

## Variation in social foraging by fishes across a coral reef landscape

P.J. Auster<sup>1</sup> and J. Lindholm<sup>2</sup>

1) National Undersea Research Center and Department of Marine Sciences, University of Connecticut at Avery Point, Groton, Connecticut 06340 USA

2) Institute for Applied Marine Ecology, Division of Science and Environmental Policy, California State University Monterey Bay, Seaside, California 93955 USA

**Abstract.** Coral reef landscapes are composed of a matrix of habitats that exhibit variation in complexity at multiple spatial scales. This variation has been shown to influence the composition of fish communities and influence the type and rate of species interactions. In this study, we quantified rates of social foraging bouts in single and mixed species groups across four habitat types (continuous reef, coral rubble-sand, reef edge, and spur and groove) at Conch Reef in the Florida Keys National Marine Sanctuary (USA). Our goal in dividing the reef landscape into particular habitat units was to ascertain if rates of social foraging vary in consistent ways in relation to habitat attributes. While there were no clear divisions in species composition that could be correlated with habitat type, rates of social foraging by mixed species groups were not equal. However, rates of social foraging bouts by single species groups were statistically equivalent across all habitat types. Fisher's diversity and species richness measures were not equal across habitat types, with lowest mean values in coral rubble habitat where rates of social foraging were highest. These results highlight the complexity of facilitative species interactions and suggest new lines of research to assess the demographic implications of such behaviors.

**Key words:** behavior, facilitation, group, mixed species, diversity

---

### Introduction

Understanding processes that mediate local patterns in the diversity of organisms is central to developing assembly rules for community structure as well as for developing strategies for conservation. Much effort has been focused on understanding the roles that recruitment limitation (bottom up) versus predation (top down) play in structuring marine communities (see Doherty 1991; Hixon 1991). However, nested within the scope of these processes is the role positive species interactions play in mediating survivorship, growth and trophic interactions, each of which may influence local species diversity within a community.

Social foraging is a common type of species interaction in coral reef fish communities and can occur in single-species and mixed-species groups. Bouts of social foraging can focus on activities of a single focal animal (producer-scrounger foraging model) or focus on multiple individuals within a group (information-sharing foraging models; Giraldeau and Beauchamp 1999). In either case 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 a group (Wolf 1987, Overholtzer and Motta 2000) and how such interactions may mediate community composition and patterns of diversity (Auster and Lindholm 2002, Auster et al. 2005).

Coral reef landscapes are composed of a matrix of habitats which exhibit a gradient of spatial complexity at multiple spatial scales (Williams 1991; Sorokin 1995). This variation has been shown, in part, to influence the composition of fish communities (Williams 1991). It follows that such variation will also influence the scope of species interactions that may mediate local patterns of diversity.

In this study, we quantified the rates of social foraging bouts in relation to community composition across four distinct habitat types at Conch Reef in the Florida Keys National Marine Sanctuary (U.S.A.). Our goal in dividing the reef landscape into particular habitat classes was to ascertain if rates of social foraging vary in consistent ways in relation to habitat attributes. We hypothesized that rates of social foraging, if mediated by attributes of habitat, would be highest over comparatively low-relief topography where the trade-offs of predation risk and access to prey would be greatest.

## Methods

Data were collected at Conch Reef (15-18.5 m depth) in the northeastern part of the Florida Keys National Marine Sanctuary from 11-18 September 2001, while using SCUBA. Conch Reef is part of the primarily Holocene reef tract along the continental margin off the south coast of Florida (Leichter et al. 2003), and is characterized by spur and groove formations. The reef landscape was divided *a priori* into four broad habitat classes (i.e., continuous reef, coral rubble-sand, reef edge, and spur and groove) in order to encompass the broadest range of spatial complexity. Reef edge and spur-and-groove habitat were similar at the scale of individual surveys in that patches contained a distinct transition zone from continuous reef to coral sand. However, these landscape features were assumed to be distinct due to differences in refuge from flow (enhanced shelter from flow within spur-and groove features) as well as differences in the location and direction of coral shelters for fishes. That is, fishes foraging in or above coral sand beyond reef edge habitat would only find shelter in the direction from where they came while fishes emerging over sand in spur-and-groove features could potentially find shelter across a sand patch in the adjacent spur (this distinction is based on unpublished observations by the authors of multiple species responding in these ways).

All data were collected during daylight hours (from 1 hr after sunrise to 1 hr before sunset). Survey patches were 5 m x 5 m (15-20 m depth). Patch delineation was estimated visually using natural landscape markers (e.g., particular coral colonies and formations). Surveys were 20 minutes in length. Observations were made while stationary in mid-water, away from patches, to minimize effects on behavior and movement of fishes but close enough to identify species. All species observed were identified to lowest the possible taxon and counted. However, no additional effort was made to census cryptic fishes (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 the number of species and the number of individuals per species involved in each bout. Actual feeding was not a pre-requisite for classification of a "bout" although one or more individuals within a group often did consume prey. Search behaviors involved non-linear swimming with individuals in each group focused on potential prey (e.g., sorting sediments, biting surfaces, attacks on vagile organisms). A bout ended when a group fully disbanded regardless of any exchange of individuals into or out of a group. The same fish may have been involved in multiple bouts within a census

period, though the incidents of this were minimal. Number of surveys within each habitat varied slightly: continuous reef (n=15), coral rubble-sand (n=16), reef edge (n=11), and spur and groove (n=12).

Bray-Curtis similarity coefficients were calculated based on species abundances from surveys within and between habitats. Non-metric multidimensional scaling (MDS; 100 restarts) was used to evaluate the level of similarity in assemblage composition between habitat types (using PRIMER software; Clarke and Gorley 2001). Abundance data were  $\log(x+1)$  transformed.

Data used to compare rates of social foraging (i.e., number of bouts per survey) were not normally distributed (Anderson-Darling tests for total, mixed-species and single species bouts all  $p < 0.05$ ). Kruskal-Wallis tests were used to determine if there were significant differences in rates of social foraging bouts between habitat types. Linear regression was used to determine if there were relationships between measures of local species diversity (i.e., species richness and Fisher's diversity of the fish community enumerated within each survey) and rates of social foraging.

## Results

Overall 36.7% of species (i.e., 33 of 90 species from community census data) participated in either single or mixed species social foraging bouts, or both. Twenty seven species participated in mixed species groups (Table 1) while 22 species participated in single species bouts (Table 2). Six species participated only in single species bouts. Yellowhead wrasse *Halichoeres garnoti* and spotted goatfish *Pseudupeneus maculatus* participated in the highest percentage of mixed species foraging bouts (33.8% and 21.6% respectively). Groups of bluehead *Thalassoma bifasciatum* composed the highest

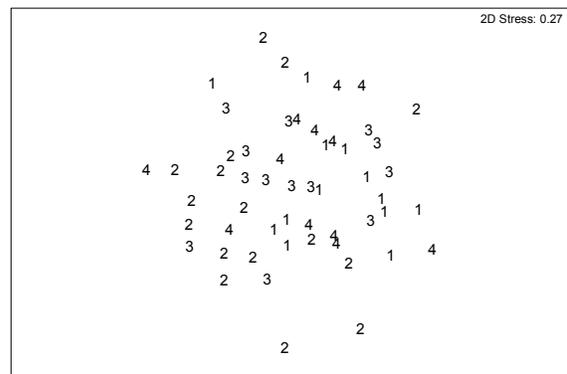


Figure 1. MDS plot illustrating similarity of species composition within and between survey sites across habitats. No habitat related associations were detected. Numbers indicate habitat type: 1 – continuous reef, 2 – coral rubble-sand, 3 – reef edge, and 4 – spur and groove.

Table 1. Percent occurrence of each species participating in mixed species foraging bouts across all surveys.

Species	Number bouts	Percent Occurrence
<i>Chromis cyaneus</i>	3	0.85%
<i>Hypoplectrus nigricans</i>	1	0.28%
<i>Acanthurus coeruleus</i>	6	1.70%
<i>Thalassoma bifasciatum</i>	17	4.83%
<i>Hypoplectrus unicolor</i>	7	1.99%
<i>Clepticus parrai</i>	2	0.57%
<i>Acanthurus chirurgus</i>	11	3.13%
<i>Lutjanus jocu</i>	1	0.28%
<i>Chaetodon capistratus</i>	1	0.28%
<i>Pomacanthus paru</i>	1	0.28%
<i>Haemulon flavolineatum</i>	2	0.57%
<i>Lutjanus griseus</i>	1	0.28%
<i>Pomacanthus arcuatus</i>	1	0.28%
<i>Lachnolaimus maximus</i>	15	4.26%
<i>Calamus bajonado</i>	3	0.85%
<i>Acanthurus bahianus</i>	5	1.42%
<i>Scarus taeniopterus</i>	2	0.57%
<i>Sparisoma aurofrenatum</i>	27	7.67%
<i>Chaetodon sedentarius</i>	1	0.28%
<i>Lactophrys triqueter</i>	9	2.56%
<i>Pseudupeneus maculatus</i>	76	21.59%
<i>Sparisoma viride</i>	2	0.57%
<i>Scarus croicensis</i>	20	5.68%
<i>Aulostomus maculatus</i>	3	0.85%
<i>Mulliodichthys martinicus</i>	4	1.14%
<i>Halichoeres garnoti</i>	119	33.81%
<i>Ocyurus chrysurus</i>	12	3.41%
<b>Total</b>	<b>352</b>	

percentage of single species bouts (19.7%) but all other species represented less than 10% each of the remaining bouts.

Results of MDS analysis (Fig. 1) indicate that there were no clear divisions in species composition that could be attributed to habitat type, although not all species occurred in all habitat types.

Comparisons of rates of social foraging based on total and mixed species bouts showed that rates of social foraging across habitats were not equal (Kruskal-Wallis tests,  $df = 3$ ,  $H = 14.78$  and  $16.94$ ;  $p = 0.002$  and  $0.001$  respectively). For both comparisons, continuous reef had the lowest mean rank of all habitats and coral rubble-sand had the highest (Fig. 2 top and middle). Paired comparisons showed that coral rubble-sand had a significantly higher rate of social foraging bouts ( $p < 0.05$ ) than the other three habitat types which were not statistically

Table 2. Percent occurrence of each species participating in single species foraging bouts across all surveys.

Species	Number bouts	Percent occurrence
<i>Caranx ruber</i>	4	2.07%
<i>Holacanthus bermudensis</i>	1	0.52%
<i>Chromis cyaneus</i>	15	7.77%
<i>Acanthurus coeruleus</i>	5	2.59%
<i>Thalassoma bifasciatum</i>	37	19.17%
<i>Clepticus parrai</i>	4	2.07%
<i>Acanthurus chirurgus</i>	8	4.15%
<i>Chaetodon capistratus</i>	16	8.29%
<i>Lutjanus griseus</i>	1	0.52%
<i>Pomacanthus arcuatus</i>	2	1.04%
<i>Serranus tigrinus</i>	1	0.52%
<i>Lachnolaimus maximus</i>	3	1.55%
<i>Acanthurus bahianus</i>	15	7.77%
<i>Sparisoma aurofrenatum</i>	5	2.59%
<i>Chaetodon sedentarius</i>	13	6.74%
<i>Holacanthus tricolor</i>	1	0.52%
<i>Canthigaster rostrata</i>	2	1.04%
<i>Chaetodon ocellatus</i>	12	6.22%
<i>Pseudupeneus maculatus</i>	15	7.77%
<i>Scarus croicensis</i>	12	6.22%
<i>Halichoeres garnoti</i>	18	9.33%
<i>Ocyurus chrysurus</i>	2	1.04%
<b>Total</b>	<b>192</b>	

different from one another. There were no significant differences in the number of single species bouts and habitat type (Kruskal-Wallis test,  $df = 3$ ,  $H = 5.33$ ,  $p = 0.149$  adjusted for ties; Fig. 2 bottom).

There was no linear relationship between the total number of social foraging bouts and species richness across all surveys (ANOVA,  $df_{1,52}$ ,  $F = 0.01$ ,  $p = 0.91$ ). However, when species abundances as well as richness were taken into account there was a significant linear relationship between Fisher's diversity and total bouts (ANOVA,  $df_{1,52}$ ,  $F = 5.25$ ,  $p = 0.03$ ). Neither Fisher's diversity nor species richness measures were equal across habitat types (Kruskal-Wallis tests,  $df = 3$ ,  $H = 14.15$  and  $10.58$ ;  $p = 0.003$  and  $0.015$  respectively) with lowest mean values in coral rubble habitat where rates of social foraging were highest (Fig. 3).

## Discussion

The benefits to individuals within a foraging group generally are considered to include enhanced vigilance to predation threats and enhanced access to prey (Lukoschek and McCormick 2002). In this study we found variable rates of social foraging among habitats within a coral reef landscape despite

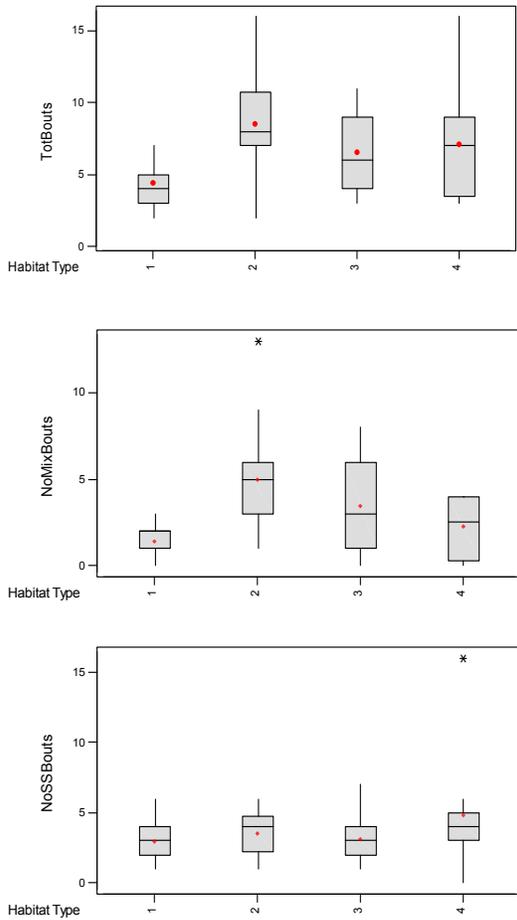


Figure 2. Boxplots of total (top), mixed species (middle) and single species (bottom) bouts per survey. Habitat types as in Figure 1. (The center-line through each box marks the median value and the solid dots mark the mean. Top and bottom of each box mark the bottom of the third and the top of first quartile of the data, respectively. The top whisker extends to the highest value in the top quartile and the bottom whisker to the lowest value in the first quartile. Stars indicate statistical outliers.)

similarity in community composition across habitats. These results suggest that structural attributes of habitat such as spatial complexity have a role in mediating behavior that balances the time and space constraints related to prey acquisition and predator avoidance.

Our *a priori* hypothesis of higher rates of social foraging in comparatively low complexity habitats was confirmed. Rates of social foraging were highest in coral rubble-sand habitats, where cover from predation was low and prey organisms are assumed to be patchy in distribution. The increased number of social foraging bouts was indicative of enhanced vigilance against threats of predation. Multiple bouts often resulted from a group breaking off and then reforming following a strike by a predator. Though predator strikes were frequent, no successful strikes were observed against individuals

participating in social foraging bouts over the course of the study. Conversely, the number of social foraging bouts was lowest over continuous reef habitat where cover from predation and potential prey was ubiquitous. Here the benefits to an individual's participation in a social foraging event are assumed to be comparatively low.

It is interesting to note that fishes in this study area exhibited a lower percentage of social foraging activities than studies elsewhere. For example, 52% of species (i.e., 34 of 65 species) from community surveys on reefs off Bonaire, Netherlands Antilles, participated in mixed or single species foraging groups (Auster and Lindholm 2002). Barber and Auster (in prep) demonstrated that approximately 45% of non-cryptic reef fish species at sites in the Gulf of California and the Great Barrier Reef occurred in mixed and single species foraging groups. While all surveys were conducted within approximately the same depth range, patterns related to latitudinal gradients and relationships to the regional species pool remain to be investigated.

Observations of foraging groups elsewhere in the Caribbean, Gulf of California, Coral Sea, and Indian Ocean revealed they can be composed of

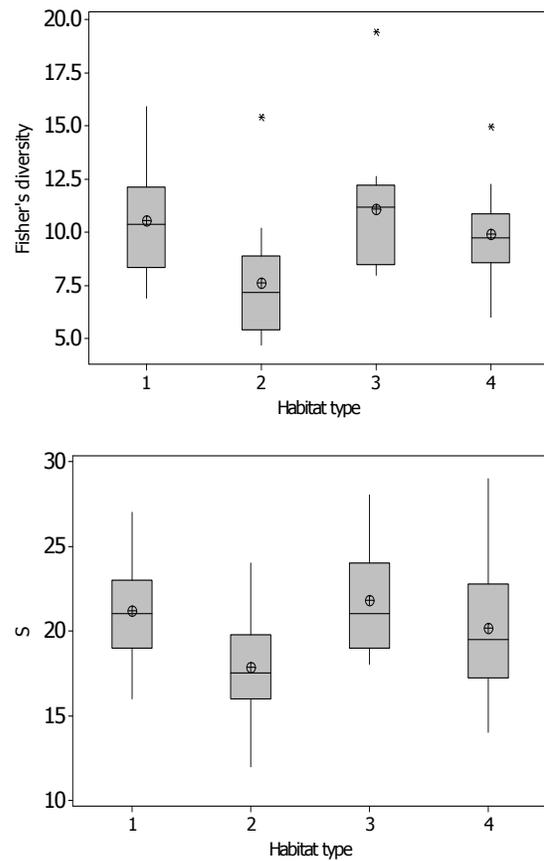


Figure 3. Boxplots of Fisher's diversity (top) and species richness (bottom) by habitat type. See legend of Figure 2 for explanation.

species representing a wide range of trophic guilds (i.e., planktivores and herbivores through piscivores; sensu Bohnsack et al. 2002) while others were limited to a particular trophic groups (Auster and Lindholm 2002, Auster 2005, 2007, Barber and Auster in prep, Auster unpublished data). Barber and Auster (in prep) showed that while all trophic guilds were represented in foraging groups at Caribbean (i.e., Bonaire) and Coral Sea (northern Great Barrier Reef) study sites, the proportions of guilds represented in foraging groups in contrast to the local community varied. While the trophic guild composition of social foraging groups at the Caribbean site reflected proportions in the local community, the guild composition of foraging groups differed significantly from the community at Coral Sea sites. Higher than expected proportions of planktivores, browsers and macro-invertivores were observed in mixed-species groups while piscivores and micro-invertivores were under-represented. However, a mechanism to explain such patterns in terms of costs and benefits remains to be discerned and will be critical for understanding the link between facilitative behaviors and population responses of component species (Auster et al. 2005, Barber and Auster in prep).

Species interactions can be explicitly linked to local patterns of diversity. For instance, 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. In the present study, local fish diversity was positively correlated with rates of group foraging, as it was at reefs off Bonaire (Auster and Lindholm 2002). In the Bahamas the combination of predator-prey and competitive interactions between reef fishes was shown to mediate patterns of local abundance of reef fishes (Carr et al. 2002). However, the role of positive (facilitative) species interactions in developing these patterns was not addressed.

Ultimately, investigating such interactions in fishes at a diversity of locations can lead to a better understanding of how behavioral interactions mediate trophic interactions and community composition. In the short term we need to better understand how quantification of such interactions can enhance our ability to evaluate the status and ecological integrity of reef fish communities.

### Acknowledgements

This work was undertaken during a saturation diving mission at the *Aquarius* undersea habitat operated by the National Undersea

Research Center at the University of North Carolina Wilmington. We would like to thank Billy Causey, Cathy Sakas, and Laddie Akins for dive support. PJA was supported by the National Oceanic and Atmospheric Administration's (NOAA's) National Undersea Research Program. NOAA's National Marine Sanctuary Program supported the habitat mission and travel for JL to participate. The views expressed herein are those of the authors and do not necessarily represent the views of NOAA or their sub-agencies.

### References

- Auster PJ (2005) Predatory behavior of piscivorous reef fishes varies with changes in landscape attributes and social context: integrating natural history observations in a conceptual model. p. 115-127. in: Diving for Science 2005, Proceedings of the American Academy of Underwater Sciences. Connecticut Sea Grant, Groton.
- Auster PJ (2007) Variation in search and predatory attack strategies of shark mackerel *Grammatorcynus bicarinatus*. J Mar Biol Assoc UK 88:847-849
- Auster PJ, Lindholm J (2002) Pattern in the local diversity of coral reef fishes versus rates of social foraging. Caribb J Sci 38:263-266
- Auster PJ, Semmens B, Barber K (2005) Pattern in the co-occurrences of fishes inhabiting the coral reefs of Bonaire, Netherlands Antilles. Environ Biol Fishes 74:187-194
- Bohnsack JA, Cantillo AY, Bello MJ (2002) Resource survey of Looe Key National Marine Sanctuary 1983. United States Department of Commerce, NOAA Technical Memorandum NMFS-SEFSC-478. 267 p.
- Barber K, Auster PJ (in preparation) A comparison of rates and structure of social foraging interactions in coral reef fishes.
- Carr MH, Anderson TW, Hixon MA (2002) Biodiversity, population regulation, and the stability of coral-reef fish communities. Proc Natl Acad Sci 99:11241-11245
- Clarke KR, Gorley RN (2001) PRIMER v5: User Manual/Tutorial. PRIMER-E Ltd, Plymouth
- Doherty PJ (1991) Spatial and temporal patterns in recruitment, pp 261-292. In: Sale, P. (ed.) The ecology of fishes on coral reefs. Academic Press, San Diego, California
- Giraldeau LA, Beauchamp G (1999) Food exploitation: searching for the optimal joining policy. Trends Ecol Evol 14:102-106
- Hixon MA (1991) Predation as a process structuring coral reef fish communities, pp 475-500. In: Sale, P. (ed.) The ecology of fishes on coral reefs. Academic Press, San Diego, California
- Leichter JJ, Stewart HL, Miller SL (2003) Episodic nutrient transport to Florida coral reefs. Limnol Oceanogr 48: 1394-1407
- Lukoschek V, McCormick MI (2000) A review of multi-species foraging associations in fishes and their ecological significance. Proc 9th Inter Coral Reef Sym 1:467-474
- Overholtzer KL, Motta PJ (2000) Effects of mixed-species foraging groups on the feeding and aggression of juvenile parrotfishes. Environ Biol Fishes 58:345-354
- Sorokin YI (1995) Coral Reef Ecology. Springer-Verlag, New York, p 465
- Williams D McB (1991) Patterns and processes in the distribution of coral reef fishes, pp 437-471. In: Sale, P. (ed.) The ecology of fishes on coral reefs. Academic Press, San Diego, California.
- Wolf NG (1987) Schooling tendency and foraging benefit in the ocean surgeonfish. Behav Ecol Sociobiol 21:59-63