Combination of trophic group habitat preferences determines coral reef fish assemblages

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ABSTRACT: We conducted an underwater survey to collect quantitative data on fish assemblages and various environmental factors on extensive reef slopes of Okinawa Island, southern Japan, and examined the relative influence of environmental factors on 6 trophic groups. Abundance and richness of most of the trophic groups were primarily affected by 1 of 2 factors, either percentage areal cover of bedrock or current velocity. For omnivores and mobile invertivores, abundance was relatively consistent across habitat types. Based on counts of fish species across 4 distinct habitat types, omnivores included more environmental generalist species occurring in multiple habitat types. In contrast, the consistent occurrence of mobile invertivores across habitat types was probably attributable to interspecific compensation, since species of this trophic function exhibited greater environmental specialization than omnivores did. Both species richness and abundance of herbivores and planktivores were more dependent on habitat type, and species included in these 2 trophic groups exhibited more consistent responses to environmental variation. Our results highlight the similarities and differences in responses to environmental variation among trophic groups, and the potential for environmental conditions to explain community structure and diversity in coral reef fishes. The realized niche width of species within each trophic group with respect to their habitat preference should be taken into consideration when developing effective conservation management strategies for coral reef fish communities.

KEY WORDS: Biodiversity · Physical and chemical environments · Environmental specialist · Environmental generalist · Ecological function · Species abundance · Species richness · Community assembly · Fringing reefs

INTRODUCTION

A central issue in community ecology is understanding the factors that determine the number and composition of species (Samuels & Drake 1997, Chase 2003). Local community structures are generally controlled by both dispersal and environmental characteristics in a variety of ecosystems (e.g. Chase 2007, Myers et al. 2013, Heino et al. 2015), but several studies in aquatic systems have shown that communities are primarily driven by environmental conditions (e.g. Urban 2004, MacNeil et al. 2009). Coral

reefs have the highest biodiversity of any marine ecosystem (Connell 1978, Hoegh-Guldberg 1999), but their decline has been documented in many regions over the last few decades. This situation highlights the urgent need to design and implement effective conservation management plans for reef resources (Bellwood et al. 2004, Wilson et al. 2006, Mora et al. 2011). Coral reef fish assemblages, which are the most speciose vertebrate communities on earth, contribute critical ecosystem functions and provide crucial ecosystem services to human societies in tropical regions (Moberg & Folke 1999), but

have been threatened by habitat degradation and overfishing (Newton et al. 2007, Wilson et al. 2010). As the first step toward the conservation of healthy coral reef ecosystems, it is important to determine the type and degree of environmental effects on the structure and diversity of fish assemblages (Agardy 1994, Botsford et al. 1997).

Distributions and abundances of coral reef fishes are influenced by a variety of environmental factors, such as live coral cover (reviewed by Coker et al. 2014), structural complexity (reviewed by Graham & Nash 2013), type of bottom substrate (Mellin et al. 2006), water movement (McGehee 1994, Depczynski & Bellwood 2005), depth (Friedlander et al. 2010), turbidity (Bejarano & Appeldoorn 2013), and water quality (Fabricius et al. 2005). To date, however, most studies have tested the significance of only one or a few environmental factors on communities, and few studies have examined the effects of multiple environmental factors (Friedlander et al. 2003, Mellin et al. 2010). To identify processes controlling community structure and to develop a sound ecosystem management strategy, it is necessary to understand the relative importance of environmental factors for communities.

Previous studies have demonstrated marked variation in responses to disturbances and habitat degradation between functional groups of reef fish (Graham et al. 2006, Wilson et al. 2006, Pratchett et al. 2008), suggesting that the type and degree of effects of environmental factors differ between functional groups. In particular, many studies have associated fish functional traits with diet and trophic level. In coral reef systems, some functionally important trophic groups, such as herbivores (Bellwood et al. 2004, Hughes et al. 2007) and corallivores (Cole et al. 2008), have been well studied, and influence phase shifts from coral to algal dominance. Thus, it may be an effective strategy to classify species into distinct groups based on trophic traits in analyses of relationships between reef fish communities and environmental factors. However, the similarity (or diversity) of responses of fish species to environmental variation within each trophic group is unclear. If responses are similar between species within trophic groups and are dependent on environmental factors, the occurrence of a trophic group may be biased toward sites with specific environment conditions. In contrast, if responses to environmental changes vary within a trophic group, these trophic groups could be less sensitive to environmental variation owing to interspecific compensation for species loss. The versatility and specialization of species composing each

trophic group across various habitats are expected to be important factors determining trophic-group-specific responses to environmental variation (Brandl et al. 2015).

To predict the dynamics of coral reef fish communities and create better management policies that sustain healthy ecosystems, it is important to understand the mechanisms underlying fish community dynamics. Understanding these mechanisms requires an examination of responses of fish communities to environmental variations and their dependence on effective functional components, such as trophic groups. In addition to the long-used taxonomic diversity, the importance of functional diversity, defined as the within-assemblage variation in functional traits, has recently been recognized (Loreau et al. 2001, Hooper et al. 2002). Some studies have demonstrated that functional diversity exerts a greater influence than taxonomic species richness (i.e. the number of species) on ecosystem functioning in mainly terrestrial ecosystems (Tilman et al. 1997, Díaz & Cabido 2001, Naeem 2002, Cadotte et al. 2011). In reef fish communities, taxonomic species richness does not necessarily reflect functional diversity (Stuart-Smith et al. 2013).

Here, we conducted an underwater survey to collect quantitative data on fish assemblages and various environmental factors on extensive reef slopes of Okinawa Island, Japan. The objectives of this study were to examine the effects of environmental variation on the abundance of 6 trophic groups of coral reef fish. Specifically, we compared the relative influence of various environmental variables on the species richness and abundance of each of the 6 trophic groups. Then, we examined the versatility and specialization of species within each trophic group with respect to their environmental preference, in order to enhance our understanding of the mechanisms that cause trophic-group-specific responses to environmental variation.

MATERIALS AND METHODS

Study sites

Field data were collected at Okinawa Island, the longest (over 100 km in length from the north to the south) and largest (1208 km²) of the Ryukyu Islands, located approximately 640 km to the southwest of Kyushu, southern Japan, in the western Pacific Ocean (26–27° N, 127° 30–128° 30′ E, Fig. S1 in the Supplement at www-int-res.com/articles/suppl/m586p141_

supp.pdf). The island is surrounded by well-developed fringing reefs that are rich in coral (Veron 1992) and fishes (Lecchini et al. 2003, Allen 2008). Coral reefs on Okinawa Island have been affected by local and global stress over the past several decades, including severe thermal stress events in 1998 that caused a catastrophic decline in corals (Loya et al. 2001) and coral-feeding fishes (Sano 2004).

Twelve sites were included in the study, including 3 stations per site, on the outer reef slope. Within each site, the stations were placed at 3- to 5-km intervals. Furthermore, at each station, 3 transects of 20 m in length, which were roughly parallel to the reef margin and separated from each other by 2–10 m, were placed haphazardly. To encompass a broad range of environmental conditions, one of the 3 sampling stations at each site was located close to a river outlet.

Field data collection

Field data were collected from boats from June to August 2011. The number of fish species and number of individuals within each species were recorded by underwater visual census (UVC) using SCUBA. All UVCs of fish species in this study were performed by the first author to eliminate potential bias between observers (Thompson & Mapstone 1997, Williams et al. 2006). After placing transect lines at the study stations and waiting at least 5 min to help fishes to resume normal behavior, the observer slowly swam unidirectionally along each transect over a 20 min period and recorded all visually identifiable fishes encountered within a 1 m width on each side of the line, except small cryptic species, such as coral-dwelling gobies. The width of the UVC enabled a visual survey, even in inner bay areas with lower visibility. When the observer encountered unidentifiable fish species, digital photographs were taken and the species was later identified from references.

The relative abundance of underlying substrate types and sessile organisms in transects was estimated using photoquadrats (Preskitt et al. 2004). While the first author performed the fish surveys at each transect, another diver took 60 photographs using a quadrat of 50 × 50 cm along another transect at the same station to avoid disturbing the fish survey. Substrate types were classified into one of 4 categories: bedrock, rubble, sand, and mud. The bedrock at study stations mostly consisted of coral rock. Sessile organisms were also classified into one of 7 categories: epilithic algal matrix (EAM; sensu Wilson et al. 2003), crustose coralline algae (CCA), macroalgae, branching corals (high-complexity hard corals, such as branching, digitate, tabular, and foliose growth forms), massive corals (low-complexity hard corals, such as massive and encrusting growth forms), soft corals, and other living organisms (e.g. sponges, ascidians, actiniae, and gorgonians). The percentage cover of each substrate type and sessile organism was estimated at 50 random points per photoquadrat. The photoquadrats were analyzed using Coral Point Count with Excel extensions (CPCe v3.3) (Kohler & Gill 2006).

Bathymetric data were obtained at each station by acoustic scanning. A boat-mounted acoustic Doppler current profiler (ADCP) equipped with real-time kinematic GPS (SonTek River Surveyor M9) was used to scan an area of approximately 90 × 90 m encompassing the 3 transects for approximately 30 min (Fig. S2 in the Supplement). In addition, each transect was scanned a few times to obtain spatially dense data points. A diver on the seawater surface tracked the transects and recorded the transect locations by GPS. Based on these data, geomorphological indices were calculated at 3 spatial scales representing different orders of magnitude: station ($\sim10^4$ m^2), transect ($\sim10^2$ m^2), and within-transect ($\sim10^0$ m^2). For the station scale, the SD of all depth data from the 90 × 90 m^2 area was calculated, and the average slope gradient of the area was estimated by least mean squares. For the transect scale, similarly, the SD of depth and average slope gradient were estimated from bathymetric data within an 8 m radius around the centroid of each transect line. For the within-transect scale, rugosity was estimated using the method proposed by Woodcock (1977). Delaunay triangles, which ranged in area between 0.09 and 1.44 m^2, were virtually drawn within each of 4 areas with 2 m radii haphazardly placed around each transect. Direction cosines of surface normal vectors of all Delaunay triangles were calculated, and the corresponding eigenvalues of their orientation tensors were computed. The natural logarithm of the ratio of second to first eigenvalues, $\ln(S_2/S_1)$, was used as an indicator of rugosity; a higher $\ln(S_2/S_1)$ indicated a more complex and rough seafloor texture. The average value of $\ln(S_2/S_1)$ for the 4 areas within each transect was used for further statistical analyses. All geomorphological calculations were conducted using MATLAB ver. 7.11 (MathWorks). For more details of the geomorphological measurements, refer to Section 2 of the Supplement.

To estimate current velocity, a plaster ball (10.5 cm in diameter and ca. 900 g in dry mass) was placed

near the centroid of each transect and retrieved after approximately 1 wk (Jokiel & Morrissey 1993, Angradi & Hood 1998). Average current velocity was then estimated using a linear regression equation previously obtained by the authors, $Y = 27.6X − 1.1$ ($R^2 = 0.85$), where Y represents the average current velocity during plaster ball deployment (cm s$^{−1}$) and X represents the average flux of plaster dissolution (g cm$^{−2}$ d$^{−1}$) estimated from the weight loss.

To characterize the chemical environments of the study locations, the concentration of suspended particulate organic carbon (POC), dissolved organic carbon (DOC), dissolved inorganic nitrogen (ammonium: NH_4-N and nitrite+nitrate: NOx-N), carbon: nitrogen ratio of suspended particulate organic matter (C:N_{POM}), and nitrogen stable isotope ratio of macroalgae ($\delta^{15}N_{MA}$) were measured. For POC and C:N_{POM}, 20 l of near-surface seawater was collected at each sampling station using a bucket. The seawater samples of known volumes were filtered through pre-combusted glass-fiber filters (Whatman GF/F) on the date of collection. In the laboratory, particles on the filters were acidified using 10% HCl to remove carbonates, rinsed with deionized water, dried in a 60°C dryer, and analyzed using a CHN Elemental Analyzer (FLASH 2000, Thermo Scientific). For DOC, NH_4-N, and NOx-N, 100 ml of near-bottom seawater was collected at each transect by SCUBA divers and immediately stored in an ice box. Samples were filtered through 0.45 μm membrane filters (Merck Millipore HA) on the date of collection. In the laboratory, the filtered seawater samples were analyzed for DOC (SHIMAZU TOC-V) and inorganic nitrogen (QUAATRO, BLTEC). For $\delta^{15}N_{MA}$, macroalgae samples were collected around transects by divers aiming to obtain as many species as possible. In the laboratory, all macroalgal samples were identified to the genus or family level, and several taxa that were relatively common throughout the study stations were selected for analysis. These macroalgal samples were rinsed with deionized water, dried in a 60°C dryer, and analyzed for the nitrogen stable isotope ratio using an isotopic ratio mass spectrometer system (Delta V Advantage + FLASH 2000; Thermo Scientific).

Data analyses

To test whether environmental features significantly affect fish species composition, the relationship between environmental and community dissimilarities was tested using the Mantel test. The environmental dissimilarity matrix was calculated as Euclidian distances between all combinations of 2 sampling locations after standardizing all measured environmental variables. Similarly, the fish species data were standardized applying Wisconsin double standardization, and the fish community dissimilarity matrix of Bray-Curtis index was obtained. The Mantel test was conducted at each of the 3 nested levels of spatial scale: transect, station, and site. To obtain data at a higher level of spatial scale (e.g. station), data at one level lower spatial scale (e.g. transect) were averaged.

Using diet information obtained from FishBase (Froese & Pauly 2015) and published references (e.g. Randall 1967, Sano et al. 1984), fish were classified into 6 trophic groups: herbivores, omnivores (consume both animal and plant materials), sessile invertivores (consume corals or sponges), zooplanktivores, mobile invertivores, and carnivores (fish and invertebrate feeders). Two fish community indices were calculated, the number of species (species richness) and the number of individuals (abundance), for the total assemblage and each trophic group for each transect. The number of trophic groups per transect was also used as a measure of trophic group richness. Correlation analyses were conducted to test the relationships among all combinations of community indices, i.e. the abundance and richness of the total assemblage and trophic groups. Furthermore, to quantify the contribution of each trophic group to the total assemblage, covariance ratios of species richness and the abundance of trophic groups to species richness and the abundance of the total assemblage, respectively, were estimated.

Principal component analysis (PCA) was used as a data reduction tool to develop a small number of uncorrelated variables that capture differences in the major environmental characteristics among transects. Subsequently, a cluster analysis was performed using Ward's method and the Euclidean distances of the principal component scores that accounted for >90% of the cumulative variation. Based on these results, transects were classified into 4 habitat types. Then, the number of habitat types in which each fish species occurred was counted to examine the relative contribution of environmental specialist and generalist species in each trophic group. Additionally, 2-level nested ANOVA was applied to estimate the variance components of environmental variables at 3 spatial levels: among individual transects within a single station, among stations within a single site, and among sites.

To examine which environmental variables affect the fish community indices, a generalized linear

mixed model (GLMM) with a Poisson distribution and log-link function was applied to transects. Prior to the GLMM analysis, the variance inflation factor (VIF) was calculated to estimate multicollinearity among 21 environmental variables. To keep VIF values below 3, percentage covers of EAM, mud, and slope gradient, which were correlated with sessile organisms, bedrock, and SD of depth, were removed. The model included each fish community index as response variables, the remaining 18 environmental variables as fixed effects, and station as a random effect. In addition, the environmental variables were standardized to compare the relative influences of the environmental variables on each community index. Model selection was carried out using stepwise backward selection with the Akaike information criterion (AIC). The marginal R^2 of the best model with the lowest AIC was also calculated as an indicator of the dependence of each trophic group on environmental condition (Nakagawa & Schielzeth 2013).

Each fish community index was compared among the 4 habitat types using 1-way ANOVA. Before the analyses, abundance data were log(x + 1) transformed to meet the assumption of normality. When variance homogeneity was not confirmed by Bartlett's test (p > 0.05), Welch's ANOVA was used to analyze the data. When ANOVA results were significant (p < 0.05), pairwise t-tests with Bonferroni correction were used to identify significant differences in the community index between pairs of habitat types. Alternatively, post hoc Games–Howell tests were used when significant differences were detected by Welch's ANOVA.

Some environmental variables had missing data for one of the 36 stations; therefore, data were analyzed for the remaining 105 transects, excluding data from the 3 transects from that particular station. All statistical analyses were conducted using R (version 2.15.3).

RESULTS

Our results showed that the fish community dissimilarity between sampling locations was significantly and positively related to the environmental dissimilarity at all 3 tested levels of spatial scales: transect (r = 0.66, p < 0.001; Mantel test), station (r = 0.50, p < 0.001) and site (r = 0.45, p < 0.001; Fig. S3 in the Supplement).

Environmental characteristics were highly variable across the Okinawa Island study locations. Based on a cluster analysis of the environmental data, the study transects clustered into 4 habitat types, and each was categorized into one of Type A, B, C, and D (Fig. S4 in the Supplement). In the PCA applied to the identical environmental data, the first principal component axis (PC1) differentiated transects along a substrate gradient from bedrock to mud (Fig. S5 in the Supplement). PC2 was negatively related to EAM and positively to NOx-N and branching coral cover. Type A transects generally had relatively higher bedrock cover, geomorphological roughness (e.g. SDs of depth, slope, and rugosity), and current velocity (n = 23; Fig. S6, Table S1 in the Supplement). Type A also had the highest live coral cover among the 4 habitat types. Type B transects were also high in bedrock cover, but lower in geomorphological roughness and live coral cover compared with those of Type A (n = 34). Type C transects generally had a slightly lower bedrock cover and current velocity compared with those of Type A and B (n = 30). Type D transects were distinctly lower in bedrock cover and current velocity, and higher in mud cover (n = 18). Type D also had relatively higher POC concentration in seawater and $\delta^{15}N_{MA}$. The 2-level nested ANOVA revealed that the environmental variables differed with respect to the major spatial scales of their variation (Table S2 in the Supplement). For 11 variables, including current velocity and percentage covers of bedrock and CCA, the variance across sites was greater than across stations or transects. Seven variables, including percentage covers of hermatypic corals, EAM, and macroalgae, showed greater variance across stations than across sites or transects. For the other 3 variables, rugosity, other sessile organisms, and NH_4-N, variance was greatest across transects, indicating substantial variation at the finest spatial scale.

A total of 24 099 ind. representing 274 species from 38 families were recorded across the 105 transects. The mean species richness and abundance per transect were 25.8 (±6.2 SD) and 223.1 (±260.0), respectively (Tables S3 & S4 in the Supplement). The most speciose group was mobile invertivores, while the most abundant group was planktivores. Omnivores had the highest richness for species occurring in all 4 habitat types, whereas herbivores, mobile invertivores, and carnivores showed the highest richness for species occurring in only one habitat type (Fig. 1). Planktivores showed relatively higher richness for species observed in 2 and 3 habitat types. Sessile invertivores had the lowest species richness, and showed no bias in the number of habitats where each species occurred. Trophic group richness, defined as the number of trophic groups, showed weak positive
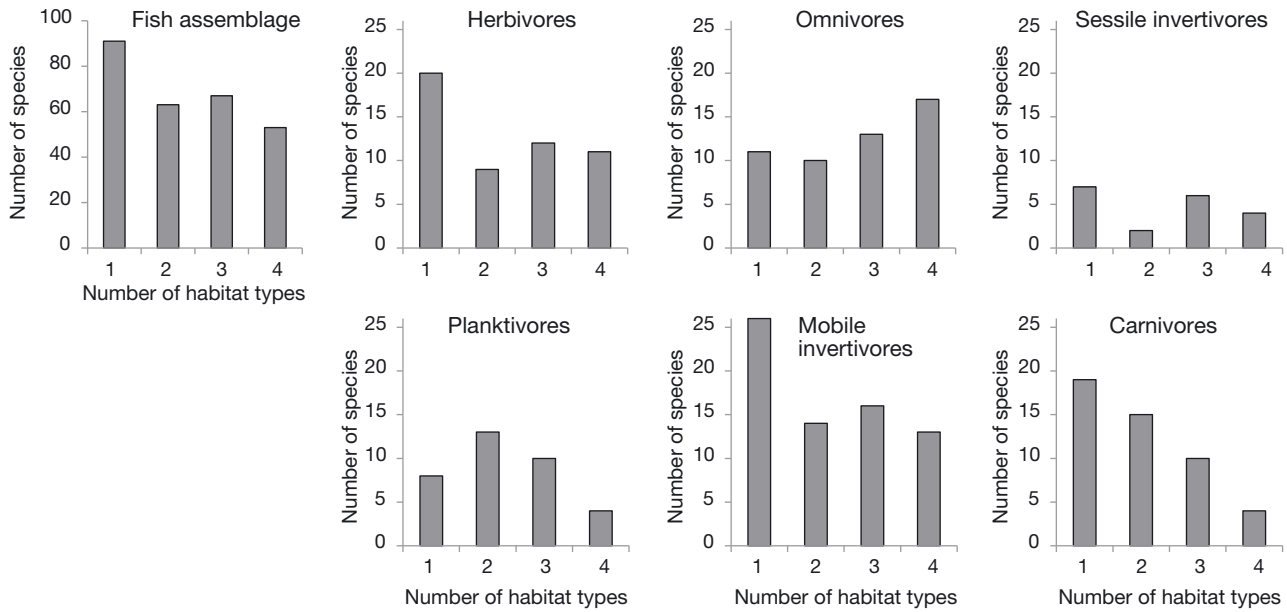
Fig. 1. Occurrence of fish species across different habitat types. The horizontal axis indicates the number of habitat types, N, at which each fish species occurs, and the vertical axis indicates the number of fish species that occur at N habitat types. The result is shown for the entire assemblage and 6 trophic groups

Table 1. Correlations between fish community indices of total assemblage/trophic groups. The correlation coefficient is shown only for significant relationships ($p < 0.05$). ri: richness; ab: abundance; EC: entire community; TG: trophic group; H: herbivore; O: omnivore; S: sessile invertivore; P: planktivore; M: mobile invertivore; C: carnivore

	ECTGri	ECri	ECab	Hri	Ori	Sri	Pri	Mri	Cri	Hab	Oab	Sab	Pab	Mab	Cab
ECTGri	–														
ECri	0.41	–													
ECab	0.20		–												
Hri		0.49		–											
Ori		0.45			–										
Sri	0.52	0.37				–									
Pri	0.30	0.62	0.19	0.26		0.20	–								
Mri		0.62		0.23			0.24	–							
Cri				−0.23			−0.27		–						
Hab				0.24			0.20			–					
Oab			0.38								–				
Sab	0.45	0.38				0.93	0.20					–			
Pab	0.20	0.20	0.86				0.38				0.23		–		
Mab			0.73	−0.25							0.22		0.31	–	
Cab	−0.21	−0.32	0.21	−0.38			−0.37	−0.32	0.46	−0.20				0.29	–

correlations with the abundance and species richness of the total assemblage (Table 1). The abundance and species richness of trophic groups other than carnivores generally exhibited weak positive correlations with those indices of some other trophic groups. In contrast, the abundance and richness of carnivores generally had negative relationships with those indices of other trophic groups.

With respect to relationships between fish community structure and environmental factors, species richness of the total fish assemblage was strongly and negatively related to current velocity, and exhibited a strong positive relationship with the percentage cover of bedrock (Table 2). Although combinations of relatively important environmental variables for fish communities differed among trophic groups, the majority of trophic groups were affected most significantly by one of 2 variables: the percentage cover of bedrock or current velocity. Specifically, species richness of herbivores, planktivores, and mobile inverti-

Table 2. Relationships between species richness and environmental factors. Standardized coefficients estimated by GLMM with stepwise model selection are shown. The significance of each coefficient based on the Wald test is also indicated (‡p < 0.1; *p < 0.05; **p < 0.01; ***p < 0.001). CCA: crustose coralline algae; POC: particulate organic carbon; C:N_{POM}: carbon:nitrogen ratio of suspended particulate organic matter; $\delta^{15}N_{MA}$: nitrogen stable isotope ratio of macroalgae; DOC: dissolved organic carbon; NOx-N: nitrite+nitrate; NH_4-N: ammonium

Explanatory variable (environmental factor)	Assemblage	Herbivores	Omnivores	Sessile invertivores	Planktivores	Mobile invertivores	Carnivores
Current velocity	−0.127***		−0.252***	−0.316*		−0.104*	−0.166*
Bedrock	0.108***	0.401***			0.615***	0.250***	
CCA	0.060*	0.189***					
POC	−0.083**		−0.082				
C:N_{POM}					0.159**		−0.184**
$\delta^{15}N_{MA}$	0.070**		0.070			0.063	0.147*
DOC					−0.116‡		
Sand					−0.513**		
Soft corals	−0.044*						−0.124‡
Rubble					0.184		0.092
SD of depth	0.039‡			0.295***	0.162***		
Massive corals					0.169**		−0.135‡
Macroalgae					−0.244***		
NOx-N							
Branching corals	0.056**	0.089*	0.053‡	0.139‡			−0.194*
Rugosity				−0.184‡			
Other organisms							
NH_4-N	−0.041‡			−0.160		−0.123**	
Marginal R^2	0.49	0.58	0.34	0.24	0.73	0.35	0.29

vores were most strongly positively related to the percentage cover of bedrock. Species richness estimates of omnivores and sessile invertivores were negatively related to current velocity. However, species richness of carnivores showed the most significant, negative relationship with the percentage cover of branching corals. In contrast, the second most important environmental variables for species richness did not overlap among trophic groups: species richness of herbivores was positively related to CCA, that of omnivores was negatively related to POC, that of sessile invertivores was positively related to SD of depth, that of planktivores was negatively related to the percentage cover of sand, that of mobile invertivores was negatively related to NH_4-N, and that of carnivores was negatively related to C:N_{POM}. The variance in the proportion of species richness explained by measured environmental variables, which is indicated by the marginal R^2, differed greatly among the trophic groups. Planktivores had the highest marginal R^2 value for species richness, followed by herbivores, mobile invertivores, omnivores, carnivores, and sessile invertivores.

The abundance of the total fish assemblage was most strongly related to the percentage cover of bedrock, and this relationship was positive (Table 3). Similarly, for the 5 trophic groups other than sessile invertivores, abundance was most strongly and positively related to bedrock cover. Herbivores had the highest marginal R^2 value for abundance, followed by planktivores, carnivores, mobile invertivores, sessile invertivores, and omnivores.

Mean trophic group richness (i.e. the total number of trophic groups found in each transect) did not differ significantly between the 4 habitat types (Fig. 2), but species richness of the total fish assemblage was significantly higher in the 3 habitat types with relatively higher coverage of consolidated substrates (i.e. Types A, B, and C) than in Type D, with low coverage of consolidated substrates. The effect of habitat type on species richness was distinctly different between the trophic groups. Specifically, the species richness values for herbivores and planktivores were significantly higher in Types A, B, and C than in Type D. While the species richness of omnivores was highest in Type C and lowest in Type B, that of mobile invertivores was higher in Types B and C and lower in Type D. The species richness of carnivores was significantly higher in Type D than in the other 3 habitat types with higher coverage of consolidated substrates, unlike the species richness of the entire assemblage and some of the other trophic groups. The species richness of sessile invertivores was generally lower than that of the other trophic groups, and

Table 3. Relationships between abundance and environmental factors. Standardized coefficients estimated by generalized linear mixed models with stepwise model selection are shown. The significance of each coefficient based on the Wald test is also indicated ([‡]p < 0.1; *p < 0.05; **p < 0.01; ***p < 0.001). CCA: crustose coralline algae; POC: particulate organic carbon; $C:N_{POM}$: carbon:nitrogen ratio of suspended particulate organic matter; $\delta^{15}N_{MA}$: nitrogen stable isotope ratio of macroalgae; DOC: dissolved organic carbon; NOx-N: nitrite+nitrate; NH_4-N: ammonium

| Explanatory variable (environmental factor)	Assemblage	Herbivores	Omnivores	Sessile invertivores	Planktivores	Mobile invertivores	Carnivores
Velocity	−0.290***			−0.371**	−1.811***	0.271**	
Bedrock	1.522***	0.872***	0.430***		2.144***	1.669***	
CCA	−0.143***				−0.469***		−0.386***
POC	0.562*					0.802*	
$C:N_{POM}$							
$\delta^{15}N_{MA}$	0.173***	−0.277*	0.293*			0.620	0.384**
DOC	0.122***	−0.055***	0.055*		0.143***	0.418***	−0.122**
Sand	−0.292***	−0.207*	−0.128***				−0.177**
Soft corals	−0.062***		0.053[‡]		−1.029***	0.190***	
Rubble	0.378***	0.228**			0.629***	0.480***	0.402***
SD of depth	−0.400***	−0.299***		0.340***	−0.631***		
Massive corals			−0.156***	−0.159	−0.185***	−0.216***	0.183*
Macroalgae	−0.112***				−0.491***	0.425***	
NOx-N	−0.100***	−0.275***	−0.274***		0.120**		0.266**
Branching corals		−0.153	0.271***	0.207*	−1.245***	0.732***	−0.442**
Rugosity	0.050***		−0.050*	−0.138	0.367***		
Other organisms	0.147***	0.085*	0.051[‡]		0.551***		
NH_4-N			0.083***	−0.294**	0.187***		
Marginal R^2	0.20	0.59	0.19	0.23	0.45	0.23	0.40
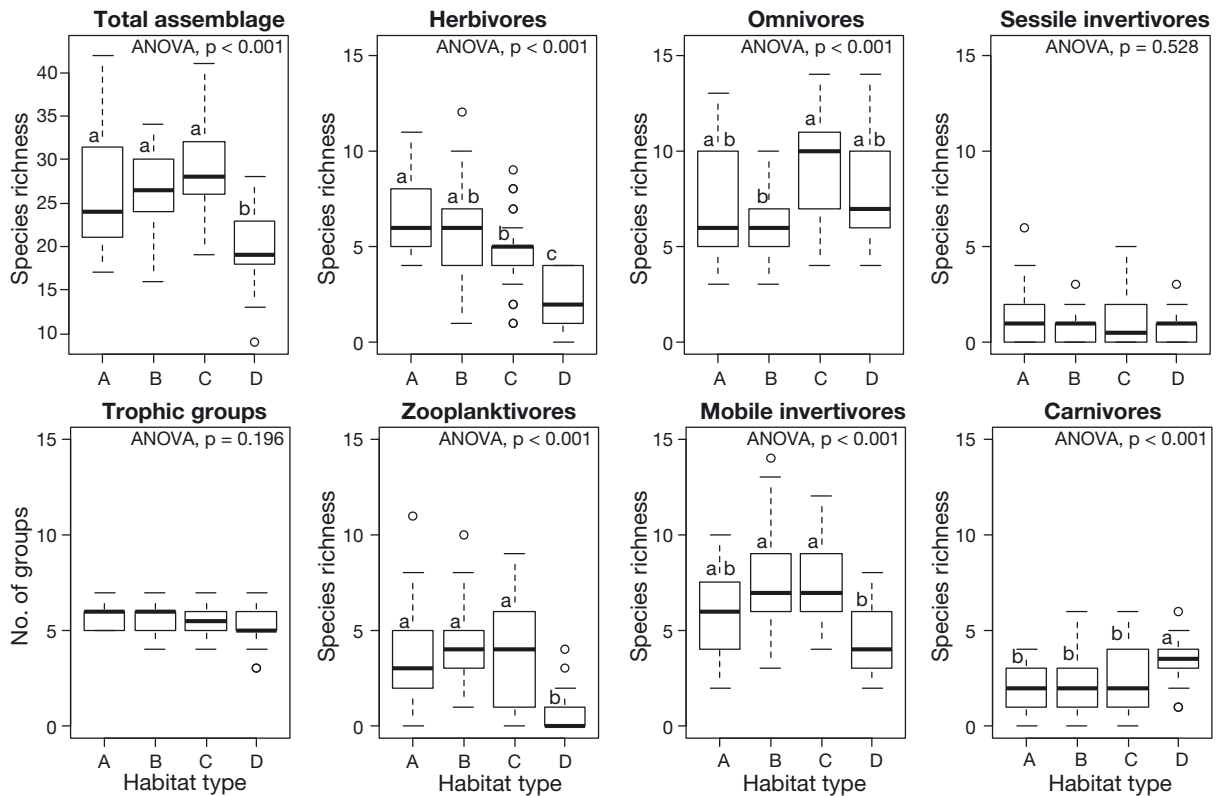
Fig. 2. Comparison of species richness of each trophic group between habitat types. The number of trophic groups found in each habitat type is also shown. Box-and-whisker plots represent the median (horizontal line within each box), upper and lower quartiles (top and bottom, respectively, of each box), maximum and minimum values (upper and lower whiskers, respectively), and outliers (open circles). Letters above boxes indicate the results of post hoc tests to assess multiple comparisons between habitat types. Boxes with the same letters are not significantly different

did not differ significantly between the 4 habitat types. Based on the covariance ratios, the variation in the species richness of the entire assemblage was most strongly affected by mobile invertivores (26.1%) and planktivores (25.9%), followed by herbivores (20.2%), omnivores (20.1%), sessile invertivores (6.9%), and carnivores (0.9%).

The abundance of the total fish assemblage did not differ significantly among the 4 habitat types, despite the significant differences in species richness (Fig. 3). Likewise, abundances of omnivores and mobile invertivores showed no significant differences among habitat types, although their species richness differed significantly among habitat types. In contrast, herbivores and planktivores were significantly lower in both abundance and species richness in Type D than in the other habitat types with higher consolidated substrates. Sessile invertivores did not differ significantly in abundance among habitat types. Based on the covariance ratios, the variation in the abundance of the entire assemblage was affected most strongly by planktivores (56.4%), followed by mobile invertivores (14.8%), herbivores (12.2%), omnivores (8.6%), sessile invertivores (8.4%), and carnivores (−0.4%).

DISCUSSION

Trophic-group-specific responses to environmental variation

Our results demonstrate that environmental features of habitat significantly affect the fish community composition in coral reefs of the studied island. Furthermore, the significant relationships between entire fish community indices, trophic group indices, and environmental variables indicate that environmental preference of trophic groups to environmental variations significantly explains fish community assembly in the coral reefs.

We detected 2 important factors that strongly and commonly affect the species richness and abundance of the identified trophic groups, bedrock cover and current velocity. Although a strong positive relationship of reef fish assemblages with the structural complexity of substrates and live coral cover has been commonly reported (e.g. Risk 1972, Graham & Nash 2013, Coker et al. 2014), the present results suggest weaker effects of these 2 environmental factors than the effects of substrate type and water movement.
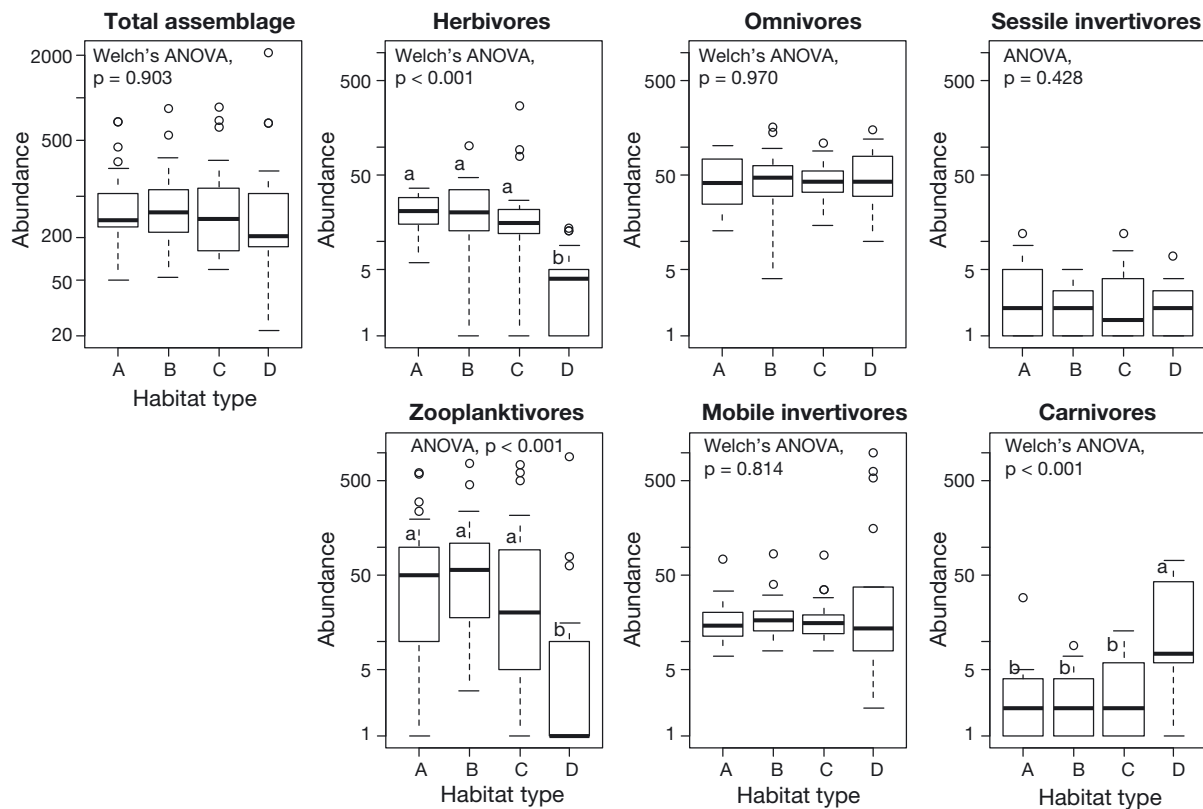

Fig. 3. Comparison of abundance of each trophic group between habitat types. Box-and-whisker plots represent the median, upper and lower quartiles, maximum and minimum values, and outliers. Letters above boxes indicate the results of post hoc tests to assess multiple comparisons between habitat types. Boxes with the same letters are not significantly different

Environmental factors influencing fish communities can vary depending on the spatial scale of the study area (Mellin et al. 2006). Several studies conducted at a relatively narrower spatial scale (less than several kilometers) have shown significant effects of live coral cover and topographic complexity on the local fish community assembly (e.g. Friedlander & Parish 1998). In the present study, the most significant environmental variables affecting fish community assembly—bedrock cover and current velocity—had the greatest variance at the largest spatial scale (between sites), whereas the variables linked to topographic complexity, such as branching coral cover and rugosity, showed the largest variance at the second-largest scale (between stations). Therefore, the incongruous results between our study and previous studies may be due to the relatively broader spatial scales of our study, over several dozen kilometers at maximum, which potentially encompasses greater variation in bedrock cover and current velocity. Furthermore, the Type D habitat had distinct environmental characteristics (e.g. lower bedrock cover and fine sediments) and fish community composition. In particular, omnivores included more species that were tolerant to a broad range of bedrock and fine sediment covers (even in the Type D habitat), whereas herbivores and zooplanktivores had distinctly lower richness and abundance in habitats with higher fine-sediment coverage. Our study—in which a broader gradient of environments was analyzed compared with those of previous studies—revealed different responses to variation in fine sediment cover among the trophic groups.

For herbivores, planktivores, and mobile invertivores, species richness increased with bedrock cover, consistent with several previous studies (e.g. Mellin et al. 2006). In general, herbivore species are more abundant in habitats with higher bedrock cover than in those with lower bedrock cover (Williams & Polunin 2001), and this is attributed to the higher periphyton abundance on consolidated substrates, which is the primary food resource for herbivores. Planktivores are known to prefer habitats with a high influx of plankton as well as high underwater visibility, which is advantageous for food acquisition (Hobson & Chess 1978, Hamner et al. 1988). The occurrence of planktivore species in the study stations with a relatively lower bedrock cover and weaker current may have been restricted by a lower availability of food resources. While consolidated habitats are considered to be advantageous for periphyton and plankton, prey invertebrates are more abundant on degraded reef frameworks and coral rubble habitats in

coral reefs (Enochs & Manzello 2012). As mobile invertivores generally have strong preferences with respect to foraging substrate (Fulton & Bellwood 2002, Glynn et al. 2014), the higher species richness of this trophic group in habitats with intermediate bedrock cover, such as Types B and C, may be due to abundant prey resources. Overall, taking these previous studies into account, the higher occurrence of fish species of these 3 trophic groups in habitats with higher bedrock cover (i.e. herbivores, planktivores, and mobile invertivores) may be explained by a higher availability of food resources specific to each trophic group.

In contrast, occurrences of the other 3 trophic groups (carnivores, sessile invertivores, and omnivores) showed either no or weak relationships with bedrock cover. Several studies in other regions have shown that the abundance of reef-associated predators is positively related to live coral cover (e.g. Pratchett et al. 2011), possibly due to an increase in the abundance of smaller prey fishes associated with topographic complexity (Graham et al. 2007, Wilson et al. 2007). However, we found negative or no relationships of carnivores with branching coral cover as well as other trophic groups, which are possible prey. Likewise, we did not detect a significant relationship between sessile invertivores and live coral cover, although corals are the most important prey for this group. Food availability may not be a major determinant of the richness and abundance of these 2 trophic groups (carnivores and sessile invertivores) at our study sites. Our results also demonstrate that the current is a major environmental factor controlling fish community structure. The swimming ability of small site-attached species is generally low and unsuitable for high-energy wave-swept locations owing to the high energetic costs of swimming (Depczynski & Bellwood 2005). Although the effects of water movement on fish are generally dependent on individual size and body shape (Bellwood & Wainwright 2001, Fulton & Bellwood 2005, Floeter et al. 2007), we found consistent negative effects of current velocity on the species richness of total fish assemblages as well as most of the trophic groups in this study. The energetic disadvantage of a high current velocity for fish may explain the negative relationships between current and fish.

Our analysis of fish assemblages classified according to diet revealed trophic-group-specific responses to various environmental factors as well as the potential importance of food availability, particularly for the occurrence of herbivores, planktivores, and mobile invertivores. Specifically, the quantity and

accessibility of food resources, which are dependent on substrate conditions, are likely to have substantially determined the species richness and abundance of each trophic group. In addition, our results suggest that current velocity also strongly restricted the species richness of most trophic groups. Substrate conditions and water movement may determine the baseline species richness and abundance for each trophic group at the studied island. Furthermore, environmental factors other than bedrock and current velocity for each trophic group had little overlap, and likely contributed to differences in species richness patterns between the groups.

Versatility and specialization of species within trophic groups

Based on our results, the trophic groups could be classified into generalist-like groups, specialist-like groups, and others, considering the number of environmental specialist and generalist species included in each trophic group. Mobile invertivores and omnivores could be defined as generalist-like groups, since their occurrences were less biased towards any particular habitat type. In addition, the richness and abundance of these 2 trophic groups were not well explained by environmental conditions, as indicated by the relatively lower R^2 estimates in the GLMM analyses. For planktivores and herbivores, both species richness and abundance were highly dependent on environmental characteristics and differed substantially among habitat types; accordingly, these trophic groups could be classified as specialist-like groups. For sessile invertivores and carnivores, although environmental conditions had relatively weak effects on their distributions, the richness and abundance of both groups were too low to evaluate their habitat preference. Thus, these 2 trophic groups could not be categorized into specialist- or generalist-like groups in our study.

For the generalist-like groups—mobile invertivores and omnivores—for which there was no significant effect of habitat type on abundance, our results further implied that the characteristics of the species differed between these 2 trophic groups. For omnivores, the number of species that occurred consistently across all 4 habitat types was greater than that of other trophic groups. Omnivores probably contained a substantial number of environmental generalist species, leading to a relatively consistent occurrence of this trophic group across habitat types (Green 1996, Depczynski & Bellwood 2003). Mean-

while, species in the generalist-like groups may exhibit diverse responses to environmental changes (Green 1996, Nunes et al. 2013), and a species loss in a particular habitat may be compensated for by other species within the same trophic group (Tilman & Downing 1994). Since species of mobile invertivores were more specialized compared with omnivores, interspecific compensation probably played an important role in the relatively consistent occurrence of this trophic function across various habitat types. In fact, labrid fishes, which comprise the majority of mobile invertivores, include various species that prefer live coral, dead coral, or soft bottoms (Fulton & Bellwood 2002). Furthermore, the species richness of mobile invertivores was still significantly lower in habitats with lower bedrock cover, but their abundance did not differ between habitat types. For instance, the mobile invertivore species *Archamia dispilus*, which formed large populations only in habitats with lower bedrock cover, compensated for the reduced abundance of other species within the same trophic group in this study. Our results demonstrate 2 different types of species-level responses to environmental variation, the occurrence of environmental generalist species and interspecific replacement with specialist species. Both responses can explain the relatively the low variation in abundance of those generalist-like groups across habitat types.

For the specialist-like groups (herbivores and planktivores), our results showed that few species belonging to these groups were common to all habitat types, while the numbers of environmentally specialized species were relatively greater. Similar patterns between species richness and abundance suggest that many of the species in these groups had similar environmental responses. Therefore, interspecific compensation, as observed in mobile invertivores, probably did not have a large effect on these specialist-like groups and led to their reduced diversity in response to environmental variation.

Implications for ecosystem management

In our study, the trophic group composition in assemblages, but not trophic group richness, differed among habitat types. In particular, the loss of specialist-like groups (herbivores and planktivores) in habitats with unconsolidated substrates was generally compensated for by the occurrence of carnivores in such habitats. Similarly, a few studies have reported that a reduction in sessile invertivores with a decrease in coral is associated with a compensatory

increase in herbivores (e.g. Wilson et al. 2009). The variation in trophic group composition implies that interactions between groups and the mechanisms by which fish communities are maintained vary among reef habitats with different environmental conditions. Furthermore, our results demonstrate that the patterns of variation in species richness and/or abundance across habitat types for some trophic groups (e.g. carnivores and sessile invertivores) differed from those of total assemblages. The overall species diversity does not necessarily reflect tropic group compositions, indicating that disregarding trophic groups can be misleading for ecosystem conservation. For example, if fishing is prohibited only in habitats with high bedrock cover based solely on species diversity estimates, important fishery stocks of large carnivores, such as those belonging to the families Serranidae and Lutjanidae, which prefer habitats with relatively higher cover of unconsolidated substrates, may be over-exploited. We should focus on community structure from the perspective of not only taxonomic species diversity, but also fully functional compositions to design and implement effective conservation strategies.

In the coastal region of Okinawa, there is ongoing pollution by terrestrial red soil, and it is feared that coral reefs may shift to muddy habitats (Nakasone 2013). Mud inputs are particularly deleterious to herbivores, a key functional group of coral reefs that sustains ecosystem processes by suppressing macroalgae and facilitating the recruitment of corals (Bellwood et al. 2004, Hughes et al. 2007). In fact, our results also showed that both species richness and abundance of herbivores, as well as planktivores, were significantly lower in habitats with relatively lower bedrock cover (in other words, higher sand/mud cover). This indicates that these trophic groups are potentially vulnerable to red soil pollution. Meanwhile, anthropogenic disturbances affecting coastal ecosystems include both top-down exploitation, such as fishing pressure, and bottom-up habitat degradation, such as coral loss and red soil pollution (e.g. Ebisawa & Nakamura 2010, Graham et al. 2011). These factors can have interactive effects on fish communities. In particular, our results indicate that for Okinawa Island, where the fishing pressure is presumably high, bedrock cover is one of the most important factors, while multiple studies in other regions have shown the importance of other factors, such as live coral cover. The relative importance of local environmental stress on the fish community depends on regional-scale characteristics of the environment and anthropogenic influences (e.g.

Brooker et al. 2013). In addition, fish communities are considered to be highly vulnerable, particularly in coral reefs, where multiple stressors co-occur (Graham et al. 2011). Our results indicate that analyses based on trophic group, which is an important ecological function, can enhance our understanding of the habitat preferences and vulnerability of fish communities, taking into account multiple responses of fish to various types of environmental change. Trophic groups should be incorporated into analyses of fish communities and decision-making for coral reef ecosystem management.

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