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Abstract Goatfishes (family Mullidae) are a common fish group and important fishery target in coral reefs. This study examined the species-specific and size-related spatial distribution of seven goatfish species in relation to environmental characteristics as well as their variations in substrate utilization for foraging in an Okinawan coral reef. All size classes (5-32 cm in total length) of four species (*Parupeneus barberinoides*, *P. barberinus*, *P. pleurostigma*, and *Mulloidichthys flavolineatus*) showed greater densities at sites with a greater coverage of sand in inner reefs and significant positive utilization of sand as feeding substrates. For *P. multifasciatus*, smaller (≤ 10 cm) and larger-sized individuals (11-25 cm) showed greater density at sites with a greater coverage of macroalgae in inner reefs and greater coverage of coral rubble in exposed and inner reefs, respectively. *Parupeneus multifasciatus* also showed positive utilization of rock and coral rubble as feeding substrates. Most size class individuals of *P. cyclostomus* (≤ 10 cm and 16-25 cm) and *M. vanicolensis* (11-25 cm) showed greater densities at sites with a greater coverage of rock, branching *Acropora* spp. and other corals. *Parupeneus cyclostomus* also utilized rock, dead corals, and coral rubble as feeding substrates but such utilization was not significant. *Mulloidichthys vanicolensis* showed no feeding behavior. This study indicated that a greater coverage of sand, coral rubble, and rock has positive effects on the spatial distribution of goatfish assemblages, suggesting that the coverage of non-coralline substrates is an important indicator for selecting candidate marine protected areas for maintaining the diversity of goatfish species.

Keywords Spatial distribution • Feeding substrate • Goatfish • Coral reef • Species diversity • Environmental characteristics

Introduction

Coral reefs support a high species diversity of marine organisms, and diverse environmental characteristics are the primary factors maintaining the high species diversity. Among marine organisms, coral reef fishes are highly diverse, and show species-specific spatial distributions in relation to various environmental characteristics which has been shown to promote the coexistence of fish species (Nanami et al., 2005; Goatley et al., 2016; Eurich et al., 2018). Marine protected areas (MPAs) are effective tools for conserving, enhancing, and restoring diverse fish assemblages (Russ, 2002; Sobel and Dahlgren, 2004; Green et al., 2013). In establishing effective MPAs, it is necessary to clarify the actual spatial distributions of target fish species in relation to their habitat characteristics (Roos et al., 2020). In addition, clarifying the spatial distribution of all life stages (e.g., newly settled juveniles, non-adult fishes and adults) should be considered in order to protect target fish species by MPAs (Green et al., 2015). Thus, species-specific and size-related spatial distributions of target fish species require individual assessment.

Various environmental characteristics (e.g., coral morphology, coral coverage, and wave exposure) that are provided by coral reefs have been considered as critical indicators of the species-specific and size-related spatial distribution of coral reef fishes (Williams, 1991; Fulton et al., 2001; Friedlander et al., 2003). Given their complex physical structure, live corals provide refuge space and shelter for many coral reef fish species. Especially, live corals with a fine structure (e.g., branching and bottlebrush corals) are frequently utilized by smaller-sized fish species such as damselfishes, gobies, cardinalfishes and angelfishes (Gardiner and Jones, 2005; Wilson et al., 2008; Wen et al., 2013; Doll et al., 2021; Nanami, 2023). Abiotic factors (e.g., reef zonation, topographic complexity, shelf position, and degree of wave exposure) can also affect the spatial distribution of coral reef fishes (Luckhurst and Luckhurst, 1978; McCormick, 1994; Fulton and Bellwood, 2002; Depczynski and Bellwood, 2005; Benthuysen et al., 2022). For example, various types of reef zonation (reef flat, reef crest and reef slope) as well as shelf position (inner, mid and outer shelfs) support species-specific fish distributions of surgeonfishes (Russ, 1984), rabbitfishes (Hoey and Bellwood, 2008), butterflyfishes (Emslie et al., 2010), wrasses (Fulton and Bellwood, 2002) and small cryptic fishes (gobies and blennies: Depczynski and Bellwood, 2005).

Identifying the feeding substrates of fishes is also essential to understand the patterns in their spatial distribution from the aspect of feeding behavior, because foraging is crucial for fish survival and growth. For example, some butterflyfish species utilize live corals as feeding substrates, suggesting that a greater coverage of live corals leads to greater fish densities (Pratchett et al., 2013). The spatial distribution of some grouper and parrotfish species was not necessarily associated with the coverage of live corals (Nanami, 2021), which is likely related to the greater density of benthic crustaceans in non-coralline substrates (dead coral and coral rubble) rather than live corals (Kramer et al., 2014, 2016), or greater availability of epilithic algae on non-coralline substrates (Nanami, 2016). In addition, some fish groups are associated with sponges because they utilize the sponges as feeding substrates (Coppock et al., 2024). These studies have suggested that the feeding substrate of fishes is a factor regulating the species-specific spatial distribution of fishes.

Goatfishes (family Mullidae) are a common fish group in coral reefs, and they primarily prey on benthic animals (Gosline, 1984; Sano et al., 1984; Wahbeh and Ajiad, 1985; Kolansinski et al., 2009, Mittelheiser et al., 2022). Given their foraging behavior using their characteristic feeding apparatus (barbels), they play an important role in coral reef ecosystems

(Uiblein, 2007). Goatfishes promote re-suspension of soft sediments (e.g., sand and coral rubble) by sweeping, excavating, and shoveling to search for prey items (McCormick, 1995; Krajewski et al., 2006). Broad-scale studies have shown the difference in goatfish assemblage structures among different reef zones with different degrees of wave exposure (McCormick, 1995; Sarhan et al., 2014). In addition, since some goatfish species are important fishery targets in coral reefs (Russ et al., 2015; Trianni et al., 2018), MPAs have been established to enable recovery of goatfish populations (Williams et al., 2006).

Although goatfishes are the main components and fishery targets in Okinawan coral reefs (Akita et al., 2016; Samejima et al., 2021; Samejima and Tachihara, 2022), conservation strategies have not been established in this region yet. Thus, ecological studies on the spatial distribution and feeding substrates of goatfishes are necessary to establish effective conservation methods. In order to do this, the relationship between spatial distribution and feeding substrates needs to be also clarified. This study investigated the spatial distribution and feeding substrate utilization of goatfish species on an Okinawan coral reef. In particular, this study examined (1) the species-specific and size-related spatial distribution in relation to environmental characteristics, (2) the species-specific substrate utilization for foraging in relation to substrate availability, and (3) the relationship between spatial distribution and feeding substrates of seven goatfish species. The results of this study help to clarify the environmental characteristics that require being focused on to propose effective conservation strategies for protecting the species diversity of goatfishes.

Materials and methods

Study site

This study was conducted at 63 study sites that were established in Sekisei Lagoon and Nagura Bay, Yaeyama Islands, Okinawa (Figs. 1a, 1b). Underwater observations of goatfishes were conducted over 14 days from June to September 2020 (12 sites in 2 days in June, 26 sites in 6 days in July, 22 sites in 4 days in August, and 3 sites in 2 days in September). The distance between two neighbor study sites among the 63 study sites was approximately 2 km. Among the 63 study sites, 29 and 34 were located in exposed reefs and inner reefs, respectively (Fig. 1c). The exposed reefs had a greater coverage of corymbose *Acropora* spp., *Pocillopora* spp., encrusting corals, foliose corals, soft corals, and rock, whereas inner reefs consisted of a greater coverage of branching *Acropora* spp., bottlebrush *Acropora* spp., mushroom corals, dead corals, coral rubble, sand, and macroalgae (Nanami, 2020).

Data collection of fish and environmental characteristics

Nanami (2018) provided details of underwater observations and measurements of environmental characteristics. A 20-min time transect was set (transect width = 5 m) in each site during the daytime (0830–1600 h). The first diver recorded the number of fish individuals and their total length (TL) on the time transect by scuba diving. The second diver followed the first diver (within 1 m behind) by scuba diving, and towed a buoy with a portable GPS receiver attached (GARMIN GPSMAP 60CS). By this procedure, the portable GPS recorded the distance of each time transect. The average distance of a 20-min transect was 353.8 m ± 38.8 standard deviation. The water depth was recorded every 1 min using a diving computer during the 20-min observation. The average water depth ranged from 3.2 m to 12.5 m.

Digital video images of the substrate were recorded to evaluate substrate availability in each site. QuickTime Player Pro (version 7.6) was used to obtain static images at 10-s intervals, and 121 static images were obtained per 20-min video image. The substrate at the center of each static image was recorded, and the data from 121 static images at each site were pooled for analysis. The substrate was categorized into 16 types for analysis, following Nanami (2018): (1) branching *Acropora* spp., (2) bottlebrush *Acropora* spp., (3) tabular *Acropora* spp., (4) branching corals except for *Acropora* spp. (e.g., branching *Pocillopora* spp., *Montipora* spp., and *Porites* spp.), (5) massive corals (e.g., massive *Porites* spp. and Faviidae spp.), (6) other live corals (e.g., encrusting corals and foliose corals), (7) dead branching *Acropora* spp., (8) dead bottlebrush *Acropora* spp., (9) dead tabular *Acropora* spp., (10) dead branching corals, (11) other dead corals, (12) soft corals, (13) rock (coral pavement with a complex physical structure), (14) coral rubble, (15) sand, and (16) macroalgae (e.g., *Padina minor* and *Sargassum* spp.).

Analysis of the spatial distribution of fish in relation to environmental characteristics

Underwater observations revealed seven dominant species (*Parupeneus barberinoides, P. barberinus, P. pleurostigma, P. multifasciatus, P. cyclostomus, Mulloidichthys flavolineatus*, and *M. vanicolensis*) across all 63 sites (Fig. S1). Thus, these species were selected in this study. Since distance of each time transect was recorded by using a portable GPS receiver, the number of individuals was converted into density (number of individuals per 100 m distance × 5 m wide) using the distance data.

Individual fish were categorized into five size classes: class 1 (TL ≤ 10 cm), class 2 (11 cm ≤ TL ≤ 15 cm), class 3 (16 cm ≤ TL ≤ 20 cm), class 4 (21 cm ≤ TL ≤ 25 cm), and class 5 (TL ≥ 26 cm). Pie charts were used to show the size-related spatial distribution of each species.

For each fish species and each size class, a generalized linear model (GLM) was applied to examine the significant difference in fish density between the exposed and inner reefs using R statistical computing language (function "glm": R Core Team, 2023). The objective and explanatory variables were fish density and reef type (i.e. exposed reefs or inner reefs), respectively. The data were assumed to follow a Poisson distribution with a log-link function. Considering that the fish count data at each site were obtained from a 20-min survey, the length of each time transect varied among the 63 sites. Thus, fish data were analyzed using the "offset" option in the R package and the length of each time transect.

The relationship between the spatial distribution of each size class individual of the each species and 17 environmental characteristics (16 types of substrates and water depth) was analyzed by performing redundancy analysis (RDA) in CANOCO software (Ter Braak and Smilauer, 2002). Before the analysis, the fish density data were log (x + 1) transformed. For environmental variables, principal component analysis (PCA) was performed to avoid multi-collinearity among the previously mentioned 17 environmental characteristics using PRIMER software (version 6). The PCA provided the principal component scores for 63 study sites along with the five PC axes. Thus, these principal scores were used as environmental variables for the RDA. Software options for forward selection were applied to extract the environmental variables (PC axes) that significantly affected the spatial distribution of fish.

Feeding substrates

To examine the foraging substrates, additional underwater observations were conducted from April to December 2022 at 17 sites (Fig. 1d). After searching for the aforementioned seven species, foraging behavior was observed while keeping a distance of several meters from the focal individual to avoid scaring the fish. The substrate that was initially foraged by the focal individual and TL of the focal individual were recorded. For analysis, substrates were categorized into seven types: (1) rock, (2) coral rubble, (3) sand, (4) live corals, (5) dead corals, (6) soft corals, and (7) macroalgae. To examine species-specific differences in feeding substrates, PCA was performed. In this method, two procedures were applied as: (1) data obtained from various size classes were pooled to examine the species-level differences in feeding substrates, and (2) data obtained from various size classes were separately analyzed to examine any size class differences in use of feeding substrates. Since the feeding behavior for *M. vanicolensis* was not observed, this species was excluded from the analysis.

In addition, resource selection ratio (Manly et al., 2002) was applied to examine the selectivity in feeding substrate which is calculated as follows:

$$w_i = o_i / \pi_i$$

where w_i is the resource selection probability function, o_i is the proportion of the *i*th substrate that was foraged by a focal fish species, and π_i is the proportion of the *i*th substrate that was available in the study area (Manly et al., 2002). For multiple comparisons, Bonferroni Z corrections was used to calculate the 95% confidence interval (CI) for each w_i which is calculated as follows:

$$95\%\ \mathrm{CI} = Z_{a/2I} \sqrt{[\, o_i (1- o_i) / (U_+ \pi_i^2)]}$$

where $Z_{a/2I}$ is the critical value of the standard normal distribution corresponding to an upper tail area of $a/2I$ (a is 0.05), I is the number of substrate categories (i.e., $I = 7$), and U_+ is the total number of individuals of the focal fish species. Substrates with $w_i \pm$ 95% CI above and below 1 indicated significantly positive and negative (non-positive, not avoidance) utilization as feeding substrates, respectively. Substrates with w_i ± 95% CI encompassing 1 indicated no significantly positive or negative utilization as feeding substrates.

Substrate data were also collected by using the 20-min video recordings at the 17 sites where the data of feeding substrates were collected (Fig. 1d). Then, the substrate data at the 17 sites were pooled for the analysis. Since the PCA revealed a similar trend in feeding substrates among the different size classes for each species (see Results), the data of feeding substrates for the different size classes were pooled for each species.

Results

Overall trends in the spatial distribution

The pie charts and results of GLM showed the species-specific and size-related spatial distribution of the seven species at the 63 sites (Fig. 2, Table 1). Five species (*Parupeneus barberinoides, P. barberinus, P. pleurostigma, Mulloidichthys flavolineatus*, and *M. vanicolensis*) primarily showed greater density in inner reefs (Figs. 2a-2c, 2f, 2g, Table 1). For *P. multifasciatus*, size class 1 individuals showed greater density in inner reefs, whereas size classes 2, 3 and 4 individuals showed no significant differences in density between the exposed and inner reefs (Fig. 2d, Table 1). For *P. cyclostomus*, size class 1 individuals were observed in the exposed reefs only, whereas size classes 2, 3, and 4 individuals showed no significant differences in density between the exposed and inner reefs (Fig. 2e, Table 1).

Species-specific and size-related spatial distribution

The results of PCA revealed the relationship between 17 environmental characteristics and five PC axes (Table S1). For PC axis 1, the plus direction represented a greater coverage of rock, whereas the minus direction represented a greater coverage of coral rubble and sand (Fig. S2a). For PC axis 2, the plus direction represented a greater coverage of sand and rock, whereas the minus direction represented a greater coverage of branching *Acropora* spp., bottlebrush *Acropora* spp., and macroalgae (Fig. S2b). For PC axis 3, the plus direction represented a greater coverage of coral rubble, whereas the minus direction represented a greater coverage of branching *Acropora* spp., bottlebrush *Acropora* spp. and macroalgae (Fig. S2c). For PC axis 4, the plus direction represented a greater coverage of macroalgae, whereas the minus direction represented a greater coverage of branching *Acropora* spp. and other live corals (Fig. S2d).

The results of RDA revealed the species-specific and size-related variations in the spatial distribution of fish in relation to substrate characteristics, and four PC axes (PC axes 1, 2, 3 and 4) significantly affected the spatial distribution of the goatfishes (Fig. 3).

Parupeneus barberinoides: the species scores of all size classes were plotted in the minus direction of PC axis 1 and at the plus directions of PC axis 2 (Fig. 3a), indicating that all size classes were primarily found at sites with a greater coverage of sand (Fig. S2).

Parupeneus barberinus: the species scores of size classes 1, 3, 4, and 5 were plotted in the minus direction of PC axis 1 and in the plus direction of PC axis 2 (Fig. 3b), indicating that these size classes were primarily found at sites with a greater coverage of sand (Fig. S2). By contrast, the species score of size class 2 was plotted in the plus direction of PC axis 4 (Fig. 3b), indicating that this size class was primarily found at sites with a greater coverage of macroalgae.

Parupeneus pleurostigma: the species scores of all size classes were plotted in the minus direction of PC axis 1 and in the plus direction of PC axis 2 (Fig. 3c), indicating that all size classes were primarily found at sites with a greater coverage of sand (Fig. S2).

Parupeneus multifasciatus: the species scores of size class 1 and three size classes (class 2, 3, and 4) were plotted in the plus directions of PC axis 4 and PC axis 3, respectively (Fig. 3d). This indicates that size class 1 was primarily found at sites with a greater coverage of macroalgae, whereas classes 2, 3, and 4 were found at sites with a greater coverage of coral rubble (Fig. S2).

Parupeneus cyclostomus: the species scores of size classes 1 and 3 were plotted in the plus direction of PC axis 1 (Fig. 3e), indicating that these size classes were primarily found at sites with a greater coverage of rock (Fig. S2). The species score of size class 2 was plotted in the plus direction of PC axis 4 (Fig. 3e), indicating that size class 2 was primarily found at sites with a greater coverage of macroalgae (Fig. S2). The species score for size class 4 was plotted at the minus direction of PC axes 3 and 4 (Fig. 3e), indicating that size class 4 was primarily found at sites with a greater coverage of branching *Acropora* spp., bottlebrush *Acropora* spp., and other live corals (Fig. S2).

Mulloidichthys flavolineatus: the species scores of all size classes were plotted in the plus direction of PC axis 2 (Fig. 3f), indicating that that all size classes were primarily found at sites with a greater coverage of sand (Fig. S2).

Mulloidichthys vanicolensis: the species score of size class 2 was plotted in the minus direction of PC axis 4 (Fig. 3g), indicating that size class 2 was primarily found at sites with a greater coverage of branching *Acropora* spp. and other live corals (Fig. S2). Species scores of two size classes (classes 3 and 4) were plotted in the plus direction of PC axis 1 (Fig. 3g), indicating that these size classes were found at sites with a greater coverage of rock (Fig. S2). The species score of size class 5 was plotted in the plus direction of PC axis 3 (Fig. 3g), indicating that size class 5 was found at sites with a greater coverage of coral rubble (Fig. S2).

Overall, the species scores of most species and size class individuals were plotted in the minus direction of PC axis 1 and plus directions of PC axes 2 and 3, indicating positive associations at sites with a lower coverage of rock as well as a greater coverage of sand and coral rubble in inner reefs (Figs. 3h, 3i).

Feeding substrates

Parupeneus barberinoides showed a greater frequency of foraging on sand and a lower frequency of foraging on rock and coral rubble (Figs. 4a, 5). This trend was relatively consistent among all size classes (Fig. S3a). This species showed a significant positive utilization of sand as a feeding substrate (Table 2).

Parupeneus barberinus showed a greater frequency of foraging on sand and a lower frequency of foraging on coral rubble (Figs. 4b, 5). This trend was relatively consistent among all size classes (Fig. S3b). This species showed a significant positive utilization of sand as a feeding substrate (Table 2).

Parupeneus pleurostigma showed foraging on sand only (Figs. 4c, 5), and this behavior was observed for all size classes (Fig. S3c). This species showed a significant positive utilization of sand as a feeding substrate (Table 2).

Parupeneus multifasciatus showed a greater frequency of foraging on rock and coral rubble, and lower frequency on sand (Figs. 4d, 5). This trend was observed for all size classes (Fig. S3d). This species showed significant positive utilizations of rock and coral rubble but negative utilization of sand as a feeding substrate (Table 2).

Parupeneus cyclostomus showed foraging on rock, dead corals, and coral rubble

(Figs. 4e, 5). This trend varied among size classes (Fig. S3e). This species showed no significant utilizations of any substrates as a feeding substrate (Table 2).

Mulloidichthys flavolineatus showed foraging on sand only (Figs. 4f, 5), and this behavior was observed for all size classes (Fig. S3f). This species showed a significant positive utilization of sand as a feeding substrate (Table 2).

Discussion

Spatial distribution of goatfishes in relation to feeding substrates

This study examined the species-specific spatial distribution of goatfishes in relation to environmental characteristics including topographic features (exposed reefs and inner reefs) as well as substrate characteristics (live corals, dead corals and non-coralline substrates). Numerous coral reef fishes showed the species-specific distribution in relation to topographic features. Namely, both exposed reef dominant and inner reef dominant species have been found in major coral reef fish groups such as damselfishes (Williams, 1991; Meekan et al., 1995; Nanami and Nishihira, 2002), wrasses (Green, 1996; Fulton et al., 2001), butterflyfishes (Emslie et al., 2010; Nanami, 2020), parrotfishes (Hoey and Bellwood, 2008; Hernández-Landa et al., 2014), groupers (Nanami, 2021) and other fish groups (Russ, 1984; Newman et al., 1997; Nemeth and Appeldoorn, 2009). This study showed that four goatfish species (*Parupeneus barberinoides*, *P. barberinus*, *P. pleurostigma* and *Mulloidichthys flavolineatus*) showed greater densities in inner reefs, or were only found in inner reefs. These four species showed greater densities at sites with a greater coverage of sand, suggesting a positive association with sand in the inner reefs. These results are contrary to that of numerous previous studies that showed positive associations between coral reef fishes and substrates with complex physical structures. For example, many coral reef fish species are positively associated with live corals with complex physical structures (Gardiner and Jones, 2005; Wilson et al., 2008; Pratchett et al., 2016; Doll et al., 2021; Nanami, 2023). The four goatfish species also showed significant positive utilizations of sand as a feeding substrate. A greater proportion of sand utilization has also been reported for two species (*P. barberinus* and *M. flavolineatus*) from the Great Barrier Reef (McCormick, 1995; Lukoschek and McCormick, 2001). These suggest that the coverage of sand is the main factor regulating the spatial distribution of the four goatfish species.

For *P. multifasciatus*, a greater density of size class 1 (TL ≤ 10 cm) was found at sites with a greater coverage of macroalgae in inner reefs. Although three size classes (classes 2, 3, and 4) did not show a significant difference in density between the exposed and inner reefs, greater densities were found at sites with a greater coverage of coral rubble. This suggests that this species was positively associated with non-coralline substrates that have less complex physical structures, which is contrary to other coral reef fish groups. Russ et al. (2015) have also shown that the density of this species increased as the live coral coverage decreased in the central Philippines. In addition, *P. multifasciatus* showed a significant positive utilization of rock and coral rubble, which is a clear difference in the feeding substrates from the aforementioned four goatfish species. This indicates that a greater coverage of coral rubble is the main factor regulating the spatial distribution of this species. However, it is also shown that a greater coverage of macroalgae does not contribute to the feeding substrates of size class 1 individuals. Size class 1 individuals might utilize the coverage of macroalgae as a refuge space, but not as a feeding substrate. By contrast, greater proportions in the utilization of algae as a feeding substrate have been reported in the Great

Barrier Reef (McCormick, 1995), suggesting a possible geographical variation in substrate utilization for feeding.

For *P. cyclostomus*, three size classes (class 1, 3, and 4) showed greater densities at sites with a greater coverage of rock, branching *Acropora* spp. and other corals. Since rock and live corals have complex physical structures, the substrate types might provide a refuge space for this species. In addition, this species utilized rock, dead corals, and coral rubble as feeding substrates, but such substrate utilization was not significant. Kramer et al. (2014, 2016) revealed that a greater abundance of small-sized crustaceans inhabited dead corals and coral rubble rather than live corals, and several species of wrasse utilized dead corals and coral rubble as feeding substrates. Thus, the greater density of crustaceans in dead corals and coral rubble is likely to explain the reason why this species utilized these substrates for feeding. These ecological aspects are different from those of the aforementioned five goatfish species. In contrast, *P. cyclostomus* showed a greater proportion in the utilization of sand as a feeding substrate in the Great Barrier Reef (McCormick, 1995). Thus, geographical variation in substrate utilization for feeding might also be observed for this species.

For *M. vanicolensis*, three size classes (size class 2, 3, and 4) showed greater densities at sites with a greater coverage of rock, branching *Acropora* spp., and other corals. Considering that no feeding behavior on these substrates was observed, these substrates were unlikely to be feeding substrates of this species. By contrast, this species has been shown to utilize sand as a feeding substrate and feed on sand-dwelling animals (Randall et al., 1997; Disalvo et al., 2007). Thus, substrates with complex physical structures could serve as a refuge space for this species.

Size-related variations in spatial distribution

This study also examined the size-related differences in the spatial distribution of the goatfishes. Among the seven species, four species (*Parupeneus barberinoides*, *P. barberinus*, *P. pleurostigma* and *Mulloidichthys flavolineatus*) showed relatively lower variations in spatial distribution among the different size classes. All size classes were found at sites with a greater coverage of sand. These four species likely settle at sites with a greater coverage of sand and grow at the sites.

For *P. multifasciatus*, size class 1 individuals showed a seven-fold greater density in inner reefs than in exposed reefs (average number of individuals per 100 m × 5 m: inner vs. exposed = 2.15 vs. 0.32), whereas other size classes (size class 2, 3, and 4) showed no significant difference in density between the exposed and inner reefs. This suggests that juveniles settle at sites in the inner reefs and expand their distributional range as they grow.

By contrast, size class 1 individuals of *P. cyclostomus* were only found in the exposed reefs, whereas the other size classes (size class 2, 3, and 4) showed no significant difference in density between the exposed and inner reefs. Although this result indicates that juveniles might preferentially settle in exposed reefs and then expand their distributions after settlement, this trend should be further examined in the future as fish densities for all size classes were low, and the overall trend in size-related spatial distributions was unclear in this study.

For *M. vanicolensis*, the pattern in size-related spatial distribution was unclear. Fish schools consisting of size classes 2, 3, and 5 occurred in the inner reefs only, whereas fish school consisting of size class 4 was found in the exposed reefs only. It is suggested that this species occurs in both exposed and inner reefs. Since no size class 1 individuals were found in this study, the ecological aspects about juvenile settlement of this species could not be examined in this study.

Implications for conservation of goatfish assemblages

Considering that live corals primarily support the diversity of fish species by providing refuge spaces and shelters for fishes, protecting coral-rich sites and restoring coral assemblages have been recommended to keep and enhance species diversity of coral reef fishes (reviews in Pratchett et al., 2008). This recommendation is particularly appropriate if such coral-rich sites are susceptible to coral bleaching and crown-of-thorns starfish outbreaks (Barton et al., 2015; Lirman and Schopmeyer, 2016). On the other hand, this study showed that the coverage of sand, coral rubble, and rock has greater positive effects on the spatial distribution for goatfish assemblages. This suggests that coverages of non-coralline substrates are useful indicators for selecting potential MPAs to maintain the species diversity of goatfishes. Russ et al. (2015) have also shown that a decrease of live coral coverage led to an increase of goatfish fish density in the central Philippines. Considering that some goatfish species showed diel movement (Holland et al., 1993; Meyer et al., 2000), the spatial distribution of the seven goatfish species might be different between daytime and nighttime. In addition, some fish species show different substrate associations between daytime and nighttime (Nanami, 2024). Thus, clarifying the species-specific nocturnal substrate associations would be useful for considering the critical sites and substrates for the conservation of goatfish assemblages.

This study did not examine the seasonal difference in the spatial distribution of goatfishes. In addition, foraging behavior of two species (*P. cyclostomus* and *M. vanicolensis*) was not sufficiently examined due to the small sample size or lack of observations. Thus, the results of this study might have some limitations to apply to an overall conservation strategy for all species of goatfishes in Okinawan coral reefs. These limitations should be improved to obtain more robust results to enable a more comprehensive understanding of ecological aspects of goatfishes in this region.

Conclusion

This study examined species-specific and size-related spatial distribution of seven goatfish species in an Okinawan coral reef, which is the first study in this region. The results demonstrated significant positive associations between goatfish species and non-coralline substrates (sand, coral rubble, and rock). These positive associations with non-coralline substrates were significantly related with their feeding substrates. Most goatfish species showed a greater proportion of utilization of sand, coral rubble, and rock. These trends also showed species-specific and size-related variations among the seven goatfish species, indicating diverse manner of substrate associations among the various size classes of the seven species. These results are different from those for other coral reef fish groups, which generally show significant positive associations with live corals as refuge space and/or feeding substrates. The results of this study indicate the importance of non-coralline substrates for protecting species diversity of goatfishes by using conservation strategies such as MPAs. Since coral reef fishes consist of very diverse species, protection of the sites with a greater coverage of sand, coral rubble and rock would contribute to protect some fish groups which are associated with these non-coralline substrates.

Acknowledgments

I express my grateful thanks to Masato Sunagawa, Masamitsu Sunagawa and Sho Sunagawa for their field guide, Nobuo Motomiya, Kenta Oishi, Fumihiko Nakamura, Minoru Yoshida and Kenji Aramoto for field assistance, and the staff of Yaeyama Field Station of Fisheries Technology Institute for support during the present study. This study was supported by Environment Research and Technology Development Fund (S-15-3(4): JPMEERF16S11513) of the Ministry of the Environment, Japan and JSPS KAKENHI Grant Number 19K06199. Constructive comments from two anonymous reviewers were much appreciated. The author would like to thank Chris Norman for the English language review. The present study complies with the current laws in Japan.

Funding This study was supported by Environment Research and Technology Development Fund (S-15-3(4): JPMEERF16S11513) of the Ministry of the Environment, Japan and JSPS KAKENHI Grant Number 19K06199.

Conflict of interest The authors declare no conflict of interest.

Ethical approval No animal testing was performed during this study

Field studies All data was obtained only by field observations, which do not require a field permit in Okinawa.

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Author contribution Atsushi Nanami conceptualized and designed the study and conducted all formal analysis, data curation and writing.

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Figure captions

Fig. 1. Maps showing the location of the Yaeyama Islands (a), study area (b), the 63 study sites used for underwater observations of spatial distributions (c), and the 17 study sites for underwater observations of feeding behavior (d). In (c), magenta and yellow symbols indicate the sites in the exposed reefs and inner reefs, respectively. The aerial photographs used in (b - d) were provided by the International Coral Reef Research and Monitoring Center.

Fig. 2. Spatial distributions of the seven goatfish species. Circle diameter and five different colors (white, yellow, green, blue and magenta) represent the fish density per 100m × 5m and different size classes, respectively. The aerial photographs were provided by the International Coral Reef Research and Monitoring Center. No individuals of size class 1 were found for *Mulloidichthys vanicolensis*. Fish photographs were taken by the author (A. Nanami).

Fig. 3. Results of redundancy analysis (RDA), demonstrating the relationship between the size-related spatial distribution of the seven goatfish species and environmental characteristics. Environmental characteristics (PC axes) that had a significant effect on spatial distributions are presented as blue vectors (see also Fig. S2). No individuals of size class 1 were found for *Mulloidichthys vanicolensis*. In (h), the species scores for all species and all size classes (a-g) were overlaid (different symbols and colors represent the different species and size classes, respectively). In (i), the site scores of 63 study sites are shown (magenta and yellow symbols represent the 29 sites in the exposed reefs and the 34 sites in the inner reefs, respectively). Fish photographs were taken by the author (A. Nanami).

Fig. 4. Relationship between the number of fish individuals that utilized the focal substrate and substrate availability. Black and gray bars represent the number of fish individuals and substrate availability, respectively. The numbers adjacent to the black bars represent the number of fish individuals that utilized the focal substrate. The result for *Mulloidichthys vanicolensis* is not shown, because no feeding behaviors were found during the observations. Fish photographs were taken by the author (A. Nanami).

Fig. 5. Results of principal component analysis (PCA), explaining the species-specific differences in feeding substrates for the six goatfish species. Pie charts represent the proportion of substrates that was foraged by the focal species. Fish species names are abbreviated (Pmul: *Parupeneus multifasciatus*; Pcyc: *P. cyclostomus*; Pbar: *P. barberinoides*; Pb: *P. barberinus*, Pple: *P. pleurostigma*; Mfla: *Mulloidichthys flavolineatus*). The result for *Mulloidichthys vanicolensis* is not shown, because no feeding behaviors were found during the observations. The vectors for three types of substrates (live corals, soft corals, and macroalgae) are not shown, because no foraging on these three types of substrates were observed. Fish photographs were taken by the author (A. Nanami).