Caribbean Journal of Science, Vol. 38, No. 3-4, 263-266

Pattern in the Local Diversity of Coral Reef Fishes Versus Rates of Social Foraging

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Social foraging in coral reef fishes occurs in single-species and mixed species groups. Many species exhibit such behaviors, and variable trophic levels are represented within and between foraging groups (Strand, 1988). Several stimuli (e.g., search behavior, predator success) elicit social foraging behaviors within and between species (Pitcher and House, 1987; Subowski, 1988). Social foraging allows individuals enhanced access to prey resources, decreases search time for patchily distributed prey, and provides increased protection from predators.

Previous studies have focused on how social foraging enhances the fitness of individuals within the group (Wolf, 1987; Overholtzer and Motta 2000). Little attention has been given to the role that the aggregate of such interactions may have in mediating community composition and patterns of diversity. For example, does the increased survivorship and prey capture efficiencies resulting from social foraging allow greater diversity of fishes to occur in local habitat patches than would be seen in the absence of such behaviors? We collected data to explore the relationship between taxa that exhibit social foraging and the composition of fish communities. In particular, we quantified the rates of social foraging bouts in relation to species diversity of coral reef fishes within local habitat patches to determine if consistent patterns emerged.

Observations were made from 3-14 April 2000 on leeward reefs off Bonaire and Klein Bonaire in the Netherlands Antilles. Twenty-three daylight hours of bottom time using snorkel and scuba were devoted to observing social foraging behaviors, including 14 20-minute census periods to quantify rates of social foraging. Habitat patches were selected in back reef-coral rubble, reef crest, and reef slope areas such that spatial boundaries for a census were easily defined. Habitat patches ranged in size from 8-60 m^2 based on visual estimates. Observations were made while stationary in mid-water and away from patches (to minimize effects on behavior and movement of fishes) but while close enough to identify species. All species observed were counted, the most abundant first. No effort was made to census cryptic fish species (e.g., blennies, gobies) as this would disrupt foraging behaviors of the more active species. Social foraging bouts (each "bout" defined as a single or mixed species group that exhibited coordinated search behavior) were enumerated as species and number of individuals involved in each bout. The same fishes may have been involved in multiple bouts within a census period if the original group disbanded and another formed.

Fifty-two percent of species observed during census periods (34 of 65 species) occurred in 108 social foraging bouts (55 single species and 53 mixed species foraging groups; Table 1). We explored the data to elucidate relationships between species diversity and rates of social foraging. Social foraging rates were computed as the total number of social foraging bouts per census, as well as the number of species participating in social foraging bouts per census. Local species richness was the total number of species observed during each census. Alpha diversity was selected as a diversity index that incorporates species richness and evenness, as it is not sensitive to small sample sizes (Magurran, 1988). Fisher's alpha diversity index was computed for each census using PRIMER software (Clarke and Gorley, 2001).

Pearson's product-moment correlation coefficients were computed using metrics normalized to 1 m^2 (to account for variation in patch size) in order to determine the relationship between species diversity metrics and rates of social foraging. The number of social foraging bouts and the number of species participating in social foraging bouts varied with species richness and alpha diversity. Pearson's product-moment correlation coefficients for all comparisons were positive and highly significant ($p<0.01$), and showed that the two diversity metrics increased with increasing measures of social foraging (Table 2).

Social foraging bouts were separated into single and mixed species categories. The number of individuals that participated in social foraging bouts (group size) within each category were compared. Single species groups were generally smaller than mixed species groups, with a mean of 2.98 individuals per bout (S.D. = 2.80) versus 31.09 individuals per bout (S.D. = 63.28). Figure 1 illustrates the pattern of increased group size and increased dominance of mixed versus single species groups, although both types of groups are represented throughout the lower range of group size. It should be noted that the range of group size is much larger for mixed species groups (2-20 individuals per single species group and 2-309 individuals per mixed species group). In general, the smaller group sizes were composed of benthivorous fishes foraging within the reef framework, while the largest group sizes were composed of planktivores that aggregated at the reef front (e.g., groups dominated by brown chromis).

A few focal species (species that others cued on to participate in mixed species social foraging bouts) dominated social foraging activities (Table 3). Yellowtail goatfish (a benthivore) and brown chromis (a planktivore) were the focal species in 54.5 % of the mixed species social foraging bouts. All other bouts were either focused on a diverse range of species or it was unclear which was the focal species.

Observations made outside census periods showed that Spanish hogfish, spotted moray, and sharptail eel were also focal species of mixed species social foraging bouts. Spotted moray and sharptail eel had several species following them during daytime movements

TABLE 1. Common name, scientific name, total number of each species observed during fish censuses, and number of occurrences in single (S) or mixed species (M) foraging bouts. A dash (—) indicates no social foraging was observed.

Common name	Scientific name	Total	S	M
banded butterflyfish	*Chaetodon striatus*	8	2	2
bar jack	*Caranx ruber*	30	2	10
barred hamlet	*Hypoplectrus puella*	2	—	—
beaugregory	*Stegastes leucostictus*	149	—	—
Bicolor damselfish	*Stegastes partitus*	749	—	—
blackbar soldierfish	*Myripristis jacobus*	42	—	—
black durgon	*Melichthys niger*	8	—	2
blue chromis	*Chromis cyanea*	28	4	8
blue parrotfish	*Scarus coeruleus*	2	—	—
blue runner	*Caranx crysos*	2	—	—
bluestriped grunt	*Haemulon sciurus*	2	—	—
blue tang	*Acanthurus coeruleus*	41	2	3
bluehead	*Thalassoma fibasciatum*	199	—	5
brown chromis	*Chromis multilineata*	668	1	13
bucktooth parrotfish	*Sparisoma radians*	6	—	—
caesar grunt	*Haemulon carbonarium*	30	4	4
chain moray	*Echidna catenata*	2	—	—
comb grouper	*Mycteroperca rubra*	10	—	—
creole wrasse	*Clepticus parrae*	56	4	3
creole-fish	*Paranthias furcifer*	12	—	1
doctorfish	*Acanthurus chirurgus*	43	4	10
dusky damselfish	*Stegastes fuscus*	48	3	3
fairy basslet	*Gramma loreto*	10	—	—
foureye butterflyfish	*Chaetodon capistratus*	16	4	—
French angelfish	*Pomacanthus paru*	2	—	—
French grunt	*Haemulon flavolineatum*	4	—	—
gray snapper	*Lutjanus griseus*	2	—	—
graysby	*Epinephelus cruentatus*	2	—	—
horse-eye jack	*Caranx latus*	8	1	3
jolthead porgy	*Calamus bajonado*	2	—	—
lane snapper	*Lutjanus synagris*	2	—	—
Caribbean longsnout butterflyfish	*Chaetodon aculeatus*	2	—	—
longspine squirrelfish	*Holocentrus rufus*	2	—	—
ocean surgeonfish	*Acanthurus bahianus*	32	1	2
peacock flounder	*Bothus lunatus*	6	—	1
princess parrotfish	*Scarus taeniopterus*	15	—	—
puddingwife	*Halichoeres radiatus*	1	—	—
queen angelfish	*Holacanthus ciliaris*	6	—	—
queen parrotfish	*Scarus vetula*	37	2	2
rainbow parrotfish	*Scarus guacamaia*	8	—	—
red hind	*Epinephelus guttatus*	19	—	—
redspotted hawkfish	*Amblycirrhitus pinos*	2	—	—
rock beauty	*Holacanthus tricolor*	12	—	—
rock hind	*Epinephelus adscensionis*	2	—	—
schoolmaster	*Lutjanus apodus*	24	—	6
sergeant major	*Abudefduf saxatilis*	58	3	12
sharpnose puffer	*Canthigaster rostrata*	2	—	—
slippery dick	*Halichoeres bivittatus*	4	—	2
smooth trunkfish	*Lactophrys triqueter*	12	1	1
Spanish hogfish	*Bodianus rufus*	14	—	3
spotfin butterflyfish	*Chaetodon ocellatus*	24	3	—
spotted goatfish	*Pseudupeneus maculatus*	6	—	3

TABLE 1. Continued.

Common name	Scientific name	Total	S	M
spotted moray	*Gymnothorax moringa*	4	—	1
spotted scorpionfish	*Scorpaena plumieri*	2	—	—
spotted trunkfish	*Lactophrys bicaudalis*	6	—	2
stoplight parrotfish	*Sparisoma viride*	21	2	1
striped parrotfish	*Scarus iserti*	2	—	—
tabaccofish	*Serranus tabacarius*	1	—	—
trumpetfish	*Aulostomus maculatus*	14	1	3
white grunt	*Haemulon plumieri*	6	—	1
whitespotted filefish	*Cantherhines macrocerus*	4	—	3
yellow goatfish	*Mulloidichthys martinicus*	48	5	20
yellowhead wrasse	*Halichoeres garnoti*	18	1	3
yellowtail damselfish	*Microspathodon chrysurus*	18	1	—
yellowtail snapper	*Ocyurus chrysurus*	18	2	3

TABLE 2. Pearson's product-moment correlation coefficients (r) and their probability (p) between measures of species diversity and rates of social foraging.

	Rates of social foraging			
	Number social foraging bouts		Number social foraging species	
Species diversity	r	p	r	p
Species richness	0.694	0.006	0.807	0.001
Fisher-s alpha	0.701	0.005	0.788	0.001

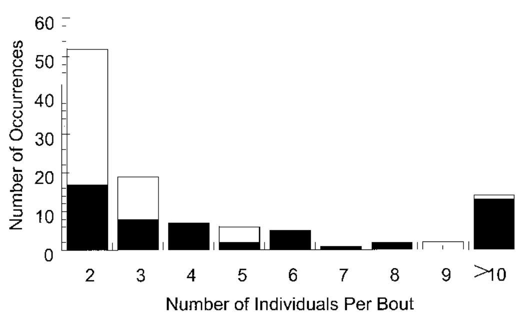

FIG. 1. Number of individuals in single species (open) and mixed species (solid) social foraging bouts.

TABLE 3. Number of occurrences of social foraging bouts focused on particular focal species (n = 55 bouts).

Taxa	Number of observations
blue chromis	1
blue tang	1
brown chromis	13
horse-eye jack	1
Spanish hogfish	1
spotted goatfish	2
spotted moray	1
white grunt	1
yellow goatfish	17
unidentified focal species	17

(Fig. 2). Movements of long duration or length (e.g., > 10 m) elicited social foraging groups with continually changing species composition, such that one individual would drop out and another (or others) of different species would join. For example, a spotted moray was initially followed by a schoolmaster which separated from the moray which was joined by a Nassau grouper.

Several observations were made of individuals exhibiting intra- and inter-specific aggression against another individual attempting to join a social foraging group. For example, bar jacks would commonly chase conspecifics away from particular goatfish they were following. Also, a yellowtail snapper chased a schoolmaster away from a spotted moray before following the moray for some distance.

Despite the small amount of data obtained in this preliminary effort, patterns emerged that can lead to further study. We found that 52 % of fishes within a local species pool participated in social foraging bouts. Is this a consistent attribute of fish communities? From a mechanistic perspective, does social foraging medi-

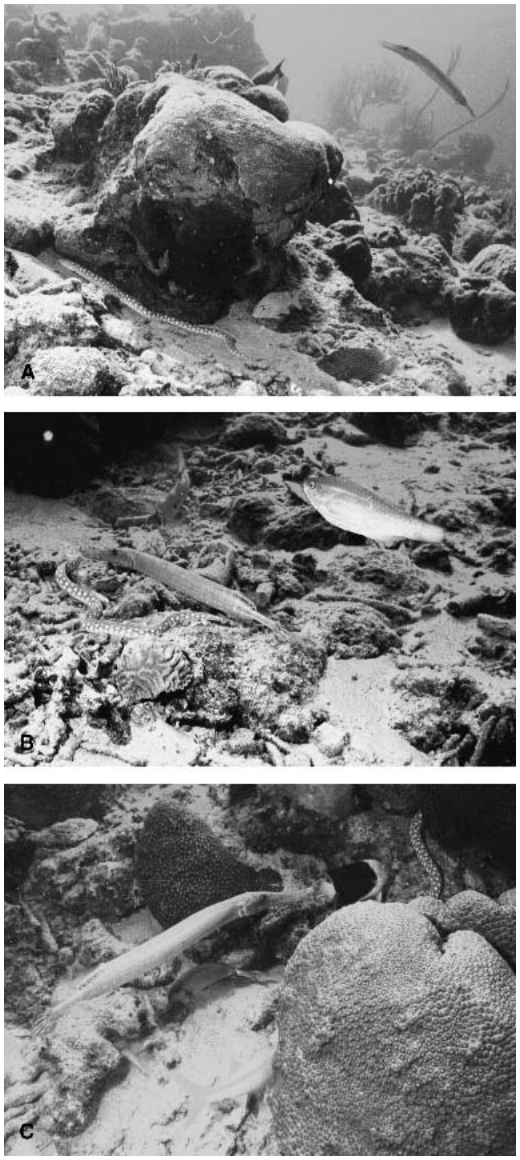

FIG. 2. Sequential mixed species social foraging with a sharptail eel as the focal species. A. A grasby and bluestriped grunt dropped off from following the sharptail eel as it entered a crevice along a coral head (note the trumpetfish in the distance). B. The trumpetfish approached the sharptail eel and followed it across the coral rubble habitat. C. The trumpetfish continued to follow the eel while a rock beauty and yellow goatfish joined the group. Obvious lunges and/or bites at potential prey were observed for all species during this extended bout.

ate patterns in the diversity of fishes within local habitats? A study of mixed flocks of Neotropical birds suggested that such behavior may contribute to enhanced richness of rainforest avifauna (Powell, 1989). The author showed that smaller bird species in mixed species flocks foraged within a larger spatial range than when foraging singly, and suggested that each species underutilized available prey resources, thus allowing coexistence of species with high niche overlap. Investigating such interactions in fishes may lead to a better understanding of how behavioral interactions mediate trophic interactions and community composition.

Acknowledgments.—This research was funded by the Pew Charitable Trusts with a Marine Conservation Fellowship to PJA and the National Undersea Research Center at the University of Connecticut. Permits were generously provided by the government of the Netherlands and Bonaire Marine Park. The MV Delphin provided exceptional surface support for diving operations. Comments by two reviewers greatly improved the paper.

LITERATURE CITED

Clarke, K.R., and R.N. Gorley. 2001. PRIMER v5: User Manual/Tutorial. PRIMER-E, Plymouth, United Kingdom.

Magurran, A.E. 1988. Ecological Diversity and Its Measurement. Princeton University Press, Princeton, New Jersey, 179 pp.

Overholtzer, K.L., and P.J. Motta. 2000. Effects of mixed-species foraging groups on the feeding and aggression of juvenile parrotfishes. Env. Biol. Fish. 58:345-354.

Pitcher, T.J., and A.C. House. 1987. Foraging rules for group feeders: area copying depends upon food density in shoaling goldfish. Ethology 76:161-167.

Powell, G.V.N. 1989. On the possible contribution of mixed species flocks to species richness in neotropical avifaunas. Behav. Ecol. Sociobiol. 24:387-393.

Strand, S. 1988. Following behavior: interspecific foraging associations among Gulf of California reef fishes. Copeia 1988:351-357.

Suboski, M.D. 1988. Acquisition and social communication of stimulus recognition by fish. Behav. Proc. 16:213-244.

Wolf, N.G. 1987. Schooling tendency and foraging benefit in the ocean surgeonfish. Behav. Ecol. Sociobiol. 21:59-63.