Nocturnal substrate association of four coral reef fish groups (parrotfishes, surgeonfishes, groupers and butterflyfishes) in relation to substrate architectural characteristics

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Although numerous coral reef fish species utilize substrates with high structural complexities as habitats and refuge spaces, quantitative analysis of nocturnal fish substrate associations has not been sufficiently examined yet. The aims of the present study were to clarify the nocturnal substrate associations of 17 coral reef fish species (nine parrotfish species, two surgeonfish species, two grouper species and four butterflyfish species) in relation to substrate architectural characteristics. Substrate architectural characteristics were categorized into seven types as follows: (1) eave-like space, (2) large inter-branch space, (3) overhang by protrusion of fine branching structure, (4) overhang by coarse structure, (5) uneven structure without large space or overhang, (6) flat and (7) macroalgae. Overall, fishes were primarily associated with three architectural characteristics (eave-like space, large inter-branch space and overhang by coarse structure). Main provisions of these three architectural characteristics were respectively due to tabular and corymbose *Acropora*, staghorn *Acropora*, and rock. Species-specific significant positive associations with particular architectural characteristics were found as follows. For the nine parrotfish species, *Chlorurus microrhinos* with large inter-branch space and overhang by coarse structure; *C. spilurus* with eave-like space and large inter-branch space; *Hipposcarus longiceps* with large inter-branch space; *Scarus ghobban* with overhang by coarse structure; five species (*Scarus forsteni*, *S. niger*, *S. oviceps*, *S. rivulatus* and *S. schlegeli*) with eave-like space. For the two surgeonfish species, *Naso unicornis* with overhang by coarse structure; *N. lituratus* with eave-like space. For the two grouper species, *Plectropomus leopardus* with eave-like space; *Epinephelus ongus* with large-inter branch space and overhang by coarse structure. For the four butterflyfish species, *Chaetodon trifascialis* with eave-like space and large inter-branch space; *C. lunulatus* and *C. ephippium* with large inter-branch space; *C. auriga* showed no significant associations with any architectural characteristics. Since three fish groups (parrotfishes,

surgeonfishes and groupers) are main fisheries targets in coral reefs, conservation and restoration of coral species that provide eave-like space (tabular and corymbose *Acropora*) and large inter-branch space (staghorn *Acropora*) as well as hard substrates with coarse structure that provide overhang (rock) should be considered for effective fisheries management in coral reefs. For butterflyfishes, coral species that provide eave-like space (tabular *Acropora*) and large inter-branch space (staghorn *Acropora)* should also be conserved and restored for provision of sleeping site. The present study revealed new insights about nocturnal substrate association of coral reef fishes, which will provide useful ecological information for effective conservational strategy.

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ABSTRACT

Although numerous coral reef fish species utilize substrates with high structural complexities as habitats and refuge spaces, quantitative analysis of nocturnal fish substrate associations has not been sufficiently examined yet. The aims of the present study were to clarify the nocturnal substrate associations of 17 coral reef fish species (nine parrotfish species, two surgeonfish species, two grouper species and four butterflyfish species) in relation to substrate architectural characteristics. Substrate architectural characteristics were categorized into seven types as follows: (1) eave-like space, (2) large inter-branch space, (3) overhang by protrusion of fine branching structure, (4) overhang by coarse structure, (5) uneven structure without large space or overhang, (6) flat and (7) macroalgae. Overall, fishes were primarily associated with three architectural characteristics (eave-like space, large inter-branch space and overhang by coarse structure). Main provisions of these three architectural characteristics were respectively due to tabular and corymbose *Acropora*, staghorn *Acropora*, and rock. Species-specific significant positive associations with particular architectural characteristics were found as follows. For the nine parrotfish species, *Chlorurus microrhinos* with large inter-branch space and overhang by coarse structure; *C. spilurus* with eave-like space and large inter-branch space; *Hipposcarus longiceps* with large inter-branch space; *Scarus ghobban* with overhang by coarse structure; five species (*Scarus forsteni*, *S. niger*, *S. oviceps*, *S. rivulatus* and *S. schlegeli*) with eave-like space. For the two surgeonfish species, *Naso unicornis* with overhang by coarse structure; *N. lituratus* with eave-like space. For the two grouper species, *Plectropomus leopardus* with eave-like space; *Epinephelus ongus* with large-inter branch space and overhang by coarse structure. For the four

butterflyfish species, *Chaetodon trifascialis* with eave-like space and large inter-branch space; *C. lunulatus* and *C. ephippium* with large inter-branch space; *C. auriga* showed no significant associations with any architectural characteristics. Since three fish groups (parrotfishes, surgeonfishes and groupers) are main fisheries targets in coral reefs, conservation and restoration of coral species that provide eave-like space (tabular and corymbose *Acropora*) and large inter-branch space (staghorn *Acropora*) as well as hard substrates with coarse structure that provide overhang (rock) should be considered for effective fisheries management in coral reefs. For butterflyfishes, coral species that provide eave-like space (tabular *Acropora*) and large inter-branch space (staghorn *Acropora)* should also be conserved and restored for provision of sleeping site. The present study revealed new insights about nocturnal substrate association of coral reef fishes, which will provide useful ecological information for effective conservational strategy.

INTRODUCTION

Coral reefs provide various substrates with high structural complexities, which are key determinants supporting high species diversity of marine organisms (Jaap, 2000; Yanovski, Nelson & Abelson, 2017). Numerous coral reef fish species utilize substrates with a high structural complexity as habitats and refuge spaces (Luckhurst & Luckhurst, 1978; Ménard et al., 2012, Richardson et al., 2017; Oren et al., 2023). Species-specific habitat associations to specific substrates or structural complexities have also been reported (Wilson et al., 2008; Ticzon et al., 2012; Untersteggaber, Mitteroecker & Herler, 2014; Nanami, 2023).

Coral reef fishes provide various ecosystem services such as natural food production, ornamental resources, aquarium resources, habitat maintenance and recreation (Moberg & Folke, 1999; Laurans et al., 2013; Elliff & Kikuchi, 2017; Sato et al., 2020). Among the diverse ecosystem services, the provision of fisheries targets is recognized as an essential service (Elliff & Kikuchi, 2017; Woodhead et al., 2019). Specifically, parrotfishes (family Labridae: Scarini), groupers (family Epinephelidae) and surgeonfishes (family Acanthuridae) are main targets of commercial fisheries in many countries in tropical and sub-tropical region (e.g., Bejarano et al., 2013; Taylor et al., 2014; Akita et al., 2016; Frisch et al., 2016). Provision of ornamental resources or aquarium resources is also an important ecosystem service in coral reefs, and butterflyfishes (family Chaetodontidae) are regarded as main target in the aquarium trade for their popularity as ornamental fishes (Tissot & Hallacher, 2003; Wabnitz et al., 2003; Lawton, Pratchett & Delbeek, 2013).

Several studies have revealed species-specific spatial distributions of these four fish groups in relation to topographic features or environmental characteristics (e.g., Newman, Williams & Russ, 1997; Hoey & Bellwood, 2008; Hernández-Landa et al. 2014; Nanami, 2020, 2021). Previous studies have also revealed the foraging substrates for parrotfishes (Bonaldo & Rotjan, 2018; Nicholson & Clements, 2020), surgeonfishes (Robertson & Gaines, 1986), groupers (Wen et al., 2013a) and butterflyfishes (Cole & Pratchett, 2013; Pratchett, 2013). In contrast, microhabitat-level substrate associations of these fish groups have not been sufficiently examined. This is because most individuals belonging to these fish groups are diurnally active and rarely show concealing behavior to specific substrates. Although some previous studies have revealed the diurnal microhabitat-level substrate associations of groupers (Nanami et al., 2013; Wen et al. 2013b), their nocturnal associations have not been examined yet.

Several previous studies have also shown high site fidelity by parrotfishes (Welsh & Bellwood, 2012; Pickholtz et al., 2022), surgeonfishes (Meyer & Holland, 2005; Marshell et al., 2011), groupers (Zeller, 1997; Matley, Heupel & Simpfendorfer, 2015; Nanami et al., 2018) and butterflyfishes (Yabuta & Berumen, 2013). For instance, Pickholtz et al. (2022) revealed that three parrotfish species repetitively used specific spaces during nocturnal periods in the Red Sea. Marshell et al. (2011) showed high site fidelity during nocturnal periods by two surgeonfish species in Guam. From the results of these studies, nocturnal microhabitat-level substrate associations might be observed due to their nocturnal high site fidelity.

Clarifying nocturnal substrate associations of fishes would provide useful ecological information for effective ecosystem management such as habitat protection and restoration by implementation of marine protected areas. This is because conservation of critical habitats for target species is crucial for marine protected area planning (Kelleher, 1999; Green, White & Kilarski, 2013). Although some previous studies have revealed nocturnal fish substrate associations (Hobson, 1965; Robertson & Sheldon, 1979; Pickholtz et al., 2023), quantitative analysis of nocturnal substrate associations in relation to substrate availability has not been sufficiently examined yet.

The aims of the present study were to clarify nocturnal substrate associations of four coral reef fish groups (parrotfishes, surgeonfishes, groupers and butterflyfishes), which provide main ecosystem services in coral reefs. Specifically, the aims were to clarify nocturnal substrate associations with substrates in terms of (1) architectural characteristics (physical structure) and (2) more precise aspects (coral morphology, live coral or dead coral, and non-coralline substrates). The results will enable a more comprehensive understanding for association between coral reef fishes and substrate characteristics.

MATERIALS AND METHODS

The study was conducted by field observations. Fish individuals that were caught for sampling were immediately killed to minimize pain. Okinawa prefectural government fisheries coordination regulation No. 37 approved the sampling procedure, which permits capture of marine fishes on Okinawan coral reefs for scientific purposes.

Fish survey and study species

This study was conducted at Sekisei lagoon and Nagura Bay in the Yaeyama Islands, Okinawa, Japan (Fig. 1). Nocturnal underwater observations (1830 h – 23:00 h) were conducted at 19 sites between November 2021 and March 2022. By using SCUBA and flashlights, the first diver swam in a zigzag manner along the seafloor and searched for inactive individuals that were associated with substrates (Fig. 2), with special care not to cover the same swimming course. Second diver followed the first diver with a data collection sheet. When the first diver found a focal fish individual, the second diver recorded the species name, total length (TL) and substrate with which the focal fish individual was associated. In some case, the whole body of fish individuals was not completely observed due to concealment behavior within the substrate. In this case, the focal fish individual was collected by spear and TL of the fish individual was measured. Over 40 minutes observation was conducted at each site (ranging from 40 to 72 minutes, average = 52.3 minutes ± 9.2 standard deviation).

During the observation period, 19, 2, 9 and 12 species were identified for parrotfishes, surgeonfishes, groupers and butterflyfishes, respectively (Table 1). Among them, 9, 2, 2 and 4 species that showed higher densities (total number of individuals was 10 or more) for parrotfishes, surgeonfishes, groupers and butterflyfishes, respectively. Thus, these 17 species were selected for the analyses.

Data collection of substrate availability

Substrate availability at the 19 study sites was recorded during daytime. Video recording mode of a digital camera was applied to record substrates on the seafloor during 20 minutes. Then, static images were extracted at 10-second 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.

Substrate categorization

Substrates were categorized into 25 types as follows with some modification from Nanami (2020) (Table 2): (1) corymbose *Acropora*, (2) tabular *Acropora*, (3) staghorn *Acropora*, (4) branching *Acropora*, (5) bottlebrush *Acropora*, (6) non-acroporid branching coral (e.g., *Seriatopora*, *Porites*, *Millepora*), (7) *Pocillopora*, (8) foliose coral (e.g., *Echinopora*), (9) massive coral (e.g., *Porites*, *Favia, Diploastrea*), (10) other coral (e.g., encrusting coral and mushroom coral), (11) dead corymbose *Acropora*, (12) dead tabular *Acropora*, (13) dead staghorn *Acropora*, (14) dead branching *Acropora*, (15) dead bottlebrush *Acropora*, (16) dead non-acroporid branching coral, (17) dead *Pocillopora*, (18) dead foliose coral, (19) dead massive coral, (20) dead other coral, (21) soft coral, (22) rock, (23) coral rubble, (24) sand and (25) macroalgae (*Padina*).

Definition of substrate architectural characteristics

Based on the above-mentioned 25 substrate types, substrate architectural characteristics (physical structure) were categorized into seven types as follows (Table 2, Fig. 3): (1) eave-like space (corymbose *Acropora*, tabular *Acropora*, foliose coral, dead corymbose *Acropora*, dead tabular *Acropora* and dead foliose coral), (2) large inter-branch space (staghorn *Acropora* and dead staghorn *Acropora*), (3) overhang provided by protrusion of fine branching structure (branching

Acropora, bottlebrush *Acropora*, non-acroporid branching coral, *Pocillopora*, dead branching *Acropora*, dead bottlebrush *Acropora*, dead non-acroporid branching coral and dead *Pocillopora*), (4) overhang by coarse structure (massive coral, dead massive coral and rock), (5) uneven structure without large space or overhang (undulating surface in several-centimeter scale: other coral, dead other coral and soft coral), (6) flat (coral rubble and sand) and (7) macroalgae.

Data analysis for substrate association

The analyses were conducted in two steps. First step was to clarify the associations between fish species and the seven types of substrate architectural characteristics (physical structure). Second step was to clarify the associations between fish species and the 25 substrate types.

Fish associations were analyzed by using "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 in 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:

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

where $Z_{a/2k}$ is the critical value of the standard normal distribution corresponding to an upper tail area of $a/2k$, a is 0.05, k is the 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 ± 95% CI above and below 1 indicate a significantly positive and negative association, respectively. Substrates with w_i ± 95% CI encompassing 1 had no significant positive or negative association. Substrates without any association with fish were excluded from the analysis.

Data preparation prior to analysis

All data for substrate associations by fish were obtained from the 19 study sites were pooled for the analysis. Although all data for substrate availability from the 19 sites were also pooled for the analysis, a modification was applied due to the difference in observation time among the 19 sites. The modification was as follows:

$$\text{Overall proportion of } i\text{th substrate} = \frac{\sum_{j=1}^{19} P_{ij}T_j}{\sum_{i=1}^{7}\sum_{j=1}^{19} P_{ij}T_j}$$

where P_{ij} is the proportion of ith substrate at site j and T_j is the observation duration (minutes) at site j.

Overall trend in substrate association

To summarize species-specific differences in substrate association, a principal component analysis (PCA) and cluster analysis using the group average linkage method with the Bray-Curtis similarity index was applied based on the number of fishes by including data from the seventeen fish species. For plotting the PCA score of each fish species, data about nocturnal substrate association were also shown by pie charts.

RESULTS

Parrotfishes

Chlorurus microrhinos was primarily associated with large inter-branch space (staghorn *Acropora*) and overhang by coarse structure (rock) (Fig. 4A). Significant positive associations with large inter-branch space (staghorn *Acropora*) and overhang by coarse structure (rock) were found (Fig. 5A).

Chlorurus spilurus was primarily associated with eave-like space (corymbose *Acropora* and tabular *Acropora*), large inter-branch space (staghorn *Acropora*) and overhang by fine branching structure (non-acroporid branching coral) (Fig. 4B). Significant positive associations with eave-like space and large inter-branch space were found (Fig. 5B). For eave-like space, no significant substrate-specific associations were found. For large inter-branch space, significant positive association with staghorn *Acropora* was found. In contrast, a significant negative association with overhang by coarse structure (rock) was found.

Hipposcarus longiceps was primarily associated with large inter-branch space (staghorn *Acropora*) and overhang by coarse structure (rock) (Fig. 4C). Significant positive and negative associations with large inter-branch space (staghorn *Acropora*) and overhang by fine branching structure was found, respectively (Fig. 5C).

Scarus ghobban was primarily associated with eave-like space (corymbose *Acropora*) and overhang by coarse structure (massive coral and rock) (Fig. 4D). Although this species showed a significant positive association with overhang by coarse structure, no significant substrate-specific associations were found (Fig. 5D).

Five species (*Scarus forsteni*, *S. niger*, *S. oviceps*, *S. rivulatus* and *S. schlegeli*) were primarily associated with eave-like space (corymbose *Acropora* and tabular *Acropora*) (Figs. 4E-4I) and showed a significant positive association with the eave-like space (Figs. 5E-5I). Three species (*S. forsteni*, *S. oviceps* and *S. rivulatus*) and one species (*S. schlegeli*) showed positive associations with tabular *Acropora* and corymbose *Acropora*, respectively (Figs. 5E, 5G-5I). In contrast, *S. niger* did not show any substrate-specific associations (Figs. 5F).

Surgeonfishes

Naso unicornis was primarily associated with overhang by coarse structure (rock: Fig. 6A) and showed a significant positive association with the substrate (Fig. 7A). A significant negative association with overhang by fine branching structure was also found (Fig. 7A).

Naso lituratus was primarily associated with eave-like space (tabular *Acropora*) and overhang by coarse structure (rock: Fig. 6B). Significant positive association with eave-like space (tabular *Acropora*) was found (Fig. 7B).

Groupers

Plectropomus leopardus was primarily associated with eave-like space (corymbose and tabular *Acropora*) and overhang by coarse structure (rock: Fig. 8A). This species showed a significant positive association with eave-like structure, although no significant substrate-specific associations were found (Fig. 9A). In contrast, a significant negative association with flat (coral rubble) was found (Fig. 9A).

Epinephelus ongus was primarily associated with overhang by fine branching structure and overhang by coarse structure (Fig. 8B). Significant positive associations with large inter-branch space and overhang by coarse structure were found (Fig. 9B). However, for substrate-specific associations, significant positive and negative associations with non-acroporid branching coral and branching *Acropora* were respectively found (Fig. 9B).

Butterflyfishes

Chaetodon trifascialis was primarily associated with eave-like space (tabular *Acropora*) and large inter-branch space (staghorn *Acropora*: Fig. 10A) and showed significant positive associations with these substrates (Fig. 11A). This species also showed a significant negative association with overhang by coarse structure (rock: Fig. 11A).

Chaetodon lunulatus was primarily associated with large inter-branch space (staghorn *Acropora*: Fig. 10B) and showed a significant positive association with the substrate (Fig. 11B). This species also showed a significant negative association with overhang by coarse structure (rock: Fig. 11B).

Chaetodon ephippium was associated with large inter-branch space (staghorn *Acropora*) and overhang by coarse structure (dead massive coral and rock: Fig. 10C) and showed a significant positive association with large inter-branch space (staghorn *Acropora*: Fig. 11C).

Chaetodon auriga was primarily associated with eave-like space (corymbose *Acropora* and dead tabular *Acropora*) and overhang by coarse structure (rock: Fig. 10D). However, no significant associations with any structural characteristics and substrates were found (Fig. 11D).

Overall trend of substrate association including the seventeen fish species

For the seven types of substrate architectural characteristics, PCA revealed that three architectural characteristics (eave-like space, large inter-branch space and overhang by coarse structure) showed major contributions for nocturnal fish associations (Fig. 12A). Cluster analysis revealed the 17 species could be divided into six groups (Figs. 12B, S1A). Two species (*Scarus ghobban* and *Naso unicornis*: group B), one species (*Chaetodon lunulatus*: group D) and five species (*Scarus forsteni*, *S. niger*, *S. oviceps*, *S. rivulatus* and *S. schlegeli*: group F) showed greater proportions in association with overhang by coarse structure, large inter-branch space and eave-like space, respectively. Other fishes belonging to three groups (group A, C and E) did not show greater proportion in association with any particular architectural characteristics.

For 25 substrate types, PCA revealed that three substrate types (tabular *Acropora*, staghorn *Acropora* and rock) showed major contributions for nocturnal fish associations (Figs. 12C). Cluster analysis revealed 17 species could be divided into eight groups (Figs. 12D, S1B). *Naso unicornis* (group A), *Chaetodon lunulatus* (group D), *Scarus schlegeli* (group F) and two species (*Scarus oviceps* and *S. rivulatus*: group H) showed greater proportions in association with rock, staghorn *Acropora*, corymbose *Acropora* and tabular *Acropora*, respectively. Other fishes belonging to four groups (group B, C, E, G) and one species (*Chaetodon trifascialis*: group D) did not show greater proportions in association with any particular substrate type.

DISCUSSION

This study examined the nocturnal microhabitat-level substrate association ~~for~~ four fish groups, which was the first study in the North Pacific (Okinawan coral reef).

Parrotfishes

Most previous studies have conducted diurnal observations to clarify the spatial distribution in relation to topographic and substrate characteristics (Hoey & Bellwood, 2008; Hernández-Landa et al., 2014; Nanami, 2021) and foraging substrates (Nanami, 2016; Bonaldo & Rotjan, 2018). However, microhabitat associations for parrotfish species have not been sufficiently examined due to their highly diurnal activity (e.g. Welsh & Bellwood, 2012). Pickholtz et al. (2023) examined nocturnal substrate associations of seven parrotfish species in the Indian Ocean (Gulf of Aqaba), in which substrates were categorized into five types (branching coral, massive coral, soft coral, rock and artificial structure). In contrast, the present study conducted in the North Pacific (Okinawa) and categorized substrates into seven types in terms of architectural characteristics and 25 types in terms of more precise aspects (e.g. coral morphology, live coral or dead coral, and other non-coralline substrates).

Three species (*Chlorurus microrhinos*, *C. spilurus* and *Hipposcarus longiceps*) showed significant positive associations with large inter-branch space (staghorn *Acropora*). Pickholtz et al. (2023) revealed nocturnal substrate associations for three closely related species in the Indian Ocean (*C. gibbus*, *C. sordidus* and *H. harid*) and showed some individuals of the three species were associated with branching corals. These results suggest that substrates that were positively associated with parrotfishes are similar among closely related species.

Scarus ghobban and *Chlorurus microrhinos* showed significant positive associations with overhang by coarse structure. Nanami & Nishihira (2004) showed smaller-sized fish species (pomacentrids and juveniles of labrids of less than 10 cm in length) were associated with the base of massive corals as shelter due to their overhang structure. In contrast, Kerry & Bellwood (2012) suggested that massive corals showed less contribution for concealment of larger-sized fishes (over 10 cm in length), although a possibility that large massive corals might provide canopy effects by overhang at the base of the colony. The results of this study support this suggestion. Namely, overhangs provided by coarse structure serve to some degree as sleeping sites for larger-sized parrotfish individuals (TLs were 24 cm and over).

The remaining five species (*Scarus forsteni*, *S. niger*, *S. oviceps*, *S. rivulatus* and *S. schlegeli*) and *C. spilurus* showed significant positive associations with eave-like space (primarily provided by corymbose *Acropora* and tabular *Acropora*). As Kerry & Bellwood (2012) suggested, it was revealed that tabular corals provide concealment for some parrotfish species as sleeping sites due to their canopy structure.

Surgeonfishes

Naso unicornis showed a significant positive association with overhang by coarse structure mainly provided by rock, suggesting that living corals were not the main sleeping sites for the species. However, such overhangs provide canopy structure and should be conserved as sleeping sites for the species. In addition, some individuals of this species were also associated with eave-like space provided by tabular *Acropora*. This suggests that conservation of tabular *Acropora* is also useful for this species. In contrast, *Naso lituratus* showed a significant positive association with eave-like space being mainly provided by tabular *Acropora*. This suggests conservation of tabular corals is effective for conservation of this species.

Naso unicornis and *N. lituratus* are main fishery targets in coral reefs (Bejarano et al., 2013; Taylor et al., 2014) and nighttime spear fishing is a common method to catch inactive individuals of these species (Taylor BM, Rhodes KL & McIlwan, 2014). Conservation of critical substrates as sleeping sites means conservation of fishing points that can be utilized by fishermen.

Groupers

Plectropomus leopardus is diurnally active and nocturnally inactive (Matley, Heupel & Simpfendorfer, 2015). Broad-scale diurnal survey (several and several-tens of kilometer scale) revealed that a greater coverage of branching *Acropora* was positively related with greater density of this species (Nanami, 2021). In contrast, this species showed a significant positive association with eave-like space (corymbose and tabular *Acropora*) as sleeping sites. These results suggest that substrate types that affect the spatial distribution of the species are different between daytime and nighttime. *Plectropomus leopardus* is a carnivore and its main prey items are small-sized fishes (St John, 1999). Since such small-sized fishes were often associated with branching *Acropora*, this species might occur at sites with greater coverage of branching *Acropora* for foraging during daytime whereas utilize eave-like space as sleeping sites during nighttime. Thus, multiple substrate types are needed to satisfy the ecological requirements of this species during both daytime and nighttime.

Diurnal observations revealed that large-sized *Epinephelus ongus* individuals (over 18 cm TL) showed a significant positive association with large inter-branch space that was created by staghorn *Acropora* (Nanami et al., 2013). In contrast, nocturnal observations by this study showed positive associations with large inter-branch space as well as overhang by coarse structure. Nanami et al. (2018) suggested that this species is nocturnally active since a greater home range size was observed at nighttime than daytime. This species might be associated with large inter-branch space and overhang by coarse structure for ambush foraging at nighttime.

Butterflyfishes

Chaetodon trifascialis showed positive associations with eave-like space (tabular *Acropora*) and large inter-branch space (staghorn *Acropora*). This species is an obligate coral polyp feeder and mainly feeds on polyp of tabular *Acropora* and corymbose *Acropora* (Pratchett, 2005; Nanami, 2020). This suggests that coral species providing large inter-branch space are important architectural structure as sleeping sites for this species, which was not indicated by diurnal observations for the clarifying foraging behavior. In contrast, tabular *Acropora* was also utilized as sleeping sites, suggesting that tabular *Acropora* is essential as both foraging and sleeping sites for this species.

Chaetodon lunulatus showed a significant positive association with large inter-branch space being provided by staghorn *Acropora*. In contrast, diurnal observations revealed that this species mainly feeds on polyp of encrusting corals and massive corals, which do not provide large inter-branch space (Nanami, 2020). This indicates that *C. lunulatus* depends on staghorn *Acropora* as sleeping sites that is not utilized as a foraging substrate, suggesting that various types of corals are essential for this species.

Chaetodon ephippium showed a significant positive association with large inter-branch space being provided by staghorn *Acropora*. In contrast, this species showed frequent bites on the surface of dead coral and rock (Nanami, 2020). This indicates that substrates utilization by *C. ephippium* was different between daytime and nighttime.

Chaetodon auriga did not show any significant associations with substrates. This species showed a greater number of bites on coral rubble and rocks (Nanami, 2020).

Overall, this study revealed large inter-branch space that created by staghorn *Acropora* was important physical structure as sleeping sites for the three species (*C. trifascialis*, *C. lunulatus* and *C. ephippium*), which was not shown by diurnal observations for clarifying their foraging substrates.

Implication about coral community degradation induced by climate change

Numerous studies have shown that coral species belonging to the genus *Acropora* is highly susceptible to coral bleaching by climate change (e.g., Marshall & Baird, 2000; Loya et al., 2001; McClanahan et al., 2004) and such degradation of the acroporid coral community causes significant declines of fish populations in coral reefs (Pratchett et al., 2008). All 17 species were nocturnally associated with acroporid coral, although the degree of association was species-specific. Especially, five species (*Scarus oviceps*, *S. rivulatus*, *S. schlegeli*, *Chaetodon lunulatus* and *C. trifascialis*) showed a greater proportion in association with acroporid corals. Some other species (*Chlorurus microrhinos*, *C. spilurus*, *Hipposcarus longiceps*, *S. forsteni*, *S. niger*, *Naso lituratus*, *Plectropomus leopardus*, *Chaetodon ephippium*) also showed positive associations with acroporid corals to some extent. These results suggest that the effects on coral degradation would cause negative impacts to the availability of sleeping sites for some fish species. This degradation would also cause a decline of fishing points for night spear fishing.

CONCLUSIONS

This study revealed nocturnal substrate associations of four coral reef fish groups (parrotfishes, surgeonfishes, groupers and butterflyfishes). Especially, the four fish groups were primarily associated with three architectural characteristics (eave-like space, large inter-branch space and overhang by coarse structure) that being primarily provided by tabular and corymbose *Acropora*, staghorn *Acropora*, and rock, which have not been clarified by diurnal observations in previous studies. These new insights will provide useful ecological information for effective conservation of biodiversity and ecosystem services of coral reef fishes. Especially, death of acroporid corals caused by coral bleaching would decrease the sleeping sites for some fish species belonging to the four fish groups. Consequently, it will lead to population declines of these fish species. Consideration of nocturnal substrate associations by fishes will enable to propose more effective strategies for conservation and restoration of coral assemblages.

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REFERENCES

Akita Y, Ohta I, Ebisawa A, Uehara M. 2016. Estimation of the fish catches of coastal species of the Yaeyama Islands. *Fauna Ryukyuana* **3**:113–127.

Bejarano S, Golbuu Y, Sapolu T, Mumby PJ. 2013. Ecological risk and the exploitation of herbivorous reef fish across Micronesia. *Marine Ecology Progress Series* **482**:197-215.

Bonaldo RM, Rotjan RD. 2018. The good, the bad, and the ugly: parrotfishes as coral predators. In: Hoey AS, Bonaldo RM. eds. *Biology of Parrotfishes*. Boca Raton: CRC Press, 197-214.

Cole AJ, Pratchett MS. 2013. Diversity in diet and feeding behavior of butterflyfishes: reliance on reef corals versus reef habitats. In: Pratchett MS, Berumen ML, Kapoor BG. eds. *Biology of Butterflyfishes*. Boca Raton, CRC Press, 107-139.

Elliff CI, Kikuchi RKP. 2017. Ecosystem services provided by coral reefs in a Southwestern Atlantic Archipelago. *Ocean and Coastal Management* **136**:49-55.

Frisch AJ, Cameron DS, Pratchett MS, Williamson DH, Williams AJ, Reynolds AD, Hoey AS, Rizzari JR, Evans L, Kerrigan B, Muldoon G, Welch DJ,

Hobbs JPA. 2016. Key aspects of the biology, fisheries and management of coral grouper. *Reviews in Fish Biology and Fisheries* **26**:303-325.

Green A, White A, Kilarski S. 2013. Designing marine protected area networks to achieve fisheries, biodiversity, and climate change objectives in tropical ecosystems: a practitioner guide. The nature Conservancy, and the USAID Coral Triangle Support Partnership, Cebu City, Philippines. viii+35pp

Hernández-Landa RC, Acosta-González G, Núñez-Lara E, Arias-González JE. 2014. Spatial distribution of surgeonfish and parrotfish in the north sector of the Mesoamerican Barrier Reef System. *Marine Ecology* **36**:423-446.

Hobson E. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia* **1965**:291-302.

Hoey AS, Bellwood DR. 2008. Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* **27:**37–47.

Jaap WC. 2000. Coral reef restoration. *Ecological Engineering* **15**:345-364.

Kerry JT, Bellwood DR. 2012. The effect of coral morphology on shelter selection by coral reef fishes. *Coral Reefs* **31**:415-424.

Kelleher G. 1999. Guidelines for Marine Protected Areas. IUCN, Gland, Switzerland and Cambridge, UK. xxiv+107 pp

Laurans Y, Pascal N, Binet T, Brander L, Clua E, David G, Rojat D, Seidl A. 2013. Economic valuation of ecosystem services from coral reefs in the South Pacific: taking stock of recent experience. *Journal of Environmental Management*

116:135-144.

Lawton RJ, Pratchett MS, Delbeek JC. 2013. Harvesting of butterflyfishes for aquarium and artisanal fisheries. In: Pratchett MS, Berumen ML, Kapoor BG, eds. *Biology of Butterflyfishes.* Boca Raton: CRC Press, 269-291.

Loya Y, Sakai K, Yamazato K, Nakano H, Sambali H, van Woesik R. 2001. Coral bleaching: the winners and the losers. *Ecology Letters* **4**:122-131.

Luckhurst BE, Luckhurst K. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* **49**:317–323.

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP. 2002. Resource selection by animals: statistical design and analysis for field studies, Second edition. Dordrecht: Kluwer Academic Publishers.

Marshall PA, Baird AH. 2000. Bleaching of corals on the Great Barrier Reef: Differential susceptibility among taxa. *Coral Reefs* **19**:155-163.

Marshell A, Mills JS, Rhodes KL, McIlwain J. 2011. Passive acoustic telemetry reveals variable home range and movement patterns among unicornfish within a marine reserve. *Coral Reefs* **30**:631-642.

Matley JK, Heupel MR, Simpfendorfer CA. 2015. Depth and space use of leopard coralgrouper *Plectropomus leopardus* using passive acoustic tracking. *Marine Ecology Progress Series* **521**:201-216.

McClanahan TR, Baird AH, Marshall PA, Toscano MA. 2004. Comparing bleaching and mortality responses of hard corals between southern Kenya and the

Great Barrier Reef, Australia. *Marine Pollution Bulletin* **48**:327-335.

Ménard A, Turgeon K, Roche DG, Binning S, Kramer DL. 2012. Shelters and their use by fishes on fringing coral reefs. *PLoS ONE* **7**:e38450.

Meyer CG, Holland KN. 2005. Movement patterns, home range size and habitat utilization of the bluespine unicornfish, *Naso unicornis* (Acanthuridae) in a Hawaiian marine reserve. *Environmental Biology of Fishes* **73**:201-210.

Moberg F, Folke C. 1999. Ecological goods and services of coral reef ecosystems. *Ecological Economics* **29**:215-233.

Nanami A. 2016. Parrotfish grazing ability: inter-specific difference in relation to jaw-lever mechanics and relative weight of adductor mandibulae on an Okinawan coral reef. *PeerJ* **4**:e2425.

Nanami A. 2020. Spatial distribution and feeding substrate of butterflyfishes (family Chaetodontidae) on an Okinawan coral reef. *PeerJ* **8**:e9666.

Nanami A. 2021. Spatial distribution of parrotfishes and groupers in an Okinawan coral reef: size-related associations in relation to habitat characteristics. *PeerJ* **9**:e12134.

Nanami A. 2023. Broad-scale spatial distribution and microhabitat-scale substrate association of seven angelfish species (family Pomacanthidae) in an Okinawan coral reef. *Environmental Biology of Fishes* **106**:1851-1863.

Nanami A, Mitamura H, Sato T, Yamaguchi T, Yamamoto K, Kawabe R, Soyano K, Arai N, Kawabata Y. 2018. Diel variation in home range size and precise returning ability after spawning migration of coral reef grouper *Epinephelus ongus*: implications for effective marine protected area design. *Marine Ecology Progress Series* **606**:119-132.

Nanami A, Nishihira M. 2004. Microhabitat association and temporal stability in reef fish assemblages on massive *Porites* microatolls. *Ichthyological Research* **51**:165-171.

Nanami A, Sato T, Takebe T, Teruya K, Soyano K. 2013. Microhabitat association in white-streaked grouper *Epinephelus ongus*: importance of *Acropora* spp. *Marine Biology* **160**:1511-1517.

Newman SJ, Williams DMcB, Russ G. 1997. Patterns of zonation of assemblages of the Lutjanidae, Lethrinidae and Serranidae (Epinephelinae) within and among mid-shelf and outer-shelf reefs in the central Great Barrier Reef. *Marine and Freshwater Research* **48**:119-128.

Nicholson GM, Clements KD. 2020. Resolving resource partitioning in parrotfishes (Scarini) using microhistology of feeding substrata. *Coral Reefs* **39**:1313-1327.

Oren A, Berman O, Neri R, Tarazi E, Parnas H, Lotan O, Zoabi M, Josef N, Shashar N. 2023. Three-dimensional-printed coral-like structures as a habitat for reef fish. *Journal of Marine Science and Engineering* **11**:882.

**Pickholtz R, Kiflawi M, Buba Y, Chaikin S, Gavriel T, Lapid G, Lazarus M, Malamud S, Marom N, Marom S, Nieger-Rachmilevitz M, Olsson K, Perevolotsky T, Rothman SBS, Salingrè S, Shapira N, Sternbach B, Wandel

H, Belmaker J. 2023. Confronting the "nocturnal problem" in coral reefs: sleeping site selection and cocoon formation in parrotfishes. *Coral Reefs* **42**:811-825.

Pickholtz R, Kiflawi M, Crossin GT, Pickholtz EY, Zamsky R, Kahan I, Gavriel T, Belmaker J. 2022. Highly repetitive space-use dynamics in parrotfishes. *Coral Reefs* **41**:1059-1073.

Pratchett MS. 2005. Dietary overlap among coral-feeding butterflyfishes (Chaetodontidae) at Lizard Island, northern Great Barrier Reef. *Marine Biology* **148**:373-382.

Pratchett MS. 2013. Feeding preferences and dietary specialization among obligate coral-feeding butterflyfishes. In: Pratchett MS, Berumen ML, Kapoor BG. eds. *Biology of Butterflyfishes*. Boca Raton, CRC Press, 140-179.

Pratchett MS, Munday PL, Wilson SK, Graham NAJ, Cinner JE, Bellwood DR, Jones GP, Polunin NVC, McClanahan TR. 2008. Effects of climate-induced coral bleaching on coral-reef fishes-ecological and economic consequences. *Oceanography and Marine Biology: An Annual Review* **46**:251-296.

Richardson LE, Graham NA, Pratchett MS, Hoey AS. 2017. Structural complexity mediates functional structure of reef fish assemblages among coral habitats. *Environmental Biology of Fishes* **100**:193-207.

Robertson DR, Sheldon JM. 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. *Journal of Experimental Marine*

Biology and Ecology **40**:285-298.

Robertson DR, Gaines SD. 1986. Interference competition structures habitat use in local assemblage of coral reef surgeonfishes. *Ecology* **67**:1372-1383.

Sato M, Nanami A, Bayne CJ, Makino M, Hori M. 2020. Changes in the potential stocks of coral reef ecosystem services following coral bleaching in Sekisei lagoon, southern Japan: implications for the future under global warming. *Sustainability Science* 1**5**:863-883.

St John J. 1999. Ontogenetic changes in the diet of the coral reef grouper *Plectropomus leopardus* (Serranidae): patterns in taxa, size and habitat of prey. *Marine Ecology Progress Series* **180**:233-246.

Taylor BM, Rhodes KL, Marshell A, McIlwan JL. 2014. Age-based demographic and reproductive assessment of orangespine *Naso lituratus* and bluespine *Naso unicornis* unicornfishes. *Journal of Fish Biology* **85**:901-916.

Ticzon VS, Mumby PJ, Samaniego BR, Bejarano-Chavarro S, David LT. 2012. Microhabitat use of juvenile coral reef fish in Palau. *Environmental Biology of Fishes* **95**:355-370.

Tissot BN, Hallacher LE. 2003. Effects of aquarium collectors on coral reef fishes in Kona, Hawaii. *Conservation Biology* **17**:1759-1768.

Untersteggaber L, Mitteroecker P, Herler J. 2014. Coral architecture affects the habitat choice and form of associated gobiid fishes. *Marine Biology* **161**:521-530.

Wabnitz C, Taylor M, Green E, Razak T. 2003. From ocean to aquarium.

UNEP-WCMC, Cambridge, UK.

Welsh JQ, Bellwood DR. 2012. Spatial ecology of the steephead parrotfish (*Chlorurus microrhinos*): an evaluation using acoustic telemetry. *Coral Reefs* **31**:55-65.

Wen CKC, Pratchett MS, Almany GR, Jones GP. 2013a. Role of prey availability in microhabitat preferences of juvenile coral trout (*Plectropomus*: Serranidae). *Journal of Experimental Marine Biology and Ecology* **443**:39-45.

Wen CKC, Pratchett MS, Almany GR, Jones GP. 2013b. Patterns of recruitment and microhabitat associations for three predatory coral reef fishes on the Great Barrier Reef, Australia. *Coral Reefs* **32**:389-398.

Wilson SK, Burgess SC, Cheal A, Emslie M, Fisher R, Miller I, Polunin NVC, Sweatman HPA. 2008. Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *Journal of Animal Ecology* **77**:220-228.

Woodhead AJ, Hicks CC, Norstöm AV, Williams GJ, Graham NAJ. 2019. Coral reef ecosystem services in the Anthropocene. *Functional Ecology* **33**:1023-1034.

Yabuta S, Berumen ML. 2013. Social structures and spawning behavior of *Chaetodon* butterflyfishes. In: Pratchett MS, Berumen ML, Kapoor BG, eds. *Biology of Butterflyfishes.* Boca Raton: CRC Press, 200-225.

Yanovski R, Nelson PA, Abelson A. 2017. Structural complexity in coral reefs: examination of a novel evaluation tool on different spatial scales. *Frontiers in Ecology and Evolution* **5**:27.

Zeller DC. 1997. Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). *Marine Ecology Progress Series* **154**:65-77.

Figure 1

Maps showing the location of the Yaeyama Islands (A), study area (B) and the 19 study sites used for examining nocturnal substrate associations of fishes (C).

The aerial photographs in (B) and (C) were provided by the International Coral Reef Research and Monitoring Center.

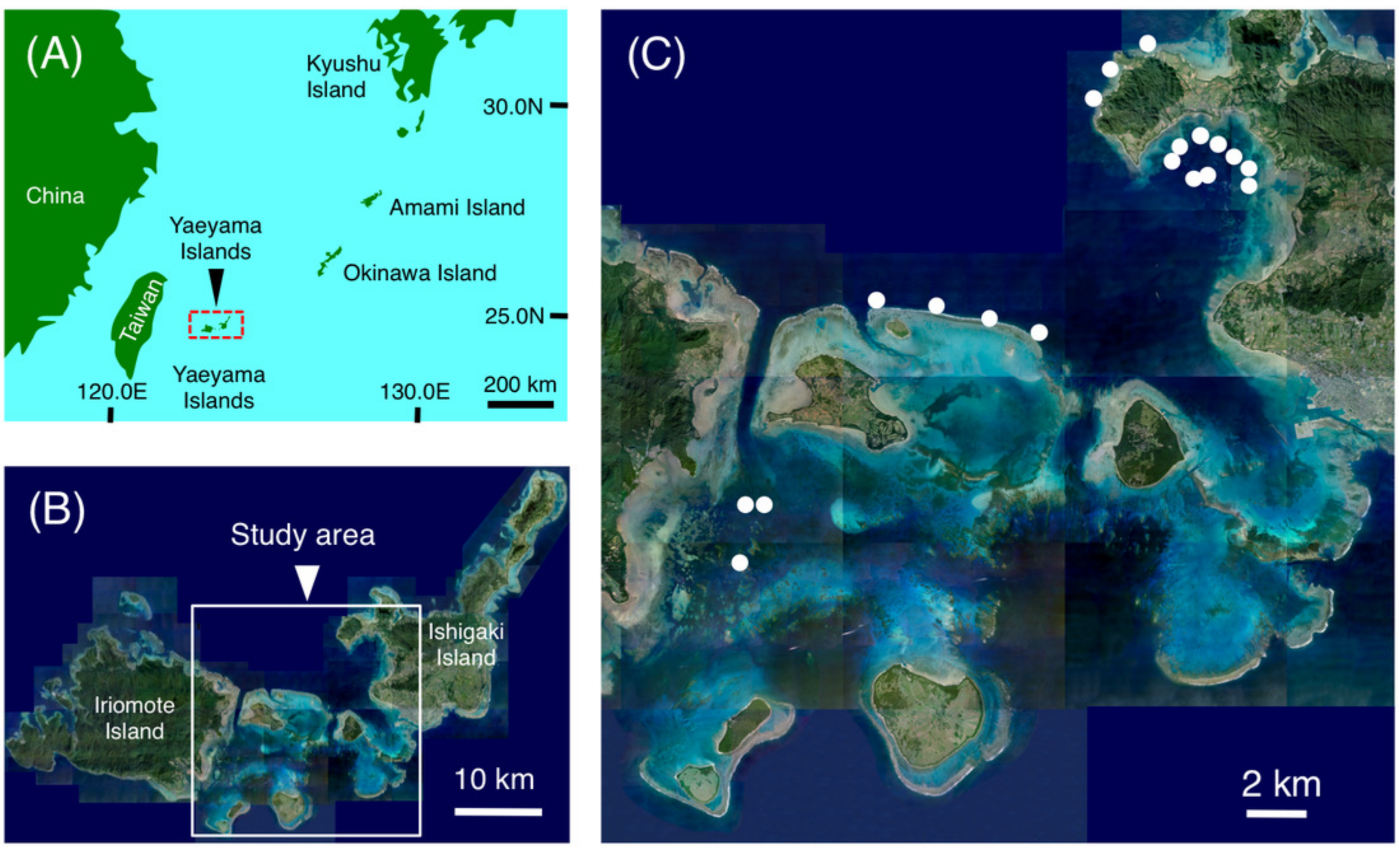


Figure 2

Examples of inactive fish individuals that were associated with substrates at nighttime for the 17 species.

One example is shown for each species. For more details about substrate associations of fishes, see figures 4, 6, 8 and 10. All fish photographs were taken by the author (A. Nanami).

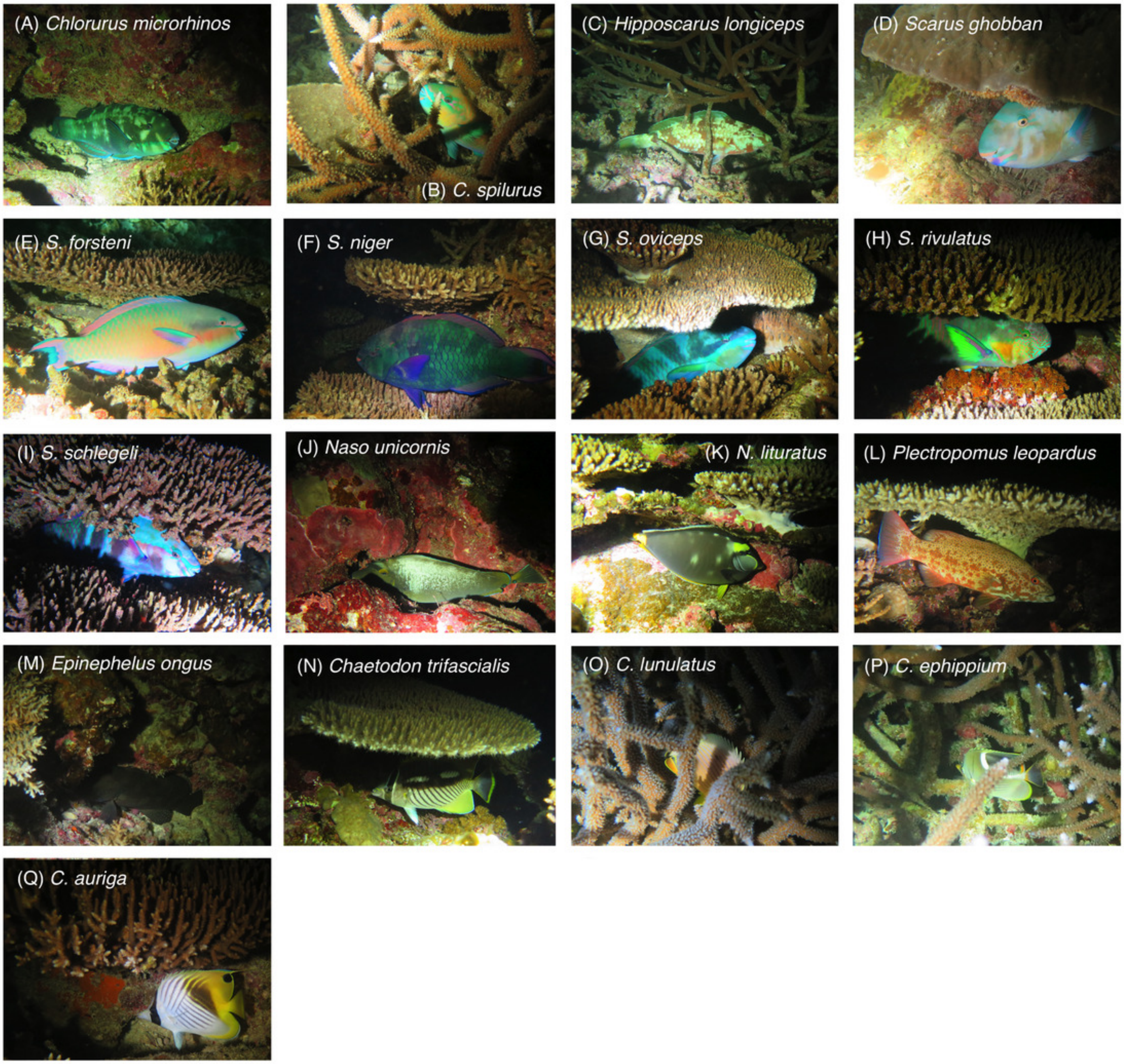

(A) Chlorurus microrhinos
(B) C. spilurus
(C) Hipposcarus longiceps
(D) Scarus ghobban
(E) S. forsteni
(F) S. niger
(G) S. oviceps
(H) S. rivulatus
(I) S. schlegeli
(J) Naso unicornis
(K) N. lituratus
(L) Plectropomus leopardus
(M) Epinephelus ongus
(N) Chaetodon trifascialis
(O) C. lunulatus
(P) C. ephippium
(Q) C. auriga

Figure 3

Schematic diagrams of the seven types of substrate architectural characteristics (physical structure) and some examples of substrates for each type.

Light green areas represent spaces that are potentially utilized by fishes as sleeping site. For more details about relationships between structural characteristics and substrates, see Table 2. All substrate photographs were taken by the author (A. Nanami).

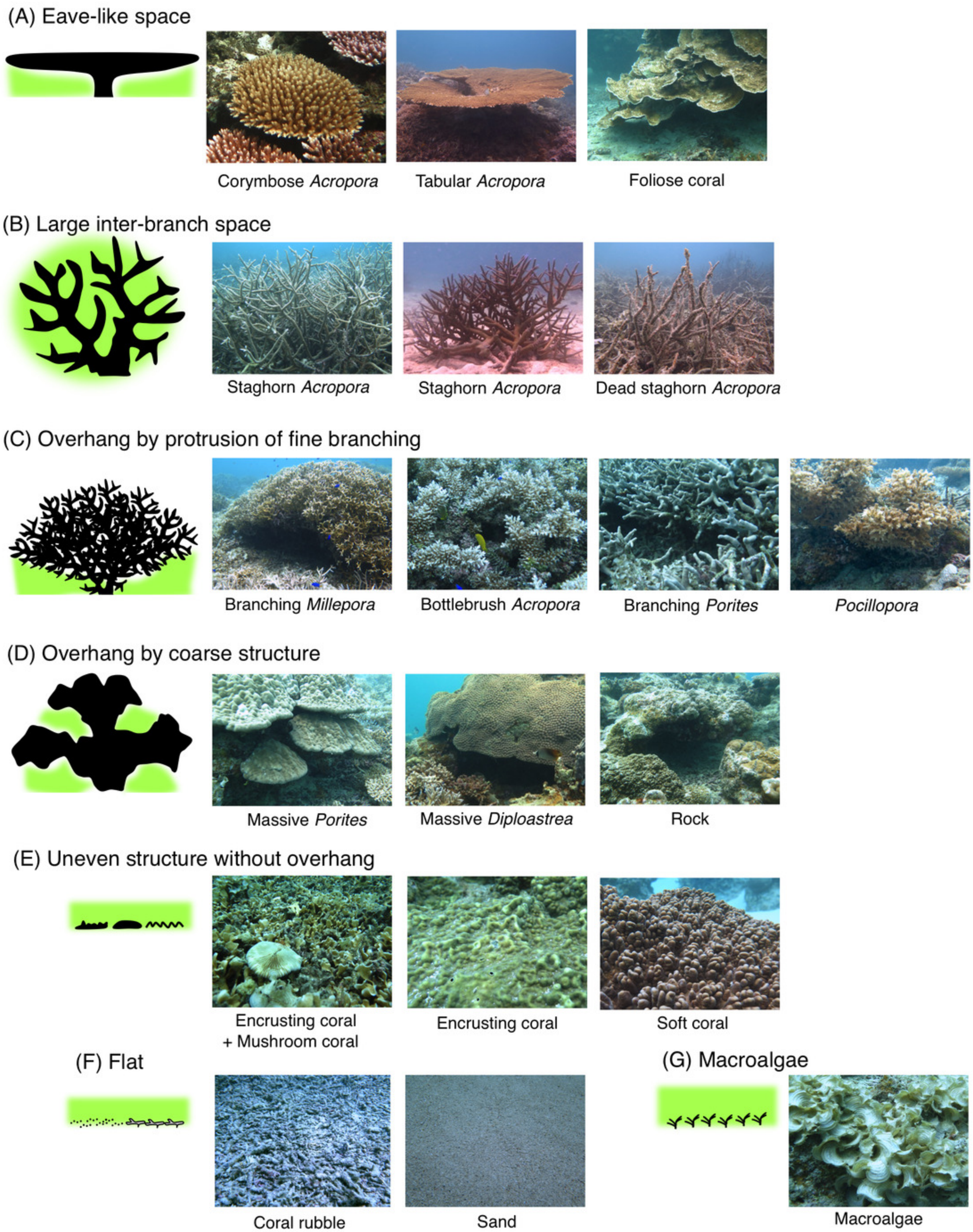

(A) Eave-like space
Corymbose Acropora
Tabular Acropora
Foliose coral
(B) Large inter-branch space
Staghorn Acropora
Staghorn Acropora
Dead staghorn Acropora
(C) Overhang by protrusion of fine branching
Branching Millepora
Bottlebrush Acropora
Branching Porites
Pocillopora
(D) Overhang by coarse structure
Massive Porites
Massive Diploastrea
Rock
(E) Uneven structure without overhang
Encrusting coral
+ Mushroom coral
Encrusting coral
Soft coral
(F) Flat
Coral rubble
Sand
(G) Macroalgae
Macroalgae

Figure 4

Relative frequency (%) of fish individuals associated with substrates and substrate availability for the nine parrotfish species.

Left and right figures represent results using the seven types of substrate architectural characteristics (physical structure) and 19 substrate types, respectively. Numbers adjacent to bars represent the number of individuals that were associated with the focal substrate. For right figures, data from 19 substrate types among 25 the substrate types are shown, since no fish individuals were associated with the remaining 6 substrate types (other coral, dead other coral, soft coral, coral rubble, sand and macroalgae). *: since one individual utilized two categories of substrates (the two substrates were closely located to each other and one focal fish individual was associated with both substrates simultaneously), 0.5 individuals were assigned for each substrate as substrate association. All fish photographs were taken by the author (A. Nanami).

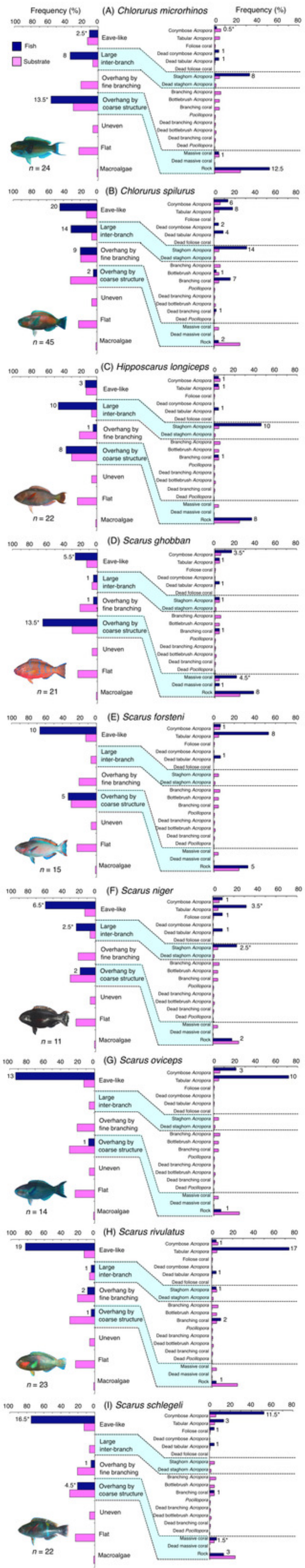

Frequency (%)
(A) Chlorurus microrhinos
Frequency (%)
Fish
Substrate
n = 24
(B) Chlorurus spilurus
n = 45
(C) Hipposcarus longiceps
n = 22
(D) Scarus ghobban
n = 21
(E) Scarus forsteni
n = 15
(F) Scarus niger
n = 11
(G) Scarus oviceps
n = 14
(H) Scarus rivulatus
n = 23
(I) Scarus schlegeli
n = 22

Figure 5

Resource selection ratio (w_i ± 95% confidence interval) for nine parrotfish species.

Left and right figures represent results using the seven types of substrate architectural characteristics and 19 substrate types, respectively. Numbers adjacent to bars represent the number of individuals that were associated with the focal substrate. Black and white arrows represent significant positive and negative associations with the substrates, respectively. The vertical red dashed line represents a selection ratio of 1 (i.e., no positive or negative association). Substrates with w_i ± 95% confidence interval above and below 1 indicate a significant positive and negative association, respectively. Substrates with w_i ± 95% confidence interval encompassing 1 have no significant positive or negative association. For right figures, data from 19 substrate types among the 25 substrate types are shown, since no fish individuals were associated with the remaining 6 substrate types (other coral, dead other coral, soft coral, coral rubble, sand and macroalgae). *: since one individual utilized two categories of substrates (the two substrates were closely located to each other and one focal fish individual was associated with both substrates simultaneously), 0.5 individuals were assigned for each substrate as substrate association. All fish photographs were taken by the author (A. Nanami).

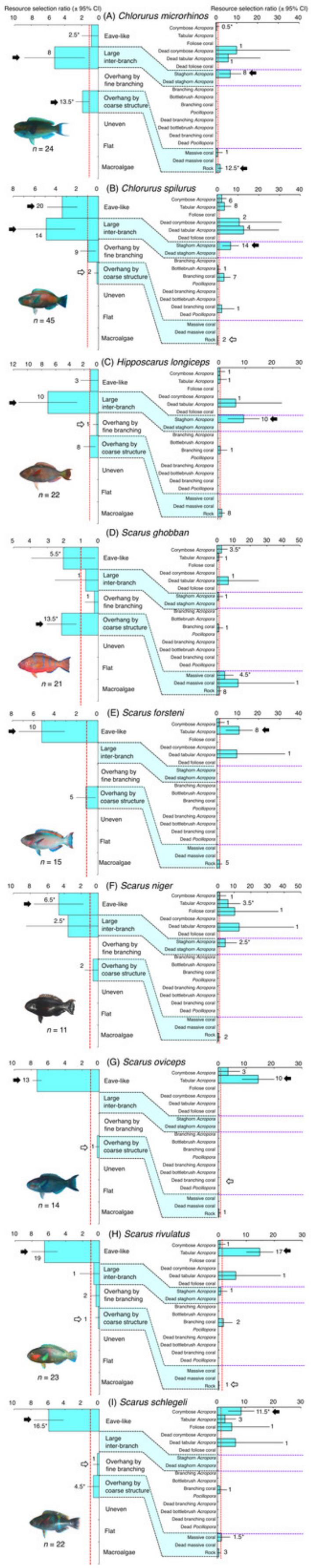


Figure 6

Relative frequency (%) of fish individuals associated with substrates and substrate availability for the two surgeonfish species.

Left and right figures represent results using the seven types of substrate architectural characteristics and 19 substrates types, respectively. Numbers adjacent to bars represent the number of individuals that were associated with the focal substrate. For right figures, data from 19 substrate types among the 25 substrate types were shown, since no fish individuals were associated with the remaining 6 substrate types (other coral, dead other coral, soft coral, coral rubble, sand and macroalgae). All fish photographs were taken by the author (A. Nanami).

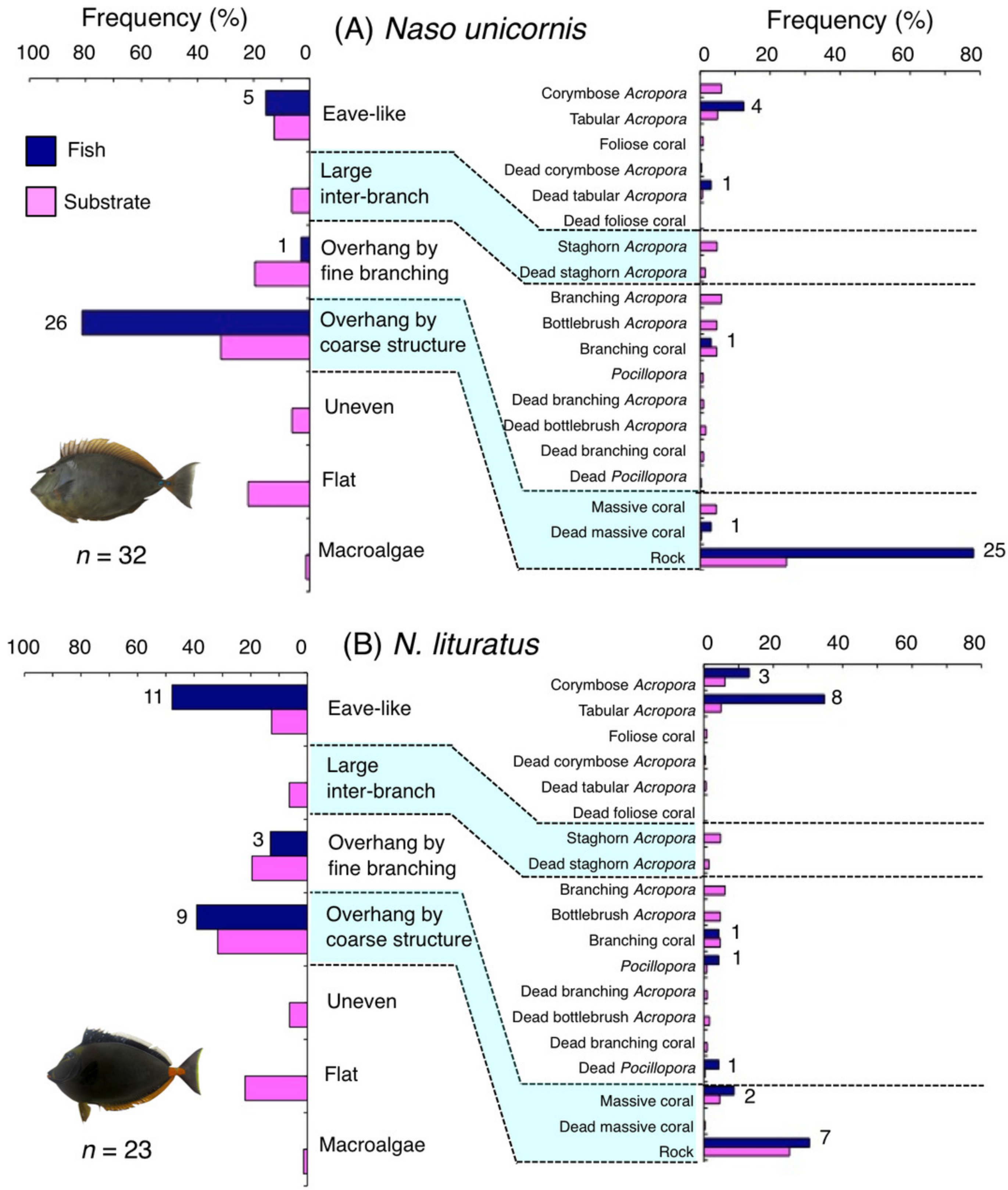
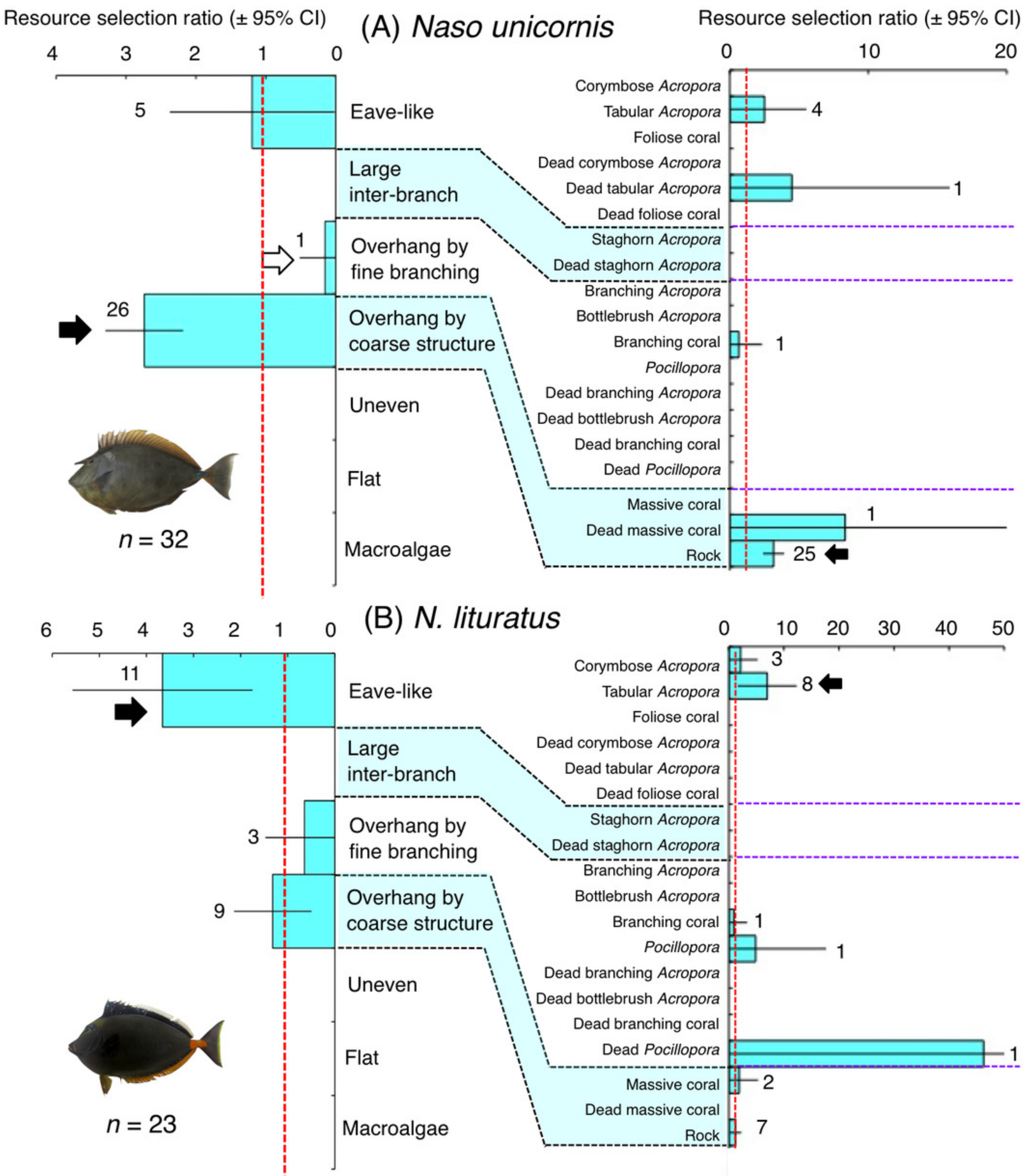

(A) Naso unicornis
Frequency (%)
100 80 60 40 20 0
0 20 40 60 80
Fish
Substrate
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular Acropora
Dead foliose coral
Staghorn Acropora
Dead staghorn Acropora
Branching Acropora
Bottlebrush Acropora
Branching coral
Pocillopora
Dead branching Acropora
Dead bottlebrush Acropora
Dead branching coral
Dead Pocillopora
Massive coral
Dead massive coral
Rock
n = 32
(B) N. lituratus
n = 23

Figure 7

Resource selection ratio (w_i ± 95% confidence interval) for the two surgeonfish species.

Left and right figures represent results using the seven types of substrate architectural characteristics and 19 substrate types, respectively. Numbers adjacent to bars represent the number of individuals that were associated with the focal substrate. Black and white arrows represent significant positive and negative association with the substrates, respectively. The vertical red dashed line represents a selection ratio of 1 (i.e., no positive or negative association). Substrates with w_i ± 95% confidence interval above and below 1 indicate a significant positive and negative association, respectively. Substrates with w_i ± 95% confidence interval encompassing 1 have no significant positive or negative association. For right figures, data from 19 substrate types among the 25 substrate types are shown, since no fish individuals were associated with the remaining 6 substrate types (other coral, dead other coral, soft coral, coral rubble, sand and macroalgae). All fish photographs were taken by the author (A. Nanami).

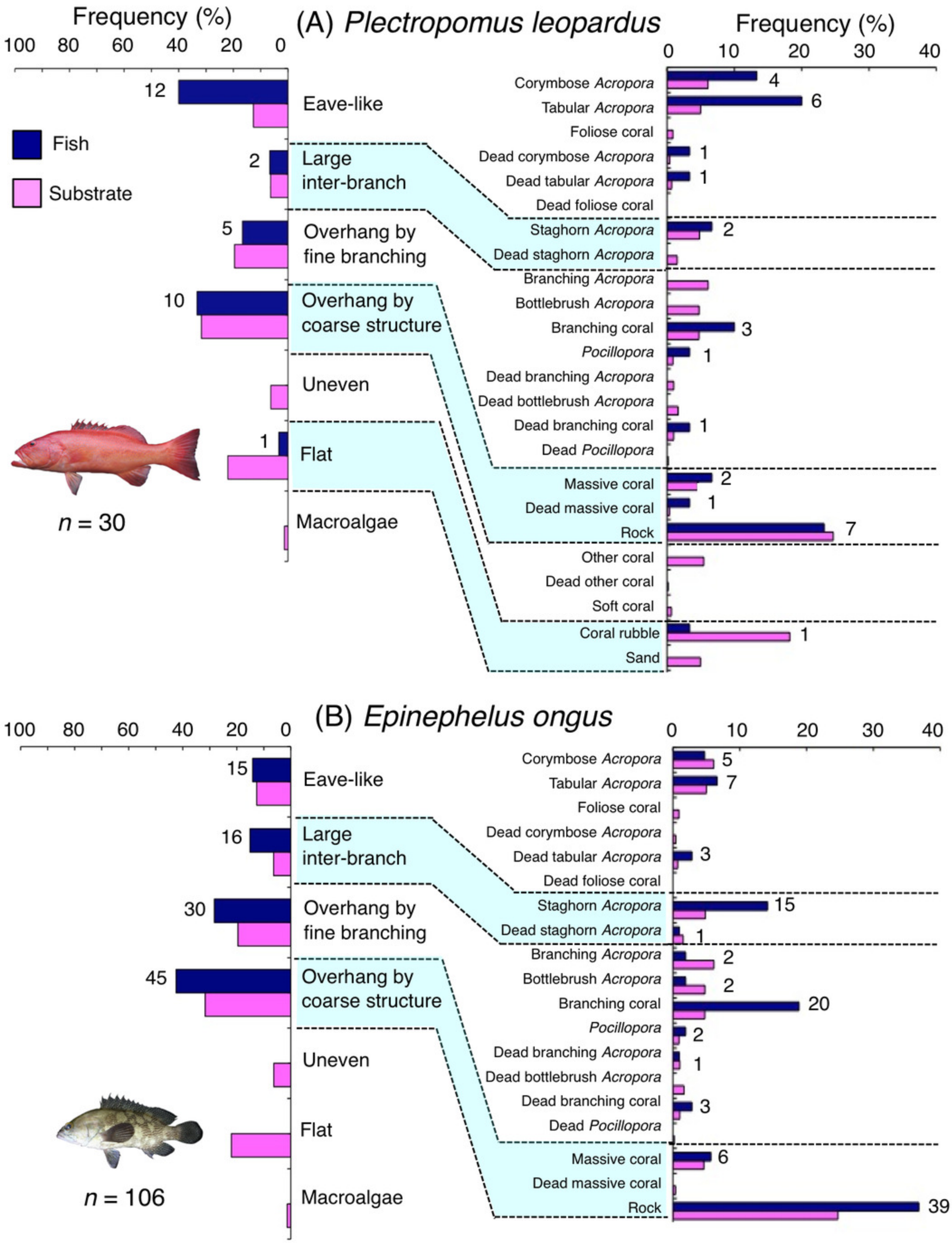


(A) Naso unicornis
Resource selection ratio (± 95% CI)
4 3 2 1 0
0 10 20
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
5
1
26
n = 32
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular Acropora
Dead foliose coral
Staghorn Acropora
Dead staghorn Acropora
Branching Acropora
Bottlebrush Acropora
Branching coral
Pocillopora
Dead branching Acropora
Dead bottlebrush Acropora
Dead branching coral
Dead Pocillopora
Massive coral
Dead massive coral
Rock
4
1
1
1
25
(B) N. lituratus
6 5 4 3 2 1 0
0 10 20 30 40 50
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
11
3
9
n = 23
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular Acropora
Dead foliose coral
Staghorn Acropora
Dead staghorn Acropora
Branching Acropora
Bottlebrush Acropora
Branching coral
Pocillopora
Dead branching Acropora
Dead bottlebrush Acropora
Dead branching coral
Dead Pocillopora
Massive coral
Dead massive coral
Rock
3
8
1
1
1
2
7

Figure 8

Relative frequency (%) of fish individuals associated with substrates and substrate availability for two grouper species.

Left figures represent results using the seven types of substrate architectural characteristics. Right figures represent results using 24 and 19 substrate types for *Plectropomus leopardus* and *Epinephelus ongus*, respectively. Numbers adjacent to bars represent the number of individuals that were associated with the focal substrate. For right figures, data from 24 and 19 substrate types among 25 substrate types are shown, since no fish individuals were associated with the remaining 1 and 6 substrate types for *Plectropomus leopardus* (microalgae) and *Epinephelus ongus* (other coral, dead other coral, soft coral, coral rubble, sand and macroalgae), respectively. All fish photographs were taken by the author (A. Nanami).



(A) Plectropomus leopardus
Frequency (%)
100 80 60 40 20 0
Fish
Substrate
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
12
2
5
10
1
n = 30
Frequency (%)
0 10 20 30 40
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular Acropora
Dead foliose coral
Staghorn Acropora
Dead staghorn Acropora
Branching Acropora
Bottlebrush Acropora
Branching coral
Pocillopora
Dead branching Acropora
Dead bottlebrush Acropora
Dead branching coral
Dead Pocillopora
Massive coral
Dead massive coral
Rock
Other coral
Dead other coral
Soft coral
Coral rubble
Sand
4
6
1
1
2
3
1
1
2
1
7
1
(B) Epinephelus ongus
100 80 60 40 20 0
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
15
16
30
45
n = 106
0 10 20 30 40
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular Acropora
Dead foliose coral
Staghorn Acropora
Dead staghorn Acropora
Branching Acropora
Bottlebrush Acropora
Branching coral
Pocillopora
Dead branching Acropora
Dead bottlebrush Acropora
Dead branching coral
Dead Pocillopora
Massive coral
Dead massive coral
Rock
5
7
3
15
1
2
2
20
2
1
3
6
39

Figure 9

Resource selection ratio (w_i ± 95% confidence interval) for the two grouper species.

Left figures represent results using seven types of substrate architectural characteristics. Right figures represent results using 24 and 19 substrate types for *Plectropomus leopardus* and *Epinephelus ongus*, respectively. Numbers adjacent to bars represent the number of individuals that were associated with the focal substrate. Black and white arrows represent significant positive and negative association with the substrates, respectively. The vertical red dashed line represents a selection ratio of 1 (i.e., no positive or negative association). Substrates with w_i ± 95% confidence interval above and below 1 indicate a significant positive and negative association, respectively. Substrates with w_i ± 95% confidence interval encompassing 1 have no significant positive or negative association. For right figures, data from 24 and 19 substrate types among the 25 substrate types are shown, since no fish individuals were associated with remaining 1 and 6 substrate types for *Plectropomus leopardus* (microalgae) and *Epinephelus ongus* (other coral, dead other coral, soft coral, coral rubble, sand and macroalgae), respectively. All fish photographs were taken by the author (A. Nanami).

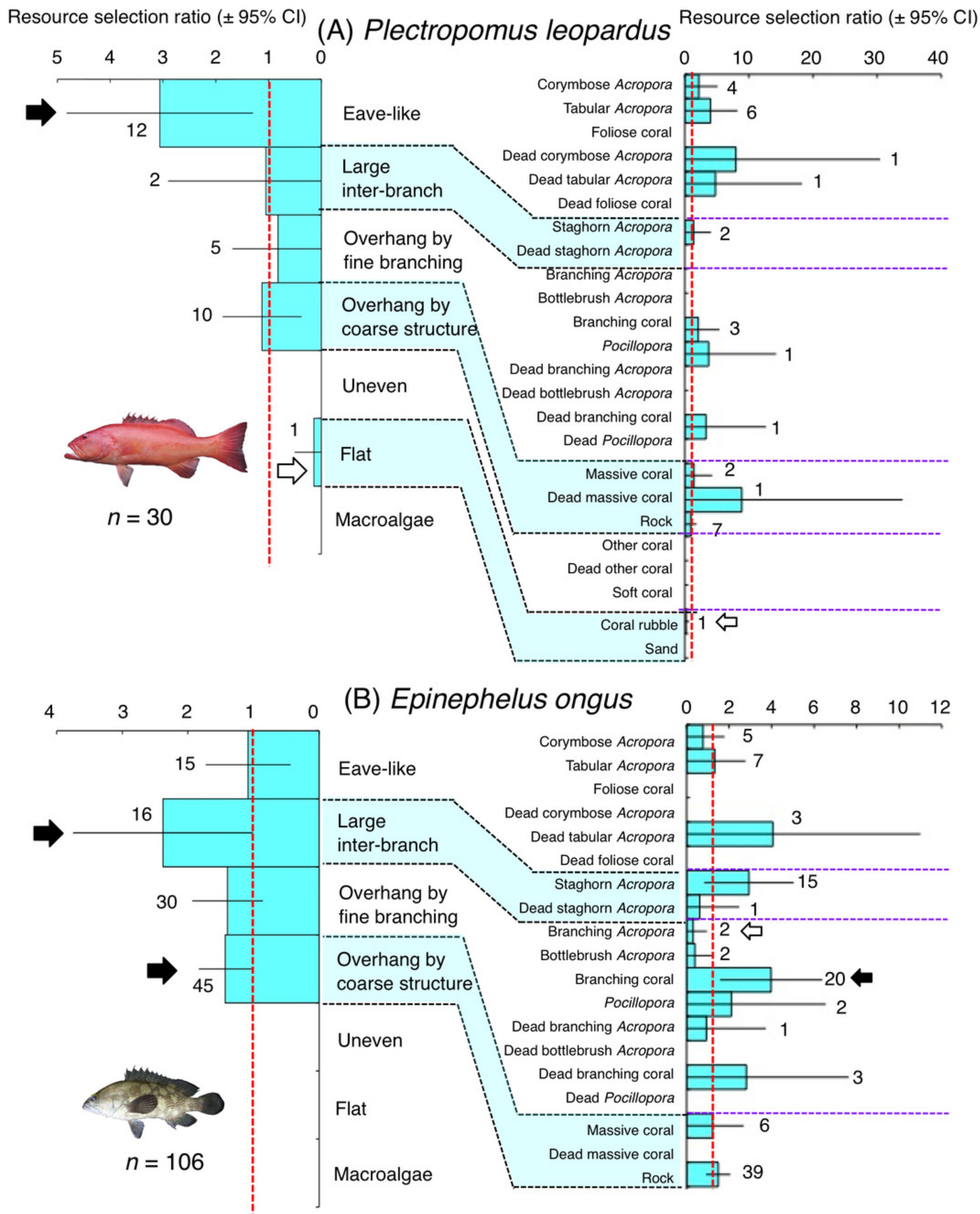
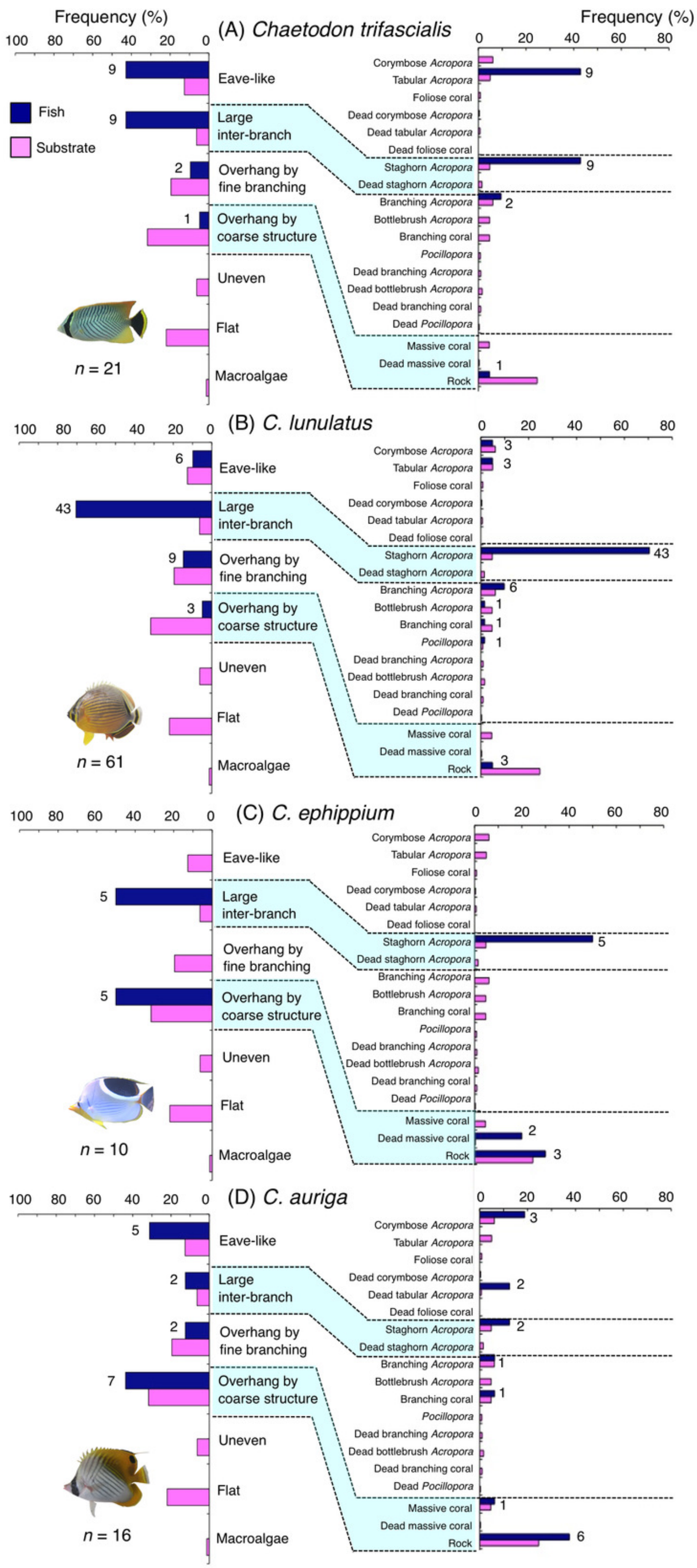

Resource selection ratio (± 95% CI)
(A) Plectropomus leopardus
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
n = 30
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular Acropora
Dead foliose coral
Staghorn Acropora
Dead staghorn Acropora
Branching Acropora
Bottlebrush Acropora
Branching coral
Pocillopora
Dead branching Acropora
Dead bottlebrush Acropora
Dead branching coral
Dead Pocillopora
Massive coral
Dead massive coral
Rock
Other coral
Dead other coral
Soft coral
Coral rubble
Sand
(B) Epinephelus ongus
n = 106

Figure 10

Relative frequency (%) of fish individuals associated with substrates and substrate availability for the four butterflyfish species.

Left and right figures represent results using the seven types of substrate architectural characteristics and 19 substrate types, respectively. Numbers adjacent to bars represent the number of individuals that were associated with the focal substrate. For right figures, data from 19 substrate types among the 25 substrate types are shown, since no fish individuals were associated with the remaining 6 substrate types (other coral, dead other coral, soft coral, coral rubble, sand and macroalgae). All fish photographs were taken by the author (A. Nanami).



Frequency (%)
(A) Chaetodon trifascialis
Fish
Substrate
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
n = 21
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular Acropora
Dead foliose coral
Staghorn Acropora
Dead staghorn Acropora
Branching Acropora
Bottlebrush Acropora
Branching coral
Pocillopora
Dead branching Acropora
Dead bottlebrush Acropora
Dead branching coral
Dead Pocillopora
Massive coral
Dead massive coral
Rock
(B) C. lunulatus
n = 61
(C) C. ephippium
n = 10
(D) C. auriga
n = 16

Figure 11

Resource selection ratio (w_i ± 95% confidence interval) for the four butterflyfish species.

Left and right figures represent results using the seven types of substrate architectural characteristics and 19 substrate types, respectively. Numbers adjacent to bars represent the number of individuals that were associated with the focal substrate. Black and white arrows represent significant positive and negative association with the substrates, respectively. The vertical red dashed line represents a selection ratio of 1 (i.e., no positive or negative association). Substrates with w_i ± 95% confidence interval above and below 1 indicate a significant positive and negative association, respectively. Substrates with w_i ± 95% confidence interval encompassing 1 have no significant positive or negative association. For right figures, data from 19 substrate types among the 25 substrate types are shown, since no fish individuals were associated with the remaining 6 substrate types (other coral, dead other coral, soft coral, coral rubble, sand and macroalgae). All fish photographs were taken by the author (A. Nanami).

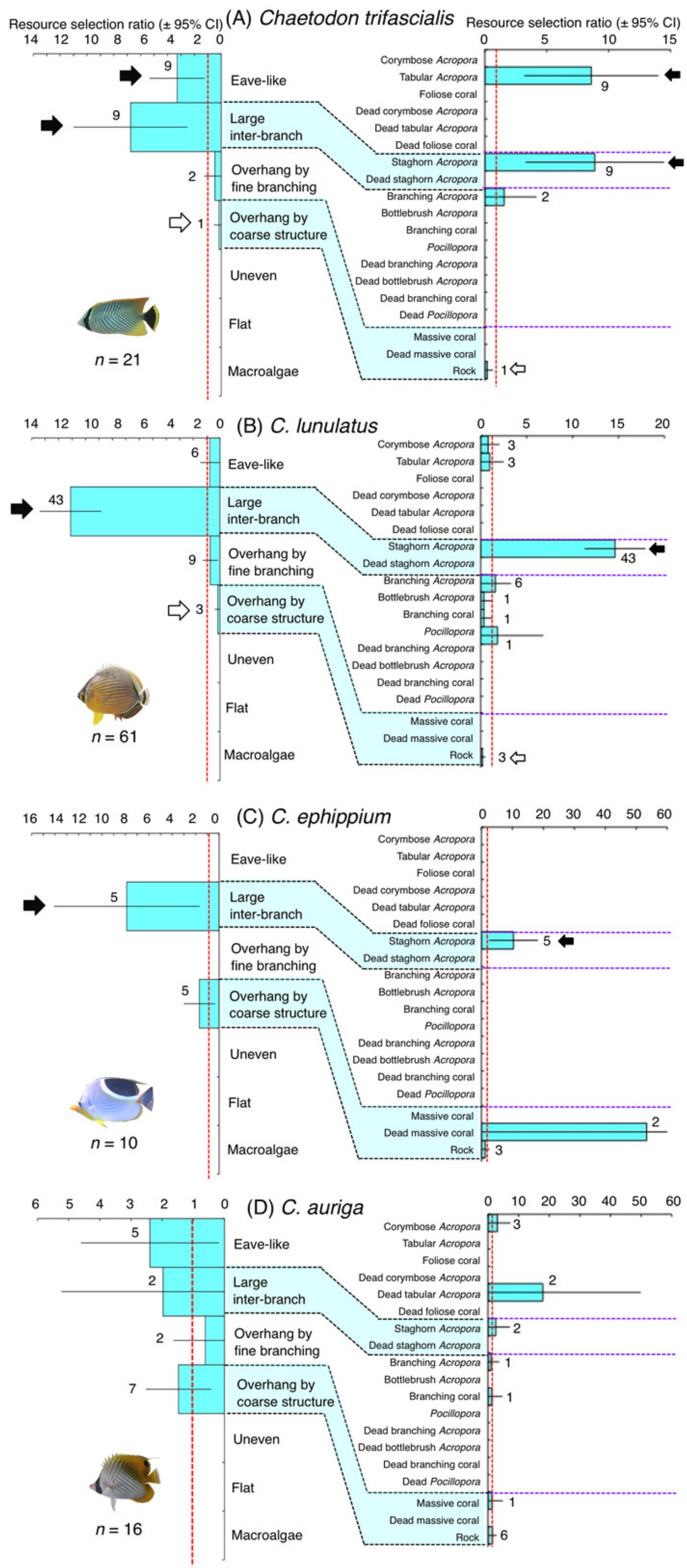

Resource selection ratio (± 95% CI)
(A) Chaetodon trifascialis
Resource selection ratio (± 95% CI)
14 12 10 8 6 4 2 0
0 5 10 15
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
n = 21
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular Acropora
Dead foliose coral
Staghorn Acropora
Dead staghorn Acropora
Branching Acropora
Bottlebrush Acropora
Branching coral
Pocillopora
Dead branching Acropora
Dead bottlebrush Acropora
Dead branching coral
Dead Pocillopora
Massive coral
Dead massive coral
Rock
(B) C. lunulatus
14 12 10 8 6 4 2 0
0 5 10 15 20
n = 61
(C) C. ephippium
16 14 12 10 8 6 4 2 0
0 10 20 30 40 50 60
n = 10
(D) C. auriga
6 5 4 3 2 1 0
0 10 20 30 40 50 60
n = 16

Figure 12

Results of principal component analysis (PCA) for substrate association of fishes based on five types of substrate architectural characteristics (A, B) and 18 substrates types (C, D).

In A and C, the vectors for two types of architectural characteristics (uneven structure and macroalgae) and seven substrate types (other coral, dead bottlebrush *Acropora*, dead foliose coral, dead other coral, soft coral, sand and macroalgae) are not shown, since no fish individuals were associated with the substrates. Divisions into multiple groups in (B) and (D) were based on the results of cluster analysis (Fig. S1). Pie charts in (B) and (D) represent proportion of nocturnal substrate association for each fish species. In (B) and (D), fish species names are shown as abbreviations (Ch.mic: *Chlorurus microrhinos*; Ch.spi: *Chlorurus spilurus*; H.lon: *Hipposcarus longiceps*; S.gho: *Scarus ghobban*; S.for: *Scarus forsteni*; S.nig: *Scarus niger*; S.ovi: *Scarus oviceps*; S.riv: *Scarus rivulatus*; S.sch: *Scarus schlegeli*; N.uni: *Naso unicornis*; N.lit: *Naso lituratus*; P.leo: *Plectropomus leopardus*; E.ong: *Epinephelus ongus*; C.tri: *Chaetodon trifascialis*; C.lun: *Chaetodon lunulatus*; C.eph: *Chaetodon ephippium*; C.arg: *Chaetodon auriga*). In (D), “Other substrates” includes 11 substrate types (bottlebrush *Acropora*, non-acroporid branching coral, foliose coral, *Pocillopora*, dead corymbose *Acropora*, dead tabular *Acropora*, dead staghorn *Acropora*, dead branching *Acropora*, dead non-acroporid branching coral, dead *Pocillopora* and coral rubble).

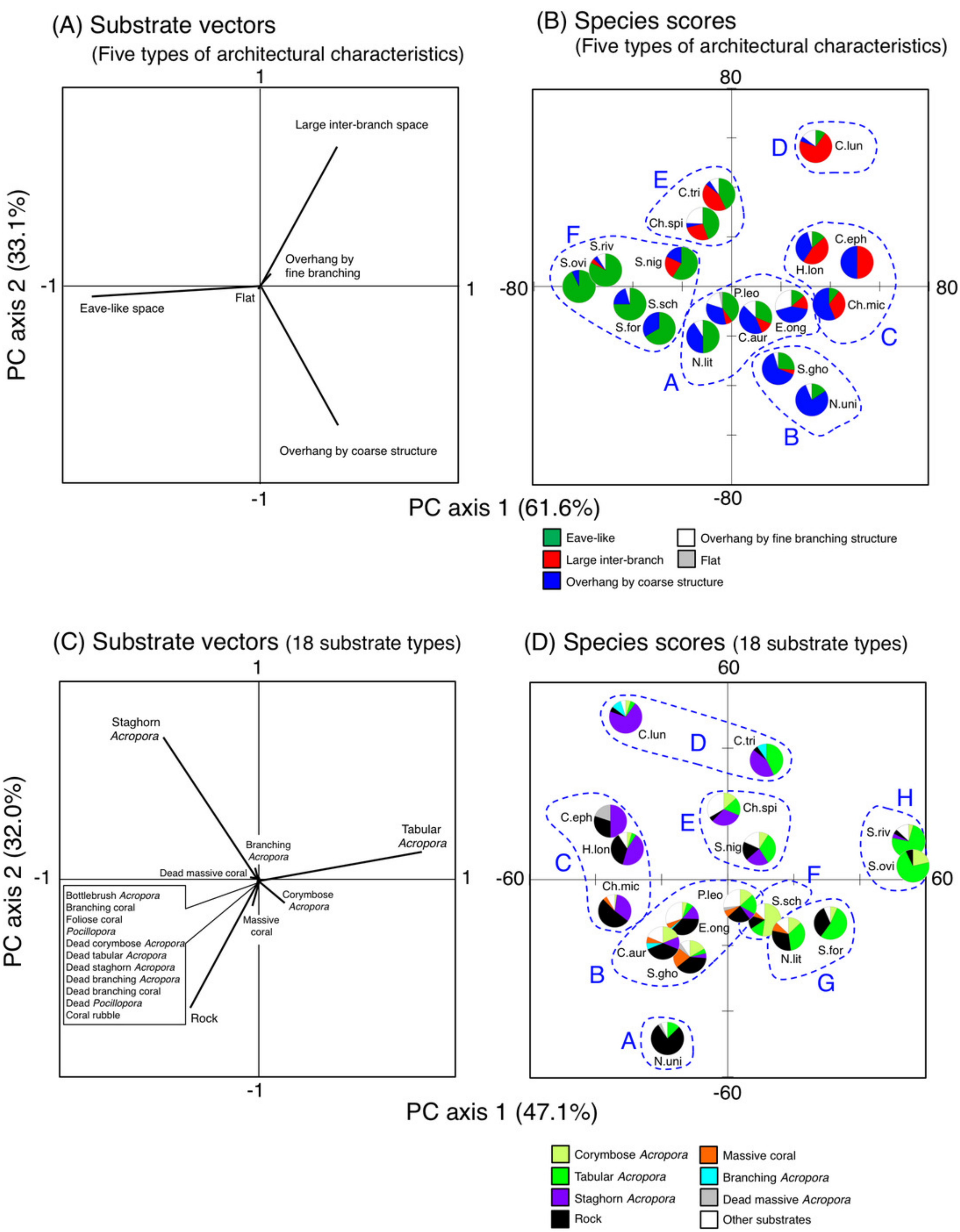

(A) Substrate vectors
(Five types of architectural characteristics)
Large inter-branch space
Overhang by fine branching
Eave-like space
Flat
Overhang by coarse structure
PC axis 2 (33.1%)
(B) Species scores
(Five types of architectural characteristics)
C.lun
C.tri
Ch.spi
S.riv
S.ovi
S.nig
S.sch
S.for
N.lit
P.leo
C.aur
E.ong
H.lon
C.eph
Ch.mic
S.gho
N.uni
PC axis 1 (61.6%)
Eave-like
Large inter-branch
Overhang by coarse structure
Overhang by fine branching structure
Flat
(C) Substrate vectors (18 substrate types)
Staghorn Acropora
Branching Acropora
Tabular Acropora
Dead massive coral
Corymbose Acropora
Massive coral
Bottlebrush Acropora
Branching coral
Foliose coral
Pocillopora
Dead corymbose Acropora
Dead tabular Acropora
Dead staghorn Acropora
Dead branching Acropora
Dead branching coral
Dead Pocillopora
Coral rubble
Rock
PC axis 2 (32.0%)
(D) Species scores (18 substrate types)
PC axis 1 (47.1%)
Corymbose Acropora
Tabular Acropora
Staghorn Acropora
Rock
Massive coral
Branching Acropora
Dead massive Acropora
Other substrates

Table 1 (on next page)

List and number of individuals of fishes belong to four fish groups (parrotfishes, surgeonfishes, groupers and butterflyfishes) that were observed for nocturnal substrate association.

X: fish species that were selected for analyses (total number of individuals were 10 individuals and over). *: since one individual utilized two categories of substrates (the two substrates were closely located to each other and one focal fish individual was associated with both substrates simultaneously), 0.5 individuals were assigned for each substrate as substrate association.

Table 1. List and number of individuals of fishes belong to four fish groups (parrotfishes, surgeonfishes, groupers and butterflyfishes) that were observed for nocturnal substrate association. X: fish species that were selected for analyses (total number of individuals were 10 individuals and over). *: since one individual utilized two categories of substrates (the two substrates were closely located to each other and one focal fish individual was associated with both substrates simultaneously), 0.5 individuals were assigned for each substrate as substrate association.

Family	Species	Number of individuals	Size range (TL: cm)	Analysis	Substrate architectural characteristics						
					Eave-like	Large Inter-branch	Overhang by fine branching	Overhang by coarse structure	Uneven	Flat	Macroalga
Parrotfishes	*Cetoscarus bicolor*	3	44 - 46		2			1			
(Labridae : Scarini)	*Chlorurus bowersi*	5	28 - 33		2	2	1				
	Chlorurus japanensis	1	33		1						
	Chlorurus microrhinos	24	25 - 62	X	2.5*	8		13.5*			
	Chlorurus spilurus	45	20 - 32	X	20	14	9	2			
	Hipposcarus longiceps	22	15 - 53	X	3	10	1	8			
	Scarus chameleon	1	25			1					
	Scarus festivus	2	27 - 40				2				
	Scarus forsteni	15	20 - 40	X	10			5			
	Scarus frenatus	3	23 - 33		2			1			
	Scarus ghobban	21	24 - 57	X	5.5*	1	1	13.5*			
	Scarus hypselopterus	6	25 - 27		4		1	1			

	Scarus niger	11	20 - 35	X	6.5*	2.5*		2	
	Scarus oviceps	14	20 - 34	X	13			1	
	Scarus prasiognathos	1	35		1				
	Scarus quoyi	1	25		1				
	Scarus rivulatus	23	25 - 35	X	19	1	2	1	
	Scarus schlegeli	22	18 - 29	X	16.5*		1	4.5*	
	Scarus spinus	5	24 - 25		2			3	
Surgeonfishes	*Naso lituratus*	23	15 - 30	X	11		3	9	
(Acanthuridae)	*Naso unicornis*	32	30 - 70	X	5		1	26	
Groupers	*Cephalopholis argus*	1	28					1	
(Epinephelidae)	*Cephalopholis miniata*	2	23 - 24		1			1	
	Epinephelus fuscoguttatus	1	59					1	
	Epinephelus hexagonatus	1	31					1	
	Epinephelus ongus	106	10 - 32	X	15	16	30	45	
	Epinephelus polyphekadion	3	25 - 40		1	2			
	Epinephelus tauvina	2	29 - 37					2	1
	Plectropomus leopardus	30	20 - 62	X	12	2	5	10	

	Variola louti	2	35 - 47		1		1	
Butterflyfishes	*Chaetodon auriga*	16	12 - 20	X	5	2	2	7
(Chaetodontidae)	*Chaetodon auripes*	1	13				1	
	Chaetodon baronessa	5	13 - 15		1	2		2
	Chaetodon bennetti	2	8 - 16				1	1
	Chaetodon ephippium	10	13 - 18	X		5		5
	Chaetodon lunulatus	61	6 - 14	X	6	43	9	3
	Chaetodon ornatissimus	6	13 - 17		1			5
	Chaetodon plebeius	2	8 - 12		1	1		
	Chaetodon trifascialis	21	5 - 13	X	9	9	2	1
	Chaetodon ulietensis	2	10 - 12			1		1
	Chaetodon vagabundus	8	10 - 15				1	7
	Forcipiger flavissimus	1	15					1

Table 2(on next page)

Relationship between seven categories of substrate architectural characteristics (physical structure) and 25 substrate types.

Table 2. Relationship between seven categories of substrate architectural characteristics (physical structure) and 25 substrate types.

Substrate architectural characteristics	Substrate
Eave-like space	Corymbose *Acropora*
	Tabular *Acropora*
	Foliose coral
	Dead corymbose *Acropora*
	Dead tabular *Acropora*
	Dead foliose coral
Large inter-branch space	Staghorn *Acropora*
	Dead staghorn *Acropora*
Overhang by fine branching structure	Branching *Acropora*
	Bottlebrush *Acropora*
	Non-acroporid branching coral
	Pocillopora
	Dead branching *Acropora*
	Dead bottlebrush *Acropora*
	Dead non-acroporid branching coral
	Dead *Pocillopora*
Overhang by coarse structure	Massive coral
	Dead massive coral
	Rock
Uneven structure without large space or overhang	Other coral
	Dead other coral
	Soft coral
Flat	Coral rubble

	Sand
Macroalgae	Macroalgae