

Spatial distribution, microhabitat association, dependence to live corals, and habitat partitioning among five grouper species (family Epinephelidae) in an Okinawan coral reef

メタデータ	言語: English 出版者: Springer Nature 公開日: 2025-10-21 キーワード: Spatial distribution; Microhabitat association; Grouper; Live coral; Habitat partitioning; Coral reef 作成者: 名波, 敦 メールアドレス: 所属:
URL	https://fra.repo.nii.ac.jp/records/2015637

1 **Spatial distributions and foraging substrates of 11 surgeonfish species (family**
2 **Acanthuridae) in an Okinawan coral reef**

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24 **ABSTRACT**

25 Surgeonfishes (family Acanthuridae) are a main fish group in coral reefs. This study aimed to
26 examine the species-specific and size-related spatial distribution, and foraging substrates of
27 11 surgeonfish species in relation to topographical features and substrate diversity. Six species
28 (*Ctenochaetus striatus*, *Acanthurus nigrofuscus*, *A. lineatus*, *A. japonicus*, *Naso lituratus*, and
29 *Zebrasoma scopas*) showed a greater density in the outer reefs with a higher coverage of rock.
30 The former five species showed a significant positive utilization of rock as foraging substrate,
31 whereas *Z. scopas* positively utilized dead corals and rock. For *A. dussumieri* and *N.*
32 *unicornis*, greater densities of smaller-sized individuals were found in the inner reefs with
33 higher coverage of coral rubble and sand, whereas larger-sized individuals were found in the
34 outer reefs with a higher coverage of rock. *Naso unicornis* showed a significantly positive
35 utilization of rock as foraging substrate. *Ctenochaetus binotatus* tended to show greater
36 density in the outer reefs and a significant positive utilization of rock as a foraging substrate.
37 *Acanthurus nigricauda* tended to show greater density in the inner reefs and a significant
38 positive utilization of sand as foraging substrate. *Zebrasoma velifer* showed greater density of
39 smaller-sized individuals in the inner reefs with higher coverage of live corals and dead corals,
40 whereas larger-sized individuals tended to be greater in the outer reefs with a higher coverage
41 of rock. *Zebrasoma velifer* showed a significant positive utilization of dead corals as foraging
42 substrate. These results indicated that non-coralline substrates are the main indicator for
43 maintaining surgeonfish species diversity.

44 **Keywords**

45 Acanthuridae; Spatial distributional pattern; Foraging behavior; Non-coralline substrates;
46 Species diversity

47 **1. Introduction**

48 Coral reefs support a high species diversity of marine organisms, which provides various
49 ecosystem services such as natural food production, ornamental resources, habitat
50 maintenance, and recreation (Moberg & Folke, 1999; Laurans et al., 2013; Elliff & Kikuchi,
51 2017). Topographical features (e.g., reef zonation), diverse substrate types (e.g., live corals
52 and non-coralline substrates), water current, and wave exposure are the main factors
53 regulating the high species diversity in coral reefs (Fulton et al., 2001; Friedlander et al.,
54 2003; Wilson et al., 2008; Lange et al., 2021; Benthuisen et al., 2022). Therefore, diverse
55 environment should be conserved to maintain such high species diversity.

56 Coral reef fishes are highly diverse. In conserving the fish species diversity, the
57 relationship between fish species and environmental characteristics should be clarified.
58 Numerous studies have shown that reef zonal variation (reef slope, reef crest, and back
59 reef) can affect the species-specific spatial distribution of coral reef fishes (Russ, 1984a,
60 1984b; Depczynski and Bellwood, 2005; Hoey and Bellwood, 2008; Emslie et al., 2010). The
61 degree of wave exposure, distance from mainland, and water depth also affect the
62 species-specific spatial distribution of fishes (Williams, 1982; Green, 1996; Fulton and
63 Bellwood, 2002; Nanami et al., 2005). For a finer spatial scale, smaller-sized fish species (e.g.,
64 damselfishes, cardinalfishes, and gobies) utilize live corals with fine structure (branching and
65 bottlebrush corals) as refuge space (Gardiner and Jones, 2005; Wilson et al., 2008; Doll et al.,
66 2021; Nanami, 2025a). Other fish species also utilize non-coralline substrates such as rock
67 and dead corals with coarse structure as refuge space and sleeping site (Donaldson, 2002;
68 Ticzon et al., 2012; Nanami, 2023, 2024).

69 Clarifying the foraging substrates of fish species is also necessary to

70 comprehensively understand the association between fishes and substrates. Coral reefs consist
71 of diverse coralline substrates (live reef-building corals and soft corals) and non-coralline
72 substrates (dead corals, rock, coral rubble, and sand). This substrate diversity provides various
73 foraging substrates of coral reef fishes. For example, butterflyfishes forage polyp of various
74 species of live corals (Pratchett and Berumen, 2008; Nanami, 2020). Predatory snapper
75 species utilize live branching corals with smaller-sized fishes as foraging substrates (Nanami
76 and Yamada, 2008). Some benthivorous wrasse species utilize dead corals and coral rubbles
77 because of a greater density of benthic crustaceans in these substrates (Kramer et al., 2016).
78 By contrast, some parrotfish and rabbitfish species utilize a rocky surface as foraging
79 substrates because rocks are covered by epilithic algal matrices and macroalgae (Clements et
80 al., 2017; Smith et al., 2018; Nanami, 2018).

81 Based on these ecological perspectives, marine protected areas (MPAs) have been
82 applied to conserve the species diversity of coral reef fishes. In selecting potential sites for
83 MPAs, the actual spatial distribution of the target species should be clarified. Protecting fishes
84 in all life stages (e.g., newly settled juveniles, non-adult fishes, and adults) and clarifying the
85 substrate types that support size-related fish spatial distribution are important (Green et al.,
86 2013; 2015). In addition, critical foraging substrates should be included in MPAs to enhance
87 the survival and growth of fishes.

88 Surgeonfishes (family Acanthuridae) are a main fish group in coral reefs, which
89 show species-specific spatial distribution in relation to environmental gradients (Choat et al.,
90 1985; Cheal et al., 2012; Hernández-Landa et al., 2014; Hernández-Landa and Aguilar-Perera,
91 2019). Surgeonfishes also show species-specific foraging substrates and feeding habits, and
92 consist of six groups (“browsers”, “brushers”, “croppers”, “concealed croppers”, “sediment

93 suckers”, and “water-column feeders”: Tebbett et al., 2022). The variety of foraging behavior
94 results in the removal of detritus, epilithic algae, and macroalgae on hard and soft substrates
95 (Montgomery et al., 1989; Choat et al., 2002a, 2002b; Brandl and Bellwood, 2014; Brandl et
96 al., 2015) and prevents algal dominance in the coral reef ecosystem (Cheal et al., 2010;
97 Marshall and Mumby, 2015; Eggertsen et al., 2019). In addition, some surgeonfish species
98 serve as main fishery targets in many countries surrounded by coral reefs (Letourneur et al.,
99 1998; Bejarano et al., 2013; 2014; Ford et al., 2016; Trianni et al., 2018; Taylor et al., 2024).
100 These findings indicate that surgeonfishes provide various ecosystem services such as habitat
101 maintenance and natural food production. Thus, this fish group should be conserved by
102 ecosystem-based management such as habitat conservation and protection of the target
103 species (e.g., Frisch et al., 2016; Harvey et al., 2018). These goals can be established by
104 MPAs, which is a useful tool to achieve ecosystem-based management (Russ, 2002; Sobel &
105 Dahlgren, 2004).

106 Although surgeonfishes serve as the main fishery targets and play a functional role
107 in Okinawan coral reefs (Akita et al., 2016; 2022), their ecological aspects, including spatial
108 distribution and foraging substrates, have not been sufficiently investigated in this region.
109 Surgeonfishes also consist of diverse species in this region (Masuda and Kobayashi, 1994).
110 Thus, this study aimed to examine (1) the species-specific and size-related spatial distribution
111 of surgeonfish species in relation to topographical features and substrate diversity, and (2) the
112 species-specific foraging substrate of surgeonfish species in relation to substrate availability.
113 Clarifying the relationship between surgeonfish species and substrate characteristics with
114 regard to habitat and foraging site promote the effective conservation of diverse surgeonfish
115 species.

116

117 **2. Materials and methods**

118 *2.1. Study site*

119 This study was conducted at 62 study sites that were established in the Sekisei Lagoon and
120 Nagura Bay, Yaeyama Islands, Okinawa (Figs. 1a, 1b). Underwater observations for
121 surgeonfishes were conducted for 9 months (between May 2018 and January 2019). The
122 distance between two neighboring study sites among the 62 study sites was approximately 2
123 km. Of the 62 study sites, 28 sites and 34 sites were located in the outer and inner reefs,
124 respectively (Fig. 1c). Outer and inner reefs were defined as the sites outside and inside the
125 reef crest, respectively.

126

127 *2.2. Data collection of fish and environmental characteristics*

128 The methods of underwater observations and measurement of environmental variables are
129 provided in detail in Nanami (2018). In brief, a 20-min time transect was set (transect width =
130 5 m) in each site during the daytime (0830–1600 h), and the number of individuals and their
131 total length (TL) were recorded by scuba diving. A portable GPS was used to measure the
132 distance of each time transect. The average distance of the 20-min time transect was 330.6 m
133 \pm 35.3 standard deviation. Water depth was recorded every 1 min using a diving computer
134 during the 20-min observation. The average water depth ranged from 3.5 m to 11.2 m.

135 Digital video images of the substrate were recorded to evaluate substrate
136 availability in each site. Static images were obtained at 10-s intervals by using QuickTime
137 Player Pro software (version 7.6). Consequently, 121 static images were obtained per 20-min
138 video image. The substrate at the center of each static image was recorded, and the data from

139 121 static images at each site were pooled for analysis. The substrate was categorized into 16
140 types for analysis in accordance with the method of Nanami (2018): (1) branching *Acropora*,
141 (2) tabular *Acropora*, (3) bottlebrush *Acropora*, (4) branching corals except for *Acropora* (e.g.,
142 branching *Pocillopora*, *Montipora*, and *Porites*), (5) massive corals (e.g., massive *Porites* and
143 Faviidae), (6) other live corals (e.g., encrusting corals and foliose corals), (7) dead branching
144 *Acropora*, (8) dead tabular *Acropora*, (9) dead bottlebrush *Acropora*, (10) dead branching
145 corals, (11) dead other corals, (12) soft corals, (13) coral rubble, (14) rock (calcium carbonate
146 substratum), (15) sand, and (16) macroalgae (e.g., *Padina* spp.).

147 Substrate data were represented as a proportion of each of the 16 types. For
148 example, if the number of points at a focal site was represented as “substrate A = 50, substrate
149 B = 30, substrate C = 20, substrate D = 21”, then the estimated coverage of each substrate at
150 the focal site was calculated as “substrate A = $50/121 \times 100 = 41.3\%$, substrate B = $30/121 \times$
151 $100 = 24.8\%$, substrate C = $20/121 \times 100 = 16.5\%$, substrate D = $21/121 \times 100 = 17.4\%$ ”.

152

153 2.3. Analysis of fish spatial distribution in relation to environmental characteristics

154 Underwater observations revealed that 11 surgeonfish species (*Ctenochaetus striatus*, *C.*
155 *binotatus*, *Acanthurus nigrofuscus*, *A. dussumieri*, *A. lineatus*, *A. nigricauda*, *A. japonicus*,
156 *Naso unicornis*, *N. lituratus*, *Zebrasoma scopas*, and *Z. velifer*) were dominant across all 62
157 sites (Fig. S1). Thus, these species were selected for analyses in this study. The 11 species
158 consisted of five functional groups of foraging behavior (Tebbett et al., 2017, 2022): (1)
159 “brushers” (*C. striatus* and *C. binotatus*), (2) “croppers” (*A. nigrofuscus*, *A. lineatus* and *A.*
160 *japonicus*), (3) “sediment suckers” (*A. dussumieri* and *A. nigricauda*), (4) “browsers” (*N.*
161 *unicornis* and *N. lituratus*) and (5) “concealed croppers” (*Z. scopas* and *Z. velifer*). Given that

162 the distance of each time transect was recorded by using a portable GPS receiver, the number
163 of individuals was converted into density (number of individuals per 100 m distance \times 5 m
164 width) using the distance data.

165 Fish individuals were categorized into six size classes for analysis: class 1 (TL \leq 10
166 cm), class 2 (11 cm \leq TL \leq 15 cm), class 3 (16 cm \leq TL \leq 20 cm), class 4 (21 cm \leq TL \leq 25
167 cm), class 5 (26 cm \leq TL \leq 30 cm), and class 6 (TL \geq 31 cm). Pie charts were used to show
168 the size-related spatial distribution of each species.

169 For each fish species and each size class, a generalized linear model (GLM) was
170 applied to examine the significant difference in fish density between the outer and inner reefs
171 using R statistical computing language (R Core Team, 2023). The objective and explanatory
172 variables were fish density and reef type (i.e., outer reefs or inner reefs), respectively. The
173 data were assumed to follow a negative binomial distribution with a log-link function. The
174 GLM was performed by using the “glm.nb” function of the “MASS” package (Venables and
175 Ripley, 2002). Considering that the fish count data at each site were obtained from a 20-min
176 survey, the length of each time transect varied among the 62 sites. Thus, fish data were
177 analyzed with the “offset” option in the R package using the length of each time transect.
178 After performing the GLM, the degree of zero-inflation was examined by using the “check
179 zeroinflation” function of the “performance” package (Lüdecke et al., 2021). The results
180 revealed that all fish species and size classes did not show zero-inflation of data distribution
181 under the assumption of a negative binomial distribution.

182 The relationship between the spatial distribution of each size class individuals of
183 each species and 17 environmental variables (16 types of substrates and water depth) was
184 analyzed by redundancy analysis (RDA) using CANOCO software (ter Braak & Smilauer

185 2002). Before analysis, the fish density data were $\log(x + 1)$ transformed. For environmental
186 variables, principal component analysis (PCA) was performed to avoid multicollinearity
187 among the abovementioned 17 environmental variables using PRIMER software (version 6).
188 The PCA provided principal component scores for the 62 study sites along with the five PC
189 axes. Thus, these principal scores were used as environmental variables for RDA. Software
190 options for forward selection were applied to extract the environmental variables (PC axes)
191 that significantly affected the spatial distribution of fish.

192

193 2.4. Foraging substrates

194 Additional underwater observations were conducted to examine the foraging substrates
195 between June 2020 and June 2025 at 24 sites (Fig. 1d). A researcher (A.N.) searched the
196 abovementioned 11 species and observed their foraging behavior while keeping a distance
197 over several meters from the focal individual to avoid scaring the fish. The focal individual
198 was followed until the researcher found the foraging behavior. The substrate that was initially
199 foraged by the focal individual and the TL of the focal individual were recorded in accordance
200 with the method of McCormick (1995) and Nanami (2025b). The following durations for each
201 fish individual were within several minutes for most species and size classes of three genera
202 (*Ctenochaetus*, *Acanthurus*, and *Zebrasoma*) as well as *Naso lituratus*, because of their
203 frequent foraging behavior. By contrast, the following duration for *N. unicornis* was
204 approximately 5 min, because this species showed less frequent foraging behavior than the
205 other fish species. Since this procedure aimed to obtain the foraging substrates at the first bite
206 of the fish individuals, the number of foraging times for each individual was not collected.
207 Since no fish individuals swam in the large group, the substrates that each individual was

208 foraging could be collected. In this analysis, substrates were categorized into seven types: (1)
209 live corals, (2) dead corals, (3) rock, (4) coral rubble, (5) sand, (6) soft corals and (7)
210 macroalgae. To examine the species and size variations in foraging substrates, PCA was
211 performed. In this procedure, two procedures were applied. First, the data obtained from six
212 size classes were pooled to examine the species-level difference in foraging substrates.
213 Second, the data obtained from six size classes were separately analyzed to examine the size
214 class difference in foraging substrates.

215 In addition, the resource selection ratio (Manly et al., 2002) was applied to examine
216 the selectivity in foraging substrate as:

$$217 \quad w_i = o_i / \pi_i$$

218 where w_i is the resource selection probability function, o_i is the proportion of the i th substrate
219 that was bitten by a focal fish species, and π_i is the proportion of the i th substrate that was
220 available in the study area (Manly et al., 2002). For multiple comparisons, the Bonferroni Z
221 correction was used to calculate the 95% confidence interval (CI) for each w_i as (Manly et al.,
222 2002):

$$223 \quad 95\% \text{ CI} = Z_{a/2I} \sqrt{[o_i(1-o_i) / (U_+ \pi_i^2)]}$$

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

230 Substrate data were also collected by using the abovementioned 20-min video
231 recordings taken at the 24 sites where the foraging substrates were investigated (Fig. 1d). The
232 121 static images were obtained from each 20-min video image, and the substrate at the center
233 of each static image was recorded. Then, the substrate data collected from the 24 sites were
234 pooled for the analysis. Considering that PCA revealed a similar trend in foraging substrates
235 among different size classes for most fish species (see Results), the data for foraging
236 substrates for different size classes were pooled for analysis.

237

238 **3. Results**

239 *3.1. Overall trends in fish spatial distribution*

240 The pie charts and results of GLM showed the overall trends in the spatial distribution of the
241 11 species at the 62 sites (Fig. 2, Table 1). Six species (*Ctenochaetus striatus*, *Acanthurus*
242 *nigrofuscus*, *A. lineatus*, *A. japonicus*, *Naso lituratus*, and *Zebrasoma scopas*) primarily
243 showed a greater density in the outer reefs (Figs. 2a, 2c–2e, 2i, 2j, Table 1). By contrast, two
244 species (*A. dussumieri* and *N. unicornis*) showed size class variations in spatial distribution.
245 For *A. dussumieri*, smaller-sized (size classes 1 and 2) and larger-sized (size classes 4–6)
246 individuals showed greater densities in the inner and outer reefs, respectively (Fig. 2f, Table
247 1). For *N. unicornis*, size class 1 individuals and other size class individuals (size classes 2–6)
248 individuals showed greater densities in the inner and outer reefs, respectively (Fig. 2h, Table
249 1). *Ctenochaetus binotatus* and *A. nigricauda* did not show a clear difference in fish density
250 between the outer and inner reefs, although a greater density of the former and latter species
251 tended to be found in the outer and inner reefs, respectively (Figs. 2b, 2g, Table 1). For *Z.*
252 *velifer*, size class 1 individuals showed a significant greater density in the inner reefs, whereas

253 other size classes (size classes 2–4) tended to show a greater density in the outer reefs (Fig. 2k,
254 Table 1).

255

256 3.2. Spatial variations of environmental variables

257 The results of PCA revealed the relationship between the 17 environmental characteristics and
258 five PC axes (Table S1). The results of RDA revealed that the two PC axes (PC axes 1 and 3)
259 significantly affected the spatial distribution of surgeonfishes ($F = 22.09$, $p < 0.001$ for PC
260 axis 1; $F = 2.27$, $p = 0.020$ for PC axis 3), whereas the three axes (PC axes 2, 4 and 5) did not
261 have significant effect ($F = 1.20$, $p = 0.260$ for PC axis 2; $F = 2.04$, $p = 0.051$ for PC axis 4; F
262 $= 0.96$, $p = 0.438$ for PC axis 5). For PC axis 1, the plus direction represented a higher
263 coverage of rock, whereas the minus direction represented a higher coverage of dead
264 branching *Acropora*, dead bottlebrush *Acropora*, coral rubble, and sand (Fig. S2a). For PC
265 axis 3, the plus direction represented a higher coverage of coral rubble, whereas the minus
266 direction represented a higher coverage of branching *Acropora*, bottlebrush *Acropora*, dead
267 branching *Acropora*, dead bottlebrush *Acropora*, and macroalgae (Fig. S2b).

268 The site score plot by RDA revealed that the sites of the outer and inner reefs were
269 primarily plotted at the plus and minus directions of PC axis 1, respectively (Figs. 3a, 3b).
270 Among the 17 environmental variables, tabular *Acropora*, massive corals, other corals, soft
271 corals, and rock showed a higher coverage in the outer reefs (Figs. 3d, 3g, 3h, 3n, 3o, S3). By
272 contrast, branching *Acropora*, bottlebrush *Acropora*, dead branching *Acropora*, dead
273 bottlebrush *Acropora*, other dead corals, coral rubble, sand, and macroalgae showed a higher
274 coverage in the inner reefs (Figs. 3c, 3e, 3i, 3k, 3m, 3p–3r, S3).

275

276 3.3. *Species-specific and size-related variations in spatial distribution*

277 The fish species score plot by RDA revealed species-specific and size-related variations in
278 spatial distribution in relation to substrate characteristics.

279 *Ctenochaetus striatus*: the species scores of size classes 1 and 2 were plotted at the
280 first quadrant of the RDA plot, whereas the species scores of size classes 3 and 4 were plotted
281 at the plus direction of PC axis 1 (Fig. 4a). This result indicates that the size classes 1 and 2
282 individuals were primarily found at sites with higher coverage of rock, tabular *Acropora*,
283 branching corals, massive corals, and other corals (Figs. 3d, 3f–3h, 3o, 4a). By contrast, the
284 size classes 3 and 4 individuals were primarily found at the sites with a higher coverage of
285 rock (Figs. S2, 3o, 4a).

286 *Ctenochaetus binotatus*: the species scores of the three size classes (size classes 1, 2,
287 and 3) and size class 4 were plotted at the plus and minus directions of PC axis 1, respectively
288 (Fig. 4b). This result indicates that the size classes 1, 2 and 3 individuals were primarily found
289 at sites with a higher coverage of rock, whereas the size class 4 individuals were primarily
290 found at sites with higher coverage of sand and coral rubble (Figs. S2, 3o–3q, 4b).

291 *Acanthurus nigrofuscus*: the species scores of all size classes were plotted at the
292 plus direction of PC axis 1 (Fig. 4c), indicating that all size class individuals were primarily
293 found at sites with a higher coverage of rock (Figs. S2, 3o, 4c).

294 *Acanthurus lineatus*: the species scores of all size classes were plotted at the plus
295 direction of PC axis 1 (Fig. 4d), indicating all size class individuals were found at sites with a
296 higher coverage of rock (Figs. S2, 3o, 4d).

297 *Acanthurus japonicus*: the species scores of all size classes were plotted at the plus
298 direction of PC axis 1 (Fig. 4e), indicating the all size class individuals were primarily found

299 at sites with a higher coverage of rock (Figs. S2, 3o, 4e).

300 *Acanthurus dussumieri*: the species scores of two size classes (size classes 1 and 2) and
301 three size classes (size classes 4–6) were plotted at the minus and plus directions of PC axis 1,
302 respectively (Fig. 4f). This result indicates that smaller-sized individuals (size classes 1 and 2)
303 were found at sites with a higher coverage of sand and coral rubble, whereas larger-sized
304 individuals (size classes 4–6) were found at sites with a higher coverage of rock (Fig. S2,
305 3o–3r, 4f). By contrast, the species score of size class 3 was plotted at the plus direction of PC
306 axis 3 (Fig. 4f), indicating the size class 3 individuals were primarily found at sites with a
307 higher coverage of coral rubble (Figs. S2, 3p, 4f).

308 *Acanthurus nigricauda*: the species scores of the four size classes (size classes 1–3 and
309 5) were plotted at the minus direction of PC axis 1 (Fig. 4g), indicating that these size class
310 individuals were primarily found at sites with higher coverage of coral rubble and sand (Figs.
311 S2, 3p, 3q, 4g). By contrast, the species score of size class 4 was plotted at the plus direction
312 of PC axis 3 (Fig. 4g), indicating that the size class 4 individuals were primarily found at sites
313 with a higher coverage of coral rubble (Figs. S2, 3p, 4g).

314 *Naso unicornis*: the species scores of size class 1 and the other five classes (size classes
315 2–6) were plotted at the minus and plus directions, respectively (Fig. 4h). This result indicates
316 that the size class 1 individuals were primarily found at sites with higher coverage of coral
317 rubble and sand (Figs. S2, 3p, 3q, 4h), whereas 1 other five class individuals were primarily
318 found at sites with a higher coverage of rock (Figs. S2, 3o, 4h).

319 *Naso lituratus*: the species scores of all size classes were plotted at the plus direction of
320 PC axis 1 (Fig. 4i), indicating that the all size class individuals were primarily found at sites
321 with a higher coverage of rock (Figs. S2, 3o, 4i).

322 *Zebrasoma scopas*: the species scores of two size classes (size classes 1 and 2) were
323 plotted at the first quadrant of the RDA plot (Fig. 4j), indicating that smaller-sized individuals
324 (size classes 1 and 2) were primarily found at sites with higher coverage of tabular *Acropora*,
325 branching corals, massive corals, other corals, and rock (Figs. 3d, 3f–3h, 3o, 4j). By contrast,
326 the species score of size class 3 was plotted at the plus direction of PC axis 1 (Fig. 4j),
327 indicating that this size class individuals were primarily found at sites with a higher coverage
328 of rock (Figs. S2, 3o, 4j).

329 *Zebrasoma velifer*: the species score of size class 1 was plotted at the second quadrant
330 of the RDA plot (Fig. 4k), indicating that size class 1 individuals were primarily found at sites
331 with higher coverage of branching *Acropora*, bottlebrush *Acropora*, dead branching *Acropora*,
332 and macroalgae (Figs. 3c, 3e, 3i, 3r, 4k). The species scores of the two size classes (size
333 classes 2 and 3) were plotted at the plus directions of PC axes 1 and 3 (Fig. 4k), indicating
334 that this size class individuals were primarily found at sites with higher coverage of rock and
335 coral rubble (Figs. S2, 3o, 3p, 4k). The species score of size class 4 was plotted at the plus
336 direction of PC axis 1 (Fig. 4k), indicating that this size class individuals were primarily
337 found at sites with a higher coverage of rock (Figs. S2, 3o, 4k).

338

339 3.4. Foraging substrates

340 Seven species (*Ctenochaetus striatus*, *C. binotatus*, *Acanthurus nigrofuscus*, *A. lineatus*, *A.*
341 *japonicus*, *Naso unicornis*, and *N. lituratus*) showed a greater proportion of foraging on rock
342 (Figs. 5a–5e, 5h, 5i, 6). This trend was relatively consistent among all size classes of the
343 seven species, except for the size class 4 individuals of *C. binotatus* (Figs. S4a–S4f, S4i, S4j).
344 These seven species showed a significant positive utilization of rock as a foraging substrate

345 (Table 2). Of the 58 individuals of *A. nigrofuscus*, three individuals showed foraging on live
346 corals, indicating a significant negative utilization of live corals for foraging (Fig. 5c, Table 2).
347 Of the 42 individuals of *N. lituratus*, one individual showed foraging on dead corals,
348 indicating a significant negative utilization of dead corals for foraging (Fig. 5i, Table 2).

349 *Acanthurus dussumieri* showed foraging on rock and macroalgae (Figs. 5f, 6). The size
350 class 1 and other size class individuals (classes 2, 4 and 5) showed foraging on macroalgae
351 and rock, respectively (Fig. S4g). Overall, these substrate utilizations were not significant
352 (Table 2).

353 *Acanthurus nigricauda* showed a greater proportion of bites on sand and a certain
354 degree of foraging on dead corals, rock, and coral rubble (Figs. 5g, 6). This trend was
355 relatively consistent among the five size classes (Fig. S4h). This species showed significant
356 positive and negative utilizations of sand and rock, respectively (Table 2).

357 Two species (*Zebrasoma scopas* and *Z. velifer*) showed a greater proportion of foraging
358 on dead corals and rock (Figs. 5j, 5k, 6). Smaller-sized individuals (size classes 1 and 2)
359 showed a greater proportion of dead corals than larger-sized individuals (size classes 3 and 4:
360 Figs. S4k, S4l). These two species showed a significant positive utilization of dead corals as a
361 foraging substrate (Table 2). *Zebrasoma scopas* also showed a significant positive utilization
362 of rock (Table 2).

363

364 **4. Discussion**

365 *4.1 Overall trend in spatial distribution*

366 This study examined the species-specific and size-related spatial distribution of 11
367 surgeonfish species in relation to topographical features (outer and inner reefs) and substrate

368 diversity (various types of live corals, dead corals and non-coralline substrates). Almost all
369 size class individuals of the six species (*Ctenochaetus striatus*, *Acanthurus nigrofuscus*, *A.*
370 *lineatus*, *A. japonicus*, *Naso lituratus*, and *Zebrasoma scopas*) and larger-sized individuals of
371 the three species (*Acanthurus dussumieri*, *N. unicornis*, and *Zebrasoma velifer*) showed
372 greater densities in the outer reefs with a higher coverage of rock. Surgeonfishes in the Great
373 Barrier Reef showed a similar trend, indicating that the density of most species belonging to
374 the three genera (*Acanthurus*, *Naso*, and *Zebrasoma*) was greater at outer reefs than at inshore
375 reefs (Russ, 1984a; Cheal et al., 2012). On the contrary, *A. nigricauda* showed a greater
376 density of all size class individuals in the inner reefs with higher coverage of coral rubble and
377 sand, which is consistent with the result obtained from the Great Barrier Reef (Cheal et al.,
378 2012). The overall trends indicated that surgeonfishes in the Okinawan coral reef preferred
379 outer reefs, which is contrary to goatfishes that showed greater densities in the inner reefs
380 (Nanami, 2025b).

381

382 4.2. Spatial distribution in relation to foraging substrates

383 For the two species of “brushers”, all size classes of *Ctenochaetus striatus* showed a
384 significant greater density in the outer reefs with a higher coverage of rock. This species
385 exhibited a significant positive utilization of rock as a foraging site, which is consistent with
386 the results of Brandl and Bellwood (2014) and Brandl et al. (2015). For *C. binotatus*, most
387 individuals tended to be found at sites with a higher coverage of rock. This species also
388 showed a significant positive utilization of rock as a foraging substrate. Considering that
389 “brushers” primarily feed on a particulate material on a hard substrate (Brandl and Bellwood,
390 2014; Brandl et al., 2015; Tebbett et al., 2022), a rocky surface is the main factor regulating

391 the spatial distribution of *C. striatus* and *C. binotatus*.

392 The three species of “croppers” (*Acanthurus nigrofuscus*, *A. lineatus*, and *A.*
393 *japonicus*) showed a greater density in the outer reefs, or were only found in the outer reefs,
394 with a higher coverage of rock. These findings indicate the positive association of the three
395 species with rock in the outer reefs. The three species also showed a significant positive
396 utilization of rock as a foraging substrate, which is consistent with the result of Brandl et al.
397 (2015) for *A. nigrofuscus* and *A. lineatus*. As “croppers” feed algae filament on a hard
398 substrate (Brandl et al., 2015; Tebbett et al., 2022), the rocky surface is the main factor
399 regulating the spatial distribution of *A. nigrofuscus*, *A. lineatus*, and *A. japonicus*. Considering
400 that the outer reefs were located outside the reef crest, the water current is likely to be greater
401 than that in the inner reefs. Some species belonging to the genus *Acanthurus* can crop algae
402 without bending the body in lateral direction, suggesting that such quick motion of foraging
403 behavior is the adaptation to a greater water flow (Mihalitsis and Wainwright, 2024;
404 Mihalitsis et al., 2025). This unique foraging behavior might be another reason that the three
405 *Acanthurus* species showed greater densities in the outer reefs.

406 For the two species of “sediment suckers”, smaller-sized individuals of *A.*
407 *dussumieri* (TL \leq 15 cm) and all size class individuals of *A. nigricauda* appeared to show a
408 greater density in the inner reefs with higher coverage of coral rubble and sand. *Acanthurus*
409 *nigricauda* also showed a significant positive utilization of sand as a foraging substrate.
410 Similar higher utilization rate of sand by *A. nigricauda* has been indicated in the Great Barrier
411 Reef (Brandl and Bellwood, 2014; Brandl et al., 2015). These results suggest that a sandy area
412 is a preferred environment for *A. nigricauda*. By contrast, *A. dussumieri* showed foraging
413 bites on microalgae or rock, which were not soft substrates. A precise diet examination of *A.*

414 *dussumieri* in Okinawan coral reefs might clarify the difference in foraging substrates
415 between the previous and the present studies.

416 For the two species of “browsers” (*N. unicornis* and *N. lituratus*), most size class
417 individuals showed a greater density in the outer reefs with a higher coverage of rock. These
418 two species also showed a significant positive utilization of rock as a foraging substrate. As
419 these two species feed on macroalgae on a hard substrate (Brandl et al., 2015), a site with a
420 higher coverage of rocky surface is likely to be a suitable environment for these two species.

421 For the “concealed croppers”, all size class individuals of *Z. scopas* showed a
422 greater density in the outer reefs with a higher coverage of rock. This species showed a
423 significant positive utilization of dead corals and rock, which is consistent with the findings of
424 Brandl et al. (2015). Considering that outer reefs were characterized by a higher coverage of
425 rock but a lower coverage of dead corals, a rocky surface rather than coverage of dead corals
426 might be a suitable environment for *Z. scopas*. However, this study did not clarify the
427 difference in precise algae availability between the outer and inner reefs. Considering that
428 surgeonfishes show a species-specific difference in algae types (Choat et al., 2002a; Clements
429 et al., 2003; Kelly et al., 2016; Duran et al., 2019), the causal relationship between *Z. scopas*
430 and a rocky surface with regard to algae availability should be examined. For *Z. velifer*, three
431 size classes (classes 2–4: TL \geq 11 cm) showed a greater density in the outer reefs with a
432 higher coverage of rock, but it showed a significant positive utilization of dead corals as a
433 foraging substrate. Although it was not significant positive utilization, 19 of 35 individuals
434 utilized rock as foraging sites, indicating that a rocky surface might be a suitable environment
435 for *Z. velifer*. However, considering that precise algae availability remained unclear, the
436 relationship between the greater density of *Z. velifer* and a rocky surface should be precisely

437 examined.

438

439 *4.3. Importance of non-coralline substrates*

440 These results suggest that non-coralline substrates (dead corals, rock, coral rubble, and sand)
441 are the key substrate types that determine the spatial distributional patterns of most
442 surgeonfish species. This result is contrary to that of numerous previous studies showing the
443 positive associations of fishes with live corals (Gardiner and Jones, 2005; Wilson et al., 2008;
444 Pratchett et al., 2008; Doll et al., 2021; Nanami, 2025a), but it is consistent with that of other
445 previous studies showing the positive associations of fishes with non-coralline substrates
446 (rock, coral rubble, and sand) (Nanami, 2021; 2025b). Non-coralline substrates, especially for
447 rock, have complex physical structures that could provide refuge space. The nocturnal
448 substrate associations of two surgeonfish species (*N. unicornis* and *N. lituratus*) revealed that
449 a rock overhang was utilized as sleeping sites (Nanami, 2024). Thus, the coarse physical
450 structure provided by a rocky surface is likely to be a suitable habitat for surgeonfishes.

451 Some previous studies revealed that inter- and intra-specific interactions determine
452 the spatial distribution and substrate utilization of surgeonfishes (Robertson, 1986; Robertson
453 et al., 1979). In addition, the nocturnal substrate associations of surgeonfishes (except for *N.*
454 *unicornis* and *N. lituratus*) remain unclear. Therefore, examining these ecological aspects
455 enable to provide comprehensive understanding of the spatial distribution of surgeonfishes.

456

457 *4.4. Importance of live corals for smaller-sized individuals*

458 Smaller-sized individuals of *Zebrasoma velifer* (size class 1) showed a greater density in the
459 inner reefs. The inner reefs showed higher coverage of live corals (branching *Acropora* and

460 bottlebrush *Acropora*) and dead corals (dead branching *Acropora* and dead other corals),
461 which provide a fine-scale structural complexity. Inner reef habitats with less wave exposure
462 serve as nursery habitats of juvenile fishes of numerous species in coral reefs (Nagelkerken,
463 2009). In addition, smaller-sized fish species (e.g., damselfishes, gobies, and cardinalfishes)
464 utilize a fine-scale structural complexity as a refuge space and habitat (Gardiner and Jones,
465 2005; Wilson et al., 2008; Doll et al., 2021; Nanami 2025a). Considering these ecological
466 aspects, smaller-sized individuals of *Z. velifer* are likely to utilize the site in the inner reefs
467 with a higher coverage of live corals as a nursery habitat.

468 In addition, smaller-sized individuals (size classes 1 and 2) of *Ctenochaetus striatus*
469 and *Z. scopas* also showed a greater density in the outer reefs with higher coverage of tabular
470 *Acropora*, branching corals, massive corals, and other corals. These results suggest that the
471 two species utilize the site in the outer reefs with a higher coverage of live corals as nursery
472 habitats, although the faunal composition of live corals was different from that in the inner
473 reefs. Considering that outer reefs are likely to be characterized by a greater degree of wave
474 exposure than inner reefs, outer reefs might not be an ideal habitat for juveniles of the two
475 species. However, considering that live corals provide complex physical structures that can
476 weaken the degree of wave action, juveniles might be closely associated with live corals to
477 avoid greater wave exposure.

478

479 *4.5. Implication of conservation for surgeonfish assemblages*

480 Considering that live corals with a structural complexity provide refuge spaces and shelters
481 for fishes, numerous studies have recommended the conservation of coral-rich areas and
482 restoration of coral assemblages (Pratchett et al., 2008; Barton et al., 2015; Lirman and

483 Schopmeyer, 2016). By contrast, this study revealed that non-coralline substrates are the key
484 ecological factors that regulate the spatial distribution and substrate utilization for foraging in
485 surgeonfishes. This finding indicates that the coarse structural complexity provided by rock,
486 as well as the foraging sites that provided by dead corals, rock, coral rubble, and sand, should
487 be considered to conserve surgeonfish species. Thus, live coral restoration is not necessarily
488 effective for conserving some surgeonfish species that are primarily found at a higher
489 coverage of non-coralline substrates. However, considering that smaller-sized individuals of
490 three species (*Ctenochaetus striatus*, *Zebrasoma scopas*, and *Z. velifer*) are primarily found at
491 sites with a higher coverage of live corals, the juveniles of these species might utilize the sites
492 as a refuge space. Thus, the live coral restoration is necessary to conserve nursery habitats
493 rather than foraging sites for these species. These ecological aspects provide several
494 indicators for establishing MPAs to maintain and enhance the overall species diversity of
495 surgeonfishes in coral reefs: (1) both outer reefs and inner reefs should be protected; (2)
496 diverse substrate types, including non-coralline substrates and various types of live corals,
497 should be protected; (3) actual species-specific spatial distribution and behavioral aspects
498 about foraging substrates should be applied.

499 A lower coverage of corals is becoming more prevalent because of degradation of
500 coral assemblages in recent years, and coral transplantation has been applied to restore coral
501 assemblages (Ferse et al., 2021). Although this technique can restore a coral reef ecosystem,
502 surgeonfishes utilize non-coralline substrates as habitat and foraging sites. Thus, in the
503 restoration of coral assemblages, it should be considered that non-coralline substrates play an
504 important role in maintaining the species diversity of coral reef fishes.

505

506 **5. Conclusion**

507 This study examined the spatial distribution and foraging substrates of 11 surgeonfish species
508 in an Okinawan coral reef, which is the first study conducted in this region. The results
509 showed positive relationships between surgeonfish species and non-coralline substrates (dead
510 corals, rock, coral rubble, and sand) as habitat and foraging sites. Three species also showed
511 that the sites with a higher coverage of live corals as nursery habitats. Although numerous
512 previous studies showed a positive relationship between coral reef fishes and live corals as
513 refuge space and foraging substrates, this study showed that the coverage of live corals is not
514 the primary factor regulating the species-specific spatial distribution of surgeonfishes. The
515 results of this study indicate the importance of non-coralline substrates for protecting
516 surgeonfish species diversity, which can be applied to ecosystem-based management. That is,
517 non-coralline substrates and live corals should be considered to establish effective MPAs for
518 maintaining and enhancing the high species diversity of surgeonfishes in coral reefs.

519

520 **Acknowledgments**

521 I express my grateful thanks to Masato Sunagawa, Masamitsu Sunagawa and Sho Sunagawa
522 for their field guide, Nobuo Motomiya, Kenta Oishi, Fumihiko Nakamura, Minoru Yoshida
523 and Kenji Aramoto for field assistance, and the staff of Yaeyama Field Station of Fisheries
524 Technology Institute for support during the present study. Constrictive comments from three
525 anonymous reviewers were much appreciated. This study was supported by Environment
526 Research and Technology Development Fund (S-15-3(4): JPMEERF16S11513) of the
527 Ministry of the Environment, Japan and JSPS KAKENHI Grant Number 15H02268 and
528 19K06199. The author would like to thank Enago (www.enago.jp) for the English language

529 review. The present study complies with the current laws in Japan.

530

531 **Funding** This study was supported by Environment Research and Technology Development
532 Fund (S-15-3(4): JPMEERF16S11513) of the Ministry of the Environment, Japan and JSPS
533 KAKENHI Grant Number 15H02268 and 19K06199.

534

535 **Conflict of interest** The authors declare no conflict of interest.

536

537 **Ethical approval** No animal testing was performed during this study

538

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

541

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

544

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

547

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782 **Figure captions**

783 **Fig. 1.** Maps of the location of the Yaeyama Islands (a), study area (b), the 62 study sites used
784 for underwater observations of spatial distributions (c), and the 24 study sites used for
785 underwater observations of foraging substrates (d). In (c), the symbols shown in magenta and
786 yellow indicate the sites in the outer and inner reefs, respectively. Outer and inner reefs were
787 defined as the sites outside and inside the reef crest. The aerial photographs used in (b), (c),
788 and (d) were provided by the International Coral Reef Research and Monitoring Center.

789
790 **Fig. 2.** Spatial distributions of the 11 surgeonfish species. The circle diameter and six
791 different colors (white, yellow, green, blue, magenta, and red) represent the fish density per
792 $100\text{ m} \times 5\text{ m}$ and different size classes, respectively. The aerial photographs were provided by
793 the International Coral Reef Research and Monitoring Center. The fish photographs were
794 taken by the author (A. Nanami).

795
796 **Fig. 3.** Results of the redundancy analysis (RDA) indicating the spatial distributional patterns
797 of environmental characteristics. The symbols of magenta and yellow represent the sites in the
798 outer and inner reefs, respectively. In (a, b), the overall difference in environmental
799 characteristics between the outer and inner reefs in relation to two PC axes was shown. In
800 (c–r), the circle diameters represent the numerical values of coverage (%) of each substrate
801 type. The cross marks represent the 0% coverage at the sites. In (s), the circle diameters
802 represent the numerical values of depth. For actual spatial distributional patterns of
803 environmental characteristics, see Figure S3.

804

805 **Fig. 4.** Results of redundancy analysis (RDA) indicating the relationship between the spatial
806 distribution of the 11 surgeonfish species and environmental characteristics. The
807 environmental characteristics that had a significant effect on spatial distributions are
808 presented as blue vectors (see also Figs. 3, S2, S3). Symbols shown by the six different colors
809 (white, yellow, green, blue, magenta, and red) represent the different size classes. The fish
810 photographs were taken by the author (A. Nanami).

811

812 **Fig. 5.** Relationship between the number of fish individuals that utilized the focal substrate
813 and substrate availability. The dark-blue and orange bars represent the number of fish
814 individuals and substrate availability, respectively. The numbers above the dark-blue bars
815 represent the number of fish individuals that utilized the focal substrate. The data for fish
816 foraging substrates and the data of substrate availability at the 24 sites were pooled for the
817 analysis. The fish photographs were taken by the author (A. Nanami).

818

819 **Fig. 6.** Results of principal component analysis (PCA) indicating the species-specific
820 difference in foraging substrates for the 11 surgeonfish species. The pie charts represent the
821 proportion of substrates that were initially foraged by the focal species. The vector for soft
822 corals was not shown because no foraging bites on soft corals were observed. Considering
823 that the score of *Acanthurus nigricauda* was (-0.673, -0.199), the score was shown in an
824 enclosed dotted square. The fish species names are abbreviated as follows: Adus, *A.*
825 *dussumieri*; Ajap, *A. japonicus*; Alin, *A. lineatus*; Anga, *A. nigricauda*; Anig, *Acanthurus*
826 *nigrofuscus*; Cstr, *Ctenochaetus striatus*; Cbin, *C. binotatus*; Nlit, *N. lituratus*; Nuni, *Naso*
827 *unicornis*; Zsco, *Zebrasoma scopas*; Zvel, *Z. velifer*.

828

829 **Fig. S1.** Total number of individuals for each species during the study periods. The data
830 enclosed in red square in (a) were shown as an enlarged figure in (b) for clarity. The blue
831 dashed line in (b) represents the threshold between the selected and unselected species for the
832 analysis.

833

834 **Fig. S2.** Results of principal component analysis (PCA) indicating the relationship between
835 the two principal component axes (PC axes 1 and 3) and 17 environmental variables.

836

837 **Fig. S3.** Spatial distributions of the 16 types of substrates (a–p), and spatial variation in water
838 depth (q). The symbols shown in magenta and yellow indicate the sites in the outer and inner
839 reefs, respectively. Outer and inner reefs were defined as the sites outside and inside the reef
840 crest. The aerial photographs were provided by the International Coral Reef Research and
841 Monitoring Center.

842

843 **Fig. S4.** Results of principal component analysis (PCA) indicating the size-related difference
844 in foraging substrates for the 11 surgeonfish species. The pie charts represent the proportion
845 of substrates that were initially foraged by the focal species. The vector for soft corals was not
846 shown, because no foraging bites on soft corals were observed. Size classes: class 1 (total
847 length ≤ 10 cm); class 2 ($11 \text{ cm} \leq \text{total length} \leq 15$ cm); class 3 ($16 \text{ cm} \leq \text{total length} \leq 20$
848 cm); class 4 ($21 \text{ cm} \leq \text{total length} \leq 25$ cm); class 5 ($26 \text{ cm} \leq \text{total length} \leq 30$ cm), class 6
849 (total length ≥ 31 cm). The fish photographs were taken by the author (A. Nanami).