within schools of intermediate individuals than in schools of large and small individuals. This may simply be because there is less potential for variation in small and large mysids which are limited by minimum and maximum species size. Considering that mysids have the ability to segregate, this change in variance may indicate that there are differing costs and benefits associated with segregation for different sized mysids. For intermediate individuals, the cost of finding a school of more similarly sized individuals may be greater than the benefits of a more homogeneous school. Larger individuals may avoid swarms of juveniles where they may be more recognized by a predator. Smaller mysids may form more homogeneous schools if they are inherently more susceptible to predation and caniballism. Population densities of mysids and the frequency of proper schooling locations may also be factors which limit the degree to which mysids segregate.

Pigmentation appears to be a strong organizing factor of mysid schools in Discovery Bay. I found only one darkly pigmented mysid within a non-pigmented school. Furthermore, dark schools were associated with dark substrates (algae/crevice) while non-pigmented schools were associated with light substrates (sand). This suggests that mysids preferentially school above substrates which make them most cryptic. Future studies could experimentally test this hypothesis by giving dark or light mysids a choice of substrates of differing darkness and observing their distributions.

Pigmentation increased as mysids became larger, indicating that an individual mysid experiences changing schooling requirements throughout its lifetime. It is likely that as a juvenile, a mysid will school with other juveniles above a sandy substrate. If mysids exhibit homing behavior , this mysid may remain with this school as it develops into a school of non-pigmented adults. However, as this mysid develops pigmentation, it may relocate to a school of pigmented adults above a darker substrate. Observing mysids in schools over the time period of several life cycles would show if mysid schools are dynamic or static in composition, and to what degree recruitment and emigration occurs within a school.

Sex ratios in adult schools varied with size. Three of the four large schools had skewed sex ratios, with high proportions of females. The embryos in these larger schools were also more developed than embryos from medium sized schools. This suggests that as females bear embryos in later stages of development and become more darkly pigmented, they benefit from selectively schooling together. Males may selectively avoid these schools in preference of schools with a greater proportion of non-gravid females to increase their reproductive efficiency. Or perhaps males do not live as long as females, possibly dying after a bout of fertilization.

LITERATURE CITED

Butler, M. 1989. A temporal study of mysid schooling behavior. Dartmouth studies in tropical reef ecology, 1989.

Clutter, R. I. 1969. Zonation of nearshore mysids. Ecology, **48**: 200-208.

Emery, A. R. 1968. Preliminary observations on coral reef plankton. Limnology and Oceanography, **13** (2): 293-303.

Modlin, R. F. 1990. Observations on the aggregative behavior of *Mysidium columbiae*, the mangrove mysid. Marine Ecology, **11** (3): 263-275.

Modlin, R. F. 1991. Population parameters, life cycle, and feeding of *Mysidium columbiae* (Simmer) in the waters surrounding a Belizian mangrove cay. Marine Ecology, **14** (1): 23-34.

O'Brien, D. P. 1988. Direct observations of clustering (schooling and swarming) behavior in mysids (Crustacea: Mysidacea). Marine Ecology Progress Series, **42**: 235-246.

Siegfried, C. A. & M. E. Kopache, 1980. Feeding of *Neomycis mercedis*. Biological Bulletin, **159**:193-205.

Wittmann, K. J. 1976. Modification of association and swarming in North Adriatic Mysidacea in relation to habitat and interacting species. Biology of Benthic Organisms. Eds., B. F. Keegan, P. O'Ceidigh and P. J. S. Boaden. Pergamon Press, Oxford: 605-612.

TRUMPETFISH COLOR MORPHOLOGY, BEHAVIOR AND SUBSTRATE ASSOCIATION ACROSS THREE SITES IN JAMAICA, W.I.

SCOTT C. BRAMAN AND MATTHEW J. UNGERER

Abstract. Trmpetfish utilize a variety of different color morphologies, behaviors, and substrates to blend into coral reef environments and ambush prey. Previous studies have proposed that prey learning may pose a limit to the frequency to which trumpetfish use different foraging behaviors. We hypothesized that if prey learning was shaping trumpetfish behavior, then trumpetfish within a given site should be evenly distributed with respect to color morphology, behavior, and substrate associations. Furthermore, we investigated color morphology and behavioral associations across sites. We surveyed a total of 175 trumpetfish from the backreef and forereef at Discovery Bay and the forereef at Pear Tree Bottom. We found that within each site, trumpetfish color morphology and foraging behavior were evenly distributed, suggesting that prey learning may be limiting color-behavior frequencies. The frequency distributions of color morphs at the forereef sites differed significantly from that at backreef site, but were not significantly different from each other. In addition, we found that blue- or yellow-headed individuals were more likely to be found at the forereef sites, and that trumpetfish with these brightly colored heads tended to be moving, while uniform-colored (tan, brown-red, or green) individuals tended to be stationary.

Key Words: Aulostomus maculatus, *Batesian mimicry, camouflage, chromatomorphy, prey-learning*

INTRODUCTION

The west Atlantic trumpetfish, *Aulostomus maculatus*, is a common chromatomorphic ambush predator found throughout the Caribbean. Trumpetfish feed on shrimp as well as a variety of reef fish, including cardinalfish (Apogonidae), blennies (Clinidae), squirrelfish (Holocentridae), damselfish and chromis (Pomacentridae), and wrasse (Labridae) (Randall 1967). Among the various color morphotypes displayed are forms with blue, violet or yellow heads and grey or brown bodies, as well as forms which are completely yellow, dull green, brown, or tan (Humann 1989, Randall 1967, Braman and Ungerer, pers. obs.). White horizontal stripes and vertical bars, as well as black spots, usually are present along the body of the fish to varying degrees.

In addition to this great variety of color morphotypes and striping patterns, trumpetfish also display a suite of different foraging behaviors which allow them to blend into many substrates found in coral reef environments: (1) They associate with large herbivorous fishes to disguise themselves and move closer to potential prey (Aronson 1983). (2) Individuals with blue snouts often are observed in association with schools of blue chromis (*Chromis cyanea*), with their snout inside the school and the rest of their grey or brown body trailing behind to confuse the visual communication of the chromis and so minimize striking distance to prey (Kaufman 1976). In a similar manner, trumpetfish with yellow heads have been seen sticking their snouts into groups of yellow juvenile or initial adult-phase blue-head wrasse (Braman and Ungerer, pers. obs.) (3) Dull green, brown, and tan individuals may align themselves horizontally, vertically or at an angle in the water column sometimes with tails curled, often near a gorgonian or coral rock overhang using their color and motionless behavior as camouflage to match their surroundings.

Previous studies have suggested that predator learning can limit the frequencies of Batesian mimics of an unpalatable species (Carpenter 1936 and Rothschild 1971 in Aronson 1983). Aronson (1983) proposed that camouflaged predators in a given area may similarly restrict the frequency with which different color morphologies and behaviors are displayed due to prey-learning. For example, if camouflaged predators are always associated with sea fans, then over time prey species will simply learn to avoid all sea fans and thus escape predation. We hypothesize that prey-learning is a factor influencing trumpetfish color and behavior, and

that trumpetfish within each site should exhibit different color morphologies, behaviors, and substrate associations with equal frequencies. To test this hypothesis, we examined trumpetfish color morphology and foraging behavior to determine the frequency of the different color morphologies, behaviors, and associated substrates at each of three different sites. In addition, we compared color morphotypes across sites to determine whether certain color morphologies are associated with specific behaviors. For example, are blue-headed trumpetfish always found horizontal and stationary in a school of blue chromis? Finally, by examining individual fish we determined to what degree trumpetfish change color and whether color changes result from different behaviors, associations with different substrates, or both.

To maximize the diversity of trumpetfish color morphotypes and behaviors as well as the types of substrates avaivable, we conducted out study in three very different habitats – a shallow backreef at the western end of Discovery Bay and forereef sites at Discovery Bay and Pear Tree Bottom.

Following the large-scale die-off of the sea urchin *Diadema antillarum* in 1983 (see Carpenter 1990), and because of intense fishing pressure on herbivorous fish, algal cover has increased dramatically in many places in and near Discovery Bay (Woodley et al 1981, Hughes 1994). However, a combination of factors seems to have led to reduced algal cover at Pear Tree Bottom. First, the forereef at Pear Tree Bottom has more-developed "spur and groove" formations, with trenches commonly 5m or more deep (Braman and Ungerer, pers. obs.), and this greater relief provides more refuge habitats for *Diadema*. Second, *Tripneustes ventucosus*, another sea urchin which emigrated to the forereef following the mass-mortality of *Diadema* is especially abundant (Ungerer and Braman, pers. obs.). These sea urchins are important herbivores which can greatly impact algal cover. Balser and Soucy (1992) found that mean percent macroalgal cover at Pear Tree Bottom was only 6.1%, compared to 28% on the forereef at Discovery Bay and 90.9% on the backreef at Discovery Bay. Percent coral cover is correspondingly much higher in Pear Tree Bottom (Braman and Ungerer, pers. obs.).

METHODS

Data were collected from 4 to 11 March 1998 along the fringing reef off the northern coast of Jamaica. Three study areas were surveyed three times each: the backreef and forereef at Discovery Bay and the forereef at Pear Tree Bottom. The three areas differed markedly in topography and percent macroalgal and coral cover. Schools of blue chromis are commonly found at both the forereef sites, but do not occur in the backreef.

Survey samples were taken during a ~ 1.5 h period and consisted of a snorkeler swimming a rough transect (~300 - 500m) and making observations of each *A. maculatus* encountered and its immediate surrounding environment. Observations included size (visually estimated in 0.5 ft. increments), head color, body color, body orientation (angled, horizontal or vertical), tail position (straight or bent) and whether the fish was stationary or moving. The substrate within 1m of the fish was classified as one of the following: algae-covered coral-rock, bare coral-rock, coral, rubble, sand, turtle grass or gorgonian (sea fan, sea whip or sea rod). In addition, the presence or absence of blue chromis (*Chromis cyanea*) and juvenile or intial adult-phase blue-headed wrasse (*Thalassoma maculatus*) was noted. 21 ten-minute focal observations of individual trumpetfish were made to obtain information about individual color change, behavior patterns, and foraging range.

Simpson's Index of evenness ($s = 1 / \sum n^2$, where n = each nominal category found at a given site) was used to examine the relative proportions of trumpetfish color, behavior and substrate associations at a given site. Values of Simpson's Index range from 1 (perfectly even) to 0 (completely uneven). Although this statistic is more commonly used to measure evenness of species abundance, it can also give a measure of the evenness of other nominal variables. Color-site associations and color-behavior associations were analyzed using G-tests and Chi-square analyses, respectively. For the analysis of color-site associations in the backreef, blue head and yellow head individuals (3 out of 42 total) were excluded because they were found in the canoe channel which links the back and fore reefs and thus were not truly representative of the trumpetfish community in the backreef. Trumpetfish behavior was combined into four categories for analysis of color-behavior associations: vertical - stationary, angled - stationary, horizontal - stationary, horizontal - moving. Differences in trumpetfish size at the different sites were analyzed with a one-way ANOVA.

RESULTS

Within each site, trumpetfish color morphologies and foraging behaviors were evenly distributed, while the evenness of trumpetfish associations with substrates varied. Trumpetfish color morphologies on the backreef were very evenly distributed ($s = 0.98$) while those at the two forereef sites exhibited fairly even distributions ($s = 0.85$ and 0.84 respectively; Fig. 1). Trumpetfish behaviors in the both the forereef of Discovery Bay and Pear Tree Bottom forereef were very evenly distributed ($s = 0.96$, 0.95 respectively; Fig.1), while the frequency of behaviors in the backreef was slightly more skewed ($s = 0.81$; Fig.1). The frequency of substrate use was skewed in the backreef ($s = 0.41$) and Pear Tree Bottom forereef ($s = 0.58$) but was relatively even in the Discovery Bay forereef ($s = 0.91$; Fig.1).

Trumpetfish were smaller in the backreef at Discovery Bay than they were at either the forereef at Discovery Bay or the forereef at Pear Tree Bottom ($F_{2,172} = 5.0$, $P = 0.008$). We found a significant difference in the frequencies of the color morphologies across the three sites ($G_8 = 19.06$, $P < 0.05$). We found significant differences in the frequencies of color morphs between the backreef and forereef of Discovery Bay ($G_3 = 15.49$, $P < 0.05$), but not between the two forereef sites ($G_3 = 6.07$, $P > 0.05$). Across sites, blue-head morphotypes were observed significantly more frequently at the forereef sites than at the backreef site ($G_2 = 11.31$, $P < 0.05$; Table 1). The frequency of green morphotypes was significantly higher at the backreef and Pear Tree Bottom forereef than at the Discovery Bay forereef ($G_2 = 7.94$, $P < 0.05$; Table 1). There were no significant differences in the frequencies of tan, brown-red, or yellow-head morphotypes across sites (all $P > 0.05$; Table 1).

Across all three sites, color morphotypes with a colored head (blue-head and yellow-head morphotypes) were more likely to be found moving than those with uniform color (tan, brown-red, and green morphotypes)($X^2_{2,171} = 16.7$, $P = 0.0001$). There was a strong trend for uniform color morphotypes to have their tail bent more than those with colored heads, but the trend was not quite statistically significant ($X^2_{2,171} = 3.1$, $P = 0.07$). For body orientation (vertical, angled, or horizontal), there was no relationship between uniform color morphotypes and those with colored heads ($X^2_{2,171} = 2.1$, $P = 0.34$).

In the 10 minute focal samples, 7 out of 21 trumpetfish changed color either from tan to brown or tan to green and vice versa. Four out of the 7 color changes occurred as the trumpetfish moved across substrates from stationary positions near a coral rock overhang. Four out of 21 were found associated in pairs for over 30 s, but there was no evidence that pairs forage using the same color morphotypes and associated behavior. Our focal samples revealed that trumpetfish moved ~ 1 to 20 m over a 10-min period.

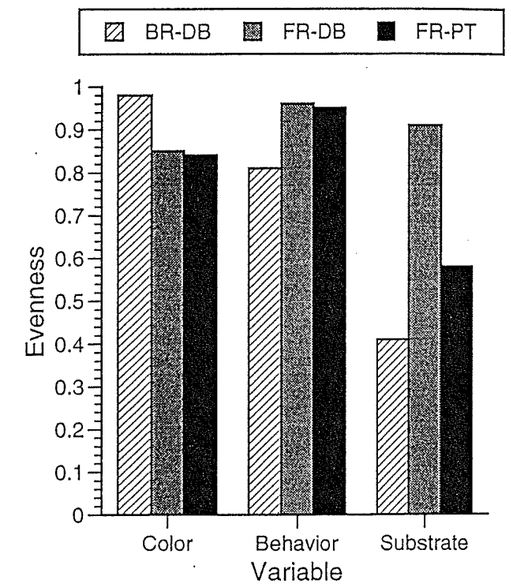

FIG. 1. Simpson's Index of evenness across three sites for trumpetfish color, behavior and the substrate on which they were observed. BR-DB = backreef at Discovery Bay, FR-DB = forereef at Discovery Bay, FR-PT = forereef at Pear Tree Bottom.

TABLE 1. Summary of trumpetfish color morphology by site. BR-DB = backreef at Discovery Bay, FR-DB = forereef at Discovery Bay, FR-PT = forereef at Pear Tree Bottom. * denotes $p < 0.05$, G-Test comparing each color morphology across sites. Means with different letters are significantly different (Tukey, $P < 0.05$)

	blue head*	yellow head	brown	tan	green*	mean size (SE)	TOTAL
BR-DB	0.05	0.02	0.29	0.33	0.31	1.29 (0.07)[a]	42
FR-DB	0.29	0.08	0.24	0.27	0.12	1.42 (0.04)	66
FR-PT	0.21	0.01	0.24	0.25	0.27	1.52 (0.05)[b]	66
TOTAL	35	7	44	48	40		174

DISCUSSION

The high evenness values that we found for trumpetfish color morphology and behavior within each site support the hypothesis that prey learning may be an important factor determining the distribution of trumpetfish color morphologies and behaviors at a given site. If prey learning is occurring, then trumpetfish would benefit from diversifying both color choices and behaviors. Such diversification limits the possibility that visually-oriented prey would learn to recognize and avoid them. Alternatively, a high degree of evenness could be explained by a high substrate diversity within each site, causing trumpetfish to change color morphology and behavior as they move across substrate types. Our data do not support this explanation since substrate associations at two of the sites appear to be highly skewed; for example, the backreef contains ~ 90% algae cover and the forereef at Pear Tree Bottom has a high degree of coral cover. The uneven distribution of substrates at these two sites may explain the low evenness index values for trumpetfish-substrate associations. Trumpetfish in the backreef and the forereef of Pear Tree Bottom may be limited to how evenly they can distribute themselves with different substrates given the prevalence of algae-covered coral rocks and coral, respectively. Our data suggest that the trumpetfish at these sites may avoid prey learning not by distributing themselves evenly over different substrates, but by utilizing equal frequencies of color morphologies and behaviors. In the forereef at Discovery Bay trumpetfish could limit prey learning by having equal frequencies of color morphologies, behaviors, and associations with different substrates.

The larger sizes of trumpetfish at both forereef sites suggests that older trumpetfish may emigrate from the backreef to the forereef, perhaps in search of larger prey items. Our data on the frequencies of different color morphs indicates that there are clear differences between the back and forereef at Discovery Bay, but not between the two forereef sites. Site characteristics may influence the abundance of some color morphotypes but does not affect the abundance of others. The blue-head morphotype was found almost exclusively at sites where blue chromis were present, although it was not always found in association with them. The green morphotype was found significantly less in the forereef at Discovery Bay, possibly due to a limited number of substrates where the green morphotype can successfully be camouflaged. Surprisingly, the proportions of trumpetfish with the tan-grey and brown-red morphologies were not greater at sites with higher algal cover. This may indicate that trumpetfish coloration and behavior mimic gorgonians and other sessile marine fauna rather than simply blending into the background substrate color. Or, these two color morphotypes may simply allow the trumpetfish to blend in well over many different substrates. Furthermore, our focal sample data indicate that individual trumpetfish change readily among the brown-red, tan-grey, and green morphotypes; this may make the uniform color morphotype adaptable to a variety of substrate types and colors.

Trumpetfish with colored heads exhibit different behavior than those with a uniform color, indicating that these two color groupings use different foraging strategies. Colored-head morphotypes seem to orient themselves horizontally in the water column and move along the substrate without bending their tail. These data support the hypothesis that blue-head morphotypes are using their color and behavior to minimize striking distance to prey (Kaufman 1973). It is not known whether yellow-head morphotypes are using a similar strategy, and our limited number of observations of this morphotype prevent us from making any conclusions about this. Blue-head morphotypes were sometimes found vertical in the water column near gorgonians where blue chromis were not found, so they do not appear to human observers to always "match" their environment. This may reflect a high cost associated with color change. Alternatively, each individual trumpetfish may not be able to exhibit the full range of color morphotypes. Out of nearly 200 different trumpetfish observations over a seven-day period, no individuals were observed changing from a colored-head morphotype to a uniform color morphotype. Future research investigating the association of yellow-head morphotypes and juvenile/initial phase adult bluehead wrasse, and the energetic cost associated with color change, should provide insight into trumpetfish behavior and camouflage predators in general.

LITERATURE CITED

Aronson, Richard B. Foraging behavior of the West Atlantic trumpetfish, *Aulostomus maculatus* : use of large herbivorous reef fishes as camouflage. Bulletin of Marine Science **33**(1): 166-171.

Balser, Teri C. and Soucy, Sheryl L. 1992. The effects of *Diadema antillarum* on two Jamaican reefs: an examination of community response. Pp. 171-180 *in* J. L. Dudycha and A. B. Shabel, editors. Dartmouth Studies in Tropical Ecology 1992.

Carpenter, R. C. 1990. Mass mortality of *Diadema antillarum*. I. Long term effects on sea-urchin population-dynamics and coral reef algal communities. Marine Biology **104**: 67-77.

Hughes, Terrence P. 1994. Castrophes, phase shifts and large-scale degredation of a Caribbean coral reef. Science **265**: 1547-1551.

Kaufman, L. 1976. Feeding behavior and functional coloration of the Atlantic trumpfish, *Aulostomus maculatus*. Copeia **2**: 377-378.

Woodley et al. 1981. Hurricane Allen's impact on Jamaican coral reefs. Science **214** : 749-755.