucci; E-mail, giovanni.masucci@oist.jp

Supplementary materials may be found in the online version of this article.

passive erosion (Griggs et al. 1994) and sediment unbalance (Martin et al. 2005, Lucrezi et al. 2010) to reductions in structural complexity and water retention properties (Airoidi et al. 2005, Firth et al. 2013, Loke et al. 2015, Hall et al. 2018). The aforementioned physical alterations may in turn drive changes in marine communities in terms of composition, abundance, and diversity (Airoidi et al. 2005, Martin et al. 2005), including favouring non-indigenous taxa, which are generally opportunistic species that can adapt to harsher environmental conditions better than native species (Airoidi et al. 2015, Oricchio et al. 2019). Although numerous works on the topic have been published in the international scientific literature from temperate regions, the effects of armouring are less studied in tropical and subtropical areas, where research has been more focused on the general effects of urbanisation and land reclamation (Reimer et al. 2015, Heery et al. 2018).

Over the years, Japan has invested considerable amounts of public budgets in coastal development (Walker & Mossa 1986, Kingston 2005). At the end of the 20th Century, about 50% of the Japanese coastline had been altered (Ministry of the Environment of Japan, 2001). The production and deployment of Tetrapods, tetrahedral concrete blocks of various sizes and weight used as armoured units for coastal defence, represent an investment of ~1500 billion yen per year (~13.5 billion USD, Hesse 2007). Coastal armouring in Japan is not subject to the national Environmental Impact Assessment law (EIA; Ministry of the Environment of Japan, 2019) and, in light of the scarcity of pre-post construction assessments, the effects of armouring on marine communities have mostly remained unclear and understudied, with few exceptions (e.g., Sane et al. 2007). Since the 1970s, coastal development has accelerated, becoming one of the main local stressors affecting the decline of the coral reefs in the Ryukyu Islands, in southern Japan (Nakano 2004). Okinawa Island, the largest of the archipelago (land area: 1213 km², Masucci & Reimer 2019; population: ~1.3 million, Okinawa Prefectural Government 2019a), has been particularly impacted by both civil and military coastal engineering projects and as of 2018 less than 40% of its coastline remained in a natural state (Masucci & Reimer 2019). Especially in the inner reefs, scleractinian corals have been reduced in abundance and diversity, with a shift in balance to stress-resistant genera (Loya et al. 2001, van Woesik et al. 2011, Hongo & Yamano 2013).

Coral mobile cryptofauna is constituted of metazoan organisms living associated with coral skeletal matrices (Enochs 2011). When dealing with degraded ecosystems, a feasible solution to conduct impact surveys beyond living coral cover is to instead examine different benthic communities, with one example being the mobile cryptofauna associated with coral rubble. Coral rubble hosts numerous benthic animals, including worms from a variety of taxa, crustaceans, molluscs, echinoderms, and fish. Overall, cryptofauna has a fundamental role in capturing nutrients and maintaining the functionality of a coral reef envi-

ronment while being an indicator of the reef trophic state and potentially general health status (Richter et al. 2001, Enochs 2011). For these reasons, mobile cryptofauna has been used in past research as a proxy for benthic diversity in a variety of different environments (Enochs 2011), including coral reefs (Takada et al. 2007, Takada et al. 2014, Wee et al. 2019).

In Okinawa, mobile rubble cryptofauna abundance and diversity has been used to compare the relative health of coral reefs, including examination of seasonal and year-to-year patterns (Biondi et al. 2020). Moreover, previous research has highlighted how the seaward sides of Okinawan breakwaters are particularly rich in small-sized rubble fragments (~2–10 cm), which tend to accumulate and form mounds (Masucci et al. 2020). The fragments generally appeared smooth with poor growth of benthic sessile species, possibly due to the abrasion occurring during displacement, but with the potential of providing a habitat for a mobile community worth investigating. Conversely, the relatively harsh hydrodynamic conditions at the seaward side of a breakwater (Eslami & Eslami 2018, Husain et al. 2018, Masucci et al. 2020) combined with the smooth and repetitive pattern of hard blocks (=fewer microhabitats, lower spatial variety and complexity), as well as other unaccounted factors, could lead instead to lower abundances and/or diversity levels (Airoidi et al. 2005, Firth et al. 2013, Masucci et al. 2020). Thus far, mobile cryptofauna communities inhabiting rubble mounds near artificial coastal barriers have not been investigated or compared with those of mounds from sites not affected by the presence of breakwaters.

In order to understand if cryptofauna communities can be impacted by the presence of coastal armouring, the aim of this research was to compare benthic abundances and high-level (phylum and class) taxonomic diversity between mobile coral rubble cryptofaunal communities sampled at armoured and natural sites in Okinawa Island, at similar depths.

Materials and Methods

Study locations and survey design

Field work was conducted in the northern part of Okinawa Island (0–500 residents/km²; Okinawa Prefectural Government, 2019b). Data were collected using scuba diving surveys over six distinct geographic locations (Fig. 1), at 12 coastal sites (Table 1), six of which were armoured (near-shore barriers placed at subtidal depths measured at lowest astronomic tide, piled up with the top part exposed; Fig. 2), each one coupled with a nearby control site. Armoured sites were labelled with the letter A, control sites with the letter B. Survey locations were selected in areas with low human population densities in order to minimize noise derived from unaccounted location-specific human-related impacts (such as water pollution, nutrient enrichment, overfishing, etc.). In addition, we selected locations

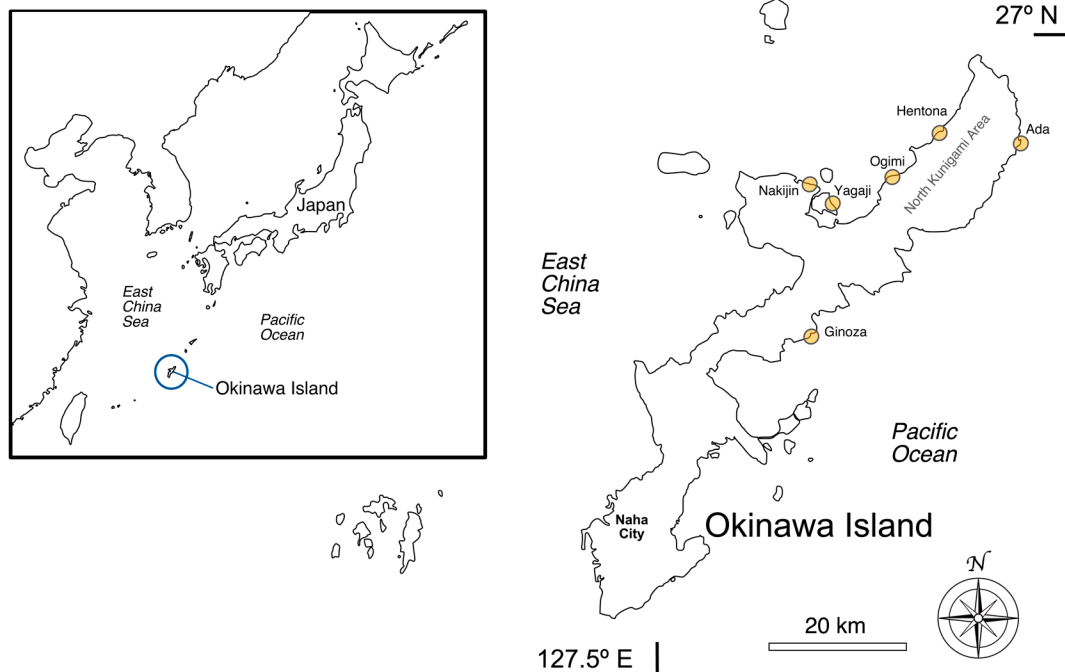


Fig. 1. Okinawa Island, southern Japan, north-west Pacific Ocean. Yellow circles represent the geographic locations surveyed during this study. Each geographic location includes two paired sites, an armoured coastline and a control one in its proximities.

with no ongoing coastal construction and where armouring was performed at least 10 years before our surveys, in order to evaluate long-term effects linked to the presence of the barrier, minimising fluctuations derived from recent construction activities (benthic succession times in the region ~ 5 years; Ohba et al. 2008). Although reclaimed areas generally have armoured shorelines, in order to clearly reconnect any measured effect to coastal armouring and not to reclamation, all selected locations faced non-reclaimed coastal areas. For each location, sites presented similar habitat characteristics between the armoured site and its respective control site, with the obvious exception of the presence of hard coastal defence structures at armoured sites. All locations were selected among shallow inner reefs. At Hentona, Nakijin, Yagaji, and Ginoza, the inner reef coral community was unhealthy with numerous dead colonies and diffused turf algal growth. Ogimi and Ada, conversely, presented a healthy inner reef coral community with little algal growth and healthy living scleractinian colonies. Compared to other sites, Ada is regularly affected by strong tidal currents. Finally, Yagaji and Ginoza were characterized by the presence of patchy seagrass meadows intertwined among the coral colonies.

Evaluation of suitable locations took place in the first half of 2017, and sampling was carried out between August and December 2017. Each location was surveyed within the same season within a three-week maximum timeframe to minimise the effects of seasonal variation.

Cryptofauna sampling and sorting

Rubble samples were collected from each site, both ar-

moured and not (=control), using buckets and lift bags (3×20 L of rubble per site; Biondi et al. 2020). For each armoured site, sampling took place at the seaward side of the wall, approximately 1 m in front of the blocks. For each corresponding control site, rubble was sampled at the same depth (Table 1) and distance from the coastline as their corresponding paired armoured site. Buckets were hermetically sealed immediately after collecting rubble to prevent mobile animals from escaping during buckets retrieval and transport. While the amount/surface area of rubble contained within each 20L bucket varied based on the shape of the rubble at each site, the volume was standard, and thus considered representative of each site's rubble.

Each animal of size ≥ 1 mm, living inside or over the surface or the scleractinian skeletal structure, was collected using tweezers or syringes, individually photographed in-vivo (Sony a6300 24.2 MP APS-C cameras, Sony E 30 mm f/3.5 macro lenses), and preserved in 99% ethanol.

Individual specimens were identified at the phylum and class levels. Coarse taxonomic levels have been used in past studies to describe and measure biodiversity (Anderson et al. 2005, Biondi et al. 2020), as well as for the purpose of quantifying human impacts and ecosystems responses to anthropogenic disturbances. Monitoring at higher taxonomic levels implies lower noise levels (Warwick 1993), higher speed of analyses, reduced costs (Khan 2006), and lower chances of mistakes due to wrong identifications. Data of higher taxonomic levels are also less affected by gaps in the baseline data from taxonomic databases. Taxonomic sufficiency (the use of higher-level taxa) has been analysed and employed in a wide range of

Table 1. Overview of the sites considered in this study.

Site Label	Location	Site category	Site description	Depth at sampling point (m)	Month	Latitude and longitude	Population density
1A	Hentona	Armoured	Breakwaters, tetrapod blocks & rubble mounds	1.6	August	26°45'27.99"N 128°11'19.97"E	0–100
2A	Ogimi	Armoured	Breakwaters, tetrapod blocks & rubble mounds	1.5	August	26°42'08.12"N 128°06'56.11"E	0–100
3A	Nakijin	Armoured	Breakwaters, rocky blocks & rubble mounds	1.7	October	26°41'25.84"N 127°59'57.15"E	100–500
4A	Yagaji	Armoured	Breakwaters, tetrapod blocks & rubble mounds	1.1	October	26°39'22.5"N 128°02'04.05"E	100–500
5A	Ada	Armoured	Breakwaters, tetrapod blocks, smaller rubble mounds	1.8	October	26°44'49.54"N 128°19'30.34"E	0–100
6A	Ginoza	Armoured	Angled groyne, tetrapod blocks & rubble mounds	2.3	November	26°28'16.12"N 127°58'44.88"E	100–500
1B	Hentona	Control	Patch reef, corals mostly dead	1.6	August	26°45'02"N 128°11'05.93"E	0–100
2B	Ogimi	Control	Patch reef, healthy <i>Montipora</i> community	1.5	August	26°42'08.12"N 128°06'56.11"E	0–100
3B	Nakijin	Control	Patch reef, corals mostly dead	1.7	October	26°41'25.84"N 127°59'57.15"E	100–500
4B	Yagaji	Control	Patch reef & seagrass meadow, corals mostly dead	1.1	October	26°39'34.67"N 128°01'55.18"E	100–500
5B	Ada	Control	Patch reef with strong currents, corals generally healthy	1.8	October	26°44'51.54"N 128°19'36.16"E	0–100
6B	Ginoza	Control	Patch reef & seagrass meadow, corals mostly dead	2.3	December	26°28'14.77"N 127°58'32.97"E	100–500

studies concerning terrestrial (Souza et al. 2016), freshwater (Cabral et al. 2017) and marine (Anderson et al. 2005, Biondi et al. 2020) ecosystems. Taxonomic accuracy was confirmed using the World Register of Marine Species (WoRMS Editorial Board 2019).

Statistics

Statistical analyses were performed using R software (version 3.6.3; R Development Core Team 2020). The level of significance for all tests was set at 95%. Normality of the variable “total abundance” was verified with the Shapiro–Wilk test (Royston 1982). Homoscedasticity of the same variable was checked using Bartlett’s test (Bartlett, 1937). Since both assumptions were respected, no transformation was performed. Differences in total cryptofauna abundances among geographic locations and between natural and armoured sites were tested with a two-way ANOVA.

Diversity was estimated with the Shannon–Wiener index (Hill 1973). Subsequently, the whole dataset was log-transformed and the effects of armoring on abundances within phyla and classes were tested with PERMANOVA (Anderson 2014), by using the ‘adonis’ function from

the *Vegan* package for R (version 2.5-5; Oksanen et al. 2019), Bray–Curtis distance, and 999 permutations. Differences between geographic locations were tested as well, as a second factor within the same analysis. Rare taxonomic groups accounting for most of the differences were revealed using the Similarity Percentages technique (SIMPER; Clarke 1993) from the *Vegan* package for R on a log-normalized dataset. SIMPER highlights the individual contribution of each variable to the overall Bray–Curtis dissimilarity, up to an overall dissimilarity percentage of 70%. Over the same dataset, correlation patterns were graphically displayed with a Principal Component Analysis (PCA), using the ‘rda’ function from the *Vegan* package for R. Results were displayed as a biplot (scaling 2; Gabriel 1971) with taxa expressed as labels and observations from different sites as triangular shapes.

Results

Cryptofauna abundance

Sites with a natural coastline featured a more abundant cryptofauna within their rubble (Fig. 3A). About 36% of

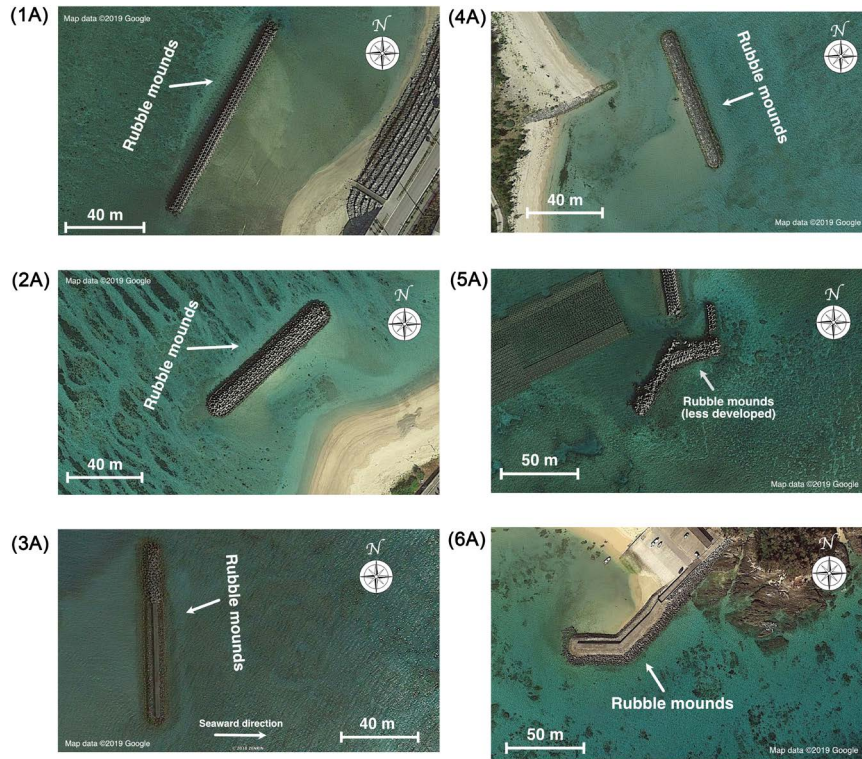


Fig. 2. Satellite view of the artificial barriers surveyed in this study. For each picture, its respective site label from Table 1 is reported in the top-left corner.

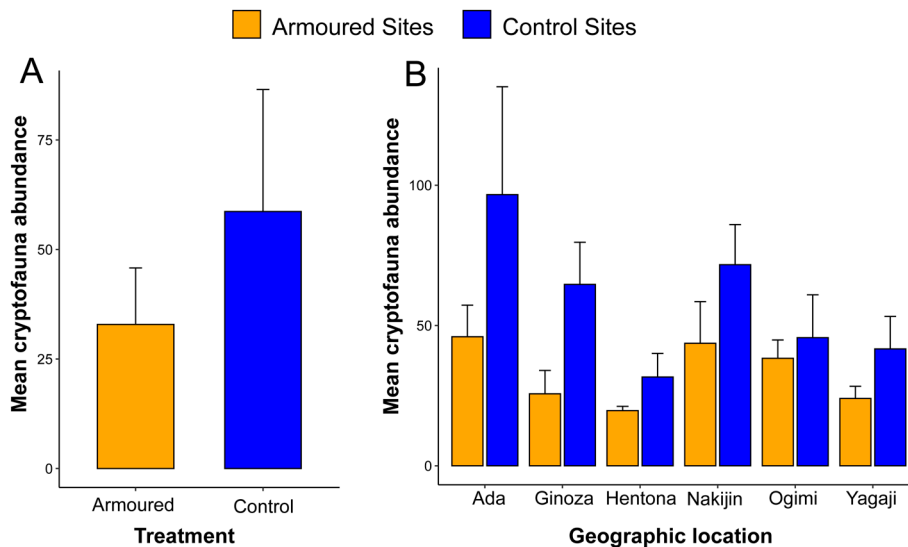


Fig. 3. Mean abundances of rubble mobile cryptofauna communities. A) Differences in mean cryptofauna abundances between armoured and control sites. Error bars represent standard deviations. B) Mean cryptofauna abundances for each site at each geographic location. Orange bars represent armoured sites, blue bars represent control sites. Error bars represent standard deviations.

the animals were sampled from armoured sites (n=590) and ~64% from natural sites (n=1055). Differences in cryptofauna abundance between natural and armoured sites were statistically significant (two-way ANOVA; $F=25.410$, $p<0.001$). The individual geographic location was also a relevant factor in influencing the abundance of the cryptofauna (Fig. 3B). Ada was the most cryptofauna-

rich geographic location, followed by Nakijin, Ginoza, Ogimi, Yagaji Island, and Hentona. Differences in cryptofauna abundance among geographic locations were also statistically significant (two-way ANOVA; $F=7.042$, $p<0.001$).

For each geographic location, rubble sampled from armoured sites hosted lower abundances than those sampled

Table 2. Total abundance per site and Shannon-Wiener biodiversity index at the phylum and class levels.

Site Label	Location	Site category	Total abundance	Shannon Index	
				Phylum	Class
1A	Hentona	Armoured	59	0.92	1.07
1B	Hentona	Control	95	1.12	1.29
2A	Ogimi	Armoured	115	0.79	0.97
2B	Ogimi	Control	137	0.99	1.33
3A	Nakijin	Armoured	129	0.93	1.08
3B	Nakijin	Control	215	1.35	1.53
4A	Yagaji	Armoured	72	0.94	1.15
4B	Yagaji	Control	124	1.09	1.24
5A	Ada	Armoured	138	1.08	1.26
5B	Ada	Control	290	1.03	1.22
6A	Ginoza	Armoured	77	0.96	1.09
6B	Ginoza	Control	194	1.20	1.39

at natural sites (Fig. 3B). Ginoza was the location where the armoured site accounted for the lowest percentage of total abundance (~28%), while Ogimi was the one with the highest percentage of cryptofauna coming from the armoured site (~46%). Interactions between the two factors (armouring status vs geographic location) were not statistically significant (two-way ANOVA; $F=1.778$ $p=0.156$). In other words, the effect of the armouring on cryptofauna abundance happened in a similar way, regardless of the specific geographic location.

In total, 1645 cryptofauna animals from 8 phyla and 16 classes were sampled, photographed, classified, and preserved (Supplementary material 1). The site with the highest abundance was 5B (Ada, control), followed by 3B (Nakijin, control), 6B (Ginoza, control), 5A (Ada, armoured), 2B (Ogimi, control), 3A (Nakijin, armoured), 4B (Yagaji Island, control), 2A (Ogimi, armoured), 1B (Hentona, control), 6A (Ginoza, armoured), 4A (Yagaji Island, armoured), and 1A (Hentona, armoured) (Table 2). Mean abundance per site (\pm SD) was 137.1 ± 66.8 animals.

Cryptofauna diversity

At the phylum level, the three most common taxonomic groups were Arthropoda (total: 907 individuals), Mollusca (total: 511 individuals), and Annelida (total: 119 individuals). Together, these groups accounted for 93% of the total abundance. At the class level, the three most common groups, accounting for 88% of the total abundance, were Malacostraca (total: 900 individuals), Gastropoda (total: 428 individuals), and Polychaeta (total: 119 individuals). Worth mentioning was the presence within rubble of fish (class Actinopterygii) (21 individuals in total, from family Gobiidae), a group not commonly associated with the benthic environmental surveys, although they are well known to live in coral rubble (e.g., Goatley & Brandl 2017; Troyer

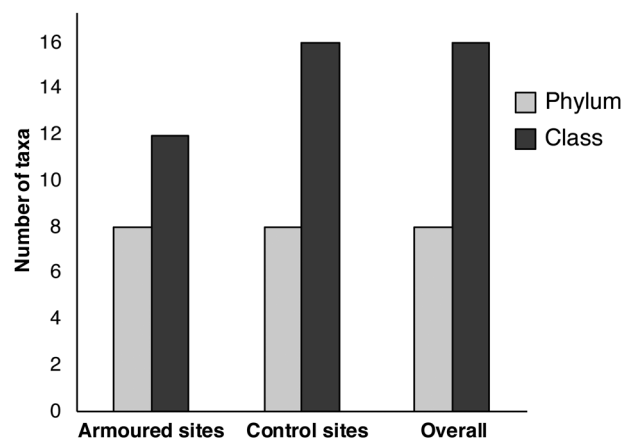


Fig. 4. Taxonomic richness in rubble mobile cryptofauna communities at the phylum and class levels, for armoured sites and control sites.

et al. 2018).

Cryptofauna communities from armoured and natural sites differed at both the phylum (2-way PERMANOVA; $df=35$, $R^2=0.19692$, $p<0.001$) and class levels (2-way PERMANOVA; $df=35$, $R^2=0.16648$, $p=0.001$). Among the three most common phyla, Arthropoda (crustaceans) and Annelida showed lower abundances at armoured sites, while Mollusca seemed relatively unaffected by coastal armouring. However, at the class level, we observed reductions in the abundance of Bivalvia, in favour of Gastropoda, at all locations to the exception of Ogimi and Ginoza. Differences between geographic locations were also significant, both at the phylum (2-way PERMANOVA; $df=35$, $R^2=0.26946$ $p=0.001$) and class level (2-way PERMANOVA; $df=35$, $R^2=0.26371$, $p<0.001$). No significant interaction was observed between armouring status

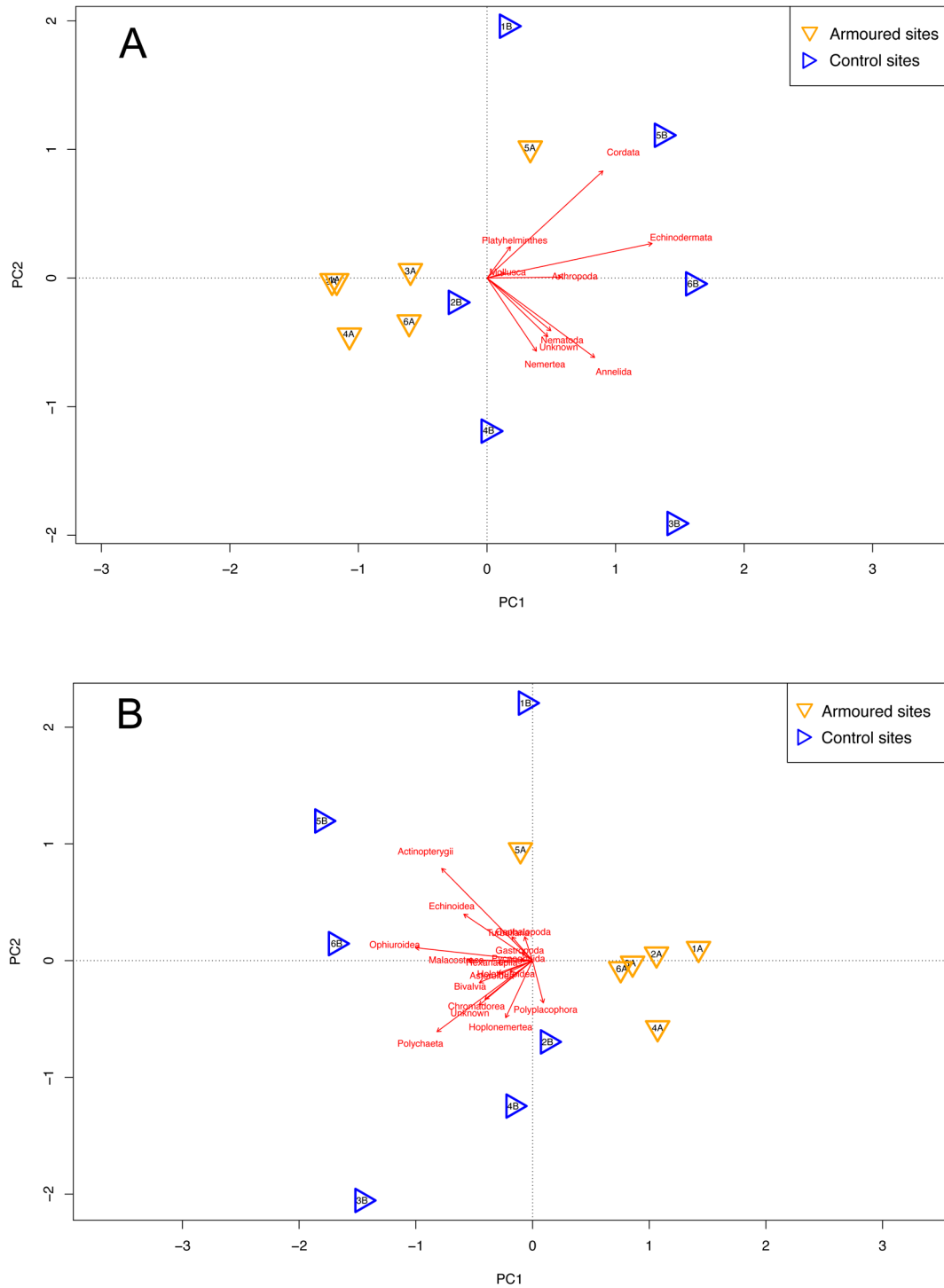


Fig. 5. Principal Component Analysis biplot of coral rubble mobile cryptofauna communities at armoured and control sites. A) Phylum level, B) class level. Results displayed as biplots, with taxa expressed as labels and observations from different sites as triangular shapes.

and geographic location.

In terms of taxonomic richness, armoured sites hosted 12 classes from eight phyla, while control sites hosted 16 classes from eight phyla (Fig 4). All the phyla and classes found at armoured sites were also present at control sites, but four classes were unique to control sites (Asterozoa, Hexanauplia, Holothuroidea, Pycnogonida).

The Shannon-Wiener index highlighted higher diversity at control sites when comparing each control site with its paired armoured site (Table 2). This was observed at both the phylum and class level, for each geographical location with the exception of Ada (sites 5A and 5B; Table 2), where diversity at phylum and class level was higher at the armoured site.

Concerning rare taxa, at the phylum level, the observed differences were mainly driven by higher relative abundances in Echinodermata, Annelida, Chordata, Arthropoda, and Nemertea at control sites. At the class level, differences between control and armoured coastlines were driven by higher abundances of Ophiuroidea, Polychaeta, Actinopterygii, Bivalvia, Echinoidea, Malacostraca, and Hoplonemertea at control sites and of Polyplacophora at armoured sites (SIMPER analysis). These associations are graphically displayed in the Principal Component Analysis biplot, which highlighted a scattered distribution for control sites, whose positions in the graph are location-specific. Conversely, armoured sites grouped closer to each other at both taxonomic levels, highlighting an increase in similarity between sites from different locations (Fig 5).

Discussion

The taxonomic richness and total and relative abundances of coral rubble cryptofauna communities differed significantly between armoured coastlines and natural sites. Notably, while different geographic locations clearly affected abundance and diversity (Fig 3, Fig 4, Fig 5), armoured sites, overall and for each location, showed lower abundances, and generally lower diversity than their control counterparts. Both the phylum and the class levels showed decreases in diversity and more similarity across armoured sites. However, a loss of taxonomic richness was only appreciable at the class level.

Each single location showed lower abundance at the armoured site. Although we lack data preceding the alteration of the armoured sites, this pattern suggests that the armouring of the coastline may have consistently caused reductions in the abundances of the benthic community at each location investigated in this study. The extent of reductions and abundances after armouring may depend on location-specific factors: as an example, Ada and Hentona were, respectively, the locations with the highest and lowest total abundance, for both natural and armoured sites. Overall, rubble mobile cryptofauna abundance provided a clear response signal to the presence of armouring.

It is worth mentioning that Ada and Nakijin, the two locations with the highest abundances, are located in areas of low urbanization and coastal development, having, among our locations, the longest uninterrupted natural coastlines, respectively, for the east and for the west coasts (Masucci & Reimer 2019). This suggests that differences between locations might reflect the general environmental state of each location. This aspect could be further investigated in future studies. Alternatively, the observed differences between locations might simply reflect peculiarities of each specific habitat. For example, in the case of Ada, the presence of strong tidal currents and a generally healthy reef could both be related to the high abundance of cryptic animals, reflected in our sampling results. It is also worth noting that seasonality and year-by-year changes may also

lead to different observations from those that we made during this study.

The lower number of taxa and the lack of low abundance-groups at armoured sites (with the exception of class Polyplacophora) is also indicative of environments with lower diversity and higher dominance, consistent with what has been reported in previous research (Airoldi et al. 2005, Firth et al. 2013, Airoldi et al. 2015). A loss of diversity can lead to a loss of ecosystem functions and, eventually, ecosystem services. Two classes of phylum Echinodermata (Asteroidea and Holothuroidea) were completely absent at armoured sites. Asteroidea have important ecological roles as predators, with both their removal and outbreaks possibly resulting in the occurrence of trophic cascades (Montecino-Latorre et al. 2016). The loss of Holothuroidea can negatively affect the remineralization of organic matter in coral reefs environments (Lee et al. 2018). Other classes showed lower abundances at armoured sites. For example, fish (class Actinopterygii) were lower in numbers in rubble sampled from armoured sites (3 juvenile individuals, compared with 18 at control sites). Shallow reefs have been shown to act as nurseries for fish species, both in the Atlantic and in the Indo-Pacific (Nagelkerken 2007, Kimirei et al. 2013), including the Ryukyus (Nakamura et al. 2012), and also harbour cryptobenthic fish communities (Goatley & Brandl 2017; Troyer et al. 2018). Functional connectivity between outer and inner reef contributes to keep reef fish populations replenished (Kimirei et al. 2013). Changes in cryptic shallow reef communities may have repercussions which go beyond the area immediately surrounding artificial barriers. For this study, the number of benthic fish sorted from rubble was limited, but future research could focus on this specific group and obtain more solid evidence on the effects of armouring on the distribution, abundance, and diversity of demersal fish.

The differences between control and armoured coastlines could at least partially be explained by a combination of reduced habitat variety, alteration of rubble sizes and surface fractal complexity combined with a more challenging environment, due to several factors, such as increased water energy and wave reflection (Eslami & Eslami 2018, Husain et al. 2018).

Regardless of the habitat found at each control site, the seaward side of the armoured barrier was consistently characterised by rubble mound formations, due to the accumulation of small rubble at the base of the blocks. Although rubble fragments host a variety of taxa and hidden diversity, they can easily be mobilised during typhoons and storm events, potentially causing breakage, displacement, and abrasion damage to the surrounding benthic communities (Cameron et al. 2016). Displacement of rubble by waves and erosion are mechanisms likely to occur at both armoured and control sites. However, the presence of hard blocks may impact the displacement dynamics, as a consequence of impoundment, alteration of longshore currents and increase of wave energy in proximity of the

breakwaters. Alterations of sedimentation and erosion rates in relation to these mechanisms have already been described for the Ogimi location in previous research (Masucci et al. 2020). Such alterations may be in part responsible for the differences that we observed in rubble infauna.

Previous surveys conducted around Okinawa Island showed that complex branching rubble formations can host a larger variety of cryptofauna than morphologically simpler rubble (Biondi et al. 2020). At different scales, biodiversity and habitat complexity show positive relations (Morse et al. 1985, Johnson et al. 2003), while a reduced substrate complexity can be associated with a decrease in both abundance and taxonomic richness (Kostylev et al. 2005).

Conclusions

Coral rubble mobile cryptofauna communities at armoured sites were significantly affected by the presence of artificial barriers, with reduced total abundances and diversity losses. Armouring a tract of coast can have measurable environmental costs.

Okinawa Island and nearby islands are surrounded by well-developed coral reefs that provide significant protection from the effects of tropical storms and typhoons. Recent research has shown that a healthy reef ecosystem is able to absorb up to 97% of wave energy (Ferrario et al. 2014). If the reef ecosystem is damaged, in the long term, the protection provided by hard blocks might come at the expense, at least partially, of the protection offered by the reef itself.

Okinawa enjoys significant benefits from its productive marine environment and landscape, yet its shorelines have been affected by an influx of large-scale coastal construction, particularly since 1972, when the prefecture reverted to Japanese sovereignty. Although a few studies have investigated coastal development in the prefecture (Nakano 2004, Reimer et al. 2015), lower levels of attention have been given to the specific problem of impacts from coastal defences. Moreover, in Japan, coastal armouring is not covered by the national Environmental Impact Assessment law (EIA, Ministry of the Environment of Japan 2019). Previous assessments conducted by the local government and private assessment companies have been focused on estimating coral cover and recruitment over single block surfaces, without considering possible negative effects on the surrounding communities or on taxa beyond corals (see Maekouchi et al. 2008 for an example of such approach). Going forward, we recommend considering several benthic components beyond hard corals when assessing environmental impacts. The cryptofauna of coral rubble is one good candidate for future utilization.

Numerous future research avenues remain unexamined. Diversity at the class level limited our analyses of the functional resolution of the community, particularly the ability to confirm shifts in the community towards the presence of non-native species. Molecular approaches can also be used

to investigate functional diversity. Another limitation in this study comes from the selection of organisms >1 mm within coral rubble, which excludes smaller class sizes of the benthic cryptofauna (such as juvenile invertebrates). Finally, the benthic diversity of the cryptic rubble ecosystem may not necessarily reflect the diversity of the entire benthic compartment.

It is still unclear how far the ‘footprint’ of armouring extends from the blocks into the surrounding benthic community, or also if artificial barriers can alter benthic diversity at lower taxonomic levels (e.g., species level). While block designs can and should be improved with the purpose of reducing impacts and improving block performance as hard substrate in mind (see Moschella et al. 2005, Loke et al. 2015, Hall et al. 2018), the amount of armoured coastline in Okinawa Island (>60%; Masucci & Reimer 2019) should also be considered when evaluating further armouring projects. Less impactful development strategies and the use of seagrass meadows, coral reefs, and coastal vegetation (including mangrove forests) as natural buffer spaces between the shoreline and human presence could help preserving remaining natural coasts in Okinawa and other tropical and subtropical locations. Conservation and restoration of native ecosystems, where possible, should be prioritised.

Acknowledgements

The authors would like to thank Dr. Hin Boo Wee, Giun Yee Soong, Dr. Hiroki Kise, and Dr. Yee Wah Lau (all MISE, University of the Ryukyus) for their help with field work and sorting of rubble cryptofauna, and Marilyn Carletti (MISE) for helping with identification of Nematoda classes. We also thank the Japan Student Services Organization (JASSO), the QUEST foundation, and Mitsubishi Corporation, for providing economic support to GDM and PB. Comments from two anonymous reviewers greatly improved an earlier version of this manuscript.

Supplementary materials

Supplementary material 1. Raw data table of rubble cryptofauna diversity and abundance (phylum and class)

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