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Does land reclamation affect small-scale benthic communities? Micro-quadrats on coral reefs around Okinawa Island, southern Japan

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Abstract

Coral reef ecosystems, such as those surrounding Okinawa Island, have high levels of biodiversity, especially among benthic communities. Over the last century, and particularly after World War II, major coastal development and reclamation works have been carried out along the coasts of Okinawa Island, and there are concerns about their adverse effects on the communities of organisms living in coral reef areas. Examples of methods for investigating the distribution and ecology of organisms that live on the seabed, as well as environmental impacts, include several transect and photo-quadrat techniques. However, such survey methods aim to roughly grasp the benthic biota at a spatial scale that does not target relatively small (< 5 cm) benthic organisms. Therefore, in this study, we focused on the microenvironment and conducted surveys of benthic organisms using quadrats of 0.0025 m^2 (5 cm × 5 cm) (hereinafter referred to as micro-quadrats). Field surveys were conducted by scuba diving at nine coastal locations on Okinawa Island, where photographs were taken including the entire micro-quadrats (5 cm per side) in the field of view. In addition to the micro-quadrats, conventional transect (10 m length) methods were also used. Benthic coverage was calculated based on the data obtained by the identification, and the similarity of the biological communities was also compared. For the similarity comparison, we confirmed differences in community composition between sites and depending on the category of coastal development (natural, armoring, land reclamation). At the sites where reclamation had occurred, the coverage of octocorals was higher in the transect method, while the coverage of sand was highest in the micro-quadrats. In addition, significant differences were found in the community composition of organisms with the transect method and between the reclaimed and unreclaimed sites ($p < 0.001$). A similarly significant difference was found in the micro-quadrat method ($p < 0.001$). Transect results indicated that sites categorized as natural and armoring were characterized by hard coral or rock and rubble, while sites categorized as land reclamation were characterized by octocorals (mainly soft corals) or sand. In addition, micro-quadrat results indicated that sites categorized as natural or armoring were more likely to have hard coral, ascidian, and CCA, and that sites categorized as land reclamation were characterized as sand. Thus, depending on the method, the organisms and categories characterized at each site were also different. By focusing on more minute environments than conventional methods, this study demonstrates the importance of understanding the biota in microhabitats at different spatial scales.

Keywords Ryukyu Islands · Benthos · Biota · Micro habitats · Coastal development

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Introduction

Coral reef areas, including Okinawa Island in southern Japan, are home to numerous species, the majority of which are still understudied. Among the marine diversity of these coral reefs are benthic organisms, many of which live on the rugose seafloor of these reefs (Enochs and Manzello 2012). Coral reefs are characterized by a complex three-dimensional structure, and the consequent increase in available spatial and ecological niches is directly related to their high levels of biodiversity (Graham and Nash 2013).

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However, over the last century, coral reef environments have been degraded by both extreme bleaching events and local stressors, and have been observed to be in decline through time (Hasegawa 2011; Hongo and Yamano 2013). For example, many coral reefs in Australia's Great Barrier Reef have been subject to substantial decline due to problems such as sediment and nutrient runoff via coastal development (De'ath and Fabricius 2010). The island of Okinawa is subject to similar problems (Hongo and Yamano 2013): the coastline, once consisting of a diverse alternation of rocky shores and sandy beaches surrounded by coral reefs, is now fragmented by seawalls and other human-made structures and more than half of it has been reclaimed and built up in shallow waters (Masucci and Reimer 2019; Nakajima et al. 2024). Furthermore, anthropogenic disturbances on Okinawa Island have been suggested to affect coral reef community compositions (Reimer et al. 2015). Coral community and fish faunal surveys conducted along the coast of Nakagusuku Bay on the east coast of Okinawa Island have suggested that coastal development has significantly reduced the diversity of both corals and fish (Clay et al. 2023; Cook et al. 2022). Survey methods such as quadrats and transects are heavily utilized for understanding the dynamics of such biota changes (Brett et al. 2007; Ogaki 2009). Each of these methods comes with its own strengths and limitations. Traditional field survey methods—such as belt transects, line-intercept transects, and quadrat sampling—have been widely used to estimate coverage and species composition across various spatial scales (Beisiegel et al. 2017). In recent years, thanks to the advent of increasingly compact, affordable, portable, and sophisticated photographic equipment and memory storage, photo and video-based surveys have become common, offering the advantage of permanent records that allow for post-survey validation, identification, and long-term monitoring (Preskitt et al. 2004). Photogrammetric approaches, such as Structure-from-Motion (SfM), have also gained popularity for generating high-resolution 3D reconstructions of reef surfaces (Burns et al. 2015). Drones, aerial photography, and satellite pictures are also widely used for studying reefs at larger spatial scales (Bennett et al. 2020). Not all methods are photographic. In situ visual surveys, destructive sampling (e.g., core sampling or scraping), settlement tiles, and coral rubble cryptofauna surveys, provide valuable data on cryptic or early life-stage organisms not easily captured in images (Biondi et al. 2020). Such methods can provide higher taxonomic resolution, but can also be labor-intensive, invasive, and restricted by local regulations. Conversely, photographic surveys can miss small or cryptic taxa, leading to biases in biodiversity estimates. Despite their widespread adoption, conventional photographic surveys based on quadrat and transect methods that obtain a broad picture of the biota of the study site usually do not target small (< 1 cm) benthic organisms (Pawlowski et al. 2022). In addition, many of the taxa that significantly differ from site to site in environmental DNA (eDNA) metabarcoding surveys are not fish or corals, but rather minor, understudied taxa (DiBattista et al. 2020). Such biota that cannot be seen easily by the naked eye are often lumped within "other" or "rocks and sand" categories in surveys. This categorization is due to image resolution limitations and observer bias. However, to better understand the mechanisms of benthic cover on coral reefs, it is important to study growth and competition processes and species composition cover at smaller scales of mm to cm (Vermeiji 2006). As well, understanding the early stages of settlement of large groups of corals and other organisms may provide important clues to understand the total biota of a coral reef area. For example, it is well known that some crustose coralline algae (CCA) that inhabit the rocky surfaces of coral reefs act as cement between coral colonies, contributing to reef-building activities (Baba 1997; Baba and Kato 2023). Furthermore, much is unknown about the ecology of most of the taxa that contribute to the diversity of coral reef areas, especially small benthic organisms such as marine invertebrates (Knowlton 2001), making studies on the distribution and diversity of these organisms important (Bolam et al. 2002).

In order to observe these smaller organisms, this study conducted a survey of benthic organisms using small 5 cm × 5 cm quadrats (hereafter "micro-quadrats"). By observing the coral reef seafloor at this smaller scale, this study aimed to (i) understand the diversity of organisms that can be surveyed by using this "micro-quadrats" method, and (ii) detect differences in biota at different sites and different levels of anthropogenic stress (specifically reclaimed, armored, and natural coastlines) that can be expected to be seen by using this method. The results obtained from this study provide knowledge and insights necessary to improve both the understanding and conservation of marine biodiversity in coral reef areas.

Materials and methods

This study was conducted at coastal reef sites around Okinawa Island in 2023 to 2024. The survey consisted of (1) field surveys using transects and micro-quadrats, (2) identification of benthic organisms using online tools (transect), (3) identification of benthic organisms using online tools (micro-quadrats), and (4) calculation of cover and statistical analyses. Details of each process are described below.

Field surveys using transects and micro-quadrats

Field surveys were conducted at nine coastal coral reef sites around Okinawa Island between February 2023 and March 2024 (Fig. 1) using scuba diving. Survey sites were selected based on site-specific data categorized by a 2019 coastal

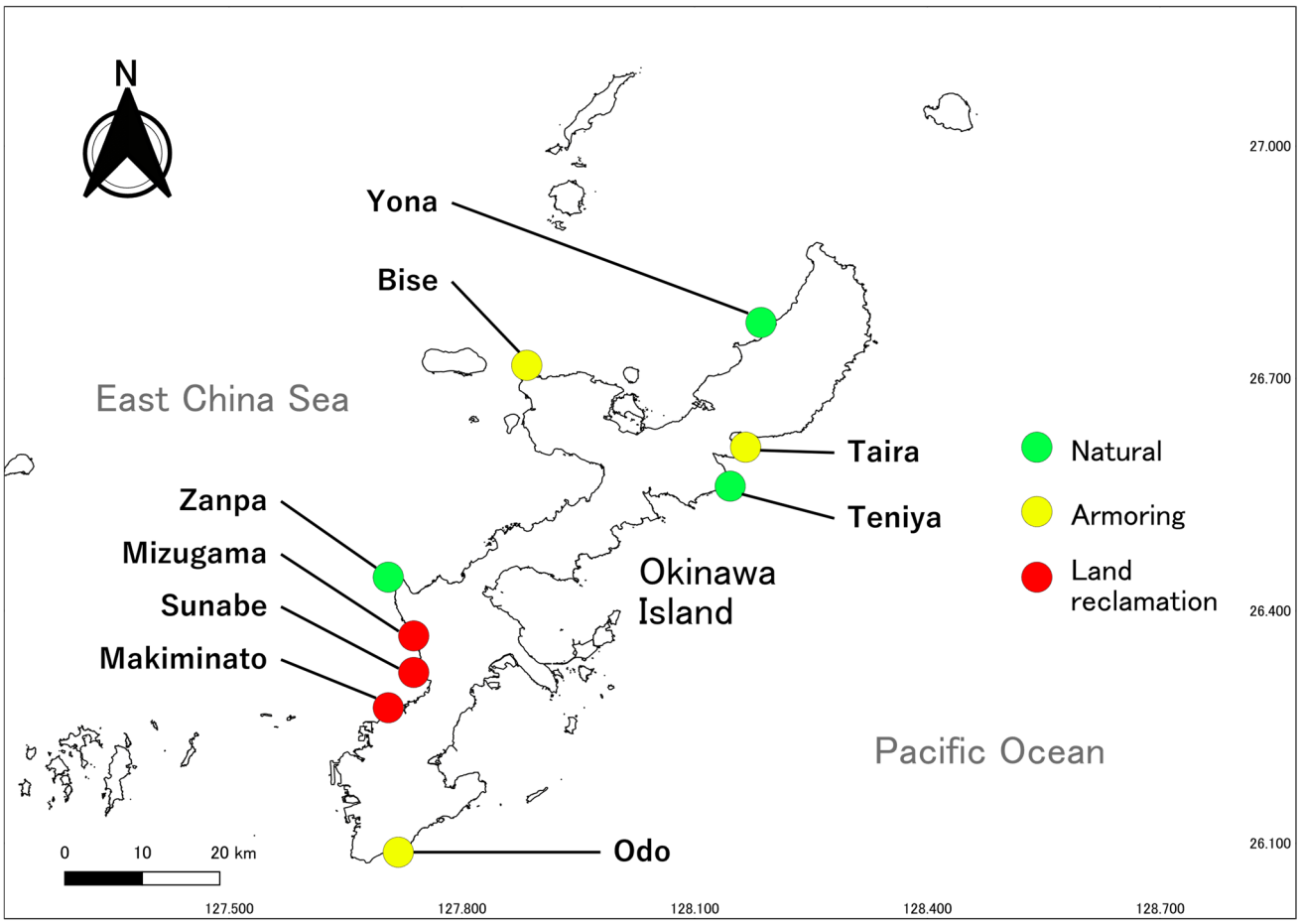

Fig. 1 Study sites in Okinawa Island, Ryukyu Archipelago, Japan

development survey (Masucci and Reimer 2019; Table 1). The categorization of the survey sites was based on the indicators of Masucci & Reimer (2019) with some modifications (soft armoring and hard armoring were merged into a single category "armoring"), classifying each site as natural (natural coast; $n=3$ locations), armored (with artificial structures such as breakwaters and wave blocks; $n=3$ locations), or as land reclamation (reclaimed land; $n=3$ locations). The sites categorized as natural in this survey were Zanpa in Yomitan Village, Teniya in Nago City, and Yona in Kunigami Village. The field survey at Zanpa was completed in March 2023, at Teniya in June 2023, and at Yona in September 2023. The sites categorized as armoring in this survey were Odo in Itoman City, Bise in Motobu Town, and Taira in Higashi Village. The field survey in Odo was in February 2023, Bise was completed in June 2023, and in Taira in October 2023. The sites categorized as land reclamation in this survey were Sunabe in Chatan Town, Makiminato in Urasoe City, and Mizugama in Kadena Town. The field survey in Sunabe was completed in March 2023, the field survey in Makiminato in October 2023, and the field survey in Mizugama in March 2024.

A Tough TG-6 camera (Olympus, Tokyo, Japan) was used to take photographs during the survey. For more accurate benthic identification, in addition to ambient light, a camera-integrated flash strobe and external lights were used to capture colors. In order to ensure uniform surveys at each site, transect lines that were 10 m in length and 40 cm in width were laid at sites that met the following three criteria: (1) flatness that could be visually confirmed, (2) the presence of some benthic organisms (e.g., hard scleractinian corals and soft corals), at (3) at a depth of 10 m (± 2 m, approximately the tidal range in Okinawa), following the contours of the reef. At each site we laid three transects of 10 m $\times$ 40 cm (20 cm on each side of the transect tape). For each transect, a total of 20 photographs were taken of the seafloor biota, one for every 50 cm of length along the 10 m line.

Within the same transects, locations categorized as "abiotic" (e.g., rock and rubble, sand, dead coral) were selected as sites for micro-quadrat photographs. For each micro-quadrat, a photograph was taken with a ruler zoomed in until the length of one side (5 cm) of the micro-quadrat was within view, and this process was repeated for a total of 40

Table 1 The list of transect/micro-quadrat sites in this study

Site no	Site name	Category	Location	Distance from the shore	Survey (month-year)	Depth
1	Zanpa1	Natural	26° 26′ 28″ N 127° 42′ 40″ E	80.2 m	Mar-23	10.3 m
2	Zanpa2	Natural	26° 26′ 29″ N 127° 42′ 39″ E	117.0 m	Mar-23	10.4 m
3	Zanpa3	Natural	26° 26′ 27″ N 127° 42′ 35″ E	181.6 m	Mar-23	11.6 m
4	Teniya1	Natural	26° 33′ 51″ N 128° 08′ 35″ E	471.0 m	Jun-23	10.9 m
5	Teniya2	Natural	26° 33′ 50″ N 128° 08′ 33″ E	413.0 m	Jun-23	9.3 m
6	Teniya3	Natural	26° 33′ 52″ N 128° 08′ 31″ E	384.9 m	Jun-23	10.3 m
7	Yona1	Natural	26° 46′ 06″ N 128° 11′ 50″ E	158.7 m	Sep-23	8.9 m
8	Yona2	Natural	26° 46′ 06″ N 128° 11′ 49″ E	168.2 m	Sep-23	8.5 m
9	Yona3	Natural	26° 46′ 05″ N 128° 11′ 46″ E	232.0 m	Sep-23	10.3 m
10	Odo1	Armoring	26° 05′ 09″ N 127° 42′ 15″ E	320.5 m	Feb-23	12.6 m
11	Odo2	Armoring	26° 05′ 09″ N 127° 42′ 18″ E	343.9 m	Feb-23	10.2 m
12	Odo3	Armoring	26° 05′ 10″ N 127° 42′ 21″ E	349.8 m	Feb-23	11.6 m
13	Bise1	Armoring	26° 42′ 44″ N 127° 52′ 56″ E	331.1 m	Jun-23	9.9 m
14	Bise2	Armoring	26° 42′ 44″ N 127° 52′ 53″ E	283.3 m	Jun-23	9.7 m
15	Bise3	Armoring	26° 42′ 46″ N 127° 52′ 49″ E	247.1 m	Jun-23	10.7 m
16	Taira1	Armoring	26° 37′ 01″ N 128° 09′ 28″ E	584.4 m	Oct-23	9.6 m
17	Taira2	Armoring	26° 36′ 56″ N 128° 09′ 28″ E	512.8 m	Oct-23	9.8 m
18	Taira3	Armoring	26° 37′ 02″ N 128° 09′ 23″ E	516.4 m	Oct-23	11.8 m
19	Sunabe1	Land reclamation	26° 19′ 18″ N 127° 44′ 39″ E	250.5 m	Mar-23	8.8 m
20	Sunabe2	Land reclamation	26° 19′ 19″ N 127° 44′ 38″ E	242.1 m	Mar-23	9.0 m
21	Sunabe3	Land reclamation	26° 19′ 20″ N 127° 44′ 38″ E	230.9 m	Mar-23	9.8 m
22	Makiminato1	Land reclamation	26° 16′ 32″ N 127° 42′ 48″ E	104.4 m	Oct-23	8.1 m
23	Makiminato2	Land reclamation	26° 16′ 34″ N 127° 42′ 50″ E	153.3 m	Oct-23	11.4 m
24	Makiminato3	Land reclamation	26° 16′ 32″ N 127° 42′ 49″ E	108.4 m	Oct-23	8.1 m
25	Mizugama1	Land reclamation	26° 21′ 32″ N 127° 44′ 17″ E	119.9 m	Mar-24	9.8 m
26	Mizugama2	Land reclamation	26° 21′ 32″ N 127° 44′ 17″ E	114.4 m	Mar-24	8.6 m
27	Mizugama3	Land reclamation	26° 21′ 33″ N 127° 44′ 18″ E	85.9 m	Mar-24	9.8 m

Each site was categorized based on the study by Masucci and Reimer (2019), partially modified

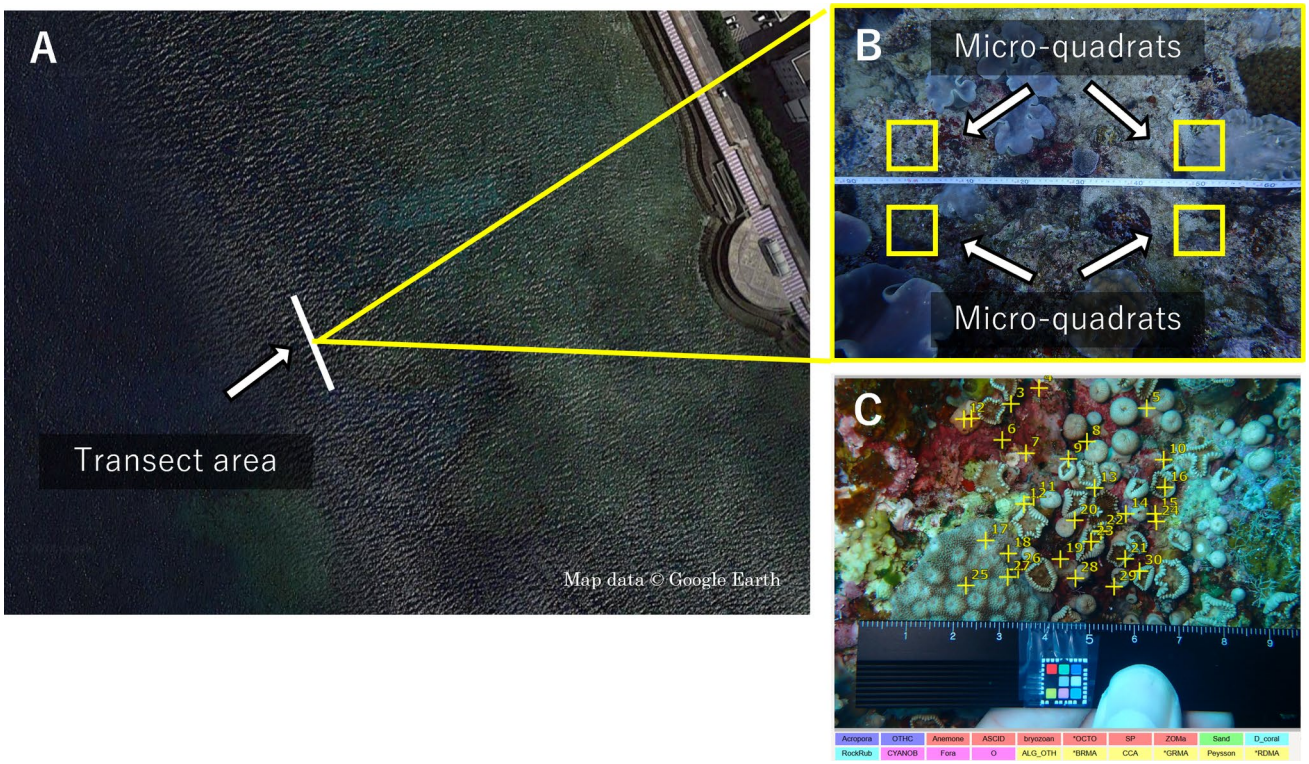

Fig. 2 Schematic of micro-quadrat method. **A** The transect method line was installed parallel to the shoreline; **B** two micro-quadrat images were taken at each side of the transect line every 50 cm length; and **C** an example of a micro-quadrat

photos, two at each end of the line for every 50 cm length of the transect line (Fig. 2). Thus, for each site, we ended up with 120 micro-quadrat photographs. The photographs were taken with an image correction color chart CASMATCH (Bear Medic Co., Ibaraki, Japan) within each picture and were taken at the same zoom level and from a similar height (approximately 20 cm) above the substrate to prevent differences in resolution depending on the height at which the photographs were taken.

Identification of benthic organisms using online tools (transect)

The online tool CoralNet (https://coralnet.ucsd.edu/) was used to identify benthic organisms for transect images.

For the transect method, in CoralNet, a 40-cm-wide (20 cm × 2) and 50-cm-long analysis area was superimposed on images. Using the CoralNet Annotation Tool, random points ($n = 30$; Tabugo 2016) were plotted within the analysis area for transects to identify the substrate and organisms.

Depth and temperature data recorded during the field survey were also recorded on CoralNet. Identification of benthic organisms was based on the Australian Institute of Marine Science (AIMS) Benthic Survey 2008 (Jonker et al. 2008), and as many subtaxa as possible were identified. In this study, only attached organisms such as anthozoans and sponges were included, while mobile organisms such as crustaceans and fishes that appeared in the photographs were categorized as "animal other." Obtained identification data were output to a CSV file.

Identification of benthic organisms using online tools (micro-quadrats)

The online tool CoralNet (https://coralnet.ucsd.edu/) was used to identify benthic organisms also for micro-quadrat images.

In CoralNet, a 5 cm × 5 cm square frame from the micro-quadrat method was superimposed on each picture based on the ruler in the photograph. Using the CoralNet Annotation Tool, random points were plotted within the analysis area for the micro-quadrats to identify the substrate and organisms. Using the CoralNet Annotation Tool, random points ($n = 30$) were plotted within the analysis area for the micro-quadrats to identify the substrate and organisms.

Depth and temperature data recorded during the field survey were also recorded on CoralNet. Identification of benthic organisms was based on the Australian Institute of Marine Science (AIMS) Benthic Survey 2008 (Jonker et al. 2008), and as many subtaxa as possible were identified. In this

study, only attached benthic organisms such as anthozoans and sponges were included, while mobile organisms such as crustaceans and fishes that appeared in the photographs were recorded in the category "Animal other," which also included hydrozoans' sessile group and polychaetes' sessile group. Obtained identification data were output to a CSV file.

Calculation of cover and statistical analyses

Percent cover in this study represented the ratio of the number of points of a given substrate to the total number of points plotted at each location and followed by average ± standard deviation. Data obtained from both transects and micro-quadrats were used to calculate the cover of each substrate and to evaluate dominant species. Dominant species in this study were defined as those taxa that had higher relative cover in each survey method. Coral cover was further divided into the sum of *Acropora* coral cover and non-*Acropora* coral cover. This distinction between *Acropora* coral and non-*Acropora* coral was based on Australian Institute of Marine Science (AIMS) Benthic Survey 2008 (Jonker et al. 2008).

The difference in overall benthic community per transect and micro-quadrat was visualized using non-metric Multidimensional Scaling (nMDS) performed on a Bray–Curtis distance matrix. To determine if community composition varied between each site, the same distance matrix was used for permutational multivariate analysis of variance (PERMANOVA). All analyses were performed in R version 4.1.3 (R Core Team 2022) using the packages vegan (Oksanen et al. 2020) and readxl (Wickham and Bryan 2019).

Results

Benthic coverage of natural sites (Figs. 3–4)

The transect method showed that rock and rubble cover was the highest at all three natural sites; Teniya (52.9 ± 12.8%), Zanpa (66.8 ± 14.3%), and Yona (40.2 ± 24.4%). After rock and rubble, the highest cover was observed for non-*Acropora* coral (22.5 ± 13.2%) at Teniya, CCA (22.0 ± 16.0%) at Zanpa, and non-*Acropora* coral (23.7 ± 16.2%) at Yona. The transect survey confirmed that natural sites had a lower cover of corals than armored sites (26.7 ± 21.4% at Teniya, 7.2 ± 10.7% at Zanpa, and 37.0 ± 32.3% at Yona) (Fig 3) (Fig 4).

Micro-quadrats revealed relatively high algal cover in Teniya (brown algae, 2.2 ± 6.9%; green algae, 1.4 ± 3.0%; red algae, 9.1 ± 10.9%; crustose coralline algae (CCA), 44.0 ± 22.1%; peyssonnelid algal crusts (PAC), 0.2 ± 1.3%). Similarly, relatively high algal cover was observed in Zanpa (brown algae, 0.3 ± 1.2%; green algae, 1.1 ± 2.9%; red algae, 4.1 ± 5.0%; PAC, 0%). For CCA, a remarkably high coverage of 71.4 ± 15.4% was observed in Zanpa. Thus, a dominance of CCA was observed in the natural micro-quadrats.

Benthic coverage of armoring sites (Figs. 3–4)

The transect method showed that non-*Acropora* coral cover was highest at all three armoring sites: Bise (50.6 ± 18.4%), Odo (46.6 ± 24.3%), and Taira (58.7 ± 18.5). In addition, rock and rubble cover was second highest at all three armoring sites: Bise (37.2 ± 15.6%), Odo (33.3 ± 17.2%), and Taira (23.8 ± 13.4%) (Figs. 3 and 4).

In the micro-quadrat method, CCA was found to be dominant at all three sites, 42.8 ± 25.1% at Bise, 37.5 ± 29.2% at Odo, and 30.6 ± 24.5% at Taira. At Odo, non-*Acropora* coral was observed at 36.9 ± 36.8% of cover, followed by CCA, and at Taira, non-*Acropora* coral was observed at 30.7 ± 33.0% of cover, showing the same dominance as CCA. At all three sites, the cover of corals in the microenvironment was more than 20% (Bise, 20.7 ± 27.4%; Odo, 40.3 ± 52.2%; and Taira, 31.6 ± 38.9%), which was higher than that at other sites.

Benthic coverage of land reclamation sites (Figs. 3–4)

Transects showed that rock and rubble cover was the highest in Sunabe and Mizugama (Sunabe, 42.8 ± 22.3%; Mizugama, 54.3 ± 21.9%). Next to rock and rubble, octocorals cover was highest (Sunabe, 38.7 ± 27.1%; Mizugama, 15.9 ± 27.5%). At Makiminato, sand was the highest at 43.7 ± 25.9%. After sand, CCA was the second-most abundant with 16.8 ± 15.3%. Thus, at the three land reclamation sites, abiotic categories were detected at higher values than in the other sites. In addition, the three sites had lower coral cover than the other sites (Sunabe, 5.7 ± 7.3%; Makiminato, 4.7 ± 8.7%; Mizugama, 5.9 ± 6.9%). In addition, *Acropora* coral was not observed at all at Makiminato (Figs. 3 and 4).

In micro-quadrats, sand cover was the highest at all three sites (Sunabe, 36.8 ± 25.5%; Makiminato, 43.7 ± 25.9%; Mizugama, 41.1 ± 30.1%). CCA cover was next highest (Sunabe, 34.0 ± 25.7%; Makiminato, 16.8 ± 15.3%; Mizugama, 31.2 ± 25.0%). Abiotic cover was detected at higher values than at other sites.

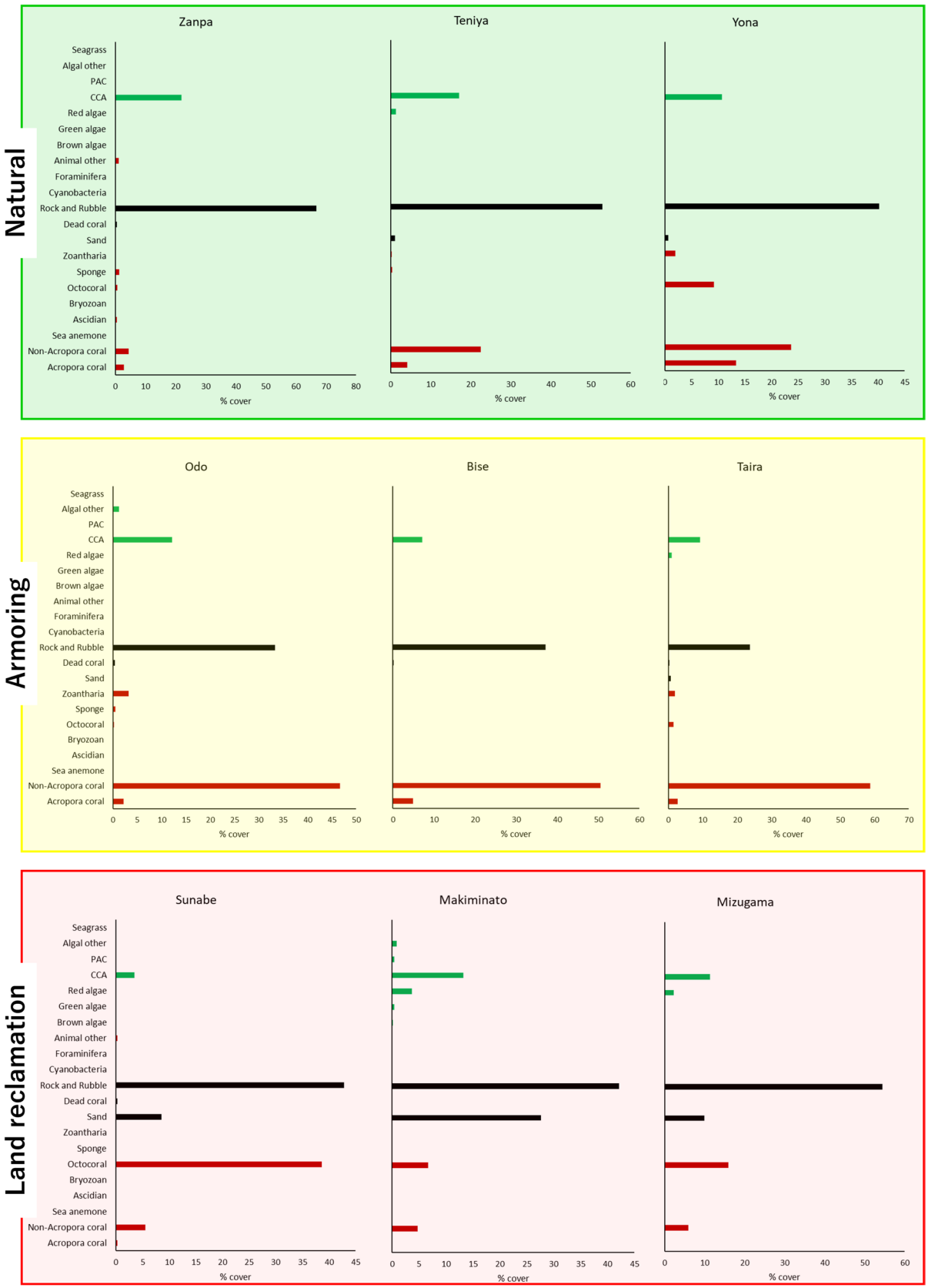

Fig. 3 The percentage cover of the benthic components from transect method

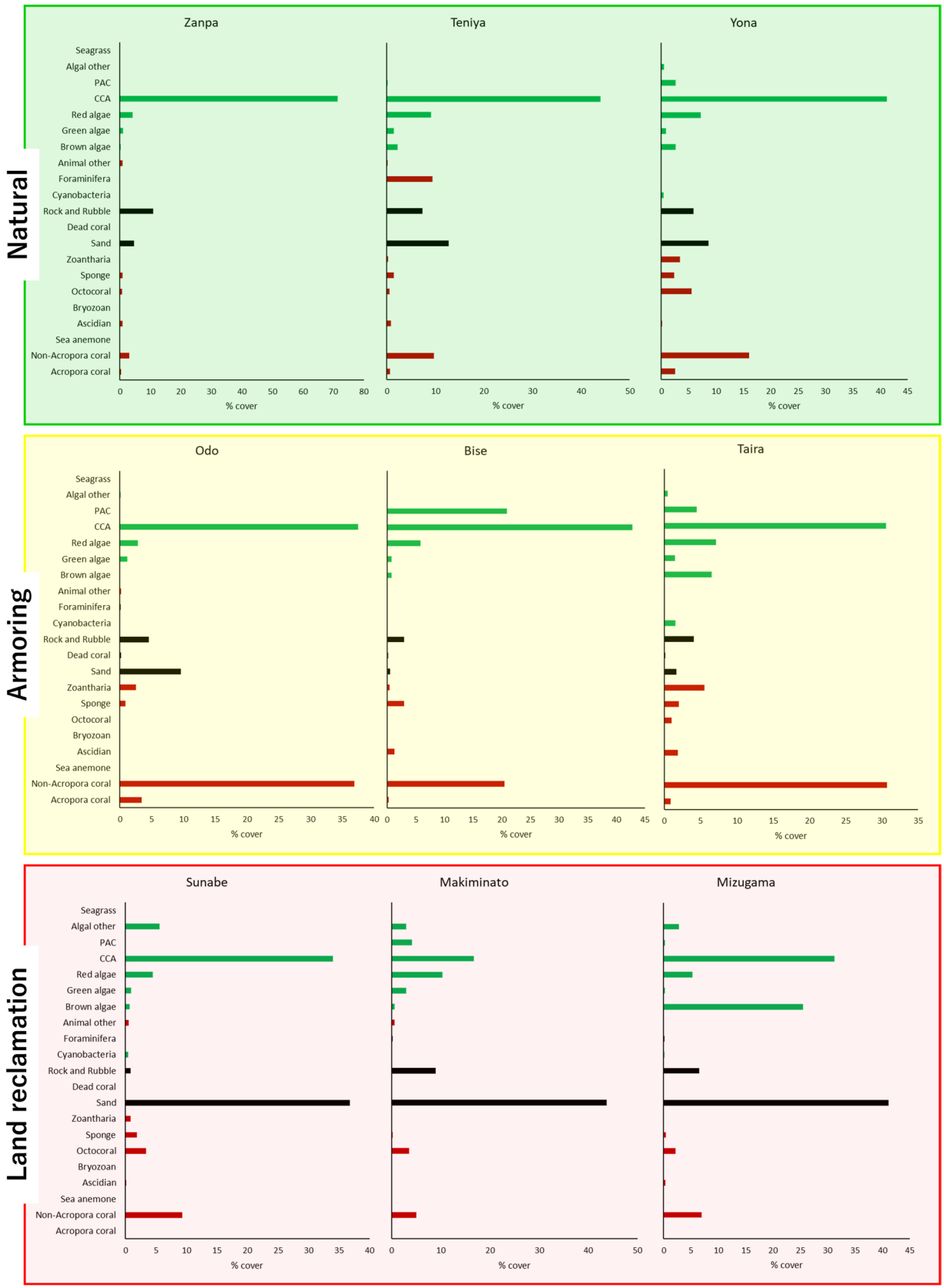

Fig. 4 The percentage cover of benthic components from the micro-quadrat method

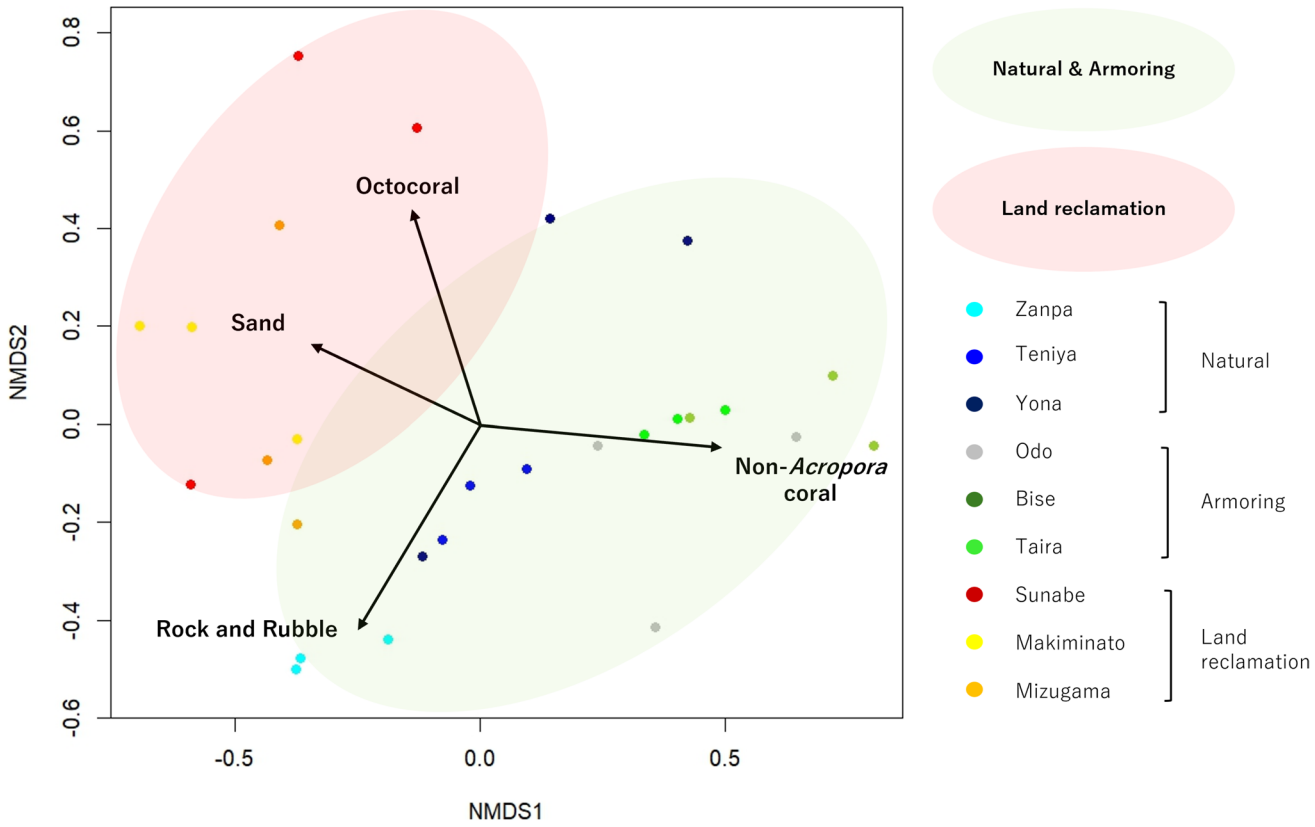

Fig. 5 Non-metric multidimensional scaling (nMDS) plot using Bray–Curtis distances of benthic components from transect data. Arrows that are fitted onto the ordination space using the envfit function in the vegan package indicate the direction and strength of significant benthic components ($p < 0.05$), with their lengths representing the degree of correlation with the ordination

Comparison of benthic community

For the transect results, there was a significant difference in benthic community between sites (PERMANOVA, df = 8, $F = 7.67$, $p < 0.001$). In addition, there were significant differences in their benthic community by coastal development category (PERMANOVA, df = 2, $F = 14.44$, $p < 0.001$; Fig. 5). The envfit results also indicated that sites categorized as natural and armoring were characterized by non-*Acropora* coral or rock and rubble, while sites categorized as land reclamation were characterized by octocoral (mainly soft corals) or sand.

As with the transects, there were significant differences in the benthic community among sites for the micro-quadrats results (PERMANOVA; df = 8, $F = 13.58$, $p < 0.001$). In addition, there were significant differences in their benthic communities by coastal development category (PERMANOVA; df = 2, $F = 15.24$, $p < 0.001$; Fig. 6). The envfit results indicated that sites categorized as natural or armoring are more likely to have non-*Acropora* coral, ascidian, and CCA, and that sites categorized as land reclamation were characterized as sand.

Discussion

This research methodology shows that coastal development is affecting marine ecosystems on a finer scale than previously thought. The changes in the environment of these microhabitats are likely to be a major factor in the overall changes in the ecosystem (Monteiro et al. 2019).

As environmental disturbances such as coastal development alter the structure of coral reefs worldwide, effective ecosystem monitoring is essential to document and understand changes in community composition (Smith et al. 2022). This study demonstrates the importance of understanding biota in microhabitats by focusing on even finer-scale measurements and scales than previous methods.

In addition, surveys using micro-quadrats at natural and armoring sites both detected CCA as the dominant species; CCA cover has been related to sedimentation, with relatively high CCA cover on coral reefs with low sedimentation (Fabricius and De'ath 2001). At least in the microenvironments seen in the present micro-quadrats, CCA and other algae were dominant. For Bise, PAC cover was also observed; PAC is a group of understudied algae, but its rapid

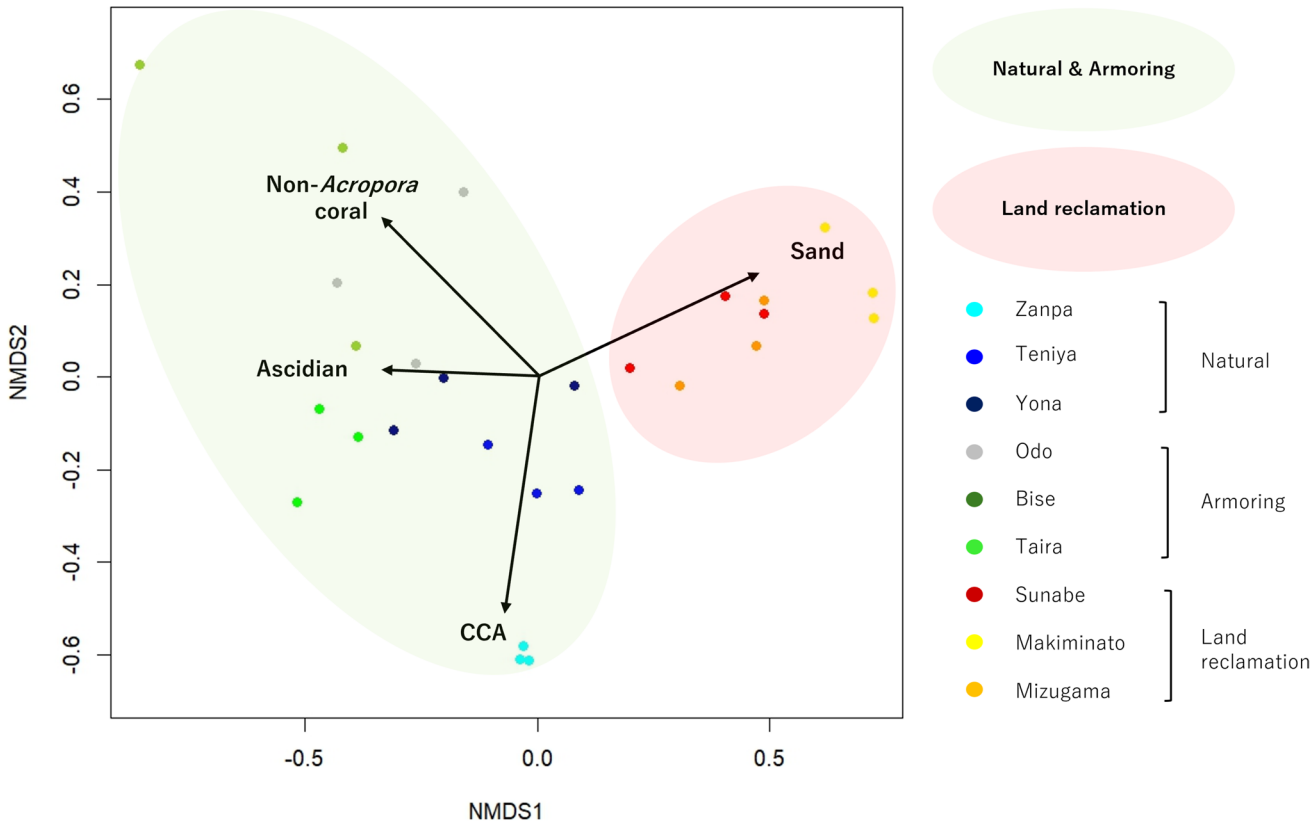

Fig. 6 Non-metric multidimensional scaling (nMDS) plot using Bray–Curtis distances of benthic components from micro-quadrat data. Arrows that are fitted onto the ordination space using the envfit function in the vegan package indicate the direction and strength of significant benthic components ($p < 0.05$), with their lengths representing the degree of correlation with the ordination

coverage expansion has been observed in the Caribbean in recent years and its impact on other organisms is a concern (Edmunds et al. 2019).

At sites categorized as land reclamation, the dominant species were unique compared to other sites. The transect method confirmed that octocoral (mainly soft corals) were the dominant inhabitants (Lalas et al. 2024). Micro-quadrats, on the other hand, had sand cover as the highest. These sites were characterized by higher turbidity due to the inflow of sand and other sediments from the reclaimed road surface drainage and the proximity of a river. Many soft coral species are comparatively less dependent on photosynthesis than many scleractinian coral species because they are able to completely satisfy respiratory losses by heterotrophic feeding (Fabricius and Klumpp 1995), and might therefore inhabit areas with high turbidity and lower levels of photosynthesis (Inoue and Takahashi 2014). In addition, on Okinawa Island, soft coral cover has been seen to be significantly higher in areas of high anthropogenic disturbance (Lalas et al. 2024). This study supports these previous studies regarding the priority of them. Sand had the highest cover at sites categorized as land reclamation, whereas a wide variety of species were detected in micro-quadrats at other sites. This result also suggests that sediments from coastal development have reduced the number of niches (Airoldi 2003).

Analysis of community composition revealed differences in benthic community composition at each site in the transect method. Similarly, the micro-quadrats revealed significant differences in biota at each site. Okinawa Islands and numerous other archipelagos located in coral reef areas have diverse shallow-water habitats due to rivers and rather complex coastlines (Nishihira and Veron 1995), which may explain the diversity of ecosystems in both the macro and microenvironments observed using transects and, particularly effectively, micro-quadrats. Micro-quadrats were conducted in transect areas that were categorized as "non-living". Despite this, a wide variety of species was observed. The benthic biodiversity in dead corals and rubble can be considered higher than the benthic diversity in living corals, which is inferred to be due to the high niche diversity in dead corals and rubble (Enochs and Manzello 2012; Kramer et al. 2014). Thus, our results also strongly suggest that living organism coverage in transect surveys may be severely underestimated.

In addition, the species found in micro-quadrats included small and relatively understudied taxa, such as CCA, and these taxa made the difference between the sites. Thus, the results obtained by this study support those of DiBattista et al. (2020) using eDNA metabarcoding. Comparison of community compositions based on the degree of coastal development (natural, armoring, land reclamation) showed significant differences among communities. This study also indicated that the coastal development that has been progressing on Okinawa Island over the past 100 years is exerting a significant impact on the coastal ecosystems of the main island (Mars Brisbin et al. 2024; Nakajima et al. 2024).

This study used the conventional transect method and a new method, the micro-quadrat method. These methods clearly show the impacts of coastal development, particularly land reclamation, on both macro and micro-ecosystems.

In benthic surveys generally conducted in coastal areas, survey sites are set up with representative locations of the surrounding environment and biota in mind and have the advantage of accurately and quantitatively determining the cover and density of emergent organisms by depth zone (Dotsu et al. 2014). However, the seafloor of Okinawa Island has a variety of environments, including gullies composed of dead corals as well as coral reefs and deep sandy mud bottoms. In this study, micro-quadrat photographs were taken by design as a subset of specific regions of the original transect (those characterized as "abiotic") and were not randomly selected, potentially introducing biases in site selection. However, given our goals of this research, this can be considered unavoidable. It is because by design, we wanted to see if abiotic and uninteresting areas would conceal interesting biomes of communities at a more resolute spatial scale. In addition, in this study, surveys were conducted only at 10 m depth. A random selection of micro-quadrats and replication at additional depths could potentially reveal the presence of taxa not recorded in the present survey or highlight different coverage percentages or distribution patterns. It is difficult to comprehensively cover such complex environments with only micro-quadrats. In fact, the photographs obtained from the micro-quadrats showed different biota, and detailed biota comparisons of each of the micro-quadrats should be conducted in the future. In addition, similarly to other methods of photo-surveys, the micro-quadrats method used in this study requires a long time for both surveys and analyses due to the large number of photographs. Therefore, to make this method more scalable, the use of machine learning may be effective to reduce this human burden (Wäldchen and Mäder 2018).

All marine biota survey methods such as transects and micro-quadrats have strengths and weaknesses. For example, satellite surveys may yield unsatisfactory results in terms of resolution and quality due to their wider survey areas (Tokuyasu et al. 1996). In addition, surveys using eDNA metabarcoding can detect organisms that are difficult to observe visually (Lafferty et al. 2021) but incur costs involved in conducting research studies, as well as have differences in effective protocols depending on the environmental conditions of the study site and target species (Takahara et al. 2016), and external factors such as the location and time of the collection site may affect the composition of the eDNA samples (Gösser et al. 2023). Therefore, to better understand marine biodiversity, it may be necessary to combine multiple survey methods. The micro-quadrat method used in this study can be considered a less expensive method to better quantify organisms at smaller scales (< 1 cm).

Future prospects

The use of 5 cm square quadrats in this study to observe coral reef areas at unconventional scales allowed us to confirm the presence of diverse small benthic organisms and biota in seemingly non-living areas as indicated by transects. In general, coral reef conservation targets fish and scleractinian corals, but other small, understudied taxa also have important ecological roles to play (Hughes et al. 2002). Moreover, fine-scale spatial assessments remain underrepresented in comparative environmental studies aimed at quantifying differences between benthic communities on natural or semi-natural reefs and those along urbanized coastlines, particularly in southern Japan. Incorporating micro-quadrat surveys at unconventional spatial scales offers an opportunity to revisit, confirm, or challenge existing assumptions about how hardened and/or reclaimed shorelines affect shallow-reef biodiversity. Such approaches can provide new insights into which aspects of reclamation design (if any), ranging from wall geometry and surface complexity to overall structure size and hydrodynamic alteration, may be more comparable to the adjacent natural coastline in supporting recruitment, diversity, and ecological functionality.

Notably, Okinawa Island, with its highly fragmented natural coastline (Masucci and Reimer 2019), extensive artificial structures in both high and relatively low-population areas, and overall easy shore access, represents an ideal setting for conducting such comparative studies. Understanding micro-environments is important when considering both the functionality of coral reef ecosystems and clarifying the extent of anthropogenic environmental changes, due to both local stressors, such as those discussed in this publication, and global-level stressors.

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Declarations

Ethics approval and consent to participate No animal testing was performed during this study.

Conflict of interest The authors declare no competing interests.

Sampling and field studies This study does not involve any sampling material, and non-extractive field surveys like this one are permitted by the Okinawa Prefecture.

Data availability Data inquiries can be directed to the corresponding author.

Author contribution Study design: DI and JDR; field work and data gathering: DI; supervision: JDR; data analyses: DI; funding acquisition: JDR; manuscript writing and editing: DI, GDM, and JDR.

References

Airoldi L (2003) The effects of sedimentation on rocky coast assemblages. Oceanography and marine biology. CRC Press, pp 169–171. https://doi.org/10.1201/9780203180570

Baba M (1997) Nongeniculate coralline algae around Akajima Island. Midoriishi 8:4–6 (**in Japanese**)

Baba M, Kato A (2023) Taxonomic and distributional accounts on the non-geniculate coralline algae in Japan. Report of Marine Ecology Research Institute 28:1–252. (**in Japanese**)

Beisiegel K, Dar A, Gogina M, Zettler ML (2017) Benefits and shortcomings of non-destructive benthic imagery for monitoring hard-bottom habitats. Mar Pollut Bull 121(1–2):5–15. https://doi.org/10.1016/j.marpolbul.2017.04.009

Bennett MK, Younes N, Joyce K (2020) Automating drone image processing to map coral reef substrates using Google earth engine. Drones 4(3):50. https://doi.org/10.3390/drones4030050

Biondi P, Masucci GD, Reimer JD (2020) Coral cover and rubble cryptofauna abundance and diversity at outplanted reefs in Okinawa, Japan. PeerJ 8:e9185. https://doi.org/10.7717/peerj.9185

Bolam SG, Fernandes TF, Huxham M (2002) Diversity, biomass, and ecosystem processes in the marine benthos. Ecol Monogr 72(4):599–615. https://doi.org/10.1890/0012-9615(2002)072[0599:DBAEPI]2.0.CO;2

Brett CE, Hendy AJ, Bartholomew AJ, Bonelli JJR, McLaughlin PI (2007) Response of shallow marine biotas to sea-level fluctuations: a review of faunal replacement and the process of habitat tracking. Palaios 22(3):228–244. https://doi.org/10.2110/palo.2005.p05-028r

Burns JHR, Delparte D, Gates RD, Takabayashi M (2015) Integrating structure-from-motion photogrammetry with geospatial software as a novel technique for quantifying 3D ecological characteristics of coral reefs. PeerJ 3:e1077. https://doi.org/10.7717/peerj.1077

Clay CG, Reimer JD, Cook KM, Yamagawa H, Gravener E, Lee THY, Beger M (2023) Temporal functional changes in coral and fish communities on subtropical coastal coral reefs. Mar Freshw Res 74(12):1081–1094. https://doi.org/10.1071/MF22253

Cook KM, Yamagiwa H, Beger M, Masucci GD, Ross S, Lee HYT, Stuart-Smith RD, Reimer JD (2022) A community and functional comparison of coral and reef fish assemblages between four decades of coastal urbanisation and thermal stress. Ecol Evol 12(3). https://doi.org/10.1002/ece3.8736

De'ath G, Fabricius K (2010) Water quality as a regional driver of coral biodiversity and macroalgae on the Great Barrier Reef. Ecol Appl 20:840–850. https://doi.org/10.1890/08-2023.1

DiBattista JD, Reimer JD, Stat M, Masucci GD, Biondi P, Brauwer MD, Wilkinson SP, Chariton CA, Bunce M (2020) Environmental DNA can act as a biodiversity barometer of anthropogenic pressures in coastal ecosystems. Sci Rep 10:8365. https://doi.org/10.1038/s41598-020-64858-9

Dotsu K, Ohta M, Takaku H, Nakao T (2014) Comparing the number of observed species of the belt transect survey and a comprehensive survey at an intertidal rocky area. Report of Marine Ecology Research Institute Contents 19:63–66 (**in Japanese**)

Edmunds PJ, Zimmermann SA, Bramanti L (2019) A spatially aggressive peyssonnelid algal crust (PAC) threatens shallow coral reefs in St. John, US Virgin Islands. Coral Reefs 38:1329–1341. https://doi.org/10.0007/s00338-019-01846-0

Enochs IC, Manzello DP (2012) Species richness of motile cryptofauna across a gradient of reef framework erosion. Coral Reefs 31:653–661. https://doi.org/10.1007/s00338-012-0886-z

Fabricius K, De'ath G (2001) Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. Coral Reefs 19:303–309. https://doi.org/10.1007/s003380000120

Fabricius KE, Klumpp DW (1995) Widespread mixotrophy in reef-inhabiting soft corals: the influence of depth, and colony expansion and contraction on photosynthesis. Mar Ecol Prog Ser 125:195–204. https://doi.org/10.3354/meps

Gösser F, Schweinsberg M, Mittelbach P, Schoenig E, Tollrian R (2023) An environmental DNA metabarcoding approach versus a visual survey for reefs of Koh Pha-ngan in Thailand. Environ DNA 5(2):297–311. https://doi.org/10.1002/edn3.378

Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315. https://doi.org/10.1007/s00338-012-0984-y

Hasegawa H (2011) The decline of coral reef conditions caused by the extensive land modification a case study of the Shiraho area on Ishigaki Island, Okinawa, Japan. J Remote Sens Soc Jpn 31:73–86. https://doi.org/10.11440/rssj.31.73. (**in Japanese**)

Hongo C, Yamano H (2013) Species-specific responses of corals to bleaching events on anthropogenically turbid reefs on Okinawa Island, Japan, over a 15-year period (1995–2009). PLoS ONE 8(4): e60952. https://doi.org/10.1371/journal.pone.0060952

Hughes TP, Bellwood DR, Connolly SR (2002) Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. Ecol Lett 5(6):775–784. https://doi.org/10.1046/j.1461-0248.2002.00383.x

Inoue S, Takahashi A (2014) Assessing the potential for community shift from hard coral to soft coral and its impact. J Jpn Coral Reef Soc 16:29–45. https://doi.org/10.3755/jcrs.16.29. (**in Japanese**)

Jonker M, Johns K, Osborne K (2008) Surveys of benthic reef communities using underwater digital photography and counts of juvenile corals. Long-Term Monitoring of the Great Barrier Reef Standard Operation Procedure Number 10:38–43

Knowlton N (2001) Coral reef biodiversity–habitat size matters. Science 292(5521):1493–1495. https://doi.org/10.1126/science.1061690

Kramer MJ, Bellwood DR, Bellwood O (2014) Benthic Crustacea on coral reefs: a quantitative survey. Mar Ecol Prog Ser 511:105–116. https://doi.org/10.3354/meps10953

Lafferty KD, Garcia-Vedrenne AE, McLaughlin JP, Childress JN, Morse MF, Jerde CL (2021) At Palmyra Atoll, the fish-community

environmental DNA signal changes across habitats but not with tides. J Fish Biol 98(2):415–425. https://doi.org/10.1111/jfb.14403

Lalas JAA, Jamodiong EA, Reimer JD (2024) Spatial patterns of soft coral (Octocorallia) assemblages in the shallow coral reefs of Okinawa Island, Ryukyu Archipelago, Japan: dominance on highly disturbed reefs. Reg Stud Mar Sci. https://doi.org/10.1016/j.rsma.2024.103405

Mars Brisbin M, Dudley KL, Yonashiro Y, Mitarai S, Ares A (2024) Urbanization of a subtropical island (Okinawa, Japan) alters physicochemical characteristics and disrupts microbial community dynamics in nearshore ecosystems. Estuaries Coasts 47(5):1266–1281. https://doi.org/10.1007/s12237-024-01366-3

Masucci GD, Reimer JD (2019) Expanding walls and shrinking beaches: loss of natural coastline in Okinawa Island, Japan. PeerJ 7:e7520. https://doi.org/10.7717/peerj.7520

Monteiro C, Zardi GI, McQuaid CD, Serrão EA, Pearson GA, Nicastro KR (2019) Canopy microclimate modification in central and marginal populations of a marine macroalga. Mar Biodivers 49:415–424. https://doi.org/10.1007/s12526-017-0824-y

Nakajima R, Masucci G, Kuba R, Wee HB, Reimer JD (2024) Son of a beach: coastal development and the loss of natural beaches over time on Okinawa Island, southern Japan. Mar Pollut Bull 212:117459. https://doi.org/10.1016/j.marpolbul.2024.117459

Nishihira M, Veron JEN (1995) Reef-building corals in Japan. Kaiyusha, Japan. (**in Japanese**)

Ogaki S (2009) Quadrats and transects: a theory of coastal survey accuracy. Argonauta 16:16–24 (**in Japanese**)

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2020) Vegan: community ecology package

Pawlowski J, Bruce K, Panksep K, Aguirre FI, Amalfitano S, Apothéloz-Perret-Gentil L, Baussant T, Bouchez A, Carugati L, Cermakova K, Cordier T, Corinaldesi C, Costa FO, Danovaro R, Dell'Anno A, Duarte S, Eisendle U, Ferrari BJD, Frontalini F, Frühe L, Haegerbaeumer A, Kisand V, Krolicka A, Lanzén A, Leese F, Lejzerowicz F, Lyautey E, Maček I, Sagova-Marečková M, Pearman JK, Pochon X, Stoeck T, Vivien R, Weigand A, Fazi S (2022) Environmental DNA metabarcoding for benthic monitoring: a review of sediment sampling and DNA extraction methods. Sci Total Environ 818:151783. https://doi.org/10.1016/j.scitotenv.2021.151783

Preskitt LB, Vroom PS, Smith CM (2004) A rapid ecological assessment (REA) quantitative survey method for benthic algae using photoquadrats with scuba. Pac Sci 58(2):201–209

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing

Reimer JD, Yang SY, White KN, Asami R, Fujita K, Hongo C, Ito S, Kawamura I, Maeda I, Mizuyama M, Obuchi M, Sakamaki T, Tachihar K, Tamura M, Takahara A, Yamaguchi A, Jenke-Kodama H (2015) Effects of causeway construction on environment and biota of subtropical tidal flats in Okinawa, Japan. Mar Pollut Bull 94(1–2):153–167. https://doi.org/10.1016/j.marpolbul.2015.02.037

Smith HA, Einarsson LB, Bourne DG (2022) A stratified transect approach captures reef complexity with canopy-forming organisms. Coral Reefs 41:897–905. https://doi.org/10.1007/s00338-022-02262-7

Tabugo SRM (2016) Coral reef assessment and monitoring made easy using Coral Point Count with Excel extensions (CPCe) software in Calangahan, Lugait, Misamis Oriental, Philippines. Comput Ecol Softw 6(1):21

Takahara T, Yamanaka H, Minamoto T, Doi H, Uchii K (2016) Current state of biomonitoring method using environment DNA analysis. J Ecol Soc Jpn 66(3):583–599. https://doi.org/10.18960/seitai.66.3_583. (**in Japanese**)

Tokuyasu T, Yamazato T, Katayama M, Ogawa A (1996) A study of the system for observing ecology of sea animals utilizing low orbit satellite. Proceedings of the Communications Society Conference of IEICE, pp 541–542. (**in Japanese**)

Vermeiji MJA (2006) Early life-history dynamics of Caribbean coral species on artificial substratum: the importance of competition, growth and variation in life-history strategy. Coral Reefs 25:59–71. https://doi.org/10.1007/s00338-005-0056-7

Wäldchen J, Mäder P (2018) Machine learning for image based species identification. Methods Ecol Evol 9(11):2216–2225. https://doi.org/10.1111/2041-210X.13075

Wickham H, Bryan J (2019) Readxl: read excel files. R package version 1.3.1. computing. R Foundation for Statistical Computing, Vienna, Austria