Broad-scale spatial distribution and microhabitat-scale substrate association of seven angelfish species (family Pomacanthidae) in an Okinawan coral reef

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Broad-scale spatial distribution and microhabitat-scale substrate association of seven angelfish species (family Pomacanthidae) in an Okinawan coral reef

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Abstract Species-specific spatial distribution in relation to environmental characteristics underpins the species diversity of coral reef fishes. This study aimed to elucidate (1) the broad-scale spatial distribution (spatial variation of fish density at intervals of several-kilometers), influenced by topographic features (exposed reef vs. inner reef), substrate characteristics and depth, and (2) the microhabitat associations (habitat association within several centimeter scale) concerning substrate availability for seven angelfish species (family Pomacanthidae) in an Okinawan coral reef. Broad-scale analysis revealed (1) *Chaetodontoplus mesoleucus* was primarily found in deep inner reefs with greater coverage of branching *Acropora* and dead coral; (2) *Centropyge bicolor* and *C. tibicen* were primarily found at shallow inner reefs with greater coverage of branching *Acropora*, dead coral, and sand; (3) *C. ferrugata* and *C. vrolikii* were primarily found at shallow exposed reefs with greater coverage of rock, and (4) *C. heraldi* and *Pygoplites diacanthus* were primarily found at deep exposed reefs with greater coverage of rock. Microhabitat-scale analysis revealed that three species (*C. mesoleucus*, *C. bicolor*, and *C. heraldi*) showed significant positive association with acroporid corals. *Centropyge tibicen* showed a significant positive association with living corals. The remaining three species (*C. ferrugata*, *C. vrolikii*, and *P. diacanthus*) did not show a positive association with living corals. This suggests that coral loss impacts angelfish population in a species-specific manner. These two spatial scale viewpoints offer valuable insight for comprehensive understandings of angelfish spatial distribution in relation to substrate characteristics.

Keywords Spatial distribution · Microhabitat association · Angelfish · Substrate characteristics · Living coral · Okinawan coral reef

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Introduction

Coral reefs support a high species diversity of fishes and the species-specific spatial distribution in relation to the environmental characteristics underpins the diversity of reef fish assemblages. Such species-specific spatial distribution of coral reef fishes can be considered from two perspectives (Syms 1995; Eagle et al. 2001; Gust et al. 2001), that is, broad-scale (spatial distribution in several tens or several kilometer scale) and microhabitat-scale (habitat use within several tens or several centimeter scale) perspectives.

Broad-scale studies have identified species-specific zonation patterns of fishes corresponding to topographic and oceanographic features (Friedlander et al. 2003; Benthuysen et al. 2022). For instance, broad-scale environmental gradients (reef slope, reef crest, and reef flat) have significant effects on fish assemblage structures such as wrasses and parrotfishes (family Labridae: Green 1996, Gust et al. 2001; Hoey and Bellwood 2008; Hernández-Landa et al. 2014; Johnson et al. 2019), butterflyfishes (family Chaetodontidae: Pratchett and Berumen 2008; Emslie et al. 2010), groupers (family Epinephelidae: Donaldson 2002) and other fish groups including surgeonfishes, snappers and rabbitfishes (family Acanthuridae, Lutjanidae and Siganidae: Russ 1984; Newman et al. 1997; Cheal et al. 2012). Broad-scale gradients in hydrodynamics and wave exposure also affect fish assemblage structure for damselfishes (family Pomacentridae: Williams 1991), wrasses (Fulton et al. 2001), butterflyfishes (Nanami 2020), and rabbitfishes (Nanami 2018).

For microhabitat-scale perspectives, diverse habitat association with various substrates has been studied for damselfishes (Wilson et al. 2008; Eurich et al. 2018), gobies (family Gobiidae: Munday et al. 1997; Doll et al. 2021), groupers (Nanami et al. 2013), and blennies (family Blenniidae: Syms 1995), demonstrating species-specific microhabitat associations. Some species showed high habitat specialization for specific substrates, whereas other species showed a broader extent of habitat selection to various types of substrates. These studies have also suggested species-specific differences in reactions to habitat loss due to coral degradation (Wilson et al. 2010).

Syms (1995) and Eagle et al. (2001) have suggested the significance of including both broad- and microhabitat-scale perspectives to better understand the relationship between fish species distribution and substrate characteristics. A single perspective (e.g. broad-scale perspective such as reef zone, depth and wave exposure) may overlook some factors that another perspectives (e.g. microhabitat-scale substrate association) might detect. Hence, integrating these perspectives could improve our understanding of fish spatial distribution in relation to substrate characteristics, which may in turn allow for more effective conservation planning of coral reef fishes such as habitat protection and coral assemblage restoration. For instance, Kelleher (1999) and Green et al. (2013) proposed that critical habitats for target species should be considered in marine protected area planning. Furthermore, identifying the precise spatial distribution of target species concerning substrate characteristics is vital for selecting restoration and conservation sites and strategies (Nanami 2021).

Angelfishes (family Pomacanthidae) are one of the major fish groups in coral reefs and highly targeted in aquarium trade for their popularity as ornamental fishes (Wood 2001; Tissot and Hallacher 2003; Okemwa et al. 2004). Thus, angelfishes provide ecosystem services (aquarium fish production and recreational diving target: Sato et al. 2020), and the proper conservation of these wild population should be achieved. To preserve the population and species diversity of angelfishes, spatial distributional patterns and microhabitat associations should be evaluated to identify potential marine protected areas and the conservation of specific microhabitat types. Previous studies have shown spatial variations in angelfish assemblage structure at the geographical scale (several-hundred kilometer scale) in the Red Sea (Roberts et al. 1992; Khalaf and Abdallah 2014). In contrast, other previous studies have shown the broad-scale spatial distribution of angelfishes (several to several tens of kilometers scale) at the Great Barrier Reef (Eagle et al. 2001) and in the Red Sea (Alwany 2012). Eagle et al. (2001) also examined microhabitat-scale habitat association of three angelfish species, revealing a preference for non-complex substrates with algae.

However, especially in the North Pacific region including the Okinawan coral reefs, broad-scale spatial distributions and microhabitat-scale substrate associations for angelfishes have not yet been sufficiently investigated. This gap exists because previous studies were conducted in the South Pacific region and the Red Sea. Thus, the aim of this study is to clarify: (1) the species-specific broad-scale spatial distribution (spatial variations of fish density at intervals of several-kilometers) in relation to various substrate characteristics, and (2) the species-specific microhabitat-scale substrate association (habitat association within several centimeter scale) in relation to substrate availability for angelfish species in an Okinawan coral reef. These two spatial scale perspectives could enable a more comprehensive understandings for relationship between angelfish spatial distribution in relation to substrate characteristics.

Materials and methods

Study species and broad-scale spatial distribution

This study was carried out at Sekisei Lagoon and Nagura Bay in the Yaeyama Islands, Okinawa, Japan (Fig. 1a, b). Underwater visual surveys were conducted from June 2016 to February 2017. A total of 68 study sites were established covering nearly the entirety of the Sekisei Lagoon and Nagura Bay area, with an inter-site distance of approximately 2 km. These study sites comprised 32 sites on exposed reefs and 36 sites on inner reefs (Fig. 1c). Exposed reefs exhibited greater coverage of non-acroporid corals and rock, whereas inner reefs exhibited greater coverage of acroporid corals, coral rubble and sand were found at the inner reef (see Results).

The underwater visual survey was performed following the methodology of Nanami (2020). A 20-min transect of a 5-m width was employed using SCUBA at each site. The length of each time transect at each site was measured with a portable GPS receiver. Average distances covered were 343.1 ± 43.9 m [mean ± standard deviation (SD), minimum length = 233 m; maximum length = 439 m]. The fish density of each angelfish species per each site (number of individuals per 500 m^2) was determined from the count of individual fish and the length of the 20-min transect. Depth profiles were also recorded using a diving computer. With a recording interval of 30 s, 40 depth values were obtained for each site (two depth points per minute × for 20 min). These 40 depth profiles were then averaged for each site and used for subsequent analysis. The water depths ranged from 2.6 m to 12.4 m (average ± SD = 7.66 ± 1.95 m).

Due to logistical limitations, underwater observations could not be conducted during one season. However, since angelfishes show high site fidelity and limited home ranges (Aldenhoven 1986; Hourigan et al. 1989; Moyer 1990; Sakai and Kohda 1997), it was assumed that seasonal variations in distribution was negligible over the nine-months periods.

During the observation period, 13 species in total were identified at the study site (Table 1) and seven species observed in higher density (*Centropyge bicolor*, *C. ferrugata*, *C. heraldi*, *C. tibicen*, *C. vrolikii*, *Chaetodontoplus mesoleucus*, and *Pygoplites diacanthus*: Fig. S1). Thus, these seven species

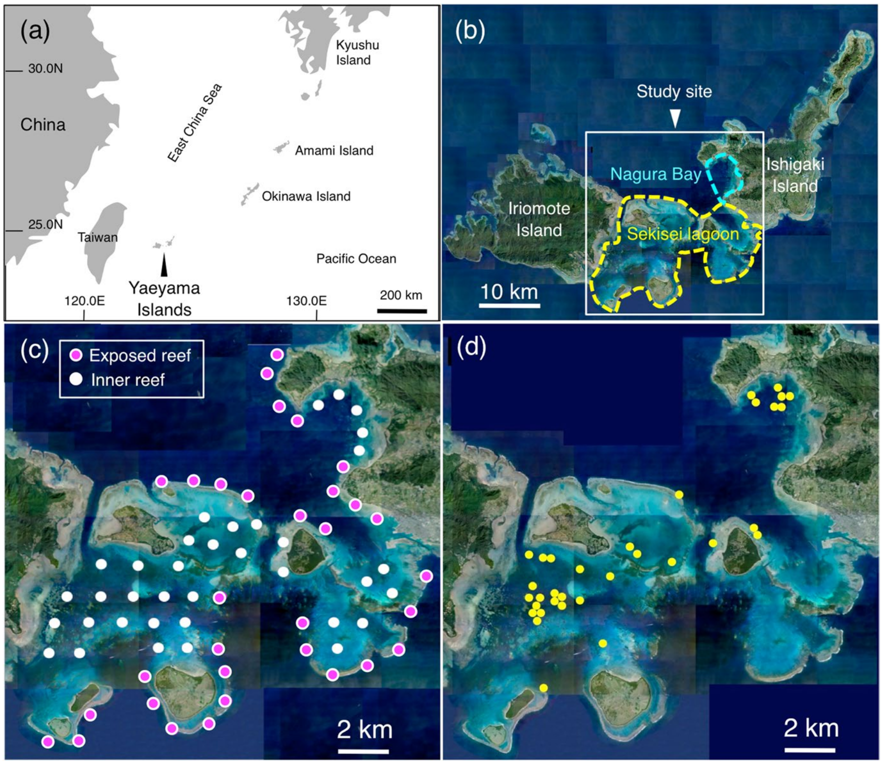

Fig. 1 Maps showing the location of the Yaeyama Islands (**a**), Sekisei Lagoon and Nagura Bay (**b**), the 68 study sites used for examining broad-scale spatial distributions (**c**), and the 33 sites for examining microhabitat association (**d**). The aerial photographs used in (**b**), (**c**) and (**d**) were provided by the International Coral Reef Research and Monitoring Center

Table 1 Number of sites with occurrence and average density of angelfish species at the 68 study sites in broad-scale survey (see Materials and methods)

Number of sites with occurrence				Average density per 500m^2 ± standard deviation			
Fish species	Total (within 68 sites)	Exposed reef (within 32 sites)	Inner reef (within 36 sites)	Total ($n=68$)	Exposed reef ($n=32$)	Inner reef ($n=36$)	Analysis
Apolemichthys trimaculatus	5	5	0	0.07 ± 0.27	0.15 ± 0.38	–	
Centropyge bicolor	24	5	19	0.35 ± 0.73	0.09 ± 0.23	0.58 ± 0.92	X
Centropyge bispinosa	1	1	0	0.00 ± 0.04	0.01 ± 0.05	–	
Centropyge ferrugata	32	18	14	0.55 ± 0.86	0.53 ± 0.84	0.57 ± 0.88	X
Centropyge heraldi	17	8	9	0.65 ± 1.96	0.87 ± 2.68	0.46 ± 0.97	X
Centropyge tibicen	33	4	29	0.51 ± 0.82	0.05 ± 0.16	0.91 ± 0.96	X
Centropyge vrolikii	43	26	17	0.83 ± 1.23	1.08 ± 1.25	0.62 ± 1.19	X
Chaetodontoplus mesoleucus	16	1	15	0.53 ± 1.54	0.01 ± 0.05	1.00 ± 2.01	X
Paracentropyge venusta	1	1	0	0.02 ± 0.14	0.04 ± 0.21	–	
Pomacanthus imperator	6	2	4	0.03 ± 0.11	0.02 ± 0.06	0.04 ± 0.14	
Pomacanthus semicirculatus	11	6	5	0.08 ± 0.21	0.07 ± 0.15	0.08 ± 0.26	
Pomacanthus sexstriatus	7	2	5	0.05 ± 0.20	0.06 ± 0.28	0.04 ± 0.11	
Pygoplites diacanthus	39	24	15	0.49 ± 0.87	0.66 ± 0.99	0.34 ± 0.73	X

Totally 13 angelfish species were observed and dominant seven species were selected for the analysis (see Fig. S1)

were selected for further analyses. Bubble plots were displayed on the study map to represent the broad-scale distributions of each species, in which bubble size represents the fish local density.

Broad-scale spatial variation in substrates

The substrate data provided by Nanami (2020) for the 68 study sites were utilized in this study with certain modifications to the substrate categorization. The substrates were classified into the following 15 categories (Table S1): (1) branching *Acropora*, (2) bottlebrush *Acropora*, (3) tabular *Acropora*, (4) corymbose *Acropora*, (5) genus *Pocillopora*, (6) branching corals other than genera *Acropora* and *Pocillopora*, (7) foliose corals, (8) massive corals, (9) other living corals, (10) soft corals, (11) dead corals, (12) coral rubble, (13) rock (calcium carbonate substratum with lower substrate complexity than living corals), (14) sand, and (15) macroalgae. Variables that demonstrated strong species associations were identified by multivariate analyses (see Data analysis section).

Microhabitat-scale substrate association

To investigate the microhabitat-scale substrate association of seven angelfish species, additional underwater observations were carried out at 33 sites from June to October 2022 (Fig. 1d), using the data collection methodology established by Nanami et al. (2013). A 20-min underwater observation was conducted at each site. During each survey at each site, the substrate at which individuals belonging to angelfish species were initially spotted was recorded.

Substrate availability at the 33 study sites was recorded during the underwater observations by a digital camera. A digital camera was attached to the data collection board, facilitating simultaneous recording of the substrate and fish. In the laboratory, static images were extracted at 10-s intervals by QuickTime Player software (version 7.6), yielding 121 static images for each site. For each image, the substrate at the center of the static image was recorded and categorized according to the above-mentioned 15 substrate categories for analysis. All data for substrate association by fish and substrate availability that were obtained from 33 study sites were pooled for the analysis.

Data analysis

Two types of data analyses were conducted in accordance with the above-mentioned two spatial scales (Fig. S2).

To evaluate the significant difference in fish density or substrate coverage between exposed and inner reefs, generalized linear model (GLM) was utilized for each fish species or each substrate using R statistical computing language (function "glm": R Core Team 2022). The objective variables were fish density and substrate coverage, explanatory variable was reef type (i.e. exposed reefs or inner reefs) and data were assumed to have a Poisson distribution with a log-link function. As fish count data at each site were obtained from 20-min survey, the length of each time transect was varied among the 68 sites. Therefore, fish data was analyzed with “offset” option in the R package using the length of each time transect.

The relationship between the broad-scale spatial distribution of the seven angelfish species and the environmental characteristics (15 substrates plus depth) was analyzed as follows: (1) detrended correspondence analysis (DCA) was performed to clarify the species response (linear or unimodal) to the environmental variables with CANOCO software (Ter Braak and Smilauer 2002); (2) as the DCA revealed the unimodal responses of species against environmental variables, canonical correspondence analysis (CCA) was carried out to clarify the relationship. Prior to the analysis, the fish density data were square-root transformed. To identify the environmental characteristics that have strong effects on the spatial distributions of the seven angelfish species, forward selection was applied using CANOCO software.

To evaluate the diversity of microhabitat-scale substrate association of fish, Hill number (q = 1) was applied:

$$\text{Hill number } (q = 1) = \exp[(-\sum p_i \log_e(p_i))]$$

where p_i is the proportion of fishes for the ith substrate.

Microhabitat-scale substrate association was analyzed by “resource selection ratio” (Manly et al. 2002). The resource selection ratio was calculated as:

$$w_i = o_i/\pi_i$$

where w_i is the resource selection probability function, o_i is the proportion of the ith substrate that was used by a focal fish species, and π_i is the proportion of the ith substrate that was available to the study area (Manly et al. 2002). For multiple comparisons, Bonferroni Z corrections were used in order to calculate the 95% confidence interval (CI) for each w_i. The formula used to calculate the 95% CI was:

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

where $Z_{a/2\ k}$ is the critical value of the standard normal distribution corresponding to an upper tail area of $a/2\ k$, a is 0.05, k is number of substrates that were used by a focal fish species, and U_+ is the total number of individuals of the focal fish species. Substrates with $w_i \pm 95\%$ CI above and below 1 indicate significantly positive and non-positive association, respectively. Substrates with $w_i \pm 95\%$ CI encompassing 1 had no significant positive or negative association. Substrates without any association with fish were excluded from the analysis.

The analysis was conducted in two steps. First step was to clarify the associations between fish species and above-mentioned 15 categories of substrates. Second step was to clarify whether fish species showed any associations of living coral or non-coralline substrates. In this step, categories constituting reef-building living coral (branching *Acropora*, corymbose *Acropora*, tabular *Acropora*, bottlebrush *Acropora*, branching coral, foliose coral, massive coral, *Pocillopora* and other coral) and other substrates (dead coral, soft coral, rock, coral rubble, sand and macroalgae) were merged and treated as hard living coral and other substrates, respectively.

Results

Broad-scale spatial distribution

The map and GLM revealed the overall trends in species-specific broad-scale spatial distributions of the seven species. Significant greater density of three species (*Chaetodontoplus mesoleucus*, *Centropyge bicolor*, and *C. tibicen*) was found in inner reefs (Fig. 2a–c, Table S2; $p < 0.01$ for the three species). One species (*C. ferrugata*) showed no significant difference in fish

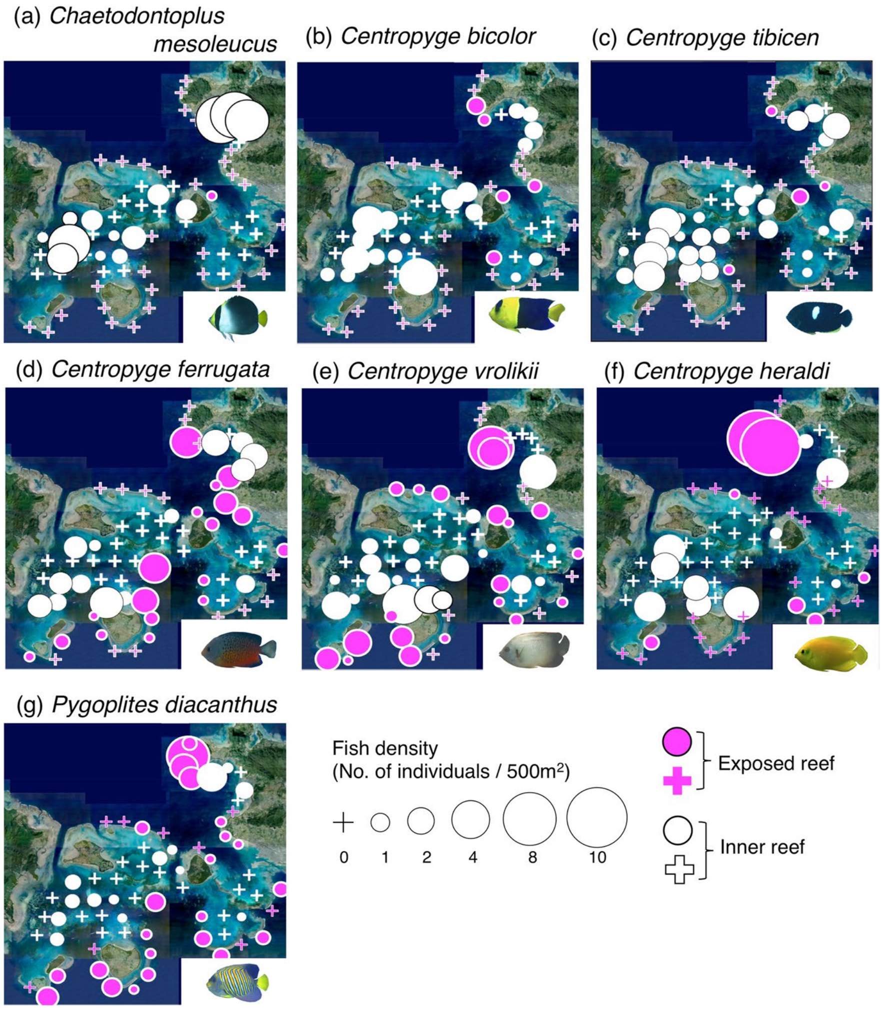

Fig. 2 Broad-scale spatial distribution of seven angelfish species on 68 sites at Sekisei Lagoon and Nagura Bay. The circle diameter represents density per 100 m × 5 m. The aerial photographs were provided by the International Coral Reef Research and Monitoring Center

density between exposed reefs and inner reefs (Fig. 2d, Table S2: $p > 0.05$). In contrast, three species (*C. vrolikii*, *C. heraldi* and *Pygoplites diacanthus*) showed significant greater density in exposed reefs (Fig. 2e, f, g, Table S2: $p < 0.05$ for the three species).

Regarding substrates, inner reefs were primarily characterized by a significant greater coverage of branching *Acropora*, bottlebrush *Acropora*, dead coral, coral rubble and sand (Table S2), whereas exposed reefs were primarily characterized by a significant greater coverage of foliose coral, massive coral, *Pocillopora*, other coral, soft coral and rock (Table S2).

The CCA revealed a broad-scale spatial distribution in relation to environmental variables. *Chaetodontoplus mesoleucus* was primarily found at deep inner reefs, where the coverage of branching *Acropora* and dead coral was greater (Fig. 3a–d, Table S2). Two species (*Centropyge bicolor* and *C. tibicen*) were primarily found in shallow inner reefs, with greater coverage of branching *Acropora*, dead coral, and sand (Fig. 3a–c, e, f, Table S2). *Centropyge ferrugata* did not show specific spatial distribution in relation to environmental variables (Fig. 3a–c, g, Table S2). *Centropyge vrolikii* tended to be found in shallow exposed reefs with greater coverage of rock, other coral and soft coral (Fig. 3a–c, h, Table S2). The remaining two species (*C. heraldi* and *P. diacanthus*) were primarily found at deep exposed reefs with a greater coverage of rock, other coral and soft coral (Fig. 3a–c, i, j, Table S2).

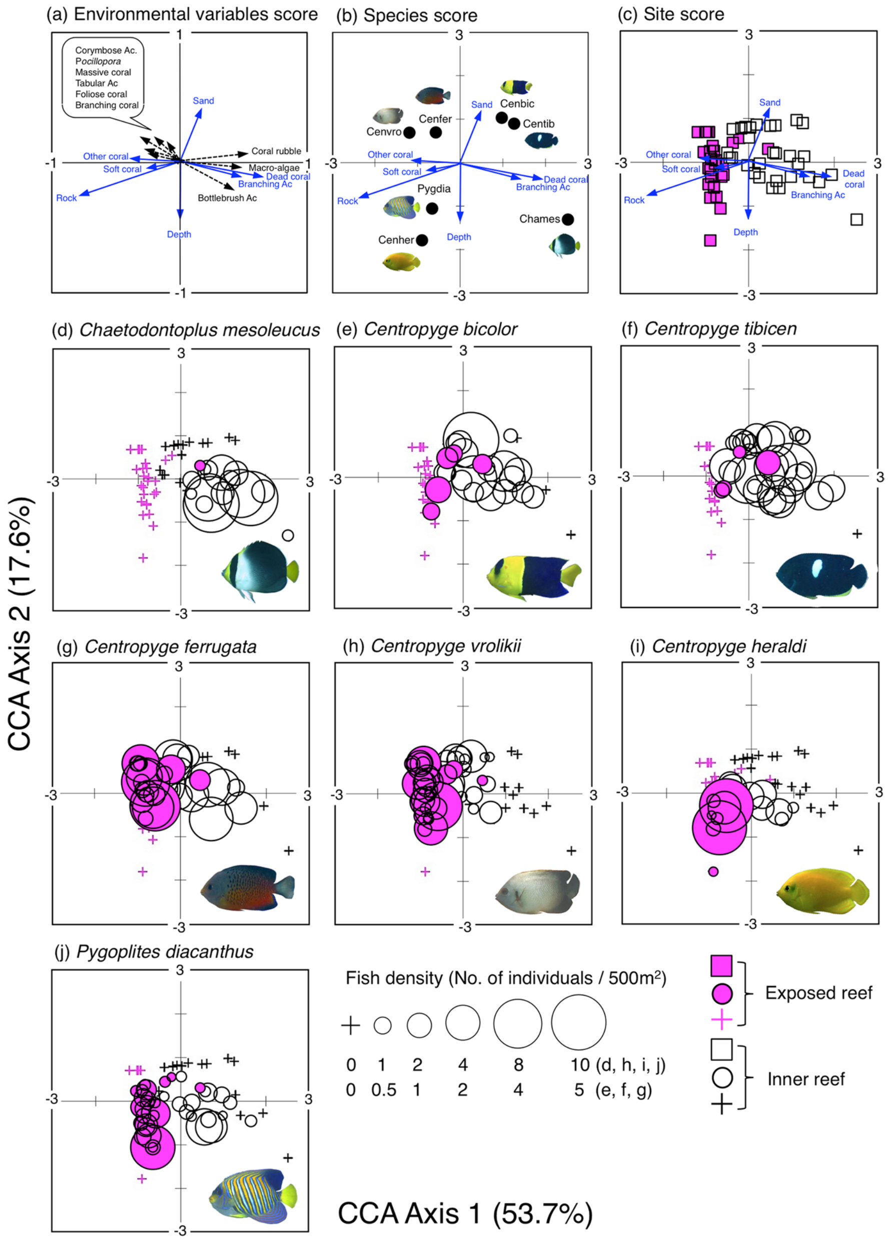

Fig. 3 The results of the canonical correspondence analysis (CCA), explaining the relationship between the spatial distribution of the seven angelfish species and environmental characteristics. In (**a**–**c**), environmental variables that have strong effects on the spatial distribution are shown as solid vectors. Several types of coral are represented as abbreviations (Branching Ac: branching *Acropora*; Bottlebrush Ac: bottlebrush *Acropora*, Corymbose Ac: corymbose *Acropora*; Tabular Ac: tabular *Acropora*). In (**b**), fish species names are indicated by abbreviations (Cenbic: *Centropyge bicolor*, Cenfer: *C ferrugata*, Cenher: *C heraldi*, Centib: *C tibicen*, Cenvro: *C vrolikii*, Chames: *Chaetodontoplus mesoleucus*, Pygdia: *Pygoplites diacanthus*)

Microhabitat-scale substrate association using 15 substrate categories

Chaetodontoplus mesoleucus was associated with six substrate categories (Hill number = 3.29: Fig. 4a). The species showed significant a positive association with branching *Acropora* and bottlebrush *Acropora*, and a significant non-positive association with dead coral and rock (Fig. 5a).

Centropyge bicolor was associated with eight substrate categories (Hill number = 5.65: Fig. 4b). The species showed a significant positive association with bottlebrush *Acropora* and a non-positive association with coral rubble (Fig. 5b).

Centropyge tibicen was associated with eight substrate categories (Hill number = 5.88: Fig. 4c) but showed no significant association with any particular substrate categories (Fig. 5c).

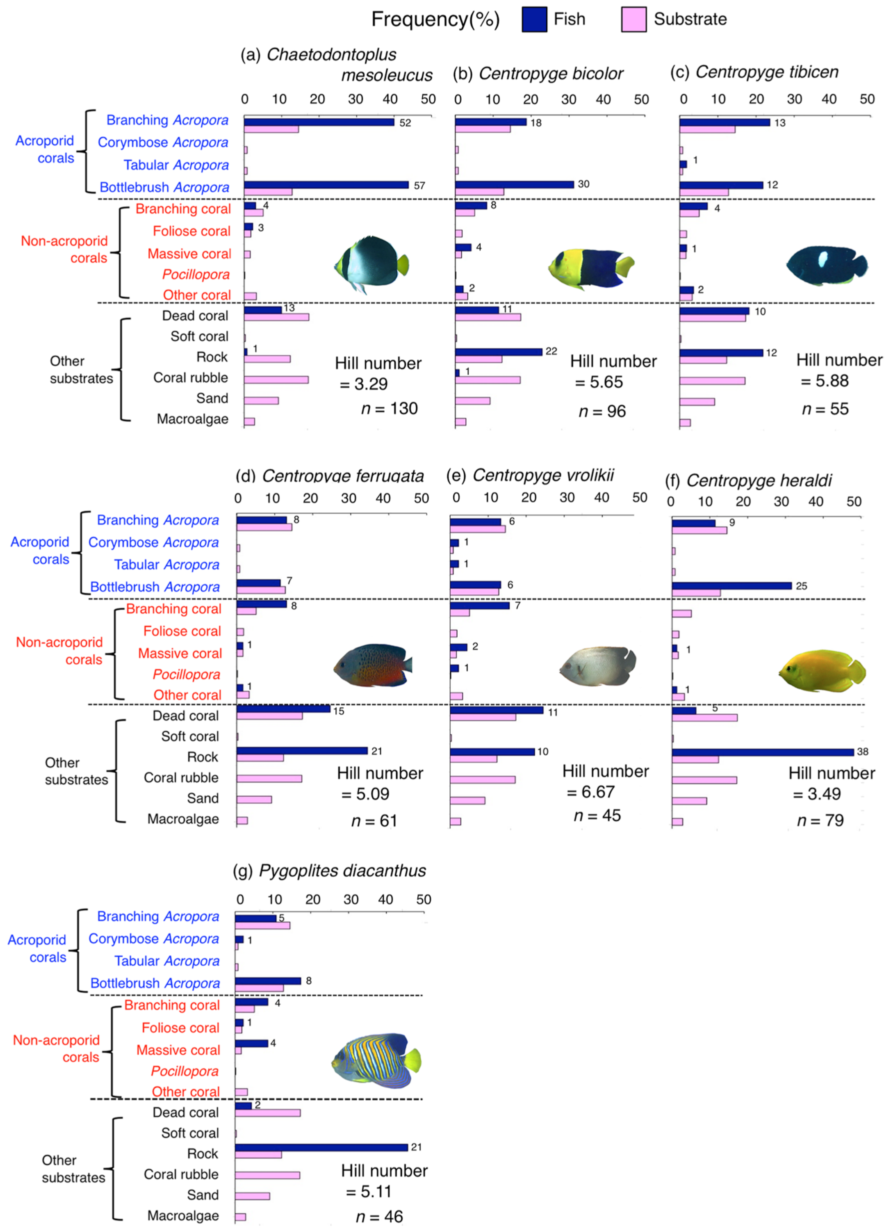

Fig. 4 Relative frequency (%) of fish individuals associated with substrates and substrate availability. Numbers above bars represent the number of individuals on the focal substrate. Horizontal dashed lines represent the division of the three groups of substrates (acroporid coral, non-acroporid coral, and other substrates)

Centropyge ferrugata was associated with seven substrate categories (Hill number = 5.09: Fig. 4d) and showed a significant positive association with rock (Fig. 5d).

Centropyge vrolikii was associated with nine substrate categories (Hill number = 6.67: Fig. 4e). The species showed no significant association with any substrates (Fig. 5e).

Centropyge heraldi was associated with six substrate categories (Hill number = 3.49: Fig. 4f). The species showed a significant positive association with bottlebrush *Acropora* and rock, and significant a non-positive association with dead coral (Fig. 5f).

Pygoplites diacanthus was associated with eight substrate categories (Hill number = 5.11: Fig. 4g). The species showed a significant positive association with rock, and a significant non-positive association with dead coral (Fig. 5g).

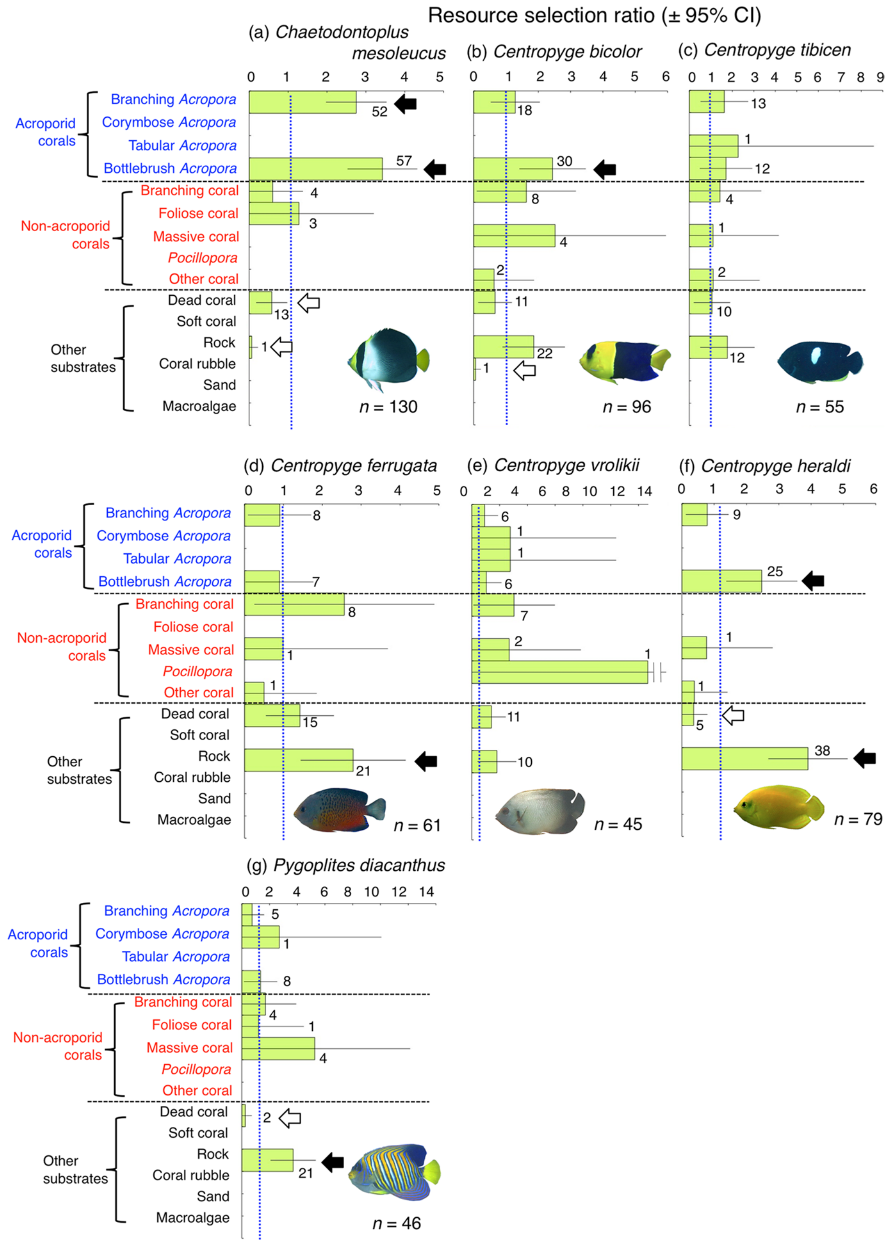

Fig. 5 Resource selection ratio ($w_i \pm 95\%$ confidence interval) for seven angelfish species. Black and white arrows represent significant positive and non-positive association for the substrates, respectively. The vertical dashed line represents a selection ratio of 1 (i.e., no positive or non-positive association). Numbers above bars represent the number of individuals. Substrates with $w_i \pm 95\%$ confidence interval above and below 1 indicate significant positive and non-positive association, respectively. Substrates with $w_i \pm 95\%$ confidence interval that encompasses 1 have no significant positive or non-positive association. Horizontal dashed lines represent the division of the three groups of substrates (acroporid coral, non-acroporid coral, and other substrates)

Microhabitat-scale substrate association: hard living coral vs. other substrates

Three species (*Chaetodontoplus mesoleucus*, *Centropyge bicolor* and *Centropyge tibicen*) showed greater number of individuals on hard living coral (60.0–89.2%) than on other substrates (10.8–40.0%: Fig. S3). For these three species, significant positive and non-positive associations with hard living coral and other substrates were shown, respectively (Figs. S4). In contrast, the remaining four fish species (*Centropyge ferrugata*, *Centropyge vrolikii*, *Centropyge heraldi* and *Pygoplites diacanthus*) showed no significant associations with hard living coral or other substrates (Fig. S4).

Discussion

Broad-scale spatial distributions in relation to environmental variables

Although three species (*Chaetodontoplus mesoleucus*, *Centropyge bicolor* and *C. tibicen*) showed greater density in the inner reefs, this contradicts the findings of Eagle et al. (2001). The latter showed that the greater abundance of three species (*C. bicolor*, *C. vrolikii*, and *C. bispinosa*) was due to their proximity to an island headland, rather than the level of wave exposure at sheltered, exposed, and intermediate sites.

At broad scale, reef zonation based on wave exposure and depth affects assemblage structure of benthic marine organisms including corals and macroalgae (Williams et al. 2013; Lange et al. 2021). This variation in species composition of benthic marine organisms, especially for corals, would affect the spatial distribution of angelfish species. The present study corroborated this hypothesis, showing that various types of substrates affect the species-specific spatial distribution of angelfish species. Notably, greater density of three species (*C. mesoleucus*, *C. bicolor* and *C. tibicen*) were found to be associated with greater coverage of branching *Acropora*. Numerous previous studies showed that branching *Acropora* provide complex structures (e.g. Wilson et al. 2008; Nanami et al. 2013), suggesting that the three fish species associated with branching *Acropora* which is a suitable refuge to avoid being eaten by predators. In contrast, four species (*C. ferrugata*, *C. vrolikii*, *C. heraldi*, and *P. diacanthus*) were found at sites with greater coverage of rock. Similar outcomes have been reported in previous studies (Ticzon et al. 2012; Nanami 2021), which suggested that rock inherently possesses uneven surfaces and large holes, creating complex structures. Although the degree of complexity is lower than that of living corals, such complexity affects the greater density of groupers and parrotfishes (Ticzon et al. 2012; Nanami 2021). Thus, the complex structures created by a non-coralline substrate might be suitable habitat and refuge space for some angelfish species.

These findings suggest that degree of dependence on living corals is species-specific on a broad-scale (several to tens kilometer scale), and living corals are not necessarily the primary factor affecting spatial distribution for several species. As the main food items of the seven angelfish species are benthic invertebrates and algae (Froese and Pauly 2022), the degree of wave exposure and substrate complexity provided by living corals and rock are likely the primary factors that responsible for the broad-scale spatial distributions.

A depth gradient in species-specific distribution was also found, that is, four species (*C. bicolor*, *C. tibicen*, *C. ferrugata* and *C. vrolikii*) and three species (*C. mesoleucus*, *C. heraldi*, and *P. diacanthus*) showed greater density at shallower and deeper sites, respectively. Similar results were also found for wrasses (Nanami et al. 2005), butterflyfishes (Bouchon-Navaro 1986), and angelfishes (Lindquist and Gilligan 1986; Alwany 2009). Species-specific depth gradients among angelfishes may be a contributing factor for the maintenance of species diversity at the study site.

Microhabitat-scale substrate association in relation to substrate availability

All seven angelfish species utilized various types of substrates (ranging from six to nine types), which was consistent with previous studies (Eagle et al. 2001; Vitelli et al. 2019). The seven angelfish species could be grouped into three categories: (1) coral specialists (*C. mesoleucus* and *C. bicolor*), (2) rock specialists (*C. ferrugata* and *P. diacanthus*) and (3) generalists (*C. tibicen*, *C. vrolikii* and *C. heraldi*). Coral specialists exhibited a significant positive association with acroporid corals. Many studies have shown that acroporid corals, owing to their complex structure, can provide habitats and refuge spaces to many coral reef fish species (e.g. Nanami et al. 2013; Wilson et al. 2010). As these acroporid corals are vulnerable to coral bleaching (Marshall and Baird 2000; Loya et al. 2001; McClanahan et al. 2004; Pratchett et al. 2008) and predation by crown-thorn starfish (Pratchett et al. 2009), these two angelfish species would be more affected by coral loss due to climate change or outbreaks of crown-thorn starfish. In contrast, Eagle et al. (2001) reported that *C. bicolor* had a positive association with non-complex substrata with algae, rather than the living corals, at Lizard Island on the Great Barrier Reef. This discrepancy might be due to the geographical differences or variations in substrate availability between the study sites.

For rock specialists, the three-dimensional structural complexity of rocks might provide suitable refuge. However, some individuals of rock specialists have been also found on reef-building hard corals, suggesting that they did not avoid living corals. Nevertheless, it is suggested that rock specialists will be less impacted by coral loss than coral specialists.

Generalists did not be associated with substrates with low complexity (i.e. soft coral, coral rubble, sand, and macroalgae), suggesting that substrates with greater complexity (various types of living corals, dead corals, and rock) are suitable habitats and refuge spaces for these species (Luckhurst and Luckhurst 1978; McCormick 1994). It is suggested that climate change has a less negative impact on these populations.

Importance of applying two spatial scale perspectives

CCA revealed that sand and soft coral have significant effects on the broad-scale spatial distribution of two species (*C. bicolor* and *C. tibicen*) and four species (*C. ferrugata*, *C. vrolikii*, *C. heraldi*, and *P. diacanthus*), respectively. However, the microhabitat-scale survey revealed no associations with sand or soft corals for these fish species. In addition, microhabitat-scale survey showed a significant positive effect of bottlebrush *Acropora* on the distribution of two species (*C. mesoleucus* and *C. bicolor*), which were not identified by the broad-scale survey. These findings highlight the importance of applying both broad-scale and microhabitat-scale perspectives to fully understand of the spatial distribution of angelfish species.

Toward the effective protection of angelfishes in relation to habitat characteristics

The present study revealed that various environmental variables, including living corals, non-coralline substrates and depth, underpin spatial distribution and habitat association of angelfish species. The degradation of coral assemblages may cause a decline in abundance of coral specialists (*C. mesoleucus and C. bicolor*) with greater dependence on acroporid corals without necessarily having a negative impact on rock specialists and generalists (*C. tibicen*, *C. ferrugata*, *C. vrolikii*, *C. heraldi* and *P. diacanthus*).

Regarding the diversity for microhabitat-scale substrate association, two species (*C. mesoleucus* and *C. heraldi*) can be considered as habitat specialist due to their lower diversity index. Specifically, over 80% of *C. mesoleucus* individuals were associated with living acroporid corals, suggesting that the decline of acroporid corals by climate change would cause greater negative impact on the species. In contrast, other five species (*C. bicolor*, *C. tibicen*, *C. ferrugata*, *C. vrolikii*, and *P. diacanthus*) can be considered as habitat generalist due to their greater diversity index. These species might be more resilient from habitat degradation by climate change compared to the two habitat specialist species.

Recently, marine protected areas are regarded as a useful tool to conserve fish population and species diversity (Green et al. 2015). Kelleher (1999) and Green et al. (2013) suggested that various ecological aspects (e.g. diverse habitat) should be taken into account when establishing marine protected areas. For the more effective conservation of angelfish populations, it is recommended: (1) sites with greater substrate complexity that are created by both living corals and non-coralline substrates should be protected; (2) both exposed and inner reefs should be included in marine protected areas; and (3) key substrates, such as living bottlebrush *Acropora* and branching *Acropora*, which have highly vulnerable to climate change, should be protected or restored in the marine protected areas. Overall, species-specific responses to habitat degradation need to be precisely clarified and the results should be considered in the effective management planning for angelfish assemblages.

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

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

Declarations

Ethical approval No animal testing or no animal sampling was performed during the study.

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

Competing interests The author declare that have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Conflict of interest The author declare no completing interests.

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