Size assortment in mixed-species groups of juvenile-phase striped parrotfish (Scarus iserti) in The Bahamas

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Abstract Striped parrotfish (Scarus iserti) often form heterospecific groups with other reef fishes. In this study, we examined the species and body size composition of these groups on reefs in The Bahamas. Groups averaged approximately 4 S. iserti and 2 associated species, with surgeonfish (Acanthurus chirurgus and A. bahianus), slippery dick (Halichoeres bivittatus), and bluehead wrasse (Thalassoma bifasciatum) as the most common associates. Fewer groups than expected had only 1 associate; groups with 3 or more associates were more common than expected. Both the S. iserti and associated species tended to be closely sizematched within a group, perhaps due to benefits of size assortment in lowering predation risk. Likewise, the high frequency of groups with greater than a single associate species suggests that associates may benefit from not being the only phenotypically different individual in a group.

Keywords Scarus iserti, Mixed-species shoals, Group Behavior, Predation risk, Size assortment

Introduction

Scarus iserti (striped parrotfish) is a common member of the reef fish community in The Bahamas (Humann and DeLoach 2002) and throughout the Caribbean (Ogden and Buckman 1973; Wolf 1985). The juvenile (i.e., striped) phase of this species forms aggregations that sometimes include other species of reef fish (Ogden and Buckman 1973; Wolf 1985). This heterospecific grouping behavior (also known as ‘‘mixed-species shoaling’’) is common in reef fish, suggesting that there are multiple benefits associated with this intriguing behavior (Alevizon 1975; Robertson et al. 1976). Such benefits may include increased foraging efficiency (Wolf 1987; Overholtzer and Motta 2000), decreased vulnerability to predators (e.g., Ehrlich and Ehrlich 1973; Wolf 1985), and benefits associated with circumventing local territorial fishes (e.g., Robertson et al. 1976).

For species found in mixed-species shoals, there may be a preference to associate with relatively homogenous, similar-sized group members (Ehrlich and Ehrlich 1973; Krause et al. 1996; Peuhkuri 1999; Crook 1999). This preferred uniformity promotes the antipredatory response commonly known as the ‘‘confusion effect’’ and reduces the ‘‘oddity effect’’ (Mueller 1971), in which a phenotypically dissimilar individual in a group may be more likely to be targeted by predators (e.g., Landeau and Terborgh 1986; Theodorakis 1989). For S. iserti, however, the common, heterospecific associates often differ greatly in color and body shape (Wolf 1985).

For our study, we investigated groups of juvenile-phase S. iserti and their heterospecific associates near Andros Island in The Bahamas. Specifically, we describe group composition in terms of species, group size, and the size of members, and use these data to address whether individuals tend to associate with phenotypically similar individuals when forming groups.

Materials and methods

Study sites

We collected data at nine reef locations off the northeast coast of Andros Island, The Bahamas (24 ° 580N, 77 ° 450W).

These included three patch reefs and four locations on the barrier reef. The Andros Island barrier reef system is the third longest barrier reef in the world. Water depth at our study sites varied between 1.5 and 3.5 m.

Field techniques

We located and recorded data on striped parrotfish groups while snorkeling between 29 May and 4 June 2009. Time of day for observations varied between 1000 and 1630 hours.A group was defined as any Scarus iserti with or without associated species (hereafter ''associates''); therefore, a single S. iserti would be a group of size 1. To be considered ''grouped'' with another fish, an individual had to remain within 0.5 mof another member of the group and travel with the group for at least 2 m and for a minimum of 30 s. Preliminary observations confirmed that these criteria were sufficient to document group membership appropriately. Based on these criteria, we recorded the number and lengths (i.e., total body length) of both S. iserti and associates in each group we encountered. Photographs were taken of all groups to confirm field identifications and to aid in determining length relationships. In addition, we lowered a weighted, 10-cm section of polyvinylchloride (PVC) pipe near most groups as a length standard. We assumed that total body length was a useful surrogate of overall size. Associates included the following species/taxa: surgeonfish (which included both Acanthurus chirurgus and A. bahianus), blue tang (A. coeruleus), slippery dick (Halichoeres bivittatus), spotted goatfish (Pseudupeneus maculatus), stoplight parrotfish (Sparisoma viride), redband parrotfish (Sparisoma aurofrenatum), redtail parrotfish (Sparisoma chrysopterum), and bluehead wrasse (Thalassoma bifasciatum).

Data analysis

For descriptive information on groups, we used data from all sites. However, for our tests of hypotheses, we only considered groups from locations on the barrier reef in order to standardize the associate pool. We used chi-square analysis to compare the observed distribution of the number of associates per group with what would be expected if individuals were randomly distributed among groups of different sizes (with the random expectation represented by a Poisson distribution). Spearman's rank correlation was used to determine the relationship between the mean length of associates and mean length of S. iserti from the same group. Finally, we used resampling techniques to compare size variability among S. iserti within each group versus randomly generated groups (same number in group) drawn from all S. iserti at that site. Statistics 101 was used to generate 10,000 random groups for each of our parrotfish groups. For each random group, we calculated the variance in length and compared the 10,000 variances with the actual variance. The percentage of those random groups that had lower variance than the observed group was then taken as the exact P value.

Results

We observed 63 groups on the various reefs, with groups averaging 4.3 ± 0.3 Scarus iserti (range 1–12); 4–6 S. iserti was the most frequent group size (Fig. 1). Groups averaged 1.8 ± 0.2 associate species (range 0–7), and total group size (S. iserti ? associates) averaged 6.1 ± 0.4 individuals (range 1–14) fish. The three most commonly associated species were Acanthurus sp. (46% of S. iserti groups), H. bivittatus (19% of groups), and T. bifasciatum (14% of groups). No other species was present in more than 8% of groups.

Analyzing groups from the main reef, the number of associates per group was not uniformly distributed. More groups had zero associates and 3 or more associates, and fewer groups had 1 or 2 associates, than expected by chance (Fig. 2 ; **v**2 = 16.2, df = 3, P\ 0.01). Scarus iserti groups that had associates did not have more S. iserti individuals than groups without associates (mean/median number of S. iserti with associates: 4.2 ± 0.4/4.0 individuals, N = 31, mean/median without associates: 4.0 ± 0.7/4.5 individuals, N = 16; Mann–Whitney U = 226.5, P = 0.62). Scarus iserti groups with associates tended to have smaller-sized individuals (10.1 ± 0.5 cm, N = 31) than groups without associates (11.8 ± 1 cm, N = 16), but this difference was not significant (t = 1.69, df = 45, P = 0.098).

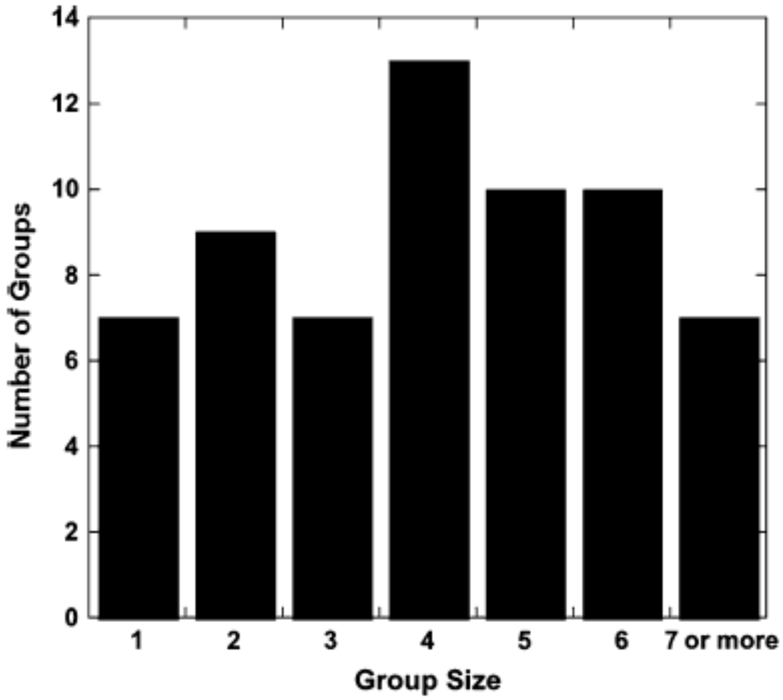

Fig. 1 Frequency distribution for the numbers of individuals in Scarus iserti groups from all reefs

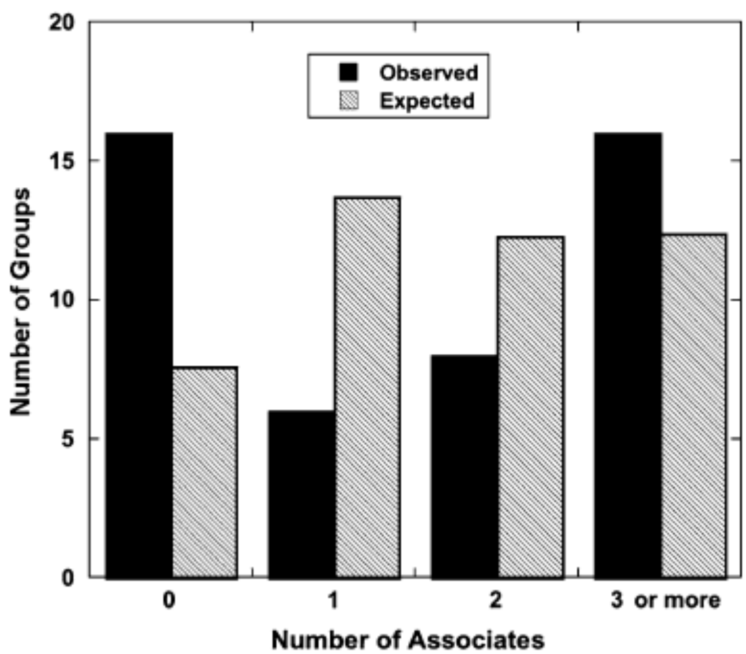

Fig. 2 Frequency distribution for the number of associates per Scarus iserti group as compared with the expected frequency via a random (Poisson) distribution (x2 = 16.2, df = 3, P<0.01). The sample represents groups from the main reef

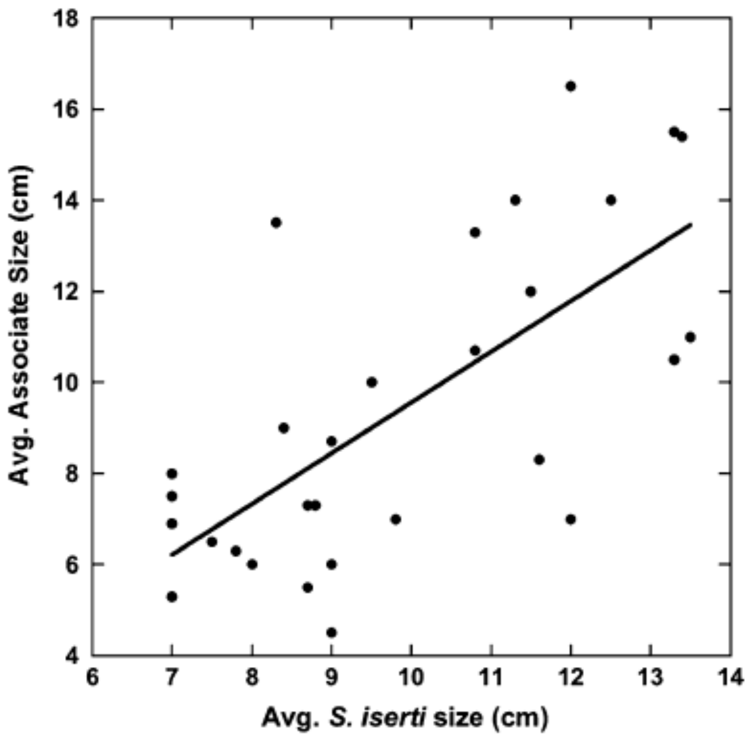

Fig. 3 Relationship between the average size of Scarus iserti individuals in a group and the average size of the associates in that group (N = 29 groups) (Spearman, rs = 0.64, z = 3.41, P<0.001). The sample represents groups from the main reef, and the line represents a simple linear regression for illustrative purposes

Size, however, did seem to affect the membership of the groups for both S. iserti and associates. When comparing the size variance among S. iserti in a group versus that expected by chance (given all the individuals in our sample), 16/41 groups had significantly lower size variance at the P = 0.05 level, and 24/41 groups had lower size variance at the P = 0.10 level. Furthermore, associates seemed to be closely size-matched to the size of the S. iserti in the group. Associates of larger size tended to be found in groups with larger-sized S. iserti (Fig. 3 ; Spearman, rs = 0.64, z = 3.41, P<0.001).

Discussion

We found that Scarus iserti groups on reefs near Andros Island most typically consisted of 4–6 conspecifics of similar sizes, and heterospecific associates were found with over half of the S. iserti groups. In this range of group sizes, Wolf (1985) reported that other parrotfish (Sparisoma sp.) and Acanthurus sp. were commonly associated with S. iserti groups on a reef in the US Virgin Islands. Our study, however, found Acanthurus sp., but not Sparisoma sp., to be the most common associate, a similar finding to that of Ogden and Buckman's (1973) Panama study. Robertson et al. (1976) found that Acanthurus sp. were attacked by territorial damselfish (Eupomacentrus planifrons) less frequently when in a S. iserti group, and Acanthurus sp. may have higher foraging rates when foraging in groups with S. iserti (Wolf 1987).

The conspecifics and heterospecifics found in the S. iserti groups tended to be of similar size, a pattern that has been found for other fish species (e.g., Blakeslee et al. 2009). Homogeneous schools can reduce predation rates on individuals by increasing the predator confusion effect (Mueller 1971), as it may become increasingly difficult for a predator to single out a group member as the number of individuals increases, especially if the members are phenotypically similar (e.g., Landeau and Terborgh 1986). Competition for resources among group members may also lead to such assortment, with small individuals avoiding larger individuals to decrease competition (Krause et al. 1996). Given the diverse feeding modes found among species within the S. iserti groups (Ogden and Buckman 1973 ; Humann and DeLoach 2002), it seems probable that, while avoiding foraging competition from larger individuals may play a role in size-matching within a species, sizematching between species is more likely to be due to avoiding predation.

The relative rarity of S. iserti groups containing only one or two heterospecific associates may relate to avoiding relatively high rates of predation by being clearly different from other group members (Mueller 1971). Wolf (1985) found that stoplight parrotfish (Sparisoma viride) and ocean surgeonfish (Acanthurus bahianus) in S. iserti groups left the group sooner if it had relatively few conspecific group members. By avoiding being the only heterospecific fish in a parrotfish group, a heterospecific associate may be avoiding being the ‘‘odd species out’’ (Wolf 1985 ; Theodorakis 1989). Avoidance of the oddity effect may be especially important for Acanthurus sp. (the most common associate in the S. iserti groups in our study), because they are very different morphologically from S. iserti .

The results of our study indicate that both member size and species are important characteristics of the structure of the mixed-species foraging groups of S. iserti . Future studies, particularly examining the formation and stability of these groups (e.g., Crook 1999), would give us more insight into the behavioral mechanisms involved in group formation. In addition, integrating these aspects of group structure into studies that examine competition and aggression among reef fishes (e.g., Mun˜oz and Motta 2000 ; Mumby and Wabnitz 2002 ; Francini-Filho et al. 2010) may increase our understanding of the complex community dynamics present in reef systems (e.g., Lokrantz et al. 2008 ; Mumby 2009).

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