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

Atsushi Nanami Corresp. [1]

[1] Environment and Fisheries Applied Techniques Research Department, Fisheries Technology Institute, Japan Fisheries Research and Education Agency, Yaeyama Field Station, Coastal and Inland Fisheries Ecosystem Division, Ishigaki, Okinawa, Japan

Corresponding Author: Atsushi Nanami
Email address: nanami_atsushi71@fra.go.jp

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; *Ch. 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 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. Four species (*Ch. microrhinos*, *H. longiceps*, *S. niger* and *N. unicornis*) also showed clear variations in substrate associations among the different fish size classes. Since 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.

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

Atsushi Nanami

Yaeyama Field Station, Coastal and Inland Fisheries Ecosystem Division, Environment and Fisheries Applied Techniques Research Department, Fisheries Technology Institute, Japan Fisheries Research and Education Agency, Fukai-Ota 148, Ishigaki, Okinawa 907-0451, Japan

Correspondence author. Atsushi Nanami
E-mail address: nanami_atsushi71@fra.go.jp
Telephone number: +81 980 88 2861
Fax number: +81 980 88 2573

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; *Ch. 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 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. Four species (*Ch. microrhinos*, *H. longiceps*, *S. niger* and *N. unicornis*) also showed clear variations in substrate associations among the different fish size classes. Since 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.

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). Such species-specific habitat associations have been shown to influence populations through survivorship (Fakan et al., 2024).

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). This diverse ecosystem services provided by coral reefs include supporting (biodiversity benefit and habitat), regulating (coastal protection and water quality), provisioning (fishery and materials) and cultural services (Woodlhead et al., 2019). 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, precise substrate characteristics (e.g., coral species, coral morphology and physical structure) that were directly associated by fish individuals 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 with specific substrates. Although some previous studies have revealed the diurnal substrate associations of groupers (Nanami et al., 2013; Wen et al. 2013b), their nocturnal associations have not been examined yet.

Several previous studies have 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 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). Thus, nocturnal substrate association of fishes should be clarified to determine the critical habitats in terms of fish nocturnal habitat utilization. In addition, parrotfishes, groupers and surgeonfishes are main fishery targets in the Pacific Islands and nighttime spear fishing is one of the methods to catch inactive individuals (Gillett & Moy, 2006)). Thus, clarifying the substrate characteristics that are utilized by fishes as sleeping sites is critical for conservation of fishing points. 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 by spear were euthanized immediately to minimize suffering. 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. The 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, 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). According to Nanami (2021), average distance of 1-minute swimming was 17.4 m. Thus, the estimated distance of each time survey was 17.4 m × survey minutes. Since the width of the time transect was 5 m, the estimated area was distance × 5 m^2.

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, the data analyses were conducted in two steps. First step was to clarify the species-level substrate associations by using above-mentioned 17 dominant species (9, 2, 2 and 4 species for parrotfishes, surgeonfishes, groupers and butterflyfishes, respectively). Second step was to clarify the family-level substrate associations by using all species including both dominant and non-dominant species (19, 2, 9 and 12 species for parrotfishes, surgeonfishes, groupers and butterflyfishes, respectively).

Data collection of substrate availability

Substrate availability at the 19 study sites was recorded during daytime. The locations of sites where nocturnal observations were conducted were recorded by a portable GPS receiver (GARMIN GPSMAP 64csx). Then, the video recording mode of a digital camera was applied to record substrates on the seafloor during 20 minutes at each sites. 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 and definition of substrate architectural characteristics

Substrates were categorized into 25 types and substrate architectural characteristics (physical structure) were categorized into seven types with some modification from several previous studies (Gardiner & Jones, 2005; Wilson et al., 2008; Nanami, 2020; Doll et al., 2021) as follows (Table 2, Fig. 3): (1) eave-like space, (2) large inter-branch space, (3) overhang provided by protrusion of fine branching structure, (4) overhang by coarse structure, (5) uneven structure without large space or overhang, (6) flat and (7) macroalgae.

Data analysis for substrate association

The analyses were conducted in two steps. The first step was to clarify the associations between fish species and the seven types of substrate architectural characteristics (physical structure). The 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). This was because many previous studies applied this index to examine the quantitative degree of substrate association of coral reef fishes to specific substrate characteristics (e.g., Gardiner & Jones, 2005; Wilson et al., 2008; Doll et al., 2021; Nanami, 2023). This index also shows 95% confidence intervals by using some parameters as described below, which can test the statistical significance of the substrate association of fishes for each substrate types.

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:

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

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 substrate categories, 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.

In addition, standardized selection ratio that indicating relative degree among substrates for habitat selection was calculated as follows:

$$B_i = w_i / \sum w_i$$

If a focal species shows Bi and Bj for ith and jth substrates, ith substrate is selected with Bi / Bj times the probability of jth substrate.

Both species level (17 species) and family level (4 families) data analyses were performed.

Variations in substrate associations among different fish size classes

Additionally, to clarify the variations in substrate associations among different fish size classes, fish individuals were divided into three size classes as follows: (1) TL ≤ 29 cm (smaller-sized); (2) TL = 30 cm – 39 cm (medium-sized) and (3) TL ≥ 40 cm (larger-sized). Then, degree of substrate association was analyzed. Five species (*Scarus schlegeli*, *Chaetodon trifascialis*, *C.*

lunulatus, *C. ephippium* and *C. auriga*) were excluded from the analysis, since total length of the all individuals were 29 cm or less for the five species.

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 (see Substrate availability raw data). Namely, substrate compositions at sites with longer fish observation durations should be included with greater proportions whereas substrate compositions at sites with shorter time observation durations should be included with lower proportions. The degree of the proportion was assigned by the observation duration at the site. Thus, 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. Analyses were performed using PRIMER (version 6) software package (Clarke & Warwick, 1994). For plotting the PCA score of each fish species, data about nocturnal substrate association were also shown by pie charts. Additional PCA was performed to clarify the variations in substrate associations among the above-mentioned three fish size classes.

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 and overhang by coarse structure were found (Tables 3, S1). However, no significant substrate associations were found for any types of 25 substrates (Tables 4, S2). For size difference, smaller-sized and medium-sized individuals were primarily associated with large inter-branch space (staghorn *Acropora*), whereas larger-sized individuals were primarily associated with overhang by coarse structure (rock: Fig. S1).

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 (Tables 3, S1). For eave-like space, no significant substrate-specific associations were found (Tables 4, S2). For large inter-branch space, significant positive association with staghorn *Acropora* was found (Tables 4, S2). In contrast, a significant negative association with overhang by coarse structure (rock) was found (Tables 3, 4, S1, S2). For size difference, smaller- and medium-sized individuals showed relatively greater proportion of association with eave-like space (corymbose and tabular *Acropora*) and large inter-branch space (staghorn *Acropora*), respectively (Fig. S2).

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 were found, respectively (Tables 3, 4, S1, S2). For size difference, smaller-, medium- and larger-sized individuals showed relatively greater proportion of association with large inter-branch space (staghorn *Acropora*), overhang by coarse structure (rock) and eave-like space (tabular and dead tabular *Acropora*), respectively (Fig. S3).

Scarus ghobban was primarily associated with eave-like space (corymbose *Acropora*) and overhang by coarse structure (massive coral and rock) (Fig. 5A). Although this species showed respectively significant positive and negative associations with overhang by coarse structure and overhang by fine branching structure (Tables 3, S1), no significant substrate-specific associations were found (Tables 4, S2). All three size classes showed relatively greater proportion of association with overhang by coarse structure (massive coral and rock: Fig. S4).

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. 5B, 5C, 6A-6C) and showed a significant positive association with the eave-like space (Tables 3, S1). Three species (*S. forsteni*, *S. oviceps* and *S. rivulatus*) and one species (*S. schlegeli*) showed positive associations with tabular *Acropora* and corymbose *Acropora*, respectively (Tables 4, S2). In contrast, *S. niger* did not show any substrate-specific associations (Tables 4, S2). For size difference, two size class (smaller- and larger-sized) and medium-sized individuals of *S. forsteni* showed greater proportion in association with eave-like space (tabular *Acropora*) and overhang by coarse structure (rock) , respectively (Fig. S5). Smaller- and medium-sized individuals of *S. niger* showed greater proportion in association with eave-like space (mainly tabular *Acropora*) and large inter-branch space (staghorn *Acropora*), respectively (Fig. S6). In contrast, all size classes of the two species (*S. oviceps* and *S. rivulatus*) were primarily associated with eave-like space ((mainly tabular *Acropora*: Figs. S7, S8).

Surgeonfishes

Naso unicornis was primarily associated with overhang by coarse structure (rock: Fig. 7A) and showed a significant positive association with the substrate (Tables 5, 6, S3, S4). A significant negative association with overhang by fine branching structure was also found (Tables 5, S3). For size difference, smaller- and larger-sized individuals were primarily associated with eave-like space (dead tabular *Acropora*) and overhang by coarse structure (rock), respectively (Figs. S9A, S9C). Medium-sized individuals was associated with both eave-like space (tabular *Acropora*) and overhang by coarse structure (rock: Fig. S9B)

Naso lituratus was primarily associated with eave-like space (tabular *Acropora*) and overhang by coarse structure (rock: Fig. 7B). Significant positive association with eave-like space was found (Tables 5, S3). However, no significant substrate associations were found for any types of 25 substrates (Tables 6, S4). For size difference, smaller- and medium-sized individuals showed greater proportion in association with eave-like space (mainly tabular *Acropora*) and overhang by coarse structure (rock), respectively (Fig. S10).

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 space (Tables 5, S3), although no significant substrate-specific associations were found (Tables 6, S4). In contrast, a significant negative association with flat (coral rubble) was found (Tables 5, 6, S3, S4). For size difference, medium-sized individuals was primarily associated with eave-like space (mainly corymbose and tabular *Acropora*: Fig. S11B). However, no clear trends were found for smaller- and larger-sized individuals (Figs. S11A, S11C).

Epinephelus ongus was primarily associated with overhang by fine branching structure (non-acroporid branching coral) and overhang by coarse structure (rock: Fig. 8B). A significant positive association with overhang by coarse structure were found (Tables 5, S3). However, for substrate-specific associations, significant positive and negative associations with non-acroporid branching coral and branching *Acropora* were respectively found (Tables 6, S4). All size class individuals showed greater proportions in association with overhang by coarse structure (rock: Fig. S12).

Butterflyfishes

Chaetodon trifascialis was primarily associated with eave-like space (tabular *Acropora*) and large inter-branch space (staghorn *Acropora*: Fig. 9A) and showed significant positive associations with these substrates (Tables 5, 6, S3, S4). This species also showed a significant negative association with overhang by coarse structure (rock: Tables 5, 6, S3, S4).

Chaetodon lunulatus was primarily associated with large inter-branch space (staghorn *Acropora*: Fig. 9B) and showed a significant positive association with the substrate (Tables 5, 6, S3, S4). This species also showed a significant negative association with overhang by coarse structure (rock: Tables 5, 6, S3, S4).

Chaetodon ephippium was associated with large inter-branch space (staghorn *Acropora*) and overhang by coarse structure (dead massive coral and rock: Fig. 9C) and showed a significant positive association with large inter-branch space (Tables 5, S3). However, no significant substrate associations were found for any types of 25 substrate types (Table, 6, S4).

Chaetodon auriga was primarily associated with eave-like space (corymbose *Acropora* and dead tabular *Acropora*) and overhang by coarse structure (rock: Fig. 9D). However, no significant associations with any structural characteristics and substrate types were found (Tables 5, 6, S3, S4).

Family-level substrate associations

Parrotfishes were primarily associated with eave-like space (corymbose *Acropora* and tabular *Acropora*), and some individuals were also associated with large inter-branch space (staghorn *Acropora*), overhang by fine branching structure (non-acroporid branching coral) and overhang by coarse structure (rock: Fig. S13A). Parrotfishes showed significant positive associations with eave-like space (corymbose *Acropora*, tabular *Acropora* and dead tabular *Acropora*) and large inter-branch space (staghorn *Acropora)* were found, whereas showed a significant negative association with overhang by fine branching structure (bottlebrush *Acropora*: Tables S5-S8).

Surgeonfishes were primarily associated with overhang by coarse structure (rock), and some individuals were also associated with eave-like space (tabular *Acropora*) and overhang by fine branching structure (non-acroporid branching coral) (Fig. S13B). Surgeonfishes showed significant positive associations with eave-like space (tabular *Acropora*) and overhang by coarse structure (rock: Tables S5-S8). A significant negative association with overhang by fine branching structure was also found (Tables S5, S7).

Groupers were primarily associated with overhang by coarse structure (rock), and some individuals were 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. S13C). For seven types of substrate architectural characteristics, groupers showed significant positive and negative associations with overhang by coarse structure and flat, respectively (Tables S5-S8). However, for 25 substrate types, a significant positive associations with non-acroporid branching corals was found (Tables S6, S8). In contrast, significant negative associations with branching *Acropora*, bottlebrush *Acropora* and coral rubble were found (Tables S6, S8).

Butterflyfishes were primarily associated with large inter-branch space (staghorn

Acropora), and some individuals were also associated with eave-like space (corymbose *Acropora* and tabular *Acropora*), overhang by fine branching structure (branching *Acropora*) and overhang by coarse structure (rock: Fig. S13D). Butterflyfishes showed a significant positive association with large inter-branch space (staghorn *Acropora*), whereas a significant negative association with overhang by fine branching structure (bottlebrush *Acropora*) (Tables S5-S8). A significant negative association with massive coral was also found (Tables S6, S8).

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. 10A). Cluster analysis revealed the 17 species could be divided into six groups (Figs. 10B, S14A). 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 fish size difference, four species (*Ch. microrhinos*, *H. longiceps*, *S. niger* and *N. unicornis*) showed relatively clear variations in substrate associations among difference size classes (Fig. S15). For the two species (*Ch. microrhinos* and *H. longiceps*,), the main associated substrates changed from large inter-branch space to overhang by coarse structure as fish size increasing (Figs. S15B, S15D). In contrast, the other two species (*S. niger* and *N. unicornis*) showed that the main associated substrates changed from eave-like space to large inter-branch space (Fig. S15G) and from eave-like space to overhang by coarse structure as fish size increasing (Fig. S15K), respectively.

For 25 substrate types, PCA revealed that three substrate types (tabular *Acropora*, staghorn *Acropora* and rock) showed major contributions for nocturnal fish associations (Figs. 10C). Cluster analysis revealed 17 species could be divided into eight groups (Figs. 10D, S14B). *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. For fish size difference, two species (*Ch. microrhinos* and *H. longiceps*,) showed that the main associated substrates changed from staghorn *Acropora* to rock as fish size increasing (Figs. S16B, S16D). Other two species (*S. niger* and *N. unicornis*) showed that the main associated substrates changed from tabular *Acropora* to staghorn *Acropora* (Fig. S16G) and from dead tabular *Acropora* to rock as fish size increasing (Fig. S16K: dead tabular *Acropora* was shown as "other substrates" in Fig. S16K. See also Fig. S9), respectively.

DISCUSSION

This study examined the nocturnal substrate association of 17 species from four fish groups, which was the first study in the North Pacific (Okinawan coral reef). The results of present study would provide useful information what types of substrates should be protected and/or restored for fish habitat at nighttime as well as fishing points for nighttime spear-fishing.

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, substrate 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 and *N. lituratus* showed significant positive associations with overhang by coarse structure mainly provided by rock and eave-like space being mainly provided by tabular *Acropora*, respectively. Some individuals of *N. unicornis* were also associated with eave-like space provided by tabular *Acropora.* These findings suggest that canopy structure (overhangs and tabular structure) should be conserved as sleeping sites for these 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, et al., 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 mainly provided by 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 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 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). Since this species was mainly associated with four types of substrate architectural characteristics (eave-like space, large inter-branch space, overhang by fine branching structure and overhang by coarse structure) but not associated with other three types of architectural characteristics (uneven surface, flat and macroalgae), this species utilized substrates with complex physical structure as sleeping site. Since these four types of substrate architectural characteristics are provided by both live corals and rock, such substrates with greater complexity should be conserved as sleeping site for the species.

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*) and substrates with complex physical structure was also important as sleeping site for *C. auriga*, which were not shown by diurnal observations for clarifying their foraging substrates.

Variations in substrate association among different fish size classes

Four species showed the clear variations in nocturnal substrate associations among different size classes. The two species (*Ch. microrhinos* and *H. longiceps*,) and one species (*N. unicornis*) showed that the main associated substrates changed from large inter-branch space (staghorn *Acropora*) to overhang by coarse structure (rock), and from eave-like space (dead tabular *Acropora*) to overhang by coarse structure (rock) as fish size increasing, respectively. These results suggest that smaller- and larger-sized individuals were respectively associated with fine and coarse habitat structures, and various types of substrate architectural characteristics are needed for the various size of the three species as nocturnal sleeping sites. In contrast, *S. niger* showed that the main associated substrates changed from eave-like space (mainly tabular *Acropora*) and large inter-branch space (staghorn *Acropora*) as fish size increasing, suggesting that various types of acroporid corals are needed for the various size of the species as nocturnal sleeping site.

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. In contrast, almost all fish species (except for one individual of *P. leopardus*) showed no associations with uneven structure without large space or overhang, flat and macroalgae, indicating fish avoidance of the three substrate architectural structure. 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 fish nocturnal substrate associations would provide more effective strategies for conservation and restoration of coral assemblages.

ACKNOWLEDGEMENTS

I express my grateful thanks to Masato Sunagawa and Sho Sunagawa for their assistance in the field, and the staff of Yaeyama Field Station, Japan Fisheries Research and Education Agency for support during the present study. Constructive comments from Chris Norman, Andy Richardson and a anonymous reviewer were much appreciated. The present study complies with current laws in Japan.

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.

Clarke KR, Warwick RM. 1994. Changes in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth.

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.

Doll PC, Munday PL, Bonin MC, Jones GP. 2021. Habitat specialization and overlap in coral reef gobies of the genus *Eviota* (Teleostei: Gobiidae). *Marine Ecology Progress Series* 677:81-94.

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

Fakan EP, McCormick MI, Jones GP, Hoey AS. 2024. Habitat and morphological characteristics affect juvenile mortality in five coral reef damselfishes. Coral Reefs 43:171-183

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.

Gardiner NM, Jones GP. 2005. Habitat specialization and overlap in a guild of coral reef cardinalfishes (Apogonidae). *Marine Ecology Progress Series* 305:163-175.

Gillett R, Moy W. 2006. Spearfishing in the Pacific Islands. Current status and management issues. FAO/Fishcode Review No. 19.

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, Belmarker 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, Belmarker 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 map in (A) was prepared by the author after processing the map from https://mapps.gsi.go.jp/maplibSearch.do#1. The aerial photographs in (B) and (C) were provided by the International Coral Reef Research and Monitoring Center.

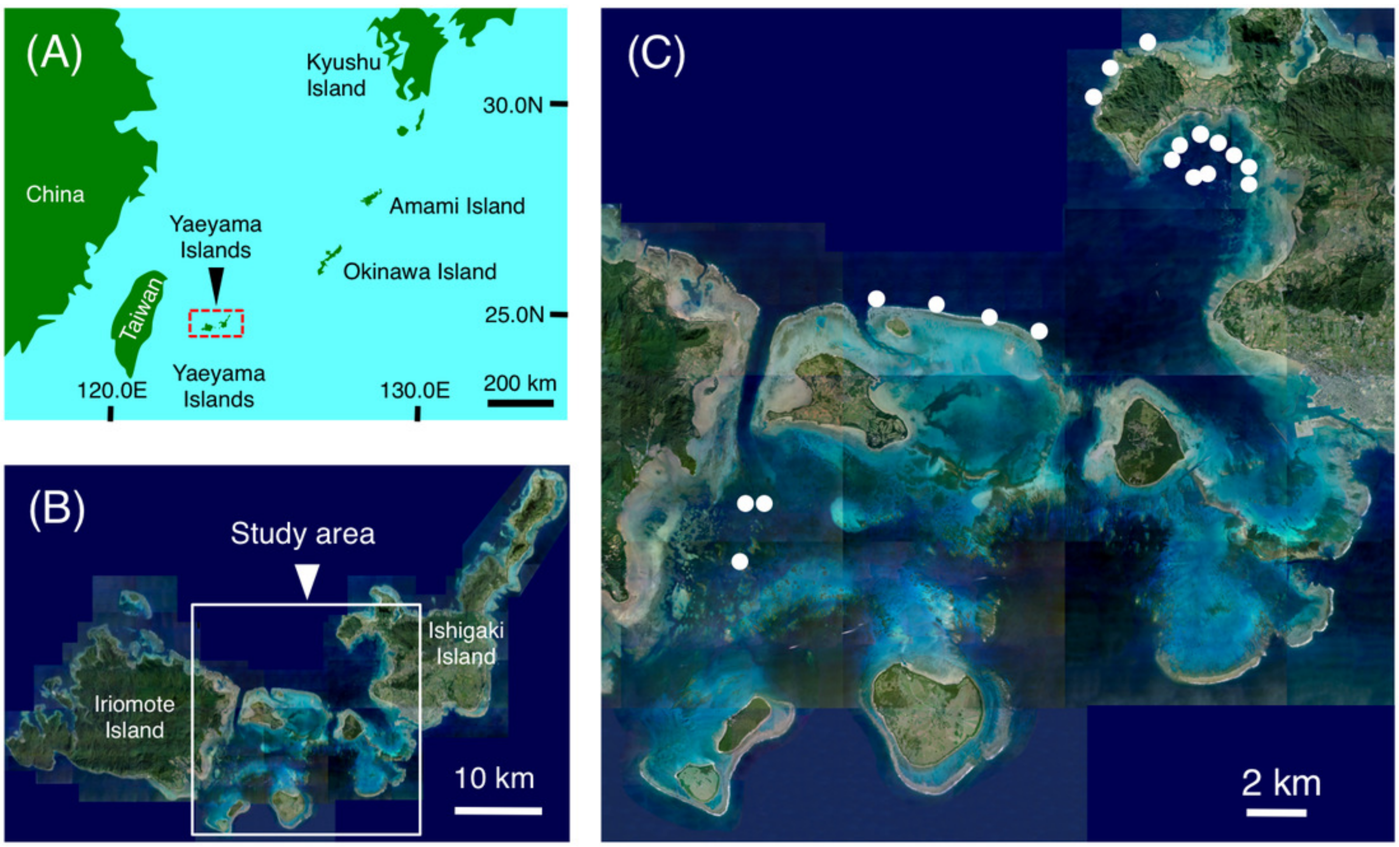


Figure 2

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, 5, 6, 7, 8 and 9. All fish photographs were taken by the author (A. Nanami).

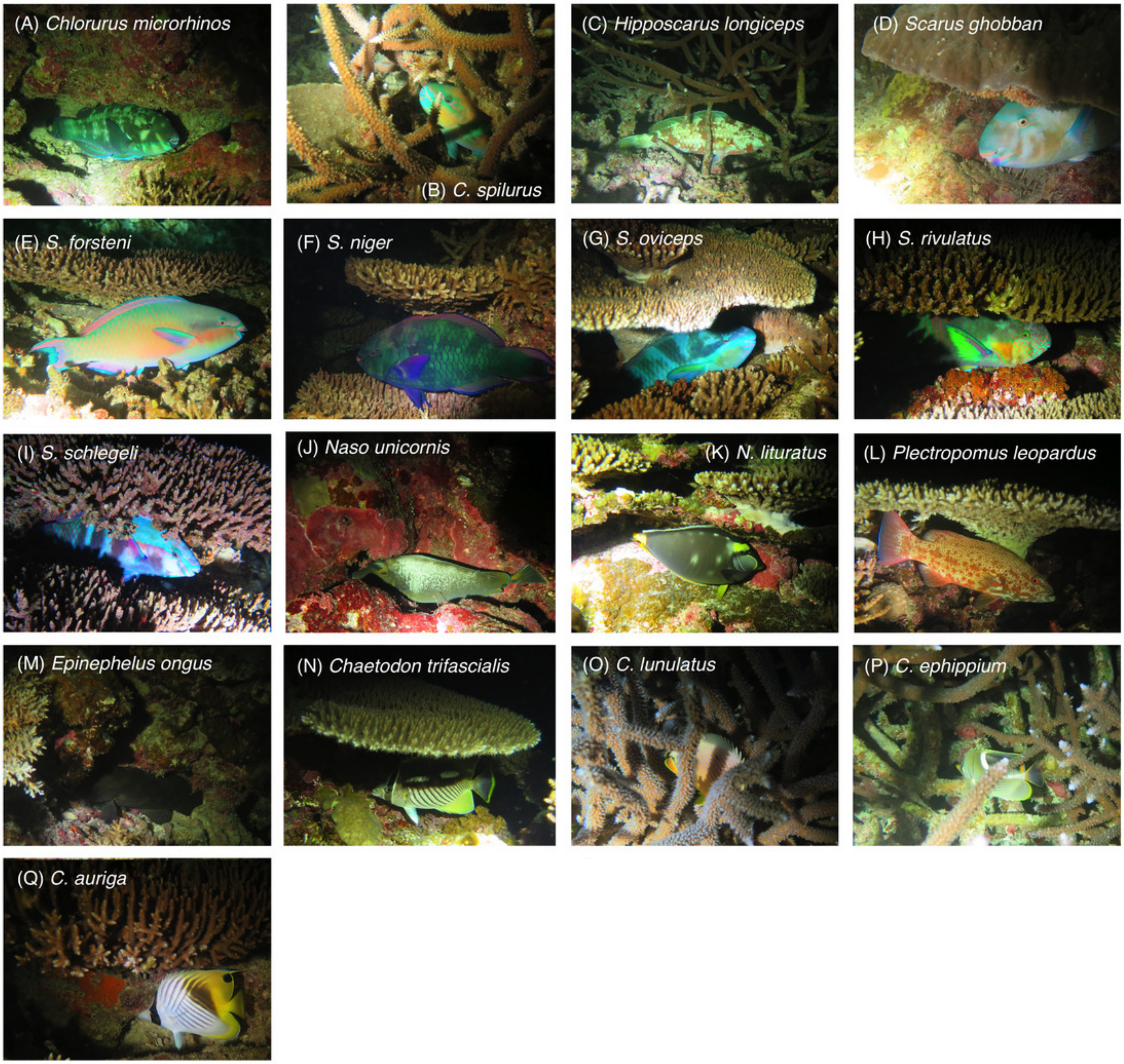

(A) Chlorurus microrhinos
(B) C. spilurus
(C) Hipposcarus longiceps
(D) Scarus ghobban
(E) S. forsteni
(F) S. niger
(G) S. oviceps
(H) S. rivulatus
(I) S. schlegeli
(J) Naso unicornis
(K) N. lituratus
(L) Plectropomus leopardus
(M) Epinephelus ongus
(N) Chaetodon trifascialis
(O) C. lunulatus
(P) C.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

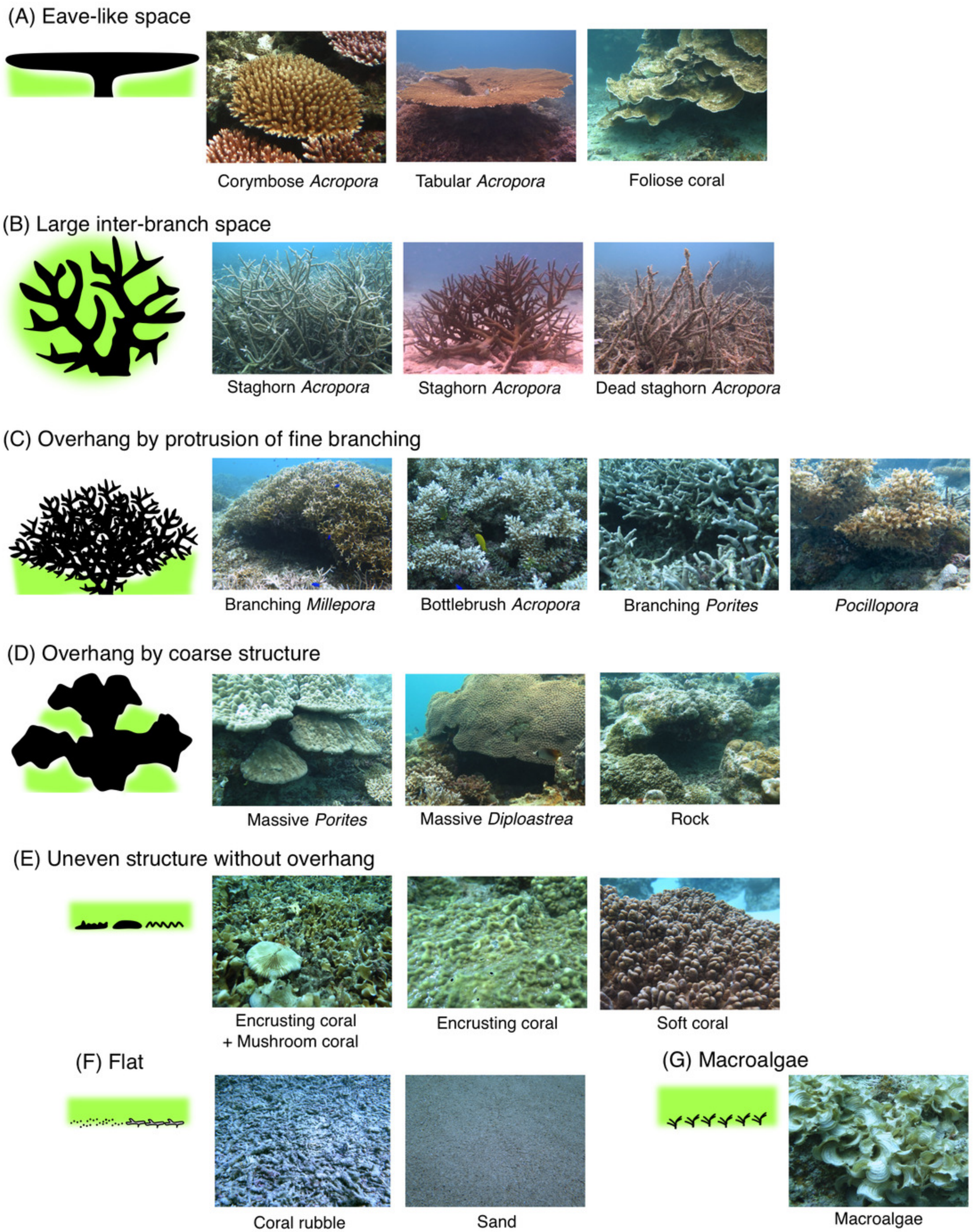

(A) Eave-like space
Corymbose Acropora
Tabular Acropora
Foliose coral
(B) Large inter-branch space
Staghorn Acropora
Staghorn Acropora
Dead staghorn Acropora
(C) Overhang by protrusion of fine branching
Branching Millepora
Bottlebrush Acropora
Branching Porites
Pocillopora
(D) Overhang by coarse structure
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 three parrotfish species *(Chlorurus microrhinos*,*C. spilurus* and *Hipposcarus longiceps*).

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).

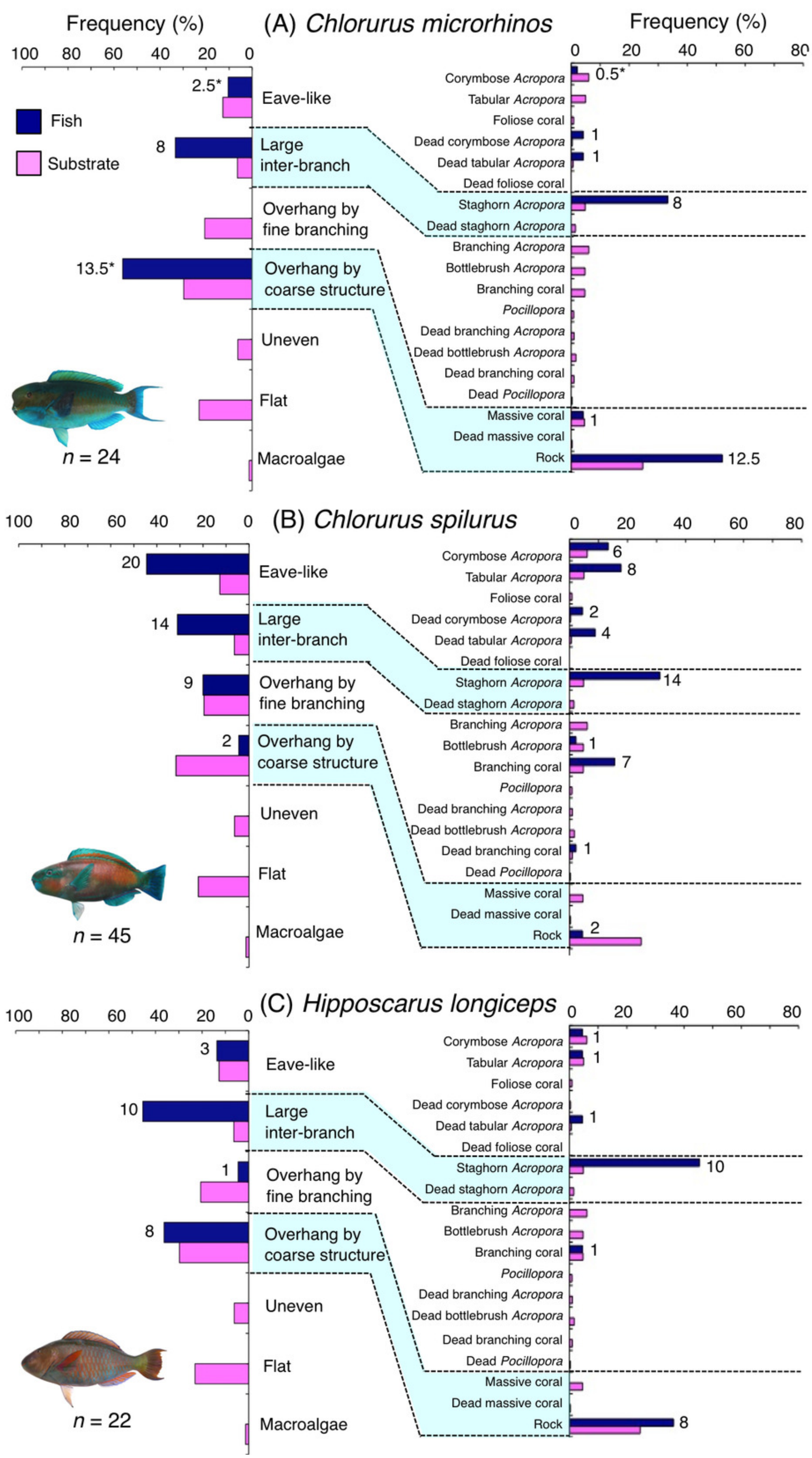
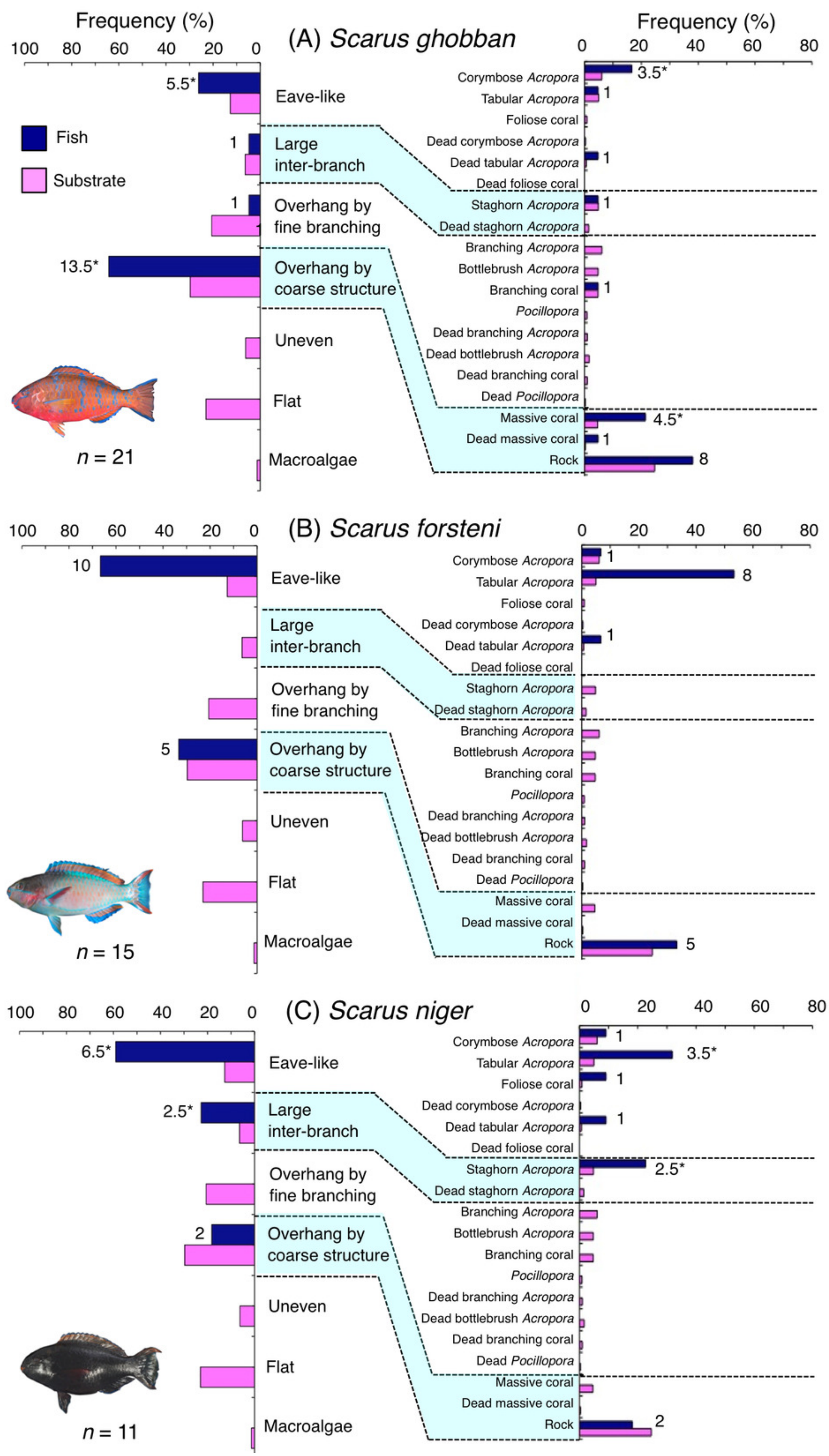

Frequency (%)
(A) Chlorurus microrhinos
Fish
Substrate
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
n = 24
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular Acropora
Dead foliose coral
Staghorn Acropora
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) Chlorurus spilurus
n = 45
(C) Hipposcarus longiceps
n = 22

Figure 5

Relative frequency (%) of fish individuals associated with substrates and substrate availability for the three parrotfish species *Scarus ghobban*,*S. forsteni* and *S. niger*).

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) Scarus ghobban
Frequency (%)
Fish
Substrate
5.5*
Eave-like
Large inter-branch
Overhang by fine branching
13.5*
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
3.5*
4.5*
8
(B) Scarus forsteni
10
5
n = 15
(C) Scarus niger
6.5*
2.5*
2
n = 11

Figure 6

Relative frequency (%) of fish individuals associated with substrates and substrate availability for the three parrotfish species *Scarus oviceps*, *S. rivulatus* and *S. schlegeli*).

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).

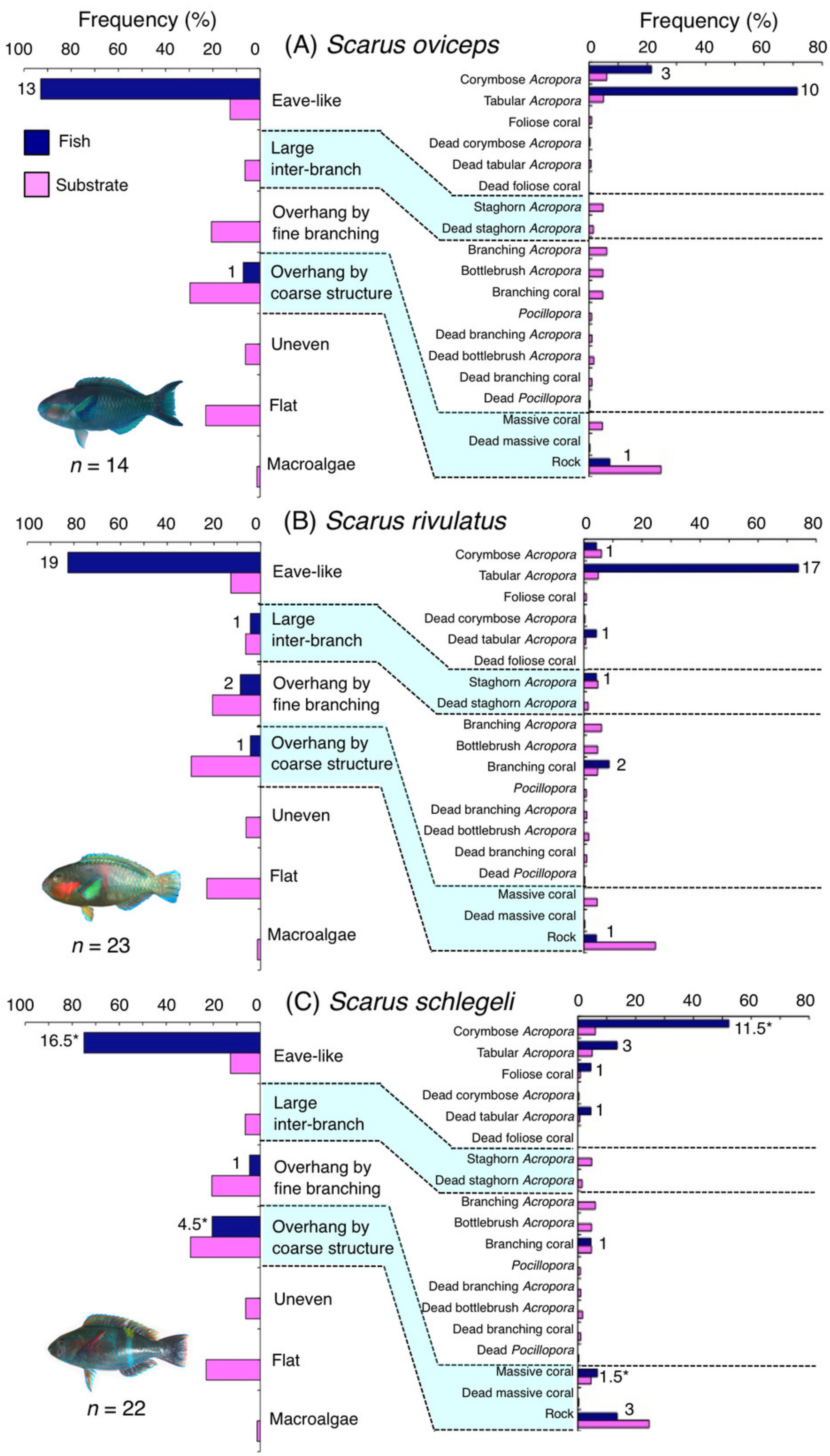

Frequency (%)
(A) Scarus oviceps
Fish
Substrate
n = 14
(B) Scarus rivulatus
n = 23
(C) Scarus schlegeli
n = 22
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular 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

Figure 7

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).

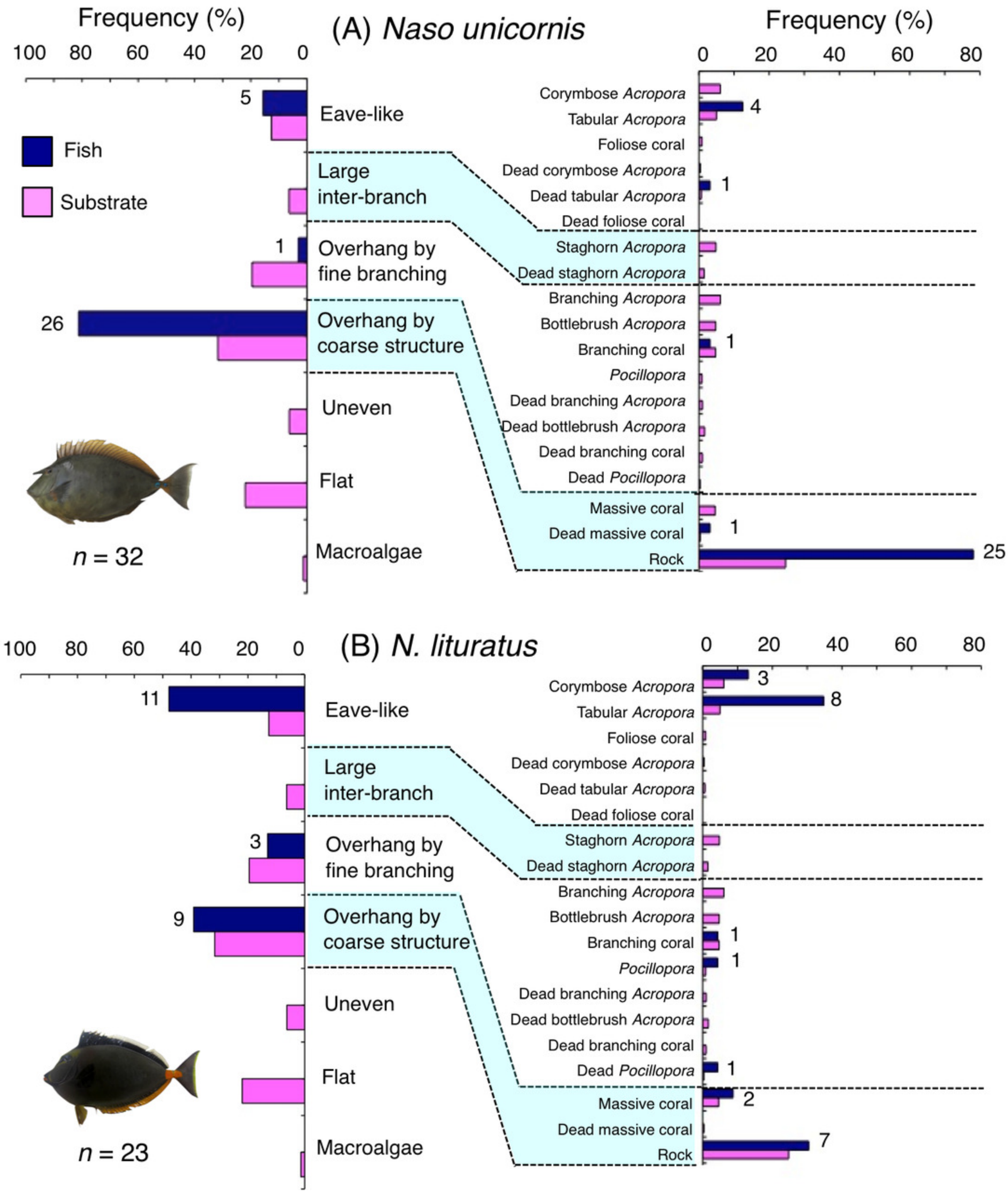
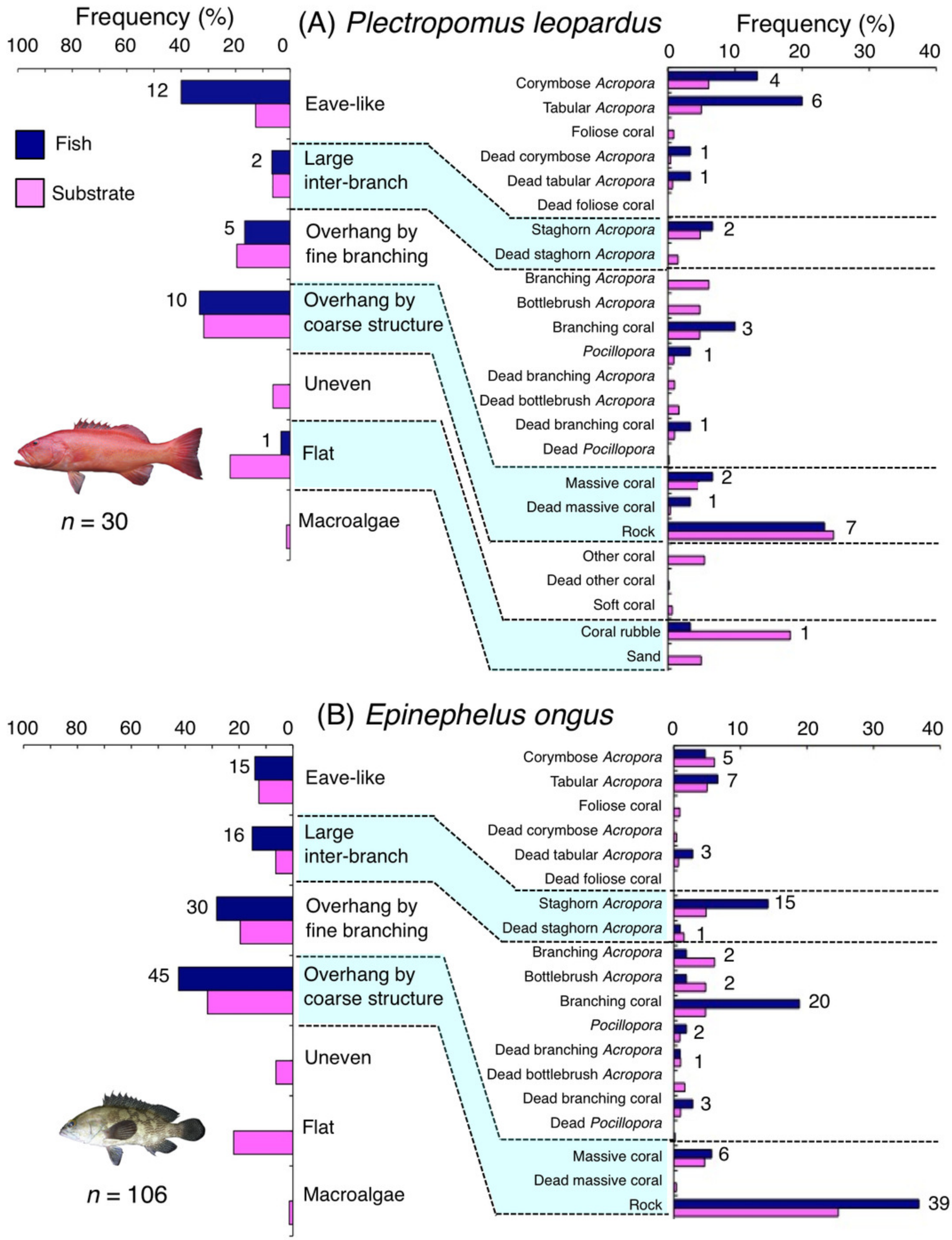

(A) Naso unicornis
Frequency (%)
100 80 60 40 20 0
Fish
Substrate
5
1
26
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
n = 32
Frequency (%)
0 20 40 60 80
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular 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
100 80 60 40 20 0
11
3
9
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
n = 23
0 20 40 60 80
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
Frequency (%)
0 10 20 30 40
Fish
Substrate
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 9

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).

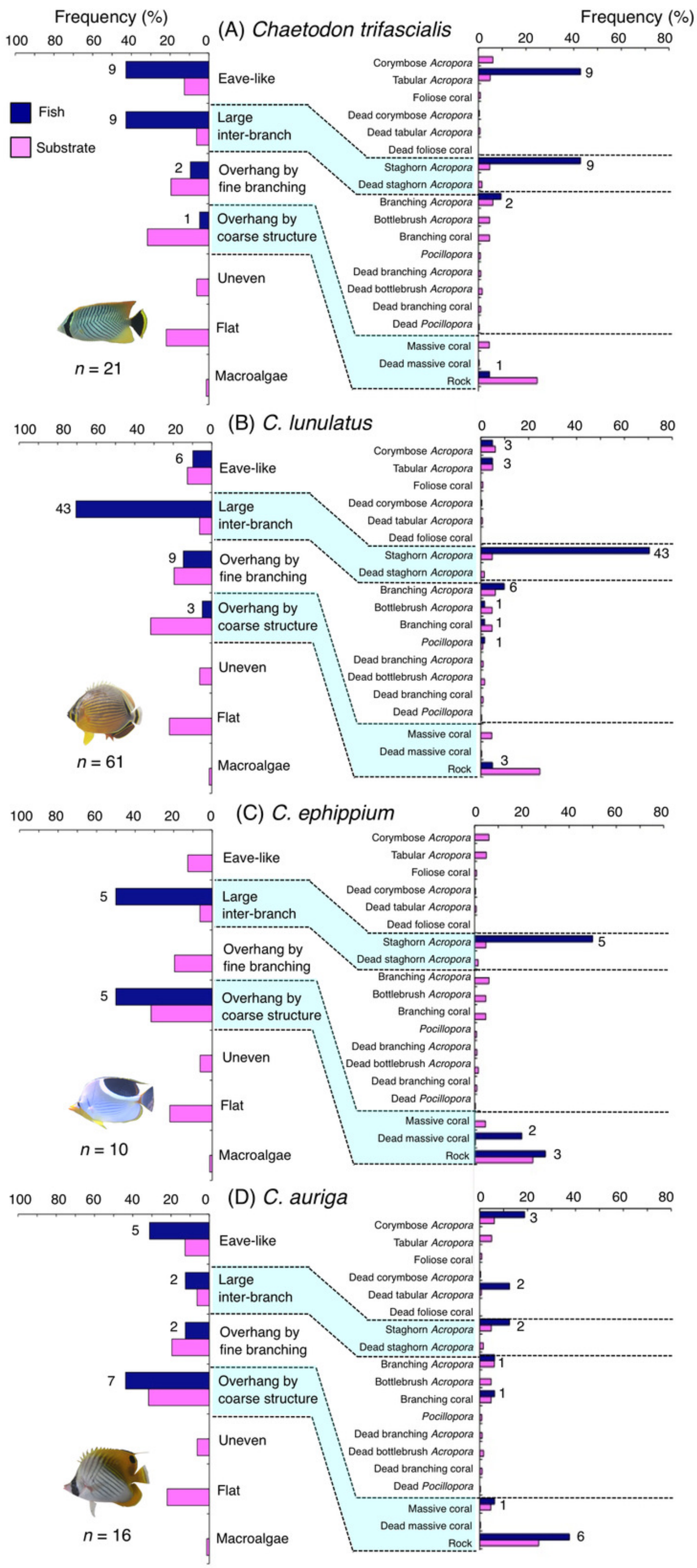

Frequency (%)
(A) Chaetodon trifascialis
Fish
Substrate
Eave-like
Large inter-branch
Overhang by fine branching
Overhang by coarse structure
Uneven
Flat
Macroalgae
n = 21
Corymbose Acropora
Tabular Acropora
Foliose coral
Dead corymbose Acropora
Dead tabular Acropora
Dead foliose coral
Staghorn Acropora
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 10

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. S2). 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). For details about data, see "Fig 10 + Fig S2 raw data.xls."

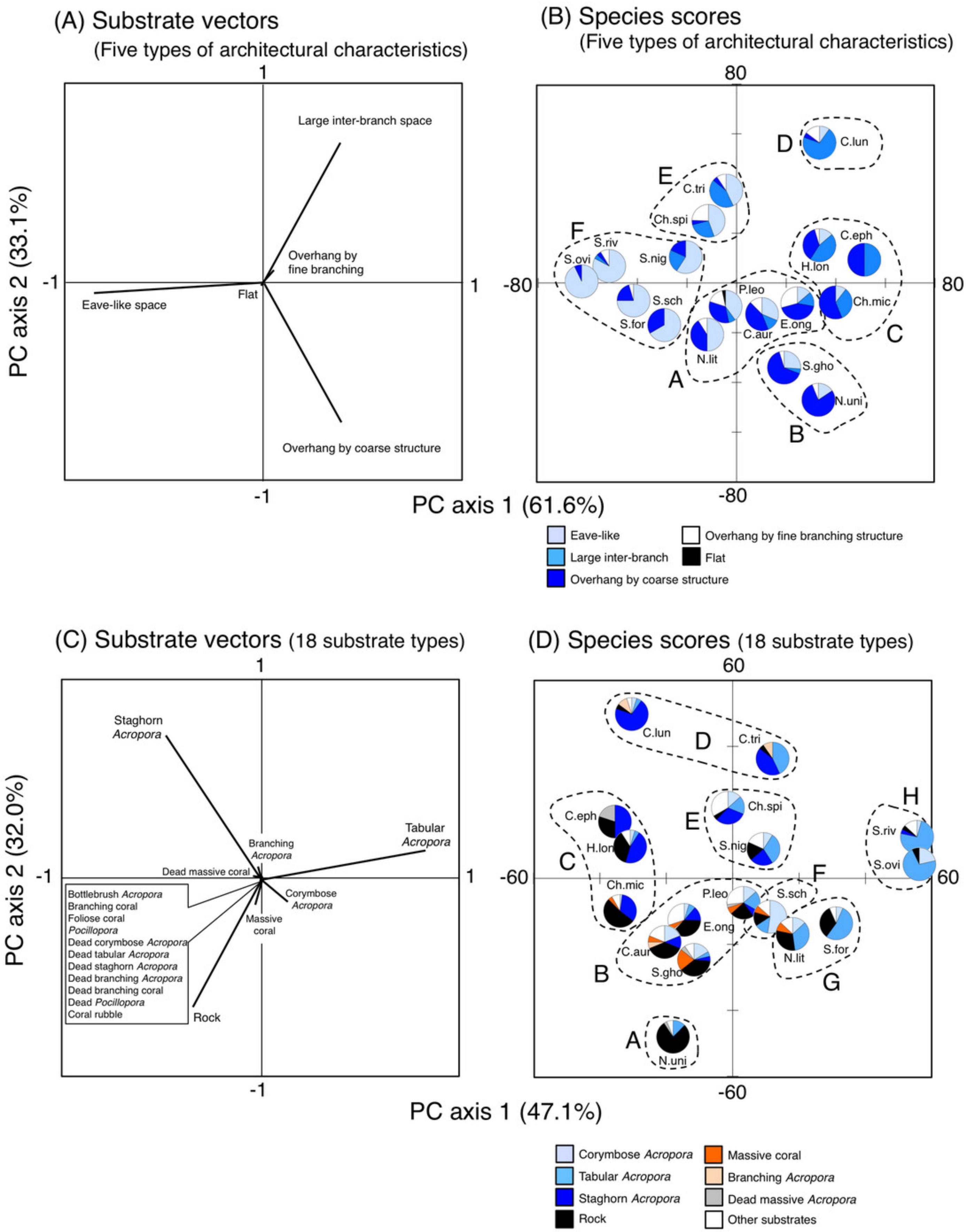

(A) Substrate vectors
(Five types of architectural characteristics)
Large inter-branch space
Overhang by fine branching
Eave-like space
Flat
Overhang by coarse structure
PC axis 2 (33.1%)
(B) Species scores
(Five types of architectural characteristics)
C.lun
C.tri
Ch.spi
S.riv
S.ovi
S.nig
C.eph
H.lon
P.leo
S.sch
S.for
Ch.mic
C.aur
E.ong
N.lit
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 species-level 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 (Chaetodontidae)	*Chaetodon auriga*	16	12 - 20	X	5	2	2	7
	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

Table 3(on next page)

Results of statistical significance of substrate association of the nine parrotfish species calculated by resource selection ratio for seven types of substrate architectural characteristics.

Significant positive associations are shown as bold characters. N.S. : non significant associations. - : no fishes were found on the substrates.

Substrate architectural characteristics	*Chlorurus microrhinos*	*Chlorurus spilurus*	*Hipposcarus longiceps*	*Scarus ghobban*	*Scarus forsteni*	*Scarus niger*	*Scarus oviceps*	*Scarus rivulatus*	*Scarus schlegeli*
Eave-like	N.S.	**Positive**	N.S.	N.S.	**Positive**	**Positive**	**Positive**	**Positive**	**Positive**
Large inter-branch	**Positive**	**Positive**	**Positive**	N.S.	-	N.S.	-	N.S.	-
Overhang by fine branching	-	N.S.	Negative	Negative	N.S.	-	-	N.S.	Negative
Overhang by coarse strure	**Positive**	Negative	N.S.	**Positive**	-	N.S.	N.S.	Negative	N.S.
Uneven	-	-	-	-	-	-	-	-	-
Flat	-	-	-	-	-	-	-	-	-
Macroalge	-	-	-	-	-	-	-	-	-

Table 4(on next page)

Results of substrate association of the nine parrotfish species calculated by resource selection ratio for 25 substrate types.

Significant positive associations are shown as bold characters. N.S. : non significant associations. - : no fishes were found on the substrates.

Substrate architectural characteristics	Substrate type	*Chlorurus microrhinos*	*Chlorurus spilurus*	*Hipposcarus longiceps*	*Scarus ghobban*	*Scarus forsteni*	*Scarus niger*	*Scarus oviceps*	*Scarus rivulatus*	*Scarus schlegeli*
Eave-like	Corymbose *Acropora*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	**Positive**
	Tabular *Acropora*	-	N.S.	N.S.	N.S.	**Positive**	N.S.	**Positive**	**Positive**	N.S.
	Foliose coral	-	-	-	-	-	N.S.	-	-	N.S.
	Dead corymbose *Acropora*	N.S.	N.S.	-	-	-	-	-	-	-
	Dead tabular *Acropora*	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	-	N.S.	N.S.
	Dead foliose coral	-	-	-	-	-	-	-	-	-
Large Inter-branch	Staghorn *Acropora*	N.S.	**Positive**	**Positive**	N.S.	-	N.S.	-	N.S.	-
	Dead staghorn *Acropora*	-	-	-	-	-	-	-	-	-
Overhang by fine branching	Branching *Acropora*	-	-	-	-	-	-	-	-	-
	Bottlebrush *Acropora*	-	N.S.	-	-	-	-	-	-	-
	Non-acroporid branching coral	-	N.S.	N.S.	N.S.	-	-	-	N.S.	N.S.
	Pocillopora	-	-	-	-	-	-	-	-	-
	Dead branching *Acropora*	-	-	-	-	-	-	-	-	-
	Dead bottlebruch *Acropora*	-	-	-	-	-	-	-	-	-
	Dead non-acroporid branching coral	-	N.S.	-	-	-	-	-	-	-
	Dead *Pocillopora*	-	-	-	-	-	-	-	-	-
Overhang by coarse structure	Massive coral	N.S.	-	-	N.S.	-	-	-	-	N.S.
	Dead massive coral	-	-	-	N.S.	-	-	-	-	-
	Rock	N.S.	Negative	N.S.	N.S.	N.S.	N.S.	N.S.	Negative	N.S.
Uneven	Other coral	-	-	-	-	-	-	-	-	-
	Dead other coral	-	-	-	-	-	-	-	-	-
	Soft coral	-	-	-	-	-	-	-	-	-
Flat	Coral rubble	-	-	-	-	-	-	-	-	-
	Sand	-	-	-	-	-	-	-	-	-
Macroalgae	Macroalgae	-	-	-	-	-	-	-	-	-

3

Table 5(on next page)

Results of statistical significance of substrate association of the two surgeonfish, two grouper and four butterflyfish species calculated by resource selection ratio for seven types of substrate architectural characteristics.

Significant positive associations are shown as bold characters. N.S. : non significant associations. - : no fishes were found on the substrates.

Substrate architectural characteristics	*Naso unicornis*	*Naso lituratus*	*Plectropomus leopardus*	*Epinephelus ongus*	*Chaetodon trifascialis*	*Chaetodon lunulatus*	*Chaetodon ephippium*	*Chaetodon auriga*
Eave-like	N.S.	**Positive**	**Positive**	N.S.	**Positive**	N.S.	-	N.S.
Large inter-branch	-	-	N.S.	N.S.	**Positive**	**Positive**	**Positive**	N.S.
Overhang by fine branching	Negative	N.S.	N.S.	N.S.	N.S.	N.S.	-	N.S.
Overhang by coarse structure	**Positive**	N.S.	N.S.	**Positive**	Negative	Negative	N.S.	N.S.
Uneven	-	-	-	-	-	-	-	-
Flat	-	-	Negative	-	-	-	-	-
Macroalge	-	-	-	-	-	-	-	-

Table 6(on next page)

Results of statistical significance of substrate association of the two surgeonfish, two grouper and four butterflyfish species calculated by resource selection ratio for 25 substrate types.

Significant positive associations are shown as bold characters. N.S. : non significant associations. - : no fishes were found on the substrates.

Substrate architectural characteristics	Substrate type	*Naso unicornis*	*Naso lituratus*	*Plectropomus leopardus*	*Epinephelus ongus*	*Chaetodon trifascialis*	*Chaetodon lunulatus*	*Chaetodon ephippium*	*Chaetodon auriga*
Eave-like	Corymbose *Acropora*	-	N.S.	N.S.	N.S.	-	N.S.	-	N.S.
	Tabular *Acropora*	N.S.	N.S.	N.S.	N.S.	**Positive**	N.S.	-	-
	Foliose coral	-	-	-	-	-	-	-	-
	Dead corymbose *Acropora*	-	-	N.S.	-	-	-	-	-
	Dead tabular *Acropora*	N.S.	-	N.S.	N.S.	-	-	-	N.S.
	Dead foliose coral	-	-	-	-	-	-	-	-
Large inter-branch	Staghorn *Acropora*	-	-	N.S.	N.S.	**Positive**	**Positive**	N.S.	N.S.
	Dead staghorn *Acropora*	-	-	-	N.S.	-	-	-	-
Overhang by fine branching	Branching *Acropora*	-	-	-	Negative	N.S.	N.S.	-	N.S.
	Bottlebrush *Acropora*	-	-	-	N.S.	-	N.S.	-	-
	Non-acroporid branching coral	N.S.	N.S.	N.S.	**Positive**	-	N.S.	-	N.S.
	Pocillopora	-	N.S.	N.S.	N.S.	-	N.S.	-	-
	Dead branching *Acropora*	-	-	-	N.S.	-	-	-	-
	Dead bottlebruch *Acropora*	-	-	-	-	-	-	-	-
	Dead non-acroporid branching coral	-	-	N.S.	N.S.	-	-	-	-
	Dead *Pocillopora*	-	N.S.	-	-	-	-	-	-
Overhang by coarse structure	Massive coral	-	N.S.	N.S.	N.S.	-	-	-	N.S.
	Dead massive coral	N.S.	-	N.S.	-	-	-	N.S.	-
	Rock	**Positive**	N.S.	N.S.	N.S.	Negative	Negative	N.S.	N.S.
Uneven	Other coral	-	-	-	-	-	-	-	-
	Dead other coral	-	-	-	-	-	-	-	-
	Soft coral	-	-	-	-	-	-	-	-
Flat	Coral rubble	-	-	Negative	-	-	-	-	-
	Sand	-	-	-	-	-	-	-	-
Macroalge	Macroalgae	-	-	-	-	-	-	-	-