



Composition and behavior of mixed-species foraging groups of reef fish in the Lakshadweep islands, India

¹ Centre for Ecological Sciences,
Indian Institute of Science, C.V.
Raman Avenue, Bangalore,
560012, India

² Dakshin Foundation, #1818, 9th
Cross, 5th Main Rd, CQAL Layout,
Sahakar Nagar, Bangalore,
560092, India

* Corresponding author email:
<anneheloise.theo@gmail.com>

Anne Heloise Theo ^{1*}
Kartik Shanker ^{1,2}

ABSTRACT.—Mixed-species foraging groups of reef fishes, although relatively common in occurrence, have historically received little attention. Most studies on this topic have been descriptive accounts of specific associations. In this study, we collected data on mixed-species foraging groups seen in the Lakshadweep islands, resulting in a dataset of 1289 groups. Data was collected from both reefs and lagoons of three islands (Kadmat, Kavaratti, and Agatti) within the Lakshadweep Archipelago over a period of three years. Cluster analysis revealed nine categories based on species composition in groups: parrotfish, juveniles, surgeonfish (small), surgeonfish (large), *Anampses* spp., wrasses, *Parupeneus macronema*, *Parupeneus barberinus*, and other goatfish groups. The clusters are named based on the nuclear species or most frequently seen species within the groups. These groups are distinct not only in terms of composition but also other parameters such as behavior (shoaling or attendant groups), habitat affinity, and group cohesion. Groups comprising herbivorous species such as parrotfish and surgeonfish were almost entirely shoaling in nature (large groups without nuclear individuals), whereas goatfish and wrasses tended to form smaller attendant associations. Groups also occupied different habitat types; for example, parrotfish and *P. barberinus* groups were seen mostly in lagoons while surgeonfish, wrasses, and *P. macronema* groups were more abundant on reefs. Our findings suggest that mixed-species foraging groups in fishes are comprised of distinct compositional categories that vary in behavior, cohesion, and habitat affinity.

Date Submitted: 16 July, 2020.
Date Accepted: 23 August, 2021.
Available Online: 24 August, 2021.

Mixed-species foraging groups (hereafter referred to as mixed-species groups), consisting of individuals of two or more species (Lukoschek and McCormick 2000), have been observed in a number of taxa, as diverse as birds (e.g., Sridhar et al. 2009), fish (Lukoschek and McCormick 2000), spiders (Hodge and Uetz 1992), cetaceans (Psarakos et al. 2003), primates (Noë and Bshary 1997), and ungulates (Fitzgibbon 1990). While observed across numerous taxa, nowhere is it as prevalent (both in terms of frequency of occurrence as well as number of participant species) as in birds and reef fishes.

Mixed-species grouping behavior is common in reef fishes; it is a complex phenomenon involving a wide diversity of species and sometimes including different trophic guilds (Lukoschek and McCormick 2000, Sazima and Grossman 2005, Sazima et al. 2007). While some associations are persistent, several species may join groups opportunistically to exploit otherwise unavailable food sources (Leitão et al. 2007, Araújo et al. 2009). In addition, several predatory fishes form associations with a variety of species that include not only fish but other phyla as well (Forsythe and Hanlon 1997, Gibran 2002). Variation exists not only in the identity of species that interact but also in the strength and durability of the association (Lukoschek and McCormick 2000).

The literature on mixed-species grouping behavior largely comprises research on birds. Based on these studies, the potential benefits of participating in mixed groups have been primarily divided into two categories: foraging benefits and antipredatory benefits (Morse 1977). Groups may also be viewed along a spectrum based on the similarity of benefits provided and asymmetry of costs and/or benefits, ranging from supplementary groups to complementary groups (Goodale et al. 2020). Supplementary groups are groups which typically gain benefits arising from group size, such as shared vigilance and dilution and confusion effects. In these groups, participants gain similar benefits, and the identity of grouping partners does not matter much. The dilution effect is the lowered probability of being targeted by a predator in a group. As the group size increases, each individual in the group benefits from the presence of others in proportion to group size (Morse 1977). The confusion effect refers to the phenomenon where the simultaneous movement of similar individuals disorients the predator and makes it difficult to target specific individuals (Bertram 1978). Conversely, complementary groups are associations in which partners provide varying benefits to each other. In these groups, benefits are strongly tied into the identity of the participating species and are a consequence of the behavior or natural history of the species involved.

Mixed-species grouping behavior in fishes is, however, poorly understood as studies on the subject are relatively scarce. Lukoschek and McCormick (2000) reported only about 45 papers published on this subject in the 30 years preceding their paper and the following years have not seen a significant change in this pattern, since most studies on grouping in fish focus on single species groups (Paijmans et al. 2019). Based on descriptions of mixed-groups within the literature and on the classification scheme suggested for these groups by Ormond (1980), Lukoschek and McCormick (2000) suggested that mixed-species associations of fishes be broadly divided into two categories: attendant associations and shoaling associations.

Shoaling associations are typically comprised of many individuals where it is unclear which species is leading foraging activities. Attendant associations are groups typically comprising a smaller number of individuals, where one or two species—known as the nuclear species—lead foraging activities and are followed by one or more attendant species. Attendant groups can be further divided into four categories (Ormond 1980). Following-and-scavenging associations are one of the most commonly observed feeding associations on the reef where individuals of a particular species (nuclear species) are followed by one or more species that scavenge on prey that are flushed out by the foraging activity of the nuclear species. Joint-hunting is an association where two or more species of predators hunt together. There is generally no clear indication of which one is the nuclear species in this type of association.

Aggressive mimicry is the mimicry of a harmless species by a predator, so that the predator may approach potential prey with relative ease (Wickler 1965). Hunting by riding is a behavior commonly exhibited by predators in coral reef systems; predators hide behind a single individual or within a shoal of a harmless species of fish, allowing them to sneak up on prey. Unlike in aggressive mimicry, there is no mimicry or change in coloration seen in this type of association, and the predators use the fish shoal merely for cover (Ormond 1980).

The foraging advantages of mixed-groups are immediately apparent in following-and-scavenging groups, as these tend to form around species that facilitate prey capture for other individuals by flushing out hidden prey items. For instance, the association between *Halichoeres hortulanus* and *Parupeneus barberinus* is frequently observed in the Indo-Pacific, where the wrasse can be seen feeding on invertebrates flushed out by the foraging activity of the goatfish (Lukoschek and McCormick 2000, Sazima et al. 2007, Krajewski 2009). Foraging in groups can also provide access to otherwise unattainable or novel food resources, such as resources defended by territorial species (Robertson et al. 1976) or access to food sources that are not primarily targeted by the species involved (Baird 1993). A common strategy used by herbivorous fishes is to create large shoals in order to overwhelm the defenses of territorial herbivores. Several studies have shown increased bite rates for large shoals of acanthurids and scarids compared to smaller groups within defended territories (Wolf 1983, Foster 1987). A very specific foraging advantage gained by predatory species is demonstrated by a number of coral reef fishes through aggressive mimicry and hunting by riding, using other harmless schooling species for camouflage or cover (Ormond 1980, Aronson 1983).

Antipredator benefits include earlier detection of predators, less time spent on vigilance, and protection due to the confusion effect or the dilution effect (Lukoschek and McCormick 2000, Pajmans et al. 2019). This is typically seen in shoaling groups; the dependence of reef fishes on such schools for antipredation defense is illustrated by the fact that several species seem to have evolved color patterns that allow them to blend with heterospecifics (Ehrlich and Ehrlich 1973, Dafni and Diamant 1984). In groups of surgeonfish *Acanthurus coeruleus* and parrotfish *Scarus coelestinus*, which are frequently seen in the Atlantic, the two species resemble each other closely in color. The parrotfish even have patches of light blue to mimic the flashes of light caused by light penetrating the thin pectoral and caudal fins of the surgeonfish (Alevizon 1976).

As is evident from the many types of mixed-species groups, this behavior is both widespread and subject to variation in terms of the behavior of participants. Mixed-species groups also vary in several aspects such as types of habitats where they are found and group permanence and cohesion (Ward et al. 2018). It is likely that benefits accrued from participation in groups may vary based on the type of group that the individual is associated with. However, few studies have focused on patterns or descriptions of mixed-species groups at the scale of the entire reef community (Ormond 1980, Strand 1988, Sazima et al. 2007).

Here, we provide a quantitative classification of the types of mixed-species foraging associations observed in the Lakshadweep Archipelago, a small group of islands located off the west coast of India, in the Arabian Sea. We use a large primary dataset of 1289 groups collected between 2012 and 2015 to describe broad-scale patterns of mixed-species groups. The sampling was stratified across the reef and lagoon, allowing us to infer patterns based on habitat type. Our objectives were to

(1) identify species that participate in mixed-species groups, (2) classify groups into compositional categories based on species composition within groups, and (3) examine patterns in group cohesion, habitat affinity, and behavioral category (shoaling, following-and-scavenging, joint-hunting) of the compositional categories identified.

METHODS

STUDY AREA.—The Lakshadweep Archipelago, located 200–400 km off the west coast of India, is an archipelago of atolls and small islands located on the Laccadives-Chagos ridge. The islands are believed to be the buried remnants of the Aravali mountain chain, around which the islands formed due to an accumulation of coral sand. The archipelago consists of 12 atolls, 3 reefs, and 5 submerged banks. There are a total of 36 islands covering an area of 32 km², of which only 10 islands are inhabited and all except one have a lagoon. The islands are quite similar to each other in topography. Each island has a north-south orientation, with a fringing reef on the eastern aspect and a lagoon surrounded by the reef on the west. The eastern and western aspect of the islands differ in terms of standing structure and live coral cover, as well as rates of recovery postbleaching due to variation in the local hydrodynamics (Arthur 2004, Arthur et al. 2006). The bulk of the rainfall in the islands is received during the south-west monsoon of India and sampling is possible only during the nonmonsoon months from October to April. Each nonmonsoon period when sampling was carried out is defined as one field season (subsequently referred to as a season). This study was carried out within the lagoon and in the reef areas of three islands within the archipelago: Kavaratti, Kadmat, and Agatti.

SAMPLING MIXED-SPECIES GROUPS.—Mixed-species groups were sampled between the months of October and April over the course of three field seasons: 2012–2013, 2013–2014, and 2014–2015. Since the lagoon and the eastern and western aspects of the reef exhibited variation in benthic structure and coral abundance, five sites were sampled within each aspect, leading to the selection of 15 sites at each of the three islands. Sites on the reef were selected arbitrarily from known dive sites established and sampled by previous researchers. Lagoon sites were selected by dividing the lagoon into 500 × 500 m square grids and picking 5 sites randomly from the set. The depth of the sites in the reef ranged from 12 to 18 m, and sites in the lagoon ranged between 0.5 and 2 m. The distribution of sites across the three islands is depicted in Figure 1.

Sampling was conducted using SCUBA in the reef and by snorkeling within the lagoon (because the shallow depths would not allow for diving), between 8:00 am and 2:00 pm. Because mixed-groups are sporadic and gathering data on one would require following it, a spatially restricted sampling technique would have been unsuitable for this study. Each site was therefore sampled for 60 min during which time the diver (A Theo) searched for groups using a random walk (swim), which covered no more than 500 m². Previous studies that attempted to sample all groups across a given area have used similar strategies for sampling (Sazima et al. 2007).

A group or collection of fishes was classified as a group only if it contained two or more species and the individuals were seen moving as well as foraging together. Upon encounter with a mixed-species group, the group was followed until it dispersed, was lost from view, or up to 3 min. Upon completion of observation of a group, the diver

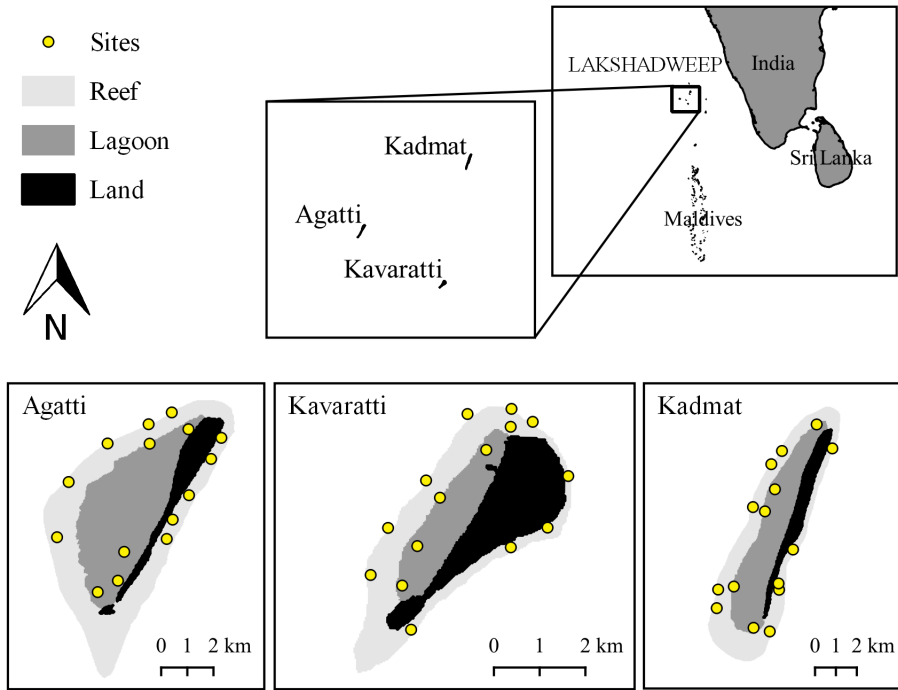


Figure 1. Map of Lakshadweep islands with the study sites demarcated on the islands of Agatti, Kadmat, and Kavaratti.

would swim away from the group in an arbitrary direction to ensure resampling of the same group did not occur. For every group encountered, the number of individuals of each species present and size classes of the individuals were visually estimated and recorded (size classe in cm = 0–5, >5–10, >10–15, >15–20, >20–30, >30–40, >40–60, >60–80, and >80). Size classes were estimated for all individuals within a group. In groups that were too large for each individual to be estimated separately, care was taken to ensure all size classes and number of individuals within each size class were recorded accurately. Video recordings of groups were also taken, and these recordings were used to gather further data on when individuals left groups and to verify the numbers/ratios of size classes within the groups. In cases where groups split or coalesced, this was counted as individuals leaving or joining the group being observed. Each site was sampled once every field season. Sampling was done by a single diver (A Theo) at each site and the same diver conducted all observations across all three seasons. During sampling, the area was scanned constantly, therefore any groups within line of sight were identified and noted. If there were species that avoided divers completely, they are likely absent from the dataset, however this would not affect the composition of groups that were observed. Among behavioral categories, shoaling groups are easier to spot than attendant groups due to their larger group size; however, focused searches were carried out in suitable habitat to detect attendant groups as well.

We collected data on habitat category (reef vs lagoon) and group cohesion for each group. Group cohesion was categorized into tight, intermediate, loose, and variable.

Groups in which the participants maintained close proximity with each other (less than three body lengths distance) were categorized as tight. Groups were termed as “loose” when the association could not be verified unless distinct acts of simultaneous movement in the same direction and ceasing of movement for foraging in the same area were seen. Intermediate group cohesiveness was assigned to groups that lay between these two ends of the spectrum, and variable cohesiveness was assigned to groups that showed a combination of the three previous categories and therefore could not be assigned to any one of them.

Behaviorally, groups were classified based on Lukoschek and McCormick (2000). During data collection, the behavior of each individual was observed and categorized as (1) nuclear if it was an individual that was followed by others, (2) follower if it followed other group members, or (3) shoaling if it was part of a large group in which no leader-follower associations could be discerned. Behavioral categorization was assigned based on the behavior of an individual during the entire duration of observation. Each group was then assigned a behavioral category based on the behavior of the individuals in the group. The video recordings were used to confirm these categorizations. Groups with large numbers of shoaling individuals with no nuclear species were categorized as shoaling. Groups where one individual or species acted in the nuclear role and other species acted as followers were categorized as following-and-scavenging groups. Groups with multiple nuclear species, in which the nuclear individuals seemed to be cooperatively hunting and maintaining proximity with each other (generally fishes in these groups took on both the nuclear and follower roles over time), were assigned the category joint-hunting. Groups of the category “hunting by riding” and “aggressive mimicry” were not observed during our sampling sessions.

ANALYSIS.—

Compositional Categorization of Groups.—During data collection, we qualitatively observed that species associations were strikingly nonrandom, i.e., species tended to group with the same species repeatedly such that species could potentially be grouped based on cooccurrence in mixed-groups. To verify this quantitatively, we ran a clustering algorithm on the dataset. For this analysis only information on species composition was used and each group was treated as a single data point. A group by species matrix of species abundance was used to generate a pairwise distance matrix of the groups observed. Distances were calculated using the Bray–Curtis dissimilarity index; this index was selected because the dataset was zero inflated. A dendrogram was generated from the distance matrix using an agglomerative hierarchical clustering algorithm (using UPGMA linkage). We used a dendrogram to visualize distance because many groups did not share any common species, making other commonly used methods unsuitable for this dataset. We then used taxonomy to categorize groups and delineated clusters visually. Each group was assigned a compositional category based on the dominant species within the group. Any species that was present either in the nuclear role or in large numbers within the group was considered the dominant species. Size class and phenotype were used to identify juveniles. The compositional category codes were used to color the branches on the dendrogram, allowing us to visually corroborate if the groups were separated based on species composition. The R package *vegan* was used to calculate distance, the

package cluster was used for the clustering, and dendextend was used to generate the dendrogram (Galili 2015, Maechler et al. 2019, Oksanen et al. 2019).

Behavior, Group Cohesion, and Habitat Affinity.—The dataset was divided into nine compositional categories based on the cluster analysis. To ascertain if the compositional categories delineated in the previous analysis also exhibited variation in parameters such as abundance in the reef and lagoon, behavior, and group cohesion, information on behavioral category, group cohesion, and habitat category was extracted for every group within a particular compositional category.

We examined differences in these parameters (habitat, behavior, and cohesion) between the different compositional categories. We also examined differences in cohesion between behavioral categories seen in our study, namely following-and-scavenging groups, joint-hunting groups, and shoaling groups. The comparisons were tested using Fisher's exact test (which is appropriate for count data and small sample sizes). All analyses were carried out in the statistical software R (R Core Team 2019).

RESULTS

GENERAL PATTERNS.—Mixed-species grouping behavior is common in the waters of the Lakshadweep islands. Data was collected on a total of 1289 groups over the course of three field seasons. Of the 302 fish species observed in Lakshadweep in this study, around 113 species belonging to 18 families were seen participating in mixed-species groups at least once (see Table 1 for a complete list of species seen in groups). Although a large number of species participated in these groups, the distribution of frequencies of participation of species within groups is extremely skewed. A great majority of the species observed were found in groups rarely. Over the course of four years, 76 species were observed in less than 10 groups (Fig. 2), while a few participated in groups almost habitually. The two species that were seen in groups most often were *Parupeneus macronema* (longbarbel goatfish) and *Chlorurus sordidus* (bullethead parrotfish), both of which were seen in over 300 groups. We observed *C. sordidus* mostly in shoaling groups and *P. macronema* in attendant associations. In general, parrotfish, goatfish, wrasses, and surgeonfish had the highest frequencies of occurrence in groups (Fig. 3).

COMPOSITIONAL CATEGORIES.—A dendrogram generated using an agglomerative clustering method based on dissimilarity of species composition within groups highlighted patterns of grouping based on species composition (Fig. 4). Based on the dominant species in each group, we designated these groups as: Scaridae (parrotfish groups predominantly composed of two species *C. sordidus* and *Scarus psittacus*); Acanthuridae (small), groups of small bodied surgeonfish species (*Acanthurus nigrofuscus*, *Acanthurus leucosternon*, and *Ctenochaetus striatus*); Acanthuridae (large), large bodied surgeonfish groups (groups including the species *Acanthurus auranticavus* and *Acanthurus nigricauda*); *Anampses* (groups that contained the wrasses *Anampses lineatus* and *Anampses meleagrides*); three categories based around goatfishes (*P. barberinus*, *P. macronema*, and a third category that contains all other goatfish species); and Labridae (mixed-groups of wrasses). Groups comprised of juveniles (which were primarily composed of parrotfish juveniles) were categorized separately; in many cases, the grouping behavior of juveniles was very different from

Table 1. Species seen in each compositional category along with the number of groups each species was seen in.

Species	Groups	Species	Groups	Species	Groups
<i>Parupeneus barberinus</i>		Mullidae (cont.)		<i>Anampses</i> spp. (cont.)	
<i>Parupeneus barberinus</i>	215	<i>Oxychelinus</i> spp.	1	<i>Scarus psittacus</i>	2
<i>Halichoeres scapularis</i>	123	<i>Wrasse</i> spp.	1	<i>Scarus</i> spp.	2
<i>Halichoeres hortulanus</i>	89			<i>Acanthurus nigrofuscus</i>	1
<i>Parupeneus macronema</i>	20	<i>Parupeneus macronema</i>		<i>Anampses caeruleopunctatus</i>	1
<i>Scolopsis bilineatus</i>	11	<i>Parupeneus macronema</i>	449	<i>Halichoeres hortulanus</i>	1
<i>Coris frerei</i>	5	<i>Halichoeres hortulanus</i>	129	<i>Hemigymnus fasciatus</i>	1
<i>Lethrinus</i> spp.	5	<i>Gomphosus caeruleus</i>	109	<i>Scarus globiceps</i>	1
<i>Acanthurus nigricauda</i>	2	<i>Stethojulis albobittata</i>	84	<i>Stethojulis trilineata</i>	1
<i>Ctenochaetus striatus</i>	2	<i>Macropharyngodon ornatus</i>	72		
<i>Mulloidichthys flavolineatus</i>	2	<i>Halichoeres scapularis</i>	51	Labridae	
<i>Parupeneus indicus</i>	2	<i>Thalassoma lunare</i>	25	<i>Stethojulis albobittata</i>	13
<i>Stethojulis albobittata</i>	2	<i>Chlorurus sordidus</i>	16	<i>Gomphosus caeruleus</i>	10
<i>Sufflamen chrysopterum</i>	2	<i>Thalassoma janseni</i>	16	<i>Parupeneus macronema</i>	10
<i>Acanthurus aurantivagus</i>	1	<i>Halichoeres cosmetus</i>	10	<i>Macropharyngodon ornatus</i>	6
<i>Acanthurus leucosternon</i>	1	<i>Hologymnosus doliatus</i>	9	<i>Halichoeres scapularis</i>	5
<i>Acanthurus triostegus</i>	1	<i>Parupeneus bifasciatus</i>	9	<i>Parupeneus barberinus</i>	4
<i>Coris africana</i>	1	<i>Parupeneus barberinus</i>	7	<i>Chlorurus sordidus</i>	3
<i>Gomphosus caeruleus</i>	1	<i>Halichoeres nebulosus</i>	5	<i>Stethojulis trilineata</i>	3
<i>Halichoeres cosmetus</i>	1	<i>Scarus psittacus</i>	5	<i>Thalassoma janseni</i>	3
<i>Lethrinus harak</i>	1	<i>Coris africana</i>	4	<i>Thalassoma lunare</i>	2
<i>Lethrinus microdon</i>	1	<i>Ctenochaetus striatus</i>	4	<i>Cirrhalabrus exquiritus</i>	1
<i>Scarus ghobban</i>	1	<i>Oxychelinus</i> spp.	3	<i>Halichoeres hortulanus</i>	1
<i>Scarus psittacus</i>	1	<i>Scarus</i> spp.	3	<i>Hologymnosus doliatus</i>	1
<i>Synodus</i> spp.	1	<i>Scolopsis bilineatus</i>	3	<i>Scarus psittacus</i>	1
<i>Wrasse</i> spp.	1	<i>Acanthurus nigrofuscus</i>	2		
<i>Zebbrasoma desjardini</i>	1	<i>Acanthurus</i> spp.	2	Juveniles	
		<i>Bodianus diana</i>	2	<i>Chlorurus sordidus</i>	72
Mullidae		<i>Parupeneus cyclostomus</i>	2	<i>Parupeneus macronema</i>	50
<i>Halichoeres hortulanus</i>	30	<i>Parupeneus pleurostigma</i>	2	<i>Scarus</i> spp.	33
<i>Parupeneus bifasciatus</i>	29	<i>Acanthurus nigricauda</i>	1	<i>Stethojulis albobittata</i>	26
<i>Parupeneus macronema</i>	29	<i>Acanthurus triostegus</i>	1	<i>Scarus scaber</i>	25
<i>Halichoeres scapularis</i>	27	<i>Anampses meleagrides</i>	1	<i>Acanthurus triostegus</i>	22
<i>Mulloidichthys flavolineatus</i>	23	<i>Bodianus</i> spp.	1	<i>Acanthurus</i> spp.	20
<i>Parupeneus barberinus</i>	21	<i>Caranx</i> spp.	1	<i>Scarus frenatus</i>	14
<i>Parupeneus cyclostomus</i>	12	<i>Cirrhalabrus exquiritus</i>	1	<i>Parupeneus barberinus</i>	12
<i>Gomphosus caeruleus</i>	8	<i>Coris</i> spp.	1	<i>Stethojulis trilineata</i>	8
<i>Parupeneus pleurostigma</i>	8	<i>Ctenochaetus strigosus</i>	1	<i>Halichoeres scapularis</i>	6
<i>Chlorurus sordidus</i>	5	<i>Epibulus insidiator</i>	1	<i>Scarus niger</i>	6
<i>Parupeneus indicus</i>	5	<i>Scarus frenatus</i>	1	<i>Scarus psittacus</i>	6
<i>Thalassoma lunare</i>	4			<i>Gomphosus caeruleus</i>	3
<i>Scolopsis bilineatus</i>	3	<i>Anampses</i> spp.		<i>Macropharyngodon ornatus</i>	3
<i>Cheilio inermis</i>	2	<i>Anampses lineatus</i>	39	<i>Thalassoma lunare</i>	3
<i>Hologymnosus doliatus</i>	2	<i>Anampses meleagrides</i>	35	<i>Chaetodon auriga</i>	2
<i>Lutjanus gibbus</i>	2	<i>Macropharyngodon ornatus</i>	19	<i>Cirrhalabrus exquiritus</i>	2
<i>Stethojulis albobittata</i>	2	<i>Stethojulis albobittata</i>	9	<i>Zebbrasoma</i> spp.	2
<i>Aethaloperca rogaa</i>	1	<i>Parupeneus macronema</i>	7	<i>Acanthurus nigrofuscus</i>	1
<i>Cheilinus trilobatus</i>	1	<i>Chlorurus sordidus</i>	6	<i>Chaetodon klenii</i>	1
<i>Ctenochaetus striatus</i>	1	<i>Thalassoma janseni</i>	5	<i>Halichoeres nebulosus</i>	1
<i>Epibulus insidiator</i>	1	<i>Anampses melanurus</i>	2	<i>Stethojulis</i> spp.	1
<i>Halichoeres cosmetus</i>	1	<i>Cirrhalabrus exquiritus</i>	2	<i>Thalassoma janseni</i>	1
<i>Halichoeres marginatus</i>	1	<i>Gomphosus caeruleus</i>	2	<i>Wrasse</i> spp.	1

Table 1. Continued.

Species	Groups	Species	Groups	Species	Groups
Scaridae		Acanthuridae (small; cont.)		Other Groups	
<i>Chlorurus sordidus</i>	243	<i>Scarus prasiognathus</i>	4	<i>Halichoeres hortulanus</i>	27
<i>Scarus psittacus</i>	153	<i>Acanthurus lineatus</i>	3	<i>Chlorurus strongylocephalus</i>	23
<i>Parupeneus macronema</i>	94	<i>Acanthurus nigricauda</i>	3	<i>Scarus prasiognathus</i>	8
<i>Scarus scaber</i>	40	<i>Acanthurus thomsonii</i>	2	<i>Pterocaesio tile</i>	6
<i>Ctenochaetus striatus</i>	28	<i>Gomphosus caeruleus</i>	2	<i>Scarus rubroviolaceus</i>	6
<i>Gomphosus caeruleus</i>	20	<i>Parupeneus macronema</i>	2	<i>Zebrasoma desjardini</i>	5
<i>Parupeneus barberinus</i>	17	<i>Scarus scaber</i>	2	<i>Caesio</i> spp.	4
<i>Acanthurus triostegus</i>	16	<i>Zebrasoma desjardini</i>	2	<i>Chlorurus atrilunula</i>	4
<i>Parupeneus bifasciatus</i>	14	<i>Chaetodon auriga</i>	1	<i>Hipposcarus harid</i>	4
<i>Stethojulis albivittata</i>	14	<i>Chaetodon trifasciatus</i>	1	<i>Thalassoma janseni</i>	4
<i>Acanthurus nigrofusus</i>	13	<i>Chaetodon xanthocephalus</i>	1	<i>Acanthurus xanthopterus</i>	3
<i>Scarus frenatus</i>	13	<i>Ctenochaetus strigosus</i>	1	<i>Hemigymmus melapterus</i>	3
<i>Halichoeres scapularis</i>	11	<i>Parupeneus bifasciatus</i>	1	<i>Lutjanus kasmira</i>	3
<i>Stethojulis trilineata</i>	7	<i>Parupeneus cyclostomus</i>	1	<i>Pterocaesio chrysozona</i>	3
<i>Thalassoma lunare</i>	6	<i>Scarus rubroviolaceus</i>	1	<i>Scarus russelli</i>	3
<i>Acanthurus auranticavus</i>	4	<i>Scarus russelli</i>	1	<i>Acanthurus nigricauda</i>	2
<i>Scarus ghobban</i>	4	<i>Scarus viridifucatus</i>	1	<i>Caesio teres</i>	2
<i>Halichoeres hortulanus</i>	3	<i>Zebrasoma scopas</i>	1	<i>Caranx melampygus</i>	2
<i>Halichoeres marginatus</i>	3	Acanthuridae (large)		<i>Gnathodentex aurolineatus</i>	2
<i>Parupeneus cyclostomus</i>	3	<i>Acanthurus auranticavus</i>	44	<i>Halichoeres scapularis</i>	2
<i>Scarus</i> spp.	3	<i>Zebrasoma desjardini</i>	37	<i>Lutjanus gibbus</i>	2
<i>Acanthurus leucosternon</i>	2	<i>Scarus prasiognathus</i>	16	<i>Mulloidichthys vanicolensis</i>	2
<i>Acanthurus</i> spp.	2	<i>Acanthurus nigricauda</i>	13	<i>Naso tuberosus</i>	2
<i>Cheilio inermis</i>	2	<i>Ctenochaetus striatus</i>	13	<i>Parupeneus bifasciatus</i>	2
<i>Chromis viridis</i>	2	<i>Chlorurus sordidus</i>	8	<i>Scarus ghobban</i>	2
<i>Mulloidichthys vanicolensis</i>	2	<i>Naso vlamingi</i>	7	<i>Scarus viridifucatus</i>	2
<i>Scarus viridifucatus</i>	2	<i>Scarus frenatus</i>	7	<i>Acanthurus auranticavus</i>	1
<i>Zebrasoma desjardini</i>	2	<i>Scarus ghobban</i>	7	<i>Bodianus axillaris</i>	1
<i>Acanthurus nigricauda</i>	1	<i>Acanthurus leucosternon</i>	6	<i>Caranx ignobilis</i>	1
<i>Bodianus diana</i>	1	<i>Scarus psittacus</i>	6	<i>Caranx</i> spp.	1
<i>Chaetodon trifascialis</i>	1	<i>Acanthurus xanthopterus</i>	5	<i>Chaetodon auriga</i>	1
<i>Cheilinus</i> spp.	1	<i>Scarus rubroviolaceus</i>	5	<i>Chaetodon citrinellus</i>	1
<i>Chlorurus atrilunula</i>	1	<i>Acanthurus nigrofusus</i>	4	<i>Chaetodon falcu</i>	1
<i>Macropharyngodon ornatus</i>	1	<i>Parupeneus barberinus</i>	4	<i>Chaetodon meyeri</i>	1
<i>Monacanthus</i> spp.	1	<i>Chlorurus atrilunula</i>	3	<i>Chlorurus enneacanthus</i>	1
<i>Naso vlamingi</i>	1	<i>Hipposcarus harid</i>	3	<i>Chlorurus sordidus</i>	1
<i>Scarus niger</i>	1	<i>Siganus argenteus</i>	3	<i>Ctenochaetus striatus</i>	1
<i>Scarus prasiognathus</i>	1	<i>Naso lituratus</i>	2	<i>Gobi wrasse</i>	1
<i>Scarus rubroviolaceus</i>	1	<i>Siganus</i> spp.	2	<i>Hemiaurichthys zoster</i>	1
<i>Siganus</i> spp.	1	<i>Acanthurus triostegus</i>	1	<i>Lethrinus</i> spp.	1
<i>Thalassoma hardwicke</i>	1	<i>Cephalopholis argus</i>	1	<i>Lutjanus monostigma</i>	1
<i>Zebrasoma scopas</i>	1	<i>Cetoscarus bicolor</i>	1	<i>Mulloidichthys flavolineatus</i>	1
Acanthuridae (small)		<i>Gomphosus caeruleus</i>	1	<i>Naso annulatus</i>	1
<i>Ctenochaetus striatus</i>	16	<i>Parupeneus bifasciatus</i>	1	<i>Naso brachycentron</i>	1
<i>Acanthurus nigrofusus</i>	14	<i>Scarus scaber</i>	1	<i>Parupeneus barberinus</i>	1
<i>Chlorurus sordidus</i>	9	<i>Scarus</i> spp.	1	<i>Elagatis bipinnulata</i>	1
<i>Scarus psittacus</i>	6	<i>Zebrasoma scopas</i>	1	<i>Scarus tricolor</i>	1
<i>Acanthurus auranticavus</i>	5			<i>Scolopsis bilineatus</i>	1
<i>Acanthurus leucosternon</i>	5			<i>Siganus argenteus</i>	1
<i>Acanthurus triostegus</i>	4			<i>Sufflamen bursa</i>	1
				<i>Thalassoma lunare</i>	1

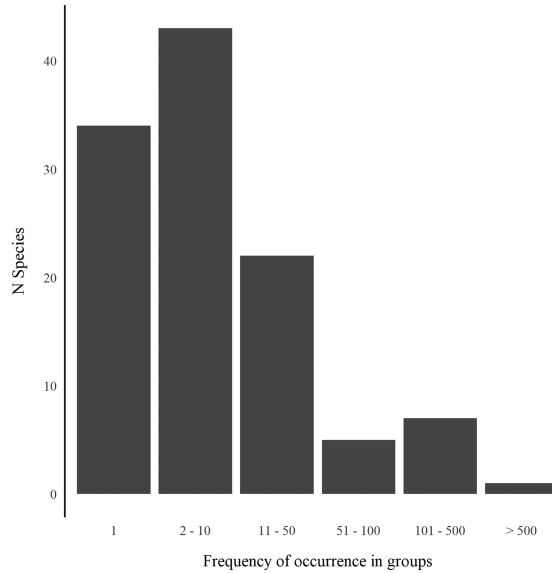


Figure 2. Species sorted by the total number of groups that they occurred in. The y-axis indicates the number of species.

the adults (juveniles tended to group with other juveniles rather than adults and were sometimes joined by goatfish of similar size classes) and binning them together might obfuscate the results.

The Scaridae, Acanthuridae (small), Acanthuridae (large), Labridae, and *Anampses* groups cluster separately within the dendrogram. The groups of juveniles, although comprised predominantly of parrotfish species, vary in species composition enough to cluster separately from the parrotfish groups (Fig. 4). The groups involving the goatfish species are distinct from the other clusters. While the *P. barberinus* and the *P. macronema* groups do segregate, they do not separate out clearly among themselves, likely due to similarities in the species that associate with goatfish. However, we chose to treat these compositional categories separately for the subsequent analysis because, although compositionally similar, they did show distinct behavioral differences. The compositional categories that the groups were divided into are henceforth referenced by the name of the primary species/family within these groups. Most of the groups we observed fell into one of these nine compositional categories, comprising 93.4% of the 1289 groups observed.

BEHAVIORAL CATEGORIES.—The groups were further categorized based on their behavior into following-and-scavenging groups, joint-hunting groups, and shoaling groups (Fig. 5A). Each compositional category showed distinct behavior. The Scaridae, juvenile, and Acanthuridae groups were almost exclusively shoaling groups. Groups comprised of wrasses and *Anampses* spp. were also predominantly shoaling groups; however, these compositional categories also showed a high incidence of attendant associations. *Parupeneus barberinus* were mostly in following-and-scavenging associations, usually followed by various species of wrasses. *Halichoeres hortulanus* (checkerboard wrasse) and *Halichoeres scapularis* (zigzag wrasse) were seen grouping

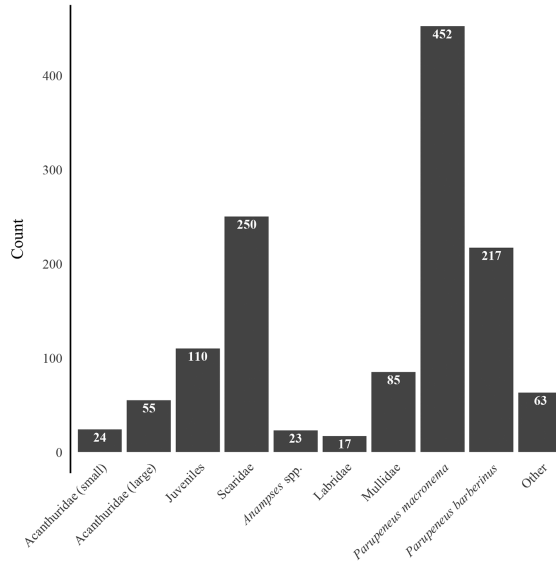


Figure 3. Number of groups within each compositional category.

with *P. barberinus* most frequently. *Parupeneus macronema* and the pooled goatfish species groups showed similar patterns of predominantly joint-hunting associations followed by following-and-scavenging and shoaling. These associations were also primarily between goatfish and wrasses. The proportion of behavioral categories varied significantly across compositional categories (Fisher's Exact test: $P < 0.05$). The groups of herbivores, Scaridae, Acanthuridae, juvenile groups, and the wrasse (Labridae) groups did not show much difference with each other (Online Table S1).

GROUP COHESION SIZE AND HABITAT AFFINITY.—The compositional categories also showed variations in parameters such as group cohesion and habitat affinity. The highest group cohesiveness was seen in Acanthuridae (small), *P. macronema*, *P. barberinus*, and other goatfish groups (Fig. 5B). Other groups exhibited a mixture of tight, intermediate, loose, and variable group cohesiveness with no patterns readily discernible (Online Table S2).

To clarify patterns, we conducted a similar analysis on groups based on the behavioral categories. We compared group cohesion between following-and-scavenging groups, joint-hunting groups, and shoaling groups pooling across compositional categories. Joint-hunting and following-and-scavenging groups were similar (Fig. 6) in terms of group cohesion, with large numbers of tight groups. However, all three behavioral categories varied significantly from each other ($P < 0.05$; Online Table S3). Shoaling groups also tended to be much larger than attendant groups [mean (shoaling) = 48.41, mean (attendant) = 2.79; Welch two sample t -test: $t = 7.4016$, $P < 0.001$].

The compositional categories also differed in the types of habitats that they occurred in. The *Anampses* and juvenile groups occurred almost exclusively in the reef and lagoon, respectively (Fig. 5C). The Scaridae and *P. barberinus* groups had similar habitat affinity (Fisher's exact test: $P = 0.637$; Online Table S4) and were

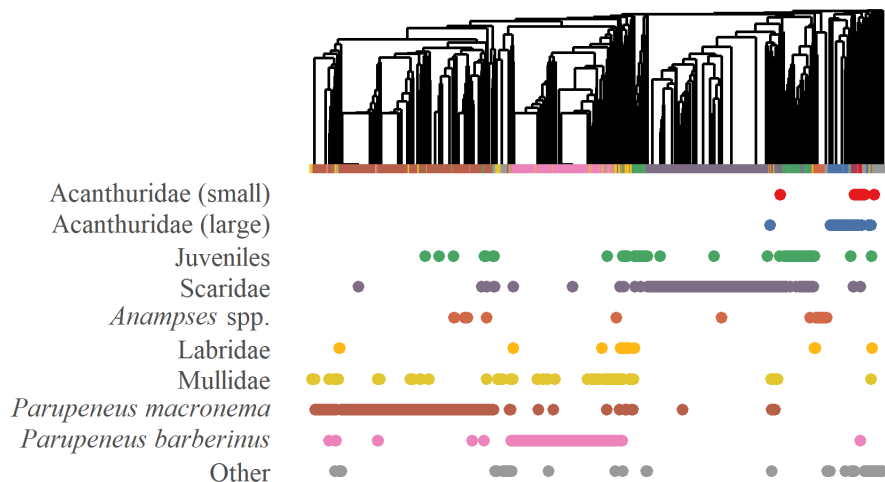


Figure 4. Groups clustered based on similarity of their species composition. The groups are assigned a category based on the dominant/nuclear species in the group and the distribution of these within the dendrogram is indicated below it.

found mostly in the lagoons. The other groups (Acanthuridae, Labridae, *Anampses* and *P. macronema*) were more frequently seen in reef habitats.

DISCUSSION

GROUPING PATTERNS IN HERBIVORES.—Here, we present the first comprehensive quantification of groups in mixed foraging groups of reef fishes based on species composition. Among herbivores, parrotfish and juveniles were seen grouping largely in the lagoon whereas surgeonfish groups were found mostly on reefs (Fig. 5C). The difference in occurrence between habitat types is possibly reflective of species abundances in these habitats. The existence of compositionally distinct groups, however, is likely not just a function of habitat since the species do overlap in habitat, differing only in abundance. Most shoaling groups we observed were also composed of similarly sized individuals, which would contribute to uniformity within the shoal. This would be beneficial if these groups were forming for antipredation benefits, as visually distinct individuals are more likely to be targeted by predators (known as the oddity effect; Alevizon 1976, Landeau and Terborgh 1986). This suggests that these fishes exhibit a preference for the species they associate with, likely based on size or other aspects of morphology.

Following the categorization of Goodale et al. (2020), shoaling groups can be viewed as supplementary groups in which the benefits gained are additive and dependent on group size. Most antipredation benefits such as the dilution effect (Foster and Treherne 1981), many eyes effect (Pulliam 1973), confusion effect (Neill and Cullen 1974), and encounter effect (Inman and Krebs 1987) are of a supplementary nature. Foraging benefits, accrued by herbivore groups due to the overwhelming of a territorial fish's defenses is also a form of supplementary benefit, gained through increasing group size. Several studies have demonstrated that larger groups have higher success feeding in defended territories compared to smaller groups (Barlow 1974, Robertson

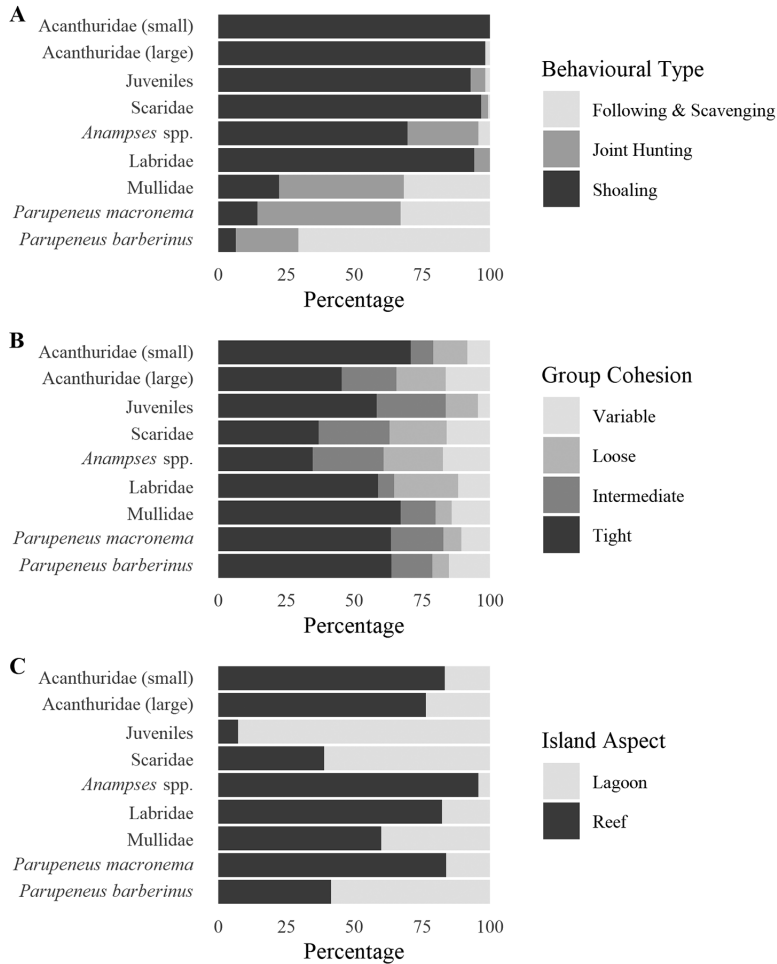


Figure 5. (A) Behavioral categories within each compositional category as a percentage of the total number of groups. (B) Group cohesion represented as a percentage of the total number of groups of each compositional category. (C) Habitat type within which the groups appeared represented as a percentage of the total number of groups.

et al. 1976, Wolf 1983, Foster 1985a). It is therefore likely that the shoaling groups we observed—which were usually comprised of either herbivores or smaller wrasses—likely form for antipredation benefits and, in the case of the herbivores, potentially in response to territorial food competitors.

Fewer surgeonfish groups were observed relative to other groups [surgeonfish (small) = 28 groups, surgeonfish (large) = 89 groups]. These groups also tended to segregate along size as smaller bodied species and larger bodied species generally grouped separately. While most of the species observed in these groups have not been reported in mixed-groups previously, there have been several reports of groups analogous to these from other areas (Barlow 1974, Alevizon 1976, Robertson et al. 1976, Foster 1985b). The most commonly seen smaller bodied species included *C. striatus* (striated surgeonfish; maximum length = 26 cm) and *A. nigrofuscus* (brown

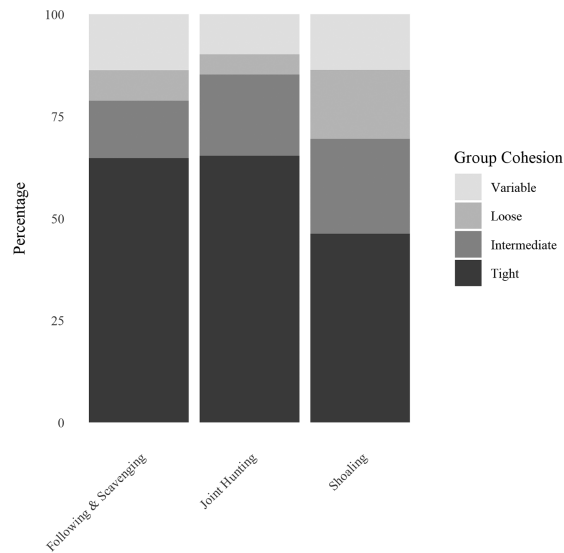


Figure 6. Group cohesion represented as a percentage of the total number of groups of each behavioral category.

surgeonfish; maximum length = 21 cm). The larger bodied surgeonfish groups were usually made up of either *A. auranticavus* (orange socket surgeonfish; maximum length = 45 cm) or *A. nigricauda* (epaulette surgeonfish; maximum length = 40 cm) present in larger numbers accompanied by 2–3 individuals of *Zebrasoma desjardini* (Desjardin's sailfin tang; maximum length = 40 cm). The powder-blue tang, *Acanthurus leucosternon* (maximum length = 54 cm, common length = 19 cm) was found in groups with both large and smaller bodied surgeonfish. These groups were occasionally accompanied by other species of surgeonfish, parrotfish, goatfish, and wrasses. Similar groups in the literature have been hypothesized to form for either antipredation benefits (Alevizon 1976) or for gaining access to defended resources (Barlow 1974, Wolf 1983, Foster 1985b).

The parrotfish groups we observed have not been previously reported. Three species of parrotfish—*C. sordidus* (bullethead parrotfish), *S. psittacus* (palenose parrotfish), and *Scarus globiceps* (violet-lined parrotfish)—were commonly seen in shoaling groups ranging in size from two to hundreds of individuals. On one occasion, a group containing nearly 2000 individuals was recorded. The groups usually consisted of initial phase (female) individuals; although terminal phase males were occasionally observed in groups, they were usually far fewer in number. While the terminal phase males of *C. sordidus* have been recorded in groups with the wrasse *Epibulus insidiator* (Ormond 1980), shoaling groups of the initial phase females are unheard of. In the initial phase, these three species are very similar in appearance, usually plainly colored varying from a dull brown to pale grey. The initial phase females of the species *C. sordidus* are the most distinct among the three, with small white dots in two rows along their sides as well as a lighter colored caudal peduncle with a dark spot. However, these features are highly plastic and at times absent altogether. Individuals of the species *C. sordidus* have been observed changing their appearance when in mixed-species groups (A Theo, Indian Institute of Science, pers observ)

Table 2. Number of groups detected of each compositional group.

Compositional groups	Frequency	Common name	Feeding habit
Acanthuridae (small)	24	Surgeonfish	Herbivore
Acanthuridae (large)	55	Surgeonfish	Herbivore
Juveniles	110	Parrotfish	Herbivore
Scaridae	248	Parrotfish	Herbivore
<i>Anampses</i> spp.	23	Wrasse	Invertivore
Labridae	17	Wrasse	Invertivore
Mullidae	39	Goatfish	Invertivore
<i>Parupeneus macronema</i>	450	Goatfish	Invertivore
<i>Parupeneus barberinus</i>	216	Goatfish	Invertivore

potentially in order to blend in with their heterospecific counterparts. This suggests that these shoals may be forming for antipredation benefits, since the odd individuals are more likely to be targeted by predators in an attack (Wolf 1985, Landeau and Terborgh 1986). These groups were often accompanied by other species (usually wrasses, goatfish, surgeonfish, and other parrotfish). Parrotfish groups were one of the most commonly seen groups (248 groups observed in total; Table 2). They were usually found within patch reefs in the lagoon and shallow reef flats. These groups tended to be short-lived and dynamic; in many cases, the groups divided or coalesced with new groups frequently and repeatedly.

Juveniles of several species of parrotfish, surgeonfish, goatfish, and occasionally wrasses were frequently seen in mixed-groups in the lagoon (138 groups observed). These groups were primarily composed of parrotfish juveniles (*C. sordidus*, *Scarus scaber*, *Scarus frenatus*). Small-sized individuals of *P. macronema* were often seen in these groups; the goatfish, however, tend to be present in smaller numbers compared to the parrotfish. There are several possible explanations as to why juveniles differ in grouping behavior from adults: they may prefer to group with similar sized individuals or they differ from adults in feeding habit, energy budget, or range size and, therefore, prefer to group with individuals with similar requirements (Overholtzer and Motta 2000, Sazima 2002).

GROUPING PATTERNS IN INVERTIVORES.—Among invertivores, although most commonly seen in attendant groups, wrasses were sometimes also observed in shoaling associations. The species seen in shoaling groups tended to be smaller bodied, the most frequently observed species being *Stethojulis albovittata*, *Macropharygodon ornatus*, *Anampses lineatus*, *Anampses meleagrides*, and *Gomphosus caeruleus*. These groups were also frequently accompanied by *P. macronema* of a similar size class. A meta-analysis of grouping in birds (Sridhar et al. 2012) concluded that species with life history traits that made them more susceptible to predation (such as smaller body size) tended to participate in mixed-groups more. A similar mechanism may be at play here as well.

Invertivores in our dataset most commonly formed attendant groups, which were either following-and-scavenging or joint-hunting groups. These groups are representative of complementary groups, as defined by Goodale et al. (2020). Complementary groups tend to form between dissimilar species, where both the nature and quantity of benefits received or given may vary and may be tied to the species identity of the group members.

A prime example of this type of group would be the groups formed around the goatfish *Parupeneus barberinus*. This species is one of the most well-known nuclear species among reef fishes (Lukoschek and McCormick 2000, Krajewski 2009). It forages primarily on sandy substrates, probing the sand for invertebrates using its barbels. This causes a substantial amount of disturbance, which flushes out invertebrates hidden in the substrate. This disturbance is used as a cue by several species of wrasses that form following-and-scavenging groups with the goatfish in order to capitalize on the newly available resource (Krajewski 2009). The wrasses *H. hortulanus* and *H. scapularis* were the most frequent followers of *P. barberinus*. Despite frequently serving as a nuclear species, it is unknown if *P. barberinus* receives any benefit within these groups. Given that it is rarely seen in a follower role or in other types of groups, this seems unlikely. These groups were, unsurprisingly, most commonly seen in the sandy habitat of the lagoon.

Some of the most commonly observed species in the nuclear role have been goatfish (Lukoschek and McCormick 2000, Sazima et al. 2007, Krajewski 2009). This pattern was corroborated in our data, with the observation of six species of goatfish as nuclear species. Of these, the most abundant were *P. barberinus* and *P. macronema*. These two species are strikingly similar visually, but have vastly different grouping behaviors. Although both species formed groups with many of the same species of wrasses, *P. macronema* usually formed joint-hunting groups and was frequently observed initiating grouping and following wrasses. This is in line with previous studies, where *P. macronema* has been reported in joint-hunting groups with *Gomphosus caeruleus* (Ormond 1980). We, however, recorded this goatfish associating with many more species as well as present in behavioral categories other than joint hunting. This species exhibited remarkable plasticity in grouping behavior, present in not only following-and-scavenging and joint-hunting groups, but also in shoaling groups with both wrasses as well as parrotfish and occasionally in shoaling groups of its own with up to 40 *P. macronema* individuals, accompanied by one or two wrasses. The incidence of *P. macronema* groups was higher in the reefs, likely due to its preference for rubble and rocky substrate. Goatfish belonging to species other than *P. macronema* and *P. barberinus* were also observed in groups, though far less frequently (81 groups; Table 2) and were categorized as other goatfish groups. These groups are similar in patterns of group cohesion and behavioral categorization to the *P. macronema* groups.

One notable association that was not highlighted in the cluster analysis because it was observed only nine times is the following-and-scavenging association between wrasses and parrotfish. In these groups, wrasses (either *H. hortulanus* or *Thalassoma jansenii*) were seen following large individuals (>30 cm), usually terminal stage males of the parrotfish species *Chlorurus strongylocephalus*. The wrasses would follow the foraging parrotfish for short periods of time, potentially feeding off invertebrates flushed out by the disturbance created by the parrotfish.

The most striking pattern among the compositional categories was the difference in the behavior of the groups. Herbivores (surgeonfish, parrotfish, and juvenile groups) were almost always shoaling associations while the invertivores were found primarily in attendant groups (Fig. 5A). When group cohesion among the three behavioral categories was compared, joint-hunting and following-and-scavenging groups were similar in the percentages of the group cohesion categories, with most groups falling within the tight or intermediate levels (Fig. 6), and both varied significantly from

shoaling groups, which had larger numbers of loose associations. It is likely that attendant groups form for foraging benefits and therefore it is necessary for individuals to maintain close proximity to each other in order to receive benefits (Lukoschek and McCormick 2000, Krajewski 2009).

CONCLUSION

Our study provides a comprehensive description of mixed-species groups found in the Lakshadweep Archipelago. We discovered that mixed-species grouping is a common occurrence in these islands, with a large diversity of species. We also found that groups tended to segregate based on species composition and most species grouped with only a subset of the species available for grouping (as evidenced by the separation of groups based on species composition). The compositional categories also varied in terms of behavior, group cohesion, and habitat affinity. Invertivores such as goatfish and wrasses were usually seen participating in attendant groups, while herbivores and sometimes smaller species of wrasses were seen in shoaling groups. This suggests that different guilds in the reef ecosystem may have varying drivers for grouping. Given that the potential costs and benefits may vary across group types (Goodale et al. 2020), we suggest that the compositional categories be studied separately when attempting to address these questions in the future.

ACKNOWLEDGMENTS

We thank the Council of Scientific and Industrial Research, Government of India, IdeaWild, and PADI Foundation for financial support towards the project and the Lakshadweep Department of Environment and Forests and the Lakshadweep Department of Science and Technology for the study permits at Lakshadweep islands. We thank the Dakshin Foundation and Nature Conservation Foundation for access to their field stations. We would also like to thank Mahima Jaini, Rucha Karkarey, Shwetha Nair, and the field staff for aiding with the data collection, Guillaume Demare for the graphs and Hari Sridhar for his advice on this paper and the project. We would like to thank Ommuni, Anwar, and Jafar from Lakshadweep for assisting with logistics in the field.

LITERATURE CITED

- Alevizon WS. 1976. Mixed schooling and its possible significance in a tropical western atlantic parrotfish and surgeonfish. *Copeia*. (4):796–798. <https://doi.org/10.2307/1443464>
- Araújo ME, Pereira PHCC, Feitosa JLLL, Gondolo G, Pimenta D, Nottingham MC. 2009. Feeding behavior and follower fishes of *Myrichthys ocellatus* (Anguilliformes: Ophichthidae) in the western Atlantic. *Neotrop Ichthyol*. 7(3):503–507. <https://doi.org/10.1590/S1679-62252009000300019>
- Aronson RB. 1983. Foraging behavior of the west Atlantic trumpetfish, *Aulostomus maculatus*: use of large, herbivorous reef fishes as camouflage. *Bull Mar Sci*. 33(1):166–171.
- Arthur R. 2004. Patterns and processes of reef recovery and human use in the Lakshadweep Islands, Indian Ocean. PhD Thesis. Townsville: James Cook University.
- Arthur R, Done TJ, Marsh H, Harriott V. 2006. Local processes strongly influence post-bleaching benthic recovery in the Lakshadweep Islands. *Coral Reefs*. 25(3):427–440. <https://doi.org/10.1007/s00338-006-0127-4>
- Baird TA. 1993. A new heterospecific foraging association between the puddingwife wrasse, *Halichoeres radiatus*, and the bar jack, *Caranx Tuber*: evaluation of the foraging consequences. *Env Biol Fishes*. 38(4):393–397. <https://doi.org/10.1007/BF00007535>

- Barlow GW. 1974. Extraspecific imposition of social grouping among surgeon fishes (Pisces: Acanthuridae). *J Zool.* 174:333–340. <https://doi.org/10.1111/j.1469-7998.1974.tb03161.x>
- Bertram B. 1978. Living in groups: predators and prey. *In*: Krebs JR, Davies NB, editors. *Behavioural ecology: an evolutionary approach*. Oxford: Blackwell Scientific Publications. p. 64–96.
- Dafni J, Diamant A. 1984. School-oriented mimicry, a new type of mimicry in fishes. *Mar Ecol Prog Ser.* 20:45–50. <https://doi.org/10.3354/meps020045>
- Ehrlich PR, Ehrlich AH. 1973. Coevolution: heterotypic schooling in Caribbean reef fishes. *Am Nat.* 107(953):157–160. <http://www.jstor.org/stable/2459572>
- Fitzgibbon CD. 1990. Mixed-species grouping in Thompson's and Grant's gazelles: the antipredator benefits. *Anim Behav.* 39:1116–1126. [https://doi.org/10.1016/S0003-3472\(05\)80784-5](https://doi.org/10.1016/S0003-3472(05)80784-5)
- Forsythe JW, Hanlon RT. 1997. Foraging and associated behavior by *Octopus cyanea* Gray, 1849 on a coral atoll, French Polynesia. *J Exp Mar Biol Ecol.* 209:15–31. [https://doi.org/10.1016/S0022-0981\(96\)00057-3](https://doi.org/10.1016/S0022-0981(96)00057-3)
- Foster SA. 1985a. Size-dependent territory defense by a damselfish. *Oecologia.* 67(4):499–505. <https://doi.org/10.1007/BF00790020>
- Foster SA. 1985b. Group foraging by a coral reef fish: a mechanism for gaining access to defended resources. *Anim Behav.* 33(3):782–792. [https://doi.org/10.1016/S0003-3472\(85\)80011-7](https://doi.org/10.1016/S0003-3472(85)80011-7)
- Foster SA. 1987. Acquisition of a defended resource: a benefit of group foraging for the neotropical wrasse, *Thalassoma lucasanum*. *Environ Biol Fishes.* 19(3):215–222. <https://doi.org/10.1007/BF00005350>
- Foster WA, Treherne JE. 1981. Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature.* 293:466–467. <https://doi.org/10.1038/293466a0>
- Galili T. 2015. dendextend: an R package for visualizing, adjusting and comparing trees of hierarchical clustering. *Bioinformatics.* 31(22):3718–3720. <https://doi.org/10.1093/bioinformatics/btv428>
- Gibran FZ. 2002. The sea basses *Diplectrum formosum* and *D. radiale* (Serranidae) as followers of the sea star *Luidia senegalensis* (Asteroidea) in southeastern Brazil. *Braz J Biol.* 62(4A):591–594. <https://doi.org/10.1590/S1519-69842002000400005>
- Goodale E, Sridhar H, Sieving KE, Bangal P, Colorado ZGJ, Farine DR, Heymann EW, Jones HH, Krams I, Martínez AE, et al. 2020. Mixed company: a framework for understanding the composition and organization of mixed-species animal groups. *Biol Rev Camb Philos Soc.* 95:889–910. <https://doi.org/10.1111/brv.12591>
- Hodge MA, Uetz GW. 1992. Antipredator benefits of single- and mixed-species grouping by *Nephila clavipes* (L.) (Araneae, Tetragnathidae). *J Arachnol.* 20(3):212–216.
- Inman AJ, Krebs J. 1987. Predation and group living. *Trends Ecol Evol.* 2(2):31–32. [https://doi.org/10.1016/0169-5347\(87\)90093-0](https://doi.org/10.1016/0169-5347(87)90093-0)
- Krajewski JP. 2009. How do follower reef fishes find nuclear fishes? *Environ Biol Fishes.* 86(3):379–387. <https://doi.org/10.1007/s10641-009-9533-0>
- Landeau L, Terborgh J. 1986. Oddity and the 'confusion effect' in predation. *Anim Behav.* 34(5):1372–1380. [https://doi.org/10.1016/S0003-3472\(86\)80208-1](https://doi.org/10.1016/S0003-3472(86)80208-1)
- Leitão RP, Caramaschi ÉP, Zuanon J. 2007. Following food clouds: feeding association between a minute loricariid and a characidiin species in an Atlantic Forest stream, Southeastern Brazil. *Neotrop Ichthyol.* 5(3):307–310. <https://doi.org/10.1590/S1679-62252007000300011>
- Lukoschek V, McCormick MI. 2000. A review of multi-species foraging associations in fishes and their ecological significance. Bali, Indonesia: Proceedings of the 9th International Coral Reef Symposium. 1:467–474.
- Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K. 2019. cluster: cluster analysis basics and extensions. Available from: <https://CRAN.R-project.org/package=cluster>
- Morse DH. 1977. Feeding behavior and predator avoidance in heterospecific groups. *Bioscience.* 27(5):332–339. <https://doi.org/10.2307/1297632>
- Neill SRJ, Cullen JM. 1974. Experiments on whether schooling by their prey affects the hunting behavior of cephalopods and fish predators. *J Zool.* 172(4):549–569. <https://doi.org/10.1111/j.1469-7998.1974.tb04385.x>

- Noë R, Bshary R. 1997. The formation of red colobus–Diana monkey associations under predation pressure from chimpanzees. *Proc Biol Sci.* 264:253–259. <https://doi.org/10.1098/rspb.1997.0036>
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, et al. 2019. *vegan*: community ecology package. Available from: <https://cran.r-project.org/package=vegan>
- Ormond RFG. 1980. Aggressive mimicry and other interspecific feeding associations among Red Sea coral reef predators. *J Zool.* 191(2):247–262. <https://doi.org/10.1111/j.1469-7998.1980.tb01458.x>
- 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. <https://doi.org/10.1023/A:1007630118383>
- Pajmians KC, Booth DJ, Wong MYL. 2019. Towards an ultimate explanation for mixed-species shoaling. *Fish Fish.* 20:921–933. <https://doi.org/10.1111/faf.12384>
- Psarakos S, Herzog DL, Marten K. 2003. Mixed-species associations between Pantropical spotted dolphins (*Stenella attenuata*) and Hawaiian spinner dolphins (*Stenella longirostris*) off Oahu, Hawaii. *Aquat Mamm.* 29:390–395. <https://doi.org/10.1578/01675420360736578>
- Pulliam HR. 1973. On the advantages of flocking. *J Theor Biol.* 38(2):419–422. [https://doi.org/10.1016/0022-5193\(73\)90184-7](https://doi.org/10.1016/0022-5193(73)90184-7)
- R Core Team. 2019. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Available from: <https://www.R-project.org/>
- Robertson DR, Sweatman HPA, Fletcher EA, Cleland MG. 1976. Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology.* 57(6):1208–1220. <https://doi.org/10.2307/1935045>
- Sazima C, Grossman A. 2005. A non-digging zoobenthivorous fish attracts two opportunistic predatory fish associates. *Neotrop Ichthyol.* 3(3):445–448. <https://doi.org/10.1590/S1679-62252005000300014>
- Sazima C, Krajewski JP, Bonaldo RM, Sazima I. 2007. Nuclear-follower foraging associations of reef fishes and other animals at an oceanic archipelago. *Environ Biol Fishes.* 80(4):351–361. <https://doi.org/10.1007/s10641-006-9123-3>
- Sazima I. 2002. Juvenile snooks (Centropomidae) as mimics of mojarras (Gerreidae), with a review of aggressive mimicry in fishes. *Environ Biol Fishes.* 65:37–45. <https://doi.org/10.1023/A:1019654721236>
- Sridhar H, Beauchamp G, Shanker K. 2009. Why do birds participate in mixed-species foraging flocks? A large-scale synthesis. *Anim Behav.* 78(2):337–347. <https://doi.org/10.1016/j.anbehav.2009.05.008>
- Sridhar H, Srinivasan U, Askins RA, Canales-Delgadillo JC, Chen C-C, Ewert DN, Gale GA, Goodale E, Gram WK, Hart PJ, et al. 2012. Positive relationships between association strength and phenotypic similarity characterize the assembly of mixed-species bird flocks worldwide. *Am Nat.* 180(6):777–790. <https://doi.org/10.1086/668012>
- Strand S. 1988. Following behavior: interspecific foraging associations among Gulf of California reef fishes. *Copeia.* (2):351–357. <https://doi.org/10.2307/1445875>
- Ward AJW, Schaerf TM, Burns ALJ, Lizier JT, Crosato E, Prokopenko M, Webster MM. 2018. Cohesion, order and information flow in the collective motion of mixed-species shoals. *R Soc Open Sci.* 5(12):181132. <https://doi.org/10.1098/rsos.181132>
- Wickler W. 1965. Mimicry and the evolution of animal communication. *Nature.* 208(5010):519–521. <https://doi.org/10.1038/208519a0>
- Wolf NG. 1983. Foraging ecology of herbivorous reef fishes in mixed-species groups. *Am Zool.* 23:985.
- Wolf NG. 1985. Odd fish abandon mixed-species groups when threatened. *Behav Ecol Sociobiol.* 17(1):47–52. <https://doi.org/10.1007/BF00299428>



