Composition Changes and Movements in Mixed-Species Groups of Algae Grazing Fish in Jamaica and Grand Cayman Island. Part II

Andrew Bloch[1], Layla Al-Shaer[1], Brandon Baumann[1], Matthew Draud[2], M. Itzkowitz[1*]

[1]Department of Biological Sciences, Lehigh University, Bethlehem, PA, USA
[2]Office of the Vice President, McMurry University, Abilene, TX, USA
Email: *mi00@lehigh.edu

Abstract

Although Caribbean mixed-species herbivorous fish groups are an important component to the reef community by helping to crop algae that often overgrow and kill corals, little is known of how they organize their foraging groups. In spite of a highly flexible membership, the basic structure of these groups consists of a "core species," that leads the group and often is either the striped parrotfish (*Scarus iserti*) or the ocean surgeon (*Acanthurus tractus*). These species lead their groups to open areas where they feed largely on low profile turf algae. Other members prefer macro algae and are termed "associate species," of which the two common species we studied were the stoplight parrotfish (*Sparisoma viride*) and the redband parrotfish (*Sparisoma aurofrenatum*). In spite of the large difference in group sizes between Jamaica and Grand Cayman Islands, the relationships between movement patterns and compositional changes were largely consistent. There was no support for the hypothesis that these dramatic and continuous group changes were related to foraging success. Instead, we speculated that these group changes perhaps were designed to maintain cohesion among a membership that was spread over a wide area. We also examined if associates species may be more than just passive followers of core species but rather instigated the attracting or the building of core groups. Both associate species do attract striped parrotfish in open areas and thus appear active in initiating mixed-species groups. Finally, given that associate species seem to derive little foraging benefit from following core species, we tested the hypothesis that associate species joined core groups to gain protection against predators. Associate species do not selectively join the larger groups of striped parrotfish but appear to join core species randomly and the groups they joined resembled the wide assortment of core groups available in the area. Thus, while associates may be joining

core groups for protection, this protection was not based on sizes of core groups.

Keywords

Caribbean, Parrotfish, *Scarus*, *Sparisoma*, Surgeonfish, *Acanthurus*

1. Introduction

Coral reef parrotfish and surgeonfish are important components in their community because their grazing behaviors appear to inhibit the overgrowth of algae [1] [2] [3]. While mixed-species groups seem especially potent at controlling a diversity of macro algae [4], few studies have examined how these species integrate their diverse types of foraging behavior while being part of the same group. Itzkowitz [5] [6] first observed these groups in Jamaica and concluded that one species, termed "core species" was usually the backbone of the group that led other species to numerous foraging sites. The species that followed core species were termed "associate species" and these species, while also herbivorous, have different food preferences compared to core species (see below). While all individuals in these groups were gregarious, the group structure was loose with individuals constantly joining and leaving. Itzkowitz [6] [7] suggested that the basic component to the foraging behavior of these fish was individuals joining groups to inspect for high quality food discoveries found by others and if none were found, groups would be disbanded with individuals leaving separately or in groups.

Here we test the hypothesis that core species continuously shift locations and group composition because they are examining the foraging success of other individuals. We predict that when given a choice, searching individuals will preferentially join others already engaged in foraging than entering a location that has no foragers. We test this prediction by comparing mixed-species groups of reef fish in Jamaica and Grand Cayman Island (herein termed "GCI"). Al-Shaer *et al.* [8] described the mixed-species groups in both Jamaica and GCI and found that Jamaican groups were similar to those described in an earlier study by Itzkowitz [6]. As before, the bulk of each group was composed of a core species, such as the striped parrotfish (*Scarus iserti*) and the ocean surgeon (*Acanthurus tractus*). Two common associate species were the stoplight parrotfish (*Sparisoma viride*) and redband parrotfish (*Sparisoma aurofrenatum*). The critical difference allowing a test of our prediction is that the striped parrotfish core group sizes are smaller in GCI, with ocean surgeons groups being extremely small and no longer functioning as a core species. Furthermore, the density of striped parrotfish is also reduced [9]. Thus, with fewer opportunities to inspect individuals already engaged in foraging, GCI striped parrotfish and ocean surgeons should be less likely to find and join other individuals already engaged in foraging.

We also considered the possibility that associate species influence the presence

of core groups in some locations. For example, Itzkowitz [7] found that associate species that arrive first at a food source could instigate mixed-species group formation by attracting other species. It was unclear from that study whether the other species were attracted to the intense feeding activity of the associate species or were attracted to the associates themselves. That is, do core species such as the striped parrotfish inspect the feeding locations of species that do not share their food preferences? This would suggest that associate species may represent a cohesive component of mixed-species groups rather than passive followers. Alternatively, this attraction to an associate individual might occur when a typical core species such as striped parrotfish are found in very small groups and become an associate species by following species in the majority [5] [6]. In this case, we predict that very small numbers of striped parrotfish would be more likely to join associate species. Because ocean surgeons did not function as a core species in Grand Cayman, we restricted the testing of this hypothesis, and the following hypothesis, to the associates' interactions with striped parrotfish.

Given that associates typically forage on different types of food than core species, we also tested the hypothesis that associates gain protection by following core groups [6]. For example, core species such as the striped parrotfish typically feed using a scraping behavior of low profiled turf algae in open areas while associate species, such as the stoplight parrotfish and the redband parrotfish, feed on leafy macro algae among rubble and coral [1] [10] [11]. Herbivores gaining protection from predators by being part of groups is a common observation in many species [12] [13] [14] and forms the foundation for this hypothesis. However, we were unable to test this hypothesis directly because we rarely observed predation. Instead, we tested this prediction by comparing the group sizes of core species joined by associate species to the available group sizes of core species in the immediate area. We predicted that associate species would join the larger of the available core groups [15].

2. Methods

This study is the second part of an initial study that was published previously, in which we presented an overview of the social dynamics of the mixed-species groups in Jamaica and GCI [8]. Because the locations, the species studied, and the data collection methods have all be described in detail [8], for the sake of brevity, here we have minimized the descriptions.

2.1. Locations and Habitat

In both Jamaica and Grand Cayman Island we selected "visually similar" locations at Discovery Bay, Jamaica and Mahogany Point Grant Cayman Island (Figure 1). Fish were observed in the back reef areas (*i.e.*, from the shoreline to the reef crest). In both locations, the distance was between 50 and 150 m. The general water depth was between 1 and 2 m. In both locations the predominate substrata was sand, small rubble (diameters between 15 and 50 cm), and larger
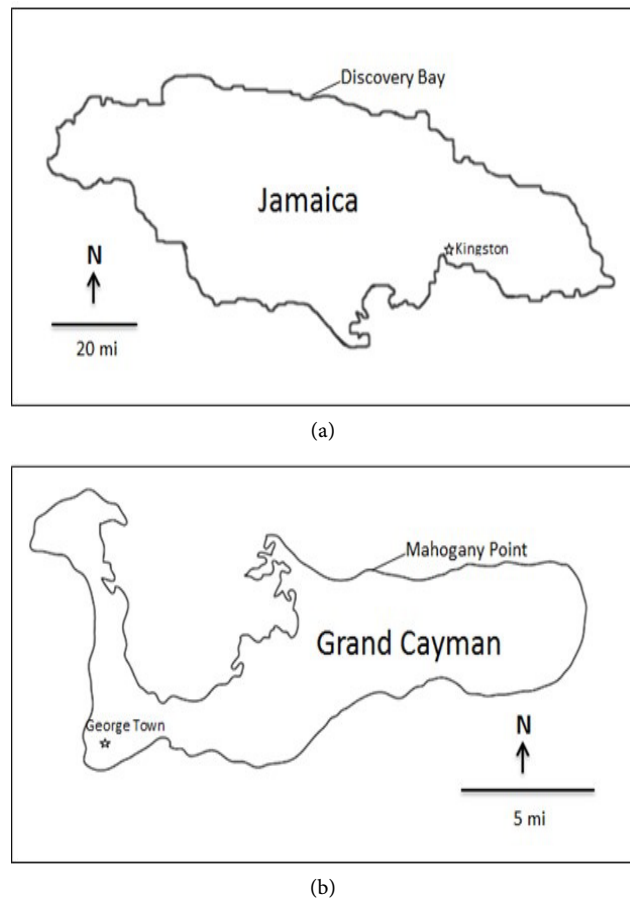
(a)

(b)

Figure 1. (a) Map of Jamaica. Study site at Discovery Bay; (b) Map of Grand Cayman Island. Study site at Mahogany Point.

rubble and coral. While Jamaica had significantly more turtle grass (*Thalassia testudinum*), none of the 4 species of fish studied utilized this type of food or habitat.

2.2. Species Observed

We studied 4 species: striped parrotfish, the ocean surgeon, the stoplight parrotfish, and the redband parrotfish. Previously, the striped parrotfish and the ocean surgeon were described as core species while the stoplight and the redband parrotfish were considered associate species [6] [7] [8] [9]. Striped parrotfish and ocean surgeons fed mainly in open areas on low profiled turf algae while both associate species feed on filamentous macro algae growing within the crevices of large rubble and coral [8] [10] [11] [16] [17].

2.3. Selection of Focal Individuals, Characterization of Groups, and Statistics

We followed 30 different individuals or groups of each of the four species in Jamaica and GCI for 15 min each. We selected individuals haphazardly and recorded when it moved, stopped, joined or left other individuals.

Core group membership changed frequently and we characterized the basic size of a core species group by treating each location used by the group as a separate group and then finding the mean after the 15 min. For example, if a group stopped 3 times and the group size was 10 individuals in each location, the mean group size was 10. These data have a parametric distribution and we calculated correlations using Pearson's Correlation Coefficient.

We divided group activities into a "movement state" and a "stationary state." The movement state occurred when a group left a location and stopped at a different location. The stationary state occurred while group remained in location (*i.e.*, essentially between movement states). For both the movement and the stationary states, we recorded the percentage of times the group increased in numbers (*i.e.*, a positive increase) and converted these numbers to percentages. For example, if a striped parrotfish group moved 20 times and had an increase in numbers 10 times, it was converted to 50%. We also recorded the total numbers of individuals of a core species gained and lost after the 15 min observation. These data have a parametric distribution and we used the ANOVA. For the remaining two hypotheses on associate species, the data were not distributed normally causing us to use either the Kruskal-Wallis nonparametric statistics or to cautiously use the one-way ANOVA. All data were analyzed using IBM SPSS Statistics Version 25.

3. Results

3.1. Core Species Inspecting Other Groups

The typical core group sampled approximately 20 - 30 new locations (see Al-Shaer *et al.* 2019). As a group moved between localities (termed "movement") it may have gained, lost, or had no changes in membership. Similarly, the same type of membership changes may have occurred while the group was stationary, *i.e.*, foraging, in a locality. To determine if larger stationary groups were more attractive to new members, we correlated the mean group size with the mean percentage of locations that the group had an increase in size by species and island. For striped parrotfish, group size was not significantly correlated with the mean percent of stationary locations that had a positive change in membership in Jamaica ($r = 0.100$, $n = 31$, $p = 0.592$) but was significantly correlated in GCI ($r = 0.593$, $n = 30$, $p = 000$). Ocean surgeon group size was not significantly correlated with percent positive additions in stationary locations in Jamaica ($r = 0.163$, $n = 28$, $p = 0.416$) but was significantly correlated in GCI ($r = 0.354$, $n = 30$, $p = 0.042$). Thus for both core species, larger stationary groups more often attracted new members in GCI but not in Jamaica.

We hypothesized that core species (striped parrotfish and ocean surgeons) would preferentially enter new locations that already had their own species foraging. The expectation is that core groups would more likely show positive member changes when they move into a location than when they are stationary in a location. Figure 2 presents the averages of the mean percentage of positive
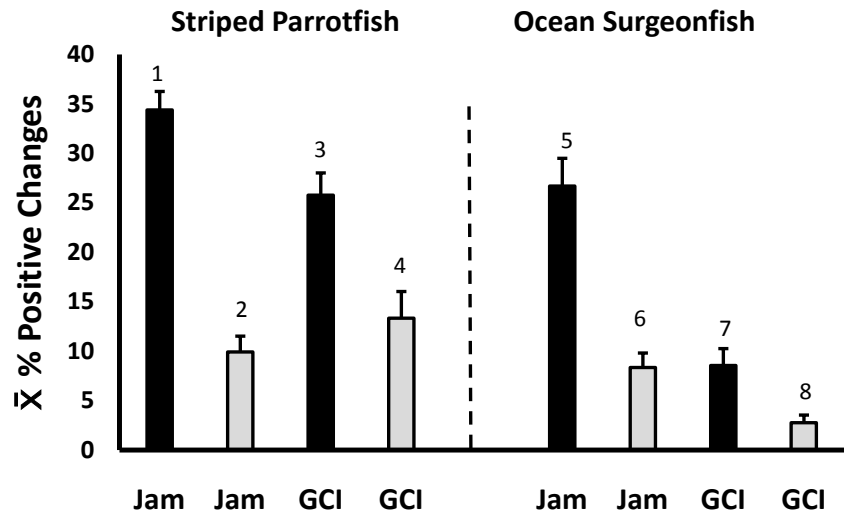
Figure 2. Mean (+S.E.) percent positive changes after moving into a foraging location (black bars) and mean percent positive changes after being stationary in a foraging location (grey bars). In Results, statistical results are referenced with bar numbers.

changes for all striped parrotfish and ocean surgeonfish groups in both Jamaica and GCI. A quick glance at the bars revealed that for both species, the positive changes were in the minority for both species in both locations. For the sake of brevity, we do not report negative changes which were almost identical to the positive changes.

A mixed-model ANOVA revealed that a significantly greater proportion of positive group changes occurred while striped parrotfish were moving ($F_{1,59}$ = 129.95, $p < 0.001$, $\eta_p^2 = 0.688$) and when ocean surgeon were moving ($F_{1,56}$ = 70.628, $p < 0.001$, $\eta_p^2 = 0.558$). There was no main effect of island on the mean percent positive changes in striped parrotfish groups ($F_{1,59}$ = 1.047, $p = 0.31$, η_p^2 = 0.017). Ocean surgeon groups in Jamaica had a significantly ($F_{1,56}$ = 31.246, $p < 0.001$, $\eta_p^2 = 0.358$) higher percent positive change than GCI ocean surgeon groups. There was a significant interaction of island and group state of striped parrotfish groups ($F_{1,59}$ = 13.822, $p < 0.001$, $\eta_p^2 = 0.19$; **Figure 2**). Planned comparisons of this interaction revealed that moving striped parrotfish groups in Jamaica have significantly higher mean percent positive changes than striped parrotfish groups in GCI ($p = 0.004$, **Figure 2**, bars 1 vs 3). When the striped parrotfish group is stationary, the percent positive changes did not differ significantly between Jamaican and GCI ($p = 0.278$, **Figure 2**, bars 2 vs 4). As Jamaican striped parrotfish groups transition from moving to stationary, the mean percent positive changes significantly decrease ($p < 0.001$, **Figure 2**, bars 1 vs 2). As GCI striped parrotfish groups transition from moving to stationary, groups significantly decrease their mean percent positive change ($p < 0.001$, **Figure 2**, bars 3 vs 4).

There was also an interaction of island and group state in ocean surgeon groups ($F_{1,56}$ = 19.177, $p < 0.001$, $\eta_p^2 = 0.255$, **Figure 2**). Planned contrasts of this interaction revealed that moving ocean surgeon groups in Jamaica have significantly higher percent positive changes than ocean surgeon groups in GCI (p

< 0.001, **Figure 2**, bars 5 vs 7). While an ocean surgeon group is stationary, the percent positive changes were significantly higher in Jamaica compared to GCI ocean surgeon groups ($p = 0.001$, **Figure 2**, bars 6 vs 8). As both Jamaican and GCI ocean surgeon groups transition from moving to stationary the mean percent positive changes significantly decrease ($p < 0.001$; $p = 0.005$, **Figure 2**, bars 5 v 6, 7 vs 8). To summarize, for both species and in both locations, the groups were more likely to increase their group size when they moved into a new location than when they remained in the location and the increase was greater in Jamaica than in GCI.

The above analysis emphasized when the core group would likely increase their membership. Next, we considered whether these changes influenced the size of the group after our 15-min observation period (**Figure 3**). We used a mixed-model ANOVA, using movement and stationary as a repeated measure. There was a significant effect of island location on mean group changes for striped parrotfish ($F_{1,59} = 4.181$, $p = 0.045$, $\eta_p^2 = 0.066$) but not for ocean surgeons ($F_{1,56} = 1.081$, $p = 0.303$, $\eta_p^2 = 0.019$). There was no interaction effect of movement/stationary on island for ocean surgeon groups ($F_{1,56} = 3.013$, $p = 0.088$, $\eta_p^2 = 0.255$). There was a significant interaction of movement/stationary and island for the striped parrotfish ($F_{1,59} = 5.249$, $p = 0.026$, $\eta_p^2 = 0.082$). A pairwise contrast revealed that there was no significant difference in moving striped parrotfish mean size change in Jamaica and GCI ($p = 0.298$, **Figure 3**, bars 1 vs 3). The Jamaican striped parrotfish stationary groups had significantly lower mean changes than GCI stationary groups ($p = 0.033$, **Figure 3**, bars 2 vs 4). As Jamaican striped parrotfish groups shifted from moving to stationary, mean group size significantly increased ($p = 0.015$, **Figure 3**, bars 1 vs 2). As GCI striped parrotfish groups transition from moving to stationary, striped parrotfish groups did not significantly alter their mean size of changes ($p = 0.463$, **Figure 3**, bars 3 vs 4). Although some changes were significant, after 15 min, the changes were small indicating that groups did not gain or lose substantial numbers of individuals when moving into a location or being stationary in a location.
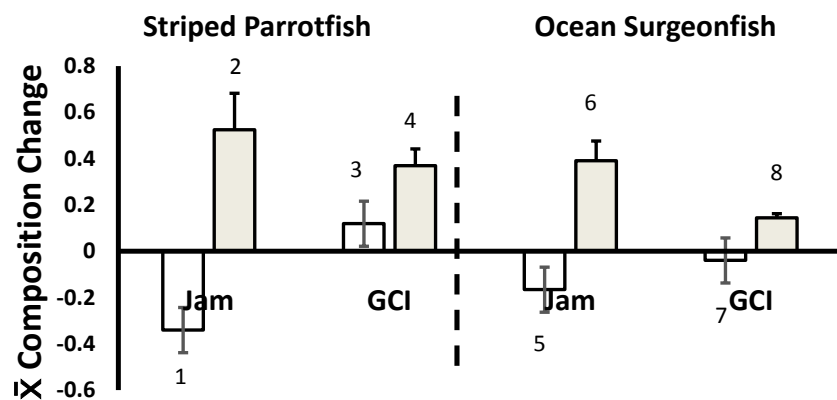

Figure 3. Mean (±S.E.) of composition changes during movements (white bars) and when stationary (foraging) for striped parrotfish and ocean surgeons in Jamaica and GCI. In Results, statistical results are referenced with bar numbers.

3.2. Associates Attracting Striped Parrotfish Core Groups

We also examined whether an associate species can initiate the presence of a core group by attracting striped parrotfish to a foraging location. This analysis is limited because the associate species, such as stoplight and redband parrotfish, often moved into habitats not frequented by striped parrotfish. For this reason, we restricted this analysis to when an associate species actually precedes the arrival of the first striped parrotfish.

In Jamaica, 56% of the redband parrotfish and 73% of stoplight parrotfish observed met the requirement of an associate individual appearing first at a location and then being joined by striped parrotfish. In GCI, 77% and 66% of the redband and stoplight parrotfish, respectively, met the above requirement. However, for both species in both locations, less than 2% of all movements attracted striped parrotfish. On the rare occasion that an associate individual met this criterion multiple times, we averaged the number of striped parrotfish groups that did join in this manner. We compared three groups of striped parrotfish; 1) groups attracted to redband parrotfish, 2) groups attracted to stoplight parrotfish, and 3) striped parrotfish groups that were found in the immediate areas. We used the Kruskal-Wallis Test because the data were not normally distributed. In Jamaica (Figure 4), comparing the three striped parrotfish groups revealed a significant difference ($p = 0.011$) and the Posthoc Paired Comparison tests revealed that redband parrotfish attracted striped parrotfish groups that were significantly smaller than the striped parrotfish groups in the area ($p = 0.008$). There was no significant difference in the number of striped parrotfish attracted to stoplight parrotfish and the groups of striped parrotfish in the area ($p = 0.471$).
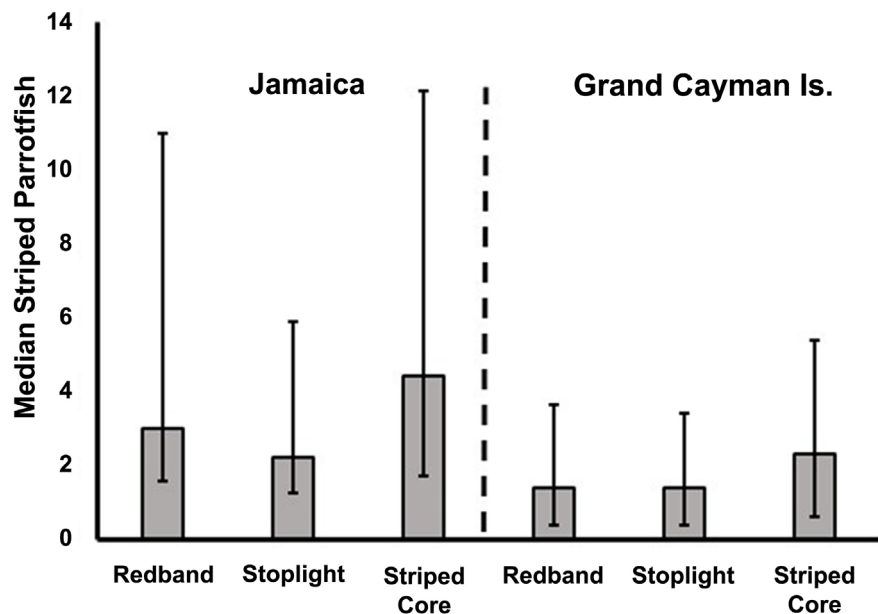

Figure 4. Median numbers (±Quartiles) of striped parrotfish attracted to redband parrotfish and stoplight parrotfish in comparison to striped parrotfish groups found in the immediate areas in Jamaica (left side of dashed line) and in GCI (right side of dashed line).

The striped parrotfish attached to redband parrotfish and stoplight parrotfish were not significantly different ($p = 0.602$). In GCI (Figure 4), there was a significant difference among the three groups of striped parrotfish (KW, $p = 0.001$). Both the striped parrotfish groups attracted to redband parrotfish and those attracted to stoplight parrotfish were significantly smaller than striped parrotfish groups in the immediate areas ($p = 0.001$, $p = 0.004$, respectively), but they were not significantly different from each other ($p = 0.716$).

To summarize, associate species typically attracted very few striped parrotfish but when they did, they typically attracted smaller numbers of striped parrotfish than typically found within the typical striped parrotfish groups. The one exception was that in Jamaica, stoplight parrotfish attracted striped parrotfish groups similar in size to other striped parrotfish groups in the area.

3.3. Core Group Size and Associates Preferences

Finally, we sought to determine if the stoplight and the redband parrotfish were attracted to the larger of the available striped parrotfish core groups. We examined the stoplight parrotfish (N = 30 groups) and redband parrotfish (N = 30 groups) that joined striped parrotfish groups that were already engaged in foraging (*i.e.*, stationary groups) to determine if these striped parrotfish groups were similar in size to the striped parrotfish groups (N = 30 groups) that were assessed separately in the same area (Figure 5). We removed from this analysis those associate species that did not join any striped parrotfish groups. In the remaining associates, individuals would often join multiple striped parrotfish groups and in those cases, we generated a mean number of striped parrotfish for those replicates. Using a one-way ANOVA, we compared the mean group sizes of striped parrotfish joined by stoplight parrotfish and redband parrotfish and
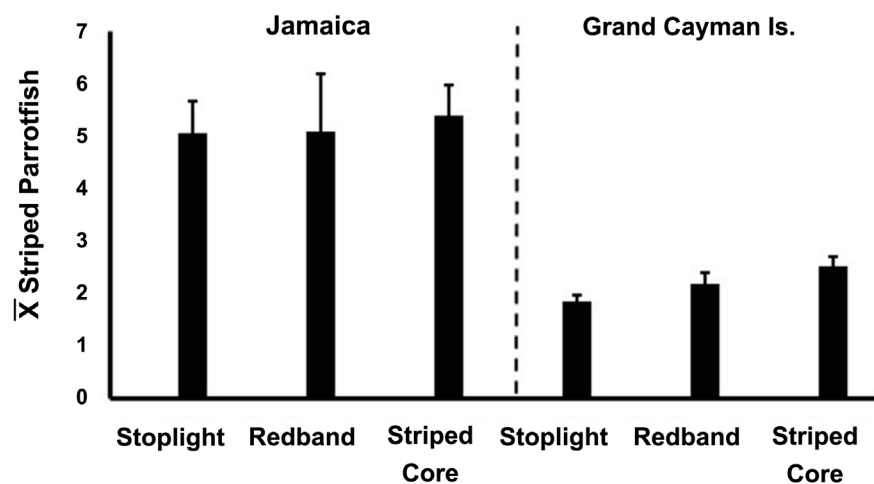

Figure 5. Mean (+S.E.) size of striped parrotfish groups that were joined by either stoplight parrotfish or redband parrotfish in Jamaica (left side of dashed line) and in Grand Cayman Island (right side of dashed line). Striped Core = the mean group sizes of the striped parrotfish groups that were found in the immediate areas of those joined by the associate species.

compared them to the mean group sizes of striped parrotfish found in the same area at approximately the same time.

In Jamaica, there were no significant differences in mean group sizes joined by stoplight parrotfish or redband parrotfish and the mean group sizes of striped parrotfish ($F_{2,85} = 0.055$, $p = 0.946$). In GCI, data were not normally distributed but nonparametric tests revealed the same results as the one-way ANOVA, which we include here. There was a significant difference among the three groups ($F_{2,77} = 3.73$, $p = 0.029$). (Note: the lower degrees of freedom for "within groups" is due to the removal of groups where the associates did not join striped parrotfish during the observation period). The Bonferroni Posthoc Test revealed that the stoplight parrotfish joined smaller groups of striped parrotfish than were available in the area ($p = 0.024$). There was no significant difference in the size of the striped parrotfish groups joined by the stoplight parrotfish and the redband parrotfish ($p = 0.641$) or between the redband and the striped parrotfish in the area ($p = 0.611$).

To summarize, with the exception of stoplight parrotfish in GCI joining the smaller of the available striped parrotfish groups, stoplight parrotfish and redband parrotfish in Jamaica and redband parrotfish in GCI joined striped parrotfish groups of similar size to those available in the area.

4. Discussion

We examined the three hypotheses regarding the composition of Caribbean mixed-species herbivore groups. The first hypothesis is that compositional changes and movements in striped parrotfish and ocean surgeonfish groups functioned to uncover high quality resources found by conspecifics. We tested 3 predictions: 1) that individuals moved into new areas where other individuals were already engaged in foraging, 2) that communities with higher densities of core species would cause an increase in the number of individuals that move to new areas, and 3) that overall, groups would show a net gain in the number of individuals after moving into all of the new areas while losing members after being in a foraging area. Some of these predictions were supported.

Regarding the 1st prediction, we found only a minority of movements into new foraging locations resulted in an increase in group membership. Thus, about a third of the new locations entered by an individual or group did increase the membership of its group by meeting an individual or group that was already foraging in that location. However, the second component to this prediction was that with more individuals foraging in the immediate area, groups would more likely gain members than in less dense areas. This was seen for both species in Jamaica, but especially striped parrotfish, where there were larger groups and more individuals than in GCI. Finally, we predicted that groups moving into a location would have a greater net positive gain than groups already in a location. This is not supported by either species in both locations. Generally, at the end of the observation period, groups showed little or no net gain when entering a loca-

tion or leaving a location. This is not surprising given that positive and negative gains were similar for both species, for entering and leaving a location, and for both islands.

We also considered two additional hypotheses regarding associate species in mixed-species groups. First, that associate species can stimulate the formation of mixed species groups by attracting core species, such as the striped parrotfish. Our strict methodology (see Methods) for testing this hypothesis resulted in only one or two replicates for each observed associate. With this limitation, stoplight parrotfish, attracted smaller groups of striped parrotfish than redband parrotfish and redband parrotfish attracted similar sized groups of striped parrotfish that were present in the immediate area. Further work is needed to determine if foraging areas of these two associate species, at least when foraging alone, caused the redband parrotfish to more likely to encounter larger groups of striped parrotfish. For example, Adams *et al.* [1] observed that Caribbean parrotfish often shared the same resources while having preferences that could take them to unique areas.

The second hypothesis regarding associates focuses on the use of core groups for predator protection. We found that both associate species were associated with a wide gamut of striped parrotfish groups whose numbers resembled the assortment found in the general area. Thus, we found no evidence that either associate species were selecting for the larger of the available striped parrotfish groups. We conclude that associate species may join striped parrotfish for protection but do not intentionally join groups based on the size of the groups.

Itzkowitz [5] [6] [7] suggested that the constant movements and group changes were designed to find individuals that already had found high quality food patches. While such groups have been observed to exploit dense growth of algae in damselfish territories [18] [19] [20], we found such activity rare. For example, in this current study, we never observed an individual discovering a high quality patch of algae that influenced composition changes or group movements. While it is clear that these groups are constantly foraging, the intent of the constant mixing of individuals with numerous location changes warrants further consideration in the future if we are to understand how these group exploit coral reef algae.

It is possible that the discovering of high quality algal patches is merely a minor byproduct of the relationship between these common herbivores and the coral reef macro algae. For this reason, in the future we intend to look more closely at how compositional changes relate to the immediate harvesting of the ubiquitous turf algae. The quantity of turf algae relates, in a general way, to the number of herbivores in an area [13] [16] [21] and this may explain the smaller groups in GCI. If composition changes are not related to immediate foraging opportunities, they may be a component of their social behavior. These species, especially the core species, often move across the reef in large groups [22] suggesting a cohesion that may require constant contact among the individual members after they divide into smaller foraging groups.

5. Conclusion

In conclusion, there was no evidence to support the hypothesis that core group species, *i.e.*, striped parrotfish and ocean surgeonfish, change foraging locations to join conspecifics already engaged in foraging. This result was applied to both Jamaica and GCI where overall group sizes were different. We now speculate that these frequent changes in composition and location have some other purposes, perhaps to maintain an overall group cohesion within a large area. There was evidence that the two associate species, *i.e.* redband and stoplight parrotfish, did attract striped parrotfish in areas devoid of fish and thus appeared instrumental in developing mixed-species groups. Finally, redband parrotfish and stoplight parrotfish did not join the larger of the available striped parrotfish groups. Thus, if core groups did provide protection to associate species, size of these groups appeared unimportant.

Acknowledgements

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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