Spatial Dispersion and Nonmigratory Spawning in the Bluehead Wrasse (Thalassoma bifasciatum)

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Abstract

Earlier studies of the behavior of the bluehead wrasse Thalassoma bifasciatum have shown it to be a migratory spawner with large terminal-phase males defending temporary spawning territories. We describe a variant social structure where fish occupy permanent home ranges, spawn within or near these home ranges, and are not territorial. Movements of identified terminal-phase and intermediate males and females were mapped in the backreef areas of three coral reefs in Puerto Rico. Locations of spawns were then compared with these home-range maps. All fish used most or all of their morning home range during the afternoon spawning period. Both terminal-phase males and females spawned within or near their home ranges. Males were relatively tolerant of other males during the afternoon spawning period: only one in five encounters between large males resulted in aggressive chases. The location of chases bore no relation to spawning sites, areas of morning foraging, or to home-range borders. A Monte Carlo computer simulation was used to measure home-range dispersion of terminal-phase and intermediate males at our main site. If males were territorial, we should expect their home ranges to be significantly overdispersed within the cumulative area they occupied. During the first year male home ranges were overdispersed but during the second year they were randomly dispersed, even though the same number of terminal-phase males occupied the same study site both years. Differences in social behavior between backreef areas and other areas reported in the literature, and found in other portions of our reefs, may be related to differences in feeding ecology between populations and between different portions of the same reef.

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Introduction

The bluehead wrasse, Thalassoma bifasciatum, is one of the best studied coral-reef fishes. It has been used to test hypotheses concerning life-history strategies and the evolution of sex change (Warner et al. 1975; Warner & Hoffman 1980a; Warner 1984, 1985), the economics of territorial defense...
Materials and Methods

Subject Species and Study Site

*T. bifasciatum* is an extremely abundant wrasse that inhabits a wide variety of Caribbean reef habitats (FIEDFERN 1965; XIMMEL 1985). It is a generalist feeder, taking zooplankton, a wide variety of bentic organisms, and ectoparasites from other fish (RANDALL 1967). Populations of *T. bifasciatum* generally contain two types of males (REINBOTH 1973). Initial-phase (IP) males are small, colored like females, and have matured directly as males. Terminal-phase (TP) males are larger and are either individuals that have changed sex and color from an earlier female stage or are initial-phase males that have changed color. TP males typically pair spawn with single females, while IP males can either pair spawning in large groups containing one female and a number of other males (WARNER et al. 1975).

Observations in Panama revealed three types of TP and INT males: territorial individuals, associated satellites and floaters (WARNER, R. R., pers. comm.). We sought evidence for such a distinction, but found a full range of variation in degree of overlap and degree of association between males of differing sizes; we found no reliable criteria for singling out discrete degrees of association.

Home-range maps and spawning locations were plotted on portions of three fringing reefs, San Cristóbal (ROGERS 1979); La India and Corona de Atravesado on the southwest coast of Puerto Rico (Fig. 1). These reefs measured approximately 225, 200, and 100 m, respectively, along their seaward crests. Study sites on all three reefs were in sheltered, backreef areas in depths of 1.0–3.5 m, where the habitat consisted of coral heads and colonies of gorgonians scattered over coral rubble and calcareous sand. Data on home range dispersion and aggressive behavior were obtained in a 50 x 50 m grid made of steel rods and polypropylene rope, divided into 225 numbered quadrats 3.3 m on a side, located at our main study site on San Cristóbal. The male : female sex ratio of IP at this site was 1 : 5.3; when 57 IP were caught in baited traps and sexed, 48 (84 %) were female and nine were male.

Home Ranges and Spawning Locations

On San Cristóbal, we mapped the home ranges of 10 TP males, 10 INT males, and 9 females whose home ranges were centered in the central 81 quadrats of the grid in two different years. We then followed selected individuals during afternoon spawning periods to locate their spawning sites. Females and INT males were selected to represent the full range of body sizes in the grid, from small females to the largest males. Data were collected between May-Aug. 1984, and between Jan.—Apr. 1985. In both years the central area was occupied by five TP males and at least five INTs. TP and INT individuals were identified by unique variations in their color (REESE 1973; WILLIAMS 1978; WARNER & HOFFMAN 1980 a), specifically in the post-opercular stripes. Females were captured in baited traps, sexed, injected subcutaneously with acrylic paints in unique patterns (THRESHER & GRONELL 1978) and released at the point of capture. Females were held for about 5 min between the time of capture and release.

Spatial Dispersion and Nonmigratory Spawning in the Bluehead Wrasse

(Fig. 1: Map showing reefs in southwestern Puerto Rico, including the three study reefs
Home range data during both years were taken between 08.19 and 12.30 h. Females were observed during five 30-min observation periods and males during 10 15-min periods. In each period, we followed the subject and recorded the number of squares entered, the proportion of total observation time spent in each quadrat. From this list we calculated the smallest set of quadrats within which the fish spent 75%, 90%, and 100% of its time (the 75%, 90% and 100% home ranges). The 100% home range included all quadrats in which the fish was ever seen during these morning observation periods.

Home range data on San Cristóbal were recorded during 239 observation periods totaling 70.3 h on 29 fish. Both 90% and 100% home range sizes approached asymptotic levels closely by the 90th min of observation in all females, INTs, and all but one TP male. Thus, our observation times were adequate to characterize home range size (Brown 1975).

We recorded spawning data for a total of ten TPs, three INTs and six females. At San Cristóbal we recorded spawning locations for five males (two TPs and three INTs), in 1984 and six females in 1985. We observed each male continuously for approximately 2.5 h during the afternoon spawning period on six days, giving a total of 74.2 observation h for all five males. The location of each spawn or courtship was recorded. Courtship was defined as the performance of any courtship behaviors (Bennett & Hoffman 1977; Robert & Forsthoff 1985). Spawning was defined as a rapid rush toward the surface by one male and one IP fish, regardless of whether or not a gamete cloud was seen (Warner & Hoffman 1980 b).

Females spawned much less frequently than some males (Warner et al. 1975; Hoffman et al. 1985); hence, methods were adjusted to increase the efficiency of observation. One of three females were marked and observed during the spawning period on the same day. The observer swam repeatedly over the grid looking for abdominal swelling, an indicator of readiness to spawn, in any marked female. Once a marked female with a swollen abdomen was detected, she was continuously followed wherever she went until she spawned. The spawning location was recorded. At the conclusion of spawning by this female, the search resumed for another spawning-ready fish. When the first-observed female spawned early, it was often possible to observe the spawning of a second or third female in the same spawning period. Female spawning behavior was observed a total 17.7 h on 10 days. Because only 1—3 females were observable on any given day, the maximum number of spawns that could have been observed with our techniques for the six marked females over the 10 observation periods, even assuming optimistically that each female spawned once daily (Warner 1986), was 18. These spawnings were, in fact, seen, suggesting that few, if any, spawns were missed with these methods.

On La India and Corna de Atravesado reefs we used an abbreviated version of the methods given above, focusing on four large TP males at each site. Large males were selected because, in Panama, they are more likely to behave territorially than small males (Warner et al. 1975). Data were collected in June, 1988. For each fish, we collected home range data during at least six 15-min observations during the morning feeding period and during at least six observations during the later spawning period by recording fish position every 15 s on detailed scale maps of the reef. The convex polygon method (Brown 1975) was used to circumscribe home-range boundaries around these points, creating a separate home range map for the morning and the afternoon periods. Spawning locations were then superimposed on these maps. Home Range Dispersion and Territorial Behavior

In the grid on San Cristóbal reef we recorded the frequency and location of courtship, spawning and aggressive encounters during the afternoon observation periods. We assumed that territoriality by males could be recognized by using any or all of the following features: (1) space used by males is virtually completely overlapping with morning home ranges for all individuals on all three reefs, would be statistically overdispersed. Thus, in the central portion of the grid, where the entire area falls within the home range of at least one male, male home ranges should be spaced apart to a greater extent than would be expected if their home ranges were placed randomly within the same area. If this assumption were not true, then males would have no exclusive area, at least, no territory, other than that provided by random occupation of space. (2) Aggressive interactions should occur in relation to whatever area or location was being defended. If males defended entire home ranges, then aggression should occur on the periphery of the home range or primarily in the area of overlap with neighboring males. If males defended courtship and spawning sites, then aggression should occur in relation to these sites. If aggression does not occur in relation to spatial features of the home range or does not indicate whether part or all of the home range is being defended, then males were not territorial. (3) Males should display low tolerance for other males approaching them. Consequently, most encounters between males during the spawning period should result in an aggressive chase.

To quantify the degree of overlap in male home ranges we calculated Pianka's index of overlap (Pianka 1975; Waser & Wiley 1979) for each possible pair of fish, based on the proportion of time each fish spent in each quadrat. This index theoretically varies from zero (no overlap) to one (both individuals spent identical amounts of time in the same quadrats). The nearest neighbor of a subject was defined as that individual with which the subject had the highest index.

To analyze spatial dispersion of male home ranges we used a Monte Carlo computer simulation (Binder & Stauffer 1987; Sokal & Rohlf 1981). Each quadrat within the home range was characterized by the proportion of time spent in it by the male. The used quadrat in a male's observed home range was placed at a randomly chosen location within a simulated grid. The home range was oriented randomly in one of four perpendicular directions, and all other used quadrats were then placed in the appropriate location with respect to the most used quadrat. This procedure was repeated for 2000 computer runs. For each quadrat in the index of overlap with any possible pair of fish, and one run of the simulation was complete. The simulation consisted of 2000 runs. We used the mean, over all fish, of Pianka's index of overlap between each fish and its nearest neighbor as our test statistic. The simulation generated a random probability distribution for this statistic. Since we wished to test whether males were territorial and their home ranges overdispersed, we employed a one-tailed test. The probability of observing an index of overlap as small or smaller than the actual value was found by comparing the observed value with the randomly generated probability distribution. If fewer than 5% of the randomly generated values were less than the observed value, p was less than .05 for a one-tailed test and we concluded statistically significant overdispersion.

Computer simulations were run separately for all 10 males, for TP males only, and for INT males only, in each of the two years of observation. The simulations would thus reveal whether TP males had spatial dispersion patterns that were the same as or different from those of INT males or from all males taken together.

Behavioral interactions were recorded for five males (three INTs and two TPs) during their afternoon spawning periods in 1984. Each male was followed as a focal animal. Whenever the focal male came within 1 m of another male for more than 5 s, an interval that approximated the error of our timing accuracy, the instance was defined as an encounter. The duration and location of encounters were recorded. When one fish swam rapidly at another fish that swam away, the interaction was called a chase and was characterized as aggressive. The number and quadrat location of chases were recorded. Levels of aggression were estimated by calculating the number of chases per observation hour and the number of chases per encounter. For comparison, similar data were also recorded during the morning observation periods of ten males (five TP and five INT males) in 1985.

To obtain an estimate of the dispersion of IP individuals, most of which were females, we censused IP fish within the central grid (Drew 1986). An observer swim slowly over the grid, spending 45 s in each quadrat counting the number of fish. Censuses were taken between 09.00 and 14.00 h on 13 days. Dispersion of fish over the central grid was analyzed by computing the variance-to-mean ratio for the number of individuals per quadrat. The value expected if fish were randomly dispersed over the central grid is 1.0 (Pielou 1977).

### Results

#### Home Ranges and Spawning Location

The area used by males during the spawning period was almost the same as the morning home range for all 13 males on all three reefs. In the grid on San Cristóbal, home range sizes did not differ significantly between 1984 and 1985 for any color phase of fish for 75%, 90%, or 100% estimates (Mann Whitney U-test, p > 0.05 for all comparisons). Consequently, data from both years were...
Table 1: Median values and 95% confidence limits (in parentheses) for the area (m²) of 75%, 90% and 100% estimates of home range for initial-phase fish (IP), intermediate males (INT), and terminal-phase males (TP)

<table>
<thead>
<tr>
<th>Fish class</th>
<th>n</th>
<th>75%</th>
<th>90%</th>
<th>100%</th>
</tr>
</thead>
<tbody>
<tr>
<td>IP</td>
<td>9</td>
<td>20 (10-30)</td>
<td>35 (10-30)</td>
<td>60 (10-70)</td>
</tr>
<tr>
<td>INT</td>
<td>10</td>
<td>55 (40-60)</td>
<td>90 (70-120)</td>
<td>150 (100-220)</td>
</tr>
<tr>
<td>TP</td>
<td>10</td>
<td>90 (30-130)</td>
<td>135 (60-200)</td>
<td>275 (190-340)</td>
</tr>
</tbody>
</table>

Kruskal Wallis ANOVA: \( p < 0.001 \) \( p < 0.001 \) \( p < 0.001 \)

Table 2: Spawning locations of terminal-phase (TP) and intermediate (INT) male *T. bifasciatum* with respect to male home range (HR). "Max distance" is the maximum observed separation between a spawning location and the nearest home range border. TL = total length

<table>
<thead>
<tr>
<th>Site</th>
<th>Fish #</th>
<th>Type</th>
<th>TL (cm)</th>
<th>Number of spawns in HR</th>
<th>out of HR</th>
<th>Max distance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Main</td>
<td>M1</td>
<td>TP</td>
<td>11.8</td>
<td>60</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Main</td>
<td>M3</td>
<td>INT</td>
<td>10.3</td>
<td>8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Main</td>
<td>M6</td>
<td>INT</td>
<td>9.8</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Main</td>
<td>M7</td>
<td>INT</td>
<td>9.8</td>
<td>9</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Main</td>
<td>M8</td>
<td>TP</td>
<td>11.5</td>
<td>37</td>
<td>2</td>
<td>12 m</td>
</tr>
<tr>
<td>Corona</td>
<td>C1</td>
<td>TP</td>
<td>10.6</td>
<td>61</td>
<td>12</td>
<td>1 m</td>
</tr>
<tr>
<td>Corona</td>
<td>C2</td>
<td>TP</td>
<td>10.7</td>
<td>4</td>
<td>??</td>
<td>5 m</td>
</tr>
<tr>
<td>Corona</td>
<td>C3</td>
<td>TP</td>
<td>10.2</td>
<td>20</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Corona</td>
<td>C4</td>
<td>TP</td>
<td>9.8</td>
<td>8</td>
<td>1</td>
<td>1 m</td>
</tr>
<tr>
<td>India</td>
<td>I1</td>
<td>TP</td>
<td>12.3</td>
<td>31</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>India</td>
<td>I2</td>
<td>TP</td>
<td>12.2</td>
<td>12</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>India</td>
<td>I3</td>
<td>TP</td>
<td>11.2</td>
<td>37</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>India</td>
<td>I4</td>
<td>TP</td>
<td>12.1</td>
<td>24</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>315</td>
<td>37</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Spatial Dispersion and Nonmigratory Spawning in the Bluehead Wrasse

From the main site, we have omitted data from these two sites from the analysis of home range size.

On all three reefs, spawning occurred within or close to the border of the morning home range of all fish. On San Cristóbal, all but one of the five males observed during afternoon spawning periods spawned exclusively within their morning home range (Table 2). The other male had 2 of his 37 spawns (5%) outside of his home range, one 3 m and the other 12 m from the nearest home range quadrate. Of a total of 121 male spawns observed at the main site, 98% were within morning home range boundaries.

At La Corona, 92 (72%) of 127 observed male spawns were inside the morning home range (Table 2). 32 spawns were within 1 m of the nearest home range border. The remaining 3 spawns were a maximum of 5 m from the nearest home range border. At La India, 100% of 104 observed male spawns were within the morning home range. Thus, of the 13 males and 352 spawns observed on all three study reefs, 9 males (accounting for 206 spawns) spawned entirely within their morning home range, and four males had a total of 37 spawns (11% of the total number of spawns) outside of their morning home range. These "outside" spawns were a mean distance of 1.68 m (max = 12 m) away from the nearest home range border.

Female spawnings were observed only at San Cristóbal. A total of six identified females were followed during the spawning period over 10 days. During this period 15 spawns by six females were observed. Each female spawned 1-4 (median 2 times). On most occasions (range 0-100%, median 88%), females spawned within their morning home ranges. When data from all females were pooled, 60% of spawns occurred within the females' home ranges. Six spawns were 3.3-13.3 m (median 6.6 m) outside of the subject female's home range. All were inside the study grid and were thus confined to a relatively small portion of the reef.

Our population differed substantially from descriptions in the literature in the number of sites at which a given male spawned. San Cristóbal males spawned in a minimum of 2 different quadrats (the male which spawned least) and in a maximum of 13 quadrats, whereas males in Panama had a maximum of 4 spawning sites (WARNER 1985). A given quadrat could contain up to three local spawning sites. We ranked spawning quadrats by the number of spawns observed within them. In total, spawns in a fish's first-ranking quadrat accounted for only 33.9% of total spawns (41 out of 121 total).

Dispersion of Home Ranges

Indices of overlap between nearest neighbor males on San Cristóbal varied widely (Table 3). Some males had home ranges that were largely exclusive of neighboring males, while others overlapped almost entirely with a neighboring male. Indices for 1984 and 1985 did not differ significantly (Mann-Whitney U-Test, \( U = 35 \), \( p > 0.05 \)).

The results of the Monte Carlo simulations differed for the two study years (Table 4). In 1984, fish were significantly overdispersed (\( p < 0.05 \)), regardless of
Table 2: Pianka's index of overlap with the nearest neighbor of each male T. bifasciatum during two successive years. (TP: terminal-phase male; INT: intermediate male).

<table>
<thead>
<tr>
<th></th>
<th>TP</th>
<th>TP</th>
<th>M1</th>
<th>M2</th>
<th>M3</th>
<th>M4</th>
<th>M5</th>
<th>M6</th>
<th>M7</th>
<th>M8</th>
<th>M9</th>
<th>INT</th>
<th>INT</th>
</tr>
</thead>
<tbody>
<tr>
<td>1984</td>
<td>Overlap</td>
<td>0.455</td>
<td>0.339</td>
<td>0.278</td>
<td>0.414</td>
<td>0.533</td>
<td>0.183</td>
<td>0.151</td>
<td>0.439</td>
<td>0.278</td>
<td>0.191</td>
<td>0.533</td>
<td>0.924</td>
</tr>
<tr>
<td>1985</td>
<td>Overlap</td>
<td>0.355</td>
<td>0.353</td>
<td>0.682</td>
<td>0.524</td>
<td>0.290</td>
<td>0.517</td>
<td>0.139</td>
<td>0.386</td>
<td>0.317</td>
<td>0.386</td>
<td>0.924</td>
<td></td>
</tr>
</tbody>
</table>

which subgroup of males (INTs only, TPs only, or all fish together) was examined. In contrast, no overdispersion was found in the 1985 data; males were randomly dispersed. Both in 1984 and in 1985, the dispersion of TPs was identical to the dispersion of INTs. Thus, even though TPs had greater reproductive success than INTs within a reef (Table 2), they dispersed themselves in identical patterns.

The mean density of IP fish (both males and females) on the central grid was 0.96 fish/quadrat or 0.88 fish/10 m². The variance-to-mean ratio for the number of IP fish per quadrat was 3.85. This ratio significantly exceeded unity, the ratio expected if fish were randomly dispersed (χ² = 308, df = 80, p < 0.001). Therefore, the IP fish were aggregated in space on the central grid.

Behavioral Interactions

The main activity of all fish during the morning was benthic feeding. During the afternoon, males mixed mating behavior with feeding, and females continued to feed benthically with a brief pause for spawning. Of 3636 feeding bites counted (n = 5 fish), only 1% were on planktonic food items.

Males encountered, i.e., moved to within 1 m of each other, a median of 8.4 and 10.8 times/h in the morning in 1985 and in the afternoon in 1984, respectively. They spent medians of 23% and 13% of the observation time in encounters during these two years. During the afternoon spawning period, the rate of chasing was 0.7-3.7 times/h, with median 2.6, and the number of chases per encounter ranged from 0.15-0.25; the median was 0.19. Thus, most encounters did not lead to aggressive chases; males were relatively tolerant of one another even during the spawning period.

The location of every aggressive act was plotted on the home range map of each male. Aggressive acts occurred in 0.25-0.64 (median 0.31) of male home-range quadrats and were not located with respect to any apparent special feature of the home range. For example, there was no consistently significant correlation, positive or negative, between quadrat usage for courtship and/or spawning and rate of aggression or between morning use for foraging and afternoon aggression (Table 5). Males behaved aggressively in central portions of their home range as well as along the periphery.

Table 3: Spearman correlation coefficients between afternoon aggression (Aggr) and courtings-and-spawnings (C/S) or morning usage (AM Use) for each of 5 males.

<table>
<thead>
<tr>
<th>Fish</th>
<th>M1</th>
<th>M3</th>
<th>M6</th>
<th>M7</th>
<th>M8</th>
</tr>
</thead>
<tbody>
<tr>
<td>C/S vs. Aggr.</td>
<td>0.03</td>
<td>-0.69</td>
<td>-0.35</td>
<td>-0.47</td>
<td>-0.39</td>
</tr>
<tr>
<td>AM Use vs. Aggr.</td>
<td>-0.52</td>
<td>0.16</td>
<td>-0.77</td>
<td>0.34</td>
<td>-0.18</td>
</tr>
</tbody>
</table>

*: terminal-phase male, b: intermediate male, #: p < 0.05 one-tailed.

Discussion

On all three study reefs, females and both INT and TP males occupied permanent all-purpose home ranges. During the morning, individuals foraged on the substrate and interacted with individual neighbors behaviorally. In the afternoon, males spawned at multiple sites almost entirely within their morning home ranges. Females spawned within their home range or close to it. In contrast, fish in Panama have been described as occupying upcurrent plankton-feeding groups in the morning and then migrating, often substantial distances, to down-current areas where TP males and females each spawn at a small number of mating sites in the afternoon (WARNER 1984, 1986, 1987; ROBERTSON & HOFFMAN 1977).

We found no convincing evidence of male territoriality in this variant of the social system. INT and TP males were relatively tolerant of other males within their home ranges. Fewer than one in four male-male encounters during the spawning period resulted in an aggressive chase. The location of chases was not correlated spatially with spawning-site location or morning usage and bore no clear relation to home range borders.
Finally, the computer simulation yielded conflicting results for two data sets in different years at the same site. In 1984, male home ranges were overdispersed, as one would expect if home ranges were defended as territories. However, these males tolerated a minimum of three out of every four intrusions by other males within their home range without chasing them. These results suggest that overdispersion of home ranges in 1984 was not caused by male-male aggression. In 1985, on the same site with the same number of TP males occupying the center of the grid, home ranges were randomly dispersed. The difference between the two years cannot be attributed to different home range sizes, different sample sizes, different techniques or different numbers of males on the grid. The most likely cause of the different dispersion patterns is the difference in identity of individual males between the two years, i.e. that different sets of males use space differently. Since choice of mating sites by females is traditional, with the same sites in use for prolonged periods (WARNER 1988), the difference in male dispersion is not likely to stem from differences in female behavior between the two years.

Whatever the cause, the variation in home range dispersion, inconsistency in location of chases, and tolerance of males for each other do not constitute convincing evidence for a consistent or well-developed system of spawning territories in this portion of our reefs. In contrast, territorial males in the San Blas Islands displayed low tolerance to the approach of another male, chasing them at high frequencies, and a substantial proportion of their time was spent defending spawning sites (WARNER & HOFFMAN 1980 b).

The most striking difference between our study populations and those described in Panama is that our fish did not migrate to the downcurrent end of the reef before spawning. Although a few fish spawned a few meters from their morning home range, no migration was seen in the backreef study areas of any of the three study reefs. When dye was released at various sites around San Cristóbal to document the speed and direction of current, the most downcurrent end of the reef was at least 100 m of almost continuous coral cover from our grid (SHAPIRO et al. 1988). The intervening area was occupied by spawning conspecifics and no physical barrier prevented migration. When the grid at San Cristóbal was divided into upcurrent and downcurrent halves, a significantly larger number of spawns were located in the upcurrent half (SHAPIRO et al. 1988). Thus, it would appear that the fish in backreef areas do not select specific spawning sites with respect to their location in the current.

In other portions of our reefs, i.e. along the forereef and in areas of vertical reef face, males and females did migrate to spawning sites and their behavior appeared to be the same as that described in Panama, i.e. individuals fed on zooplankton during the morning and migrated to other sites in the afternoon where TP males defended temporary territories. Females either spawned in pairs within these territories or spawned in groups with IP males in nearby areas. Thus, the populations in our reefs are organized into at least two variants of social and mating structures. Similar variation in social and mating structure has been documented in another protogynous labrid, Halichoeres maculipinna (THRESHER 1979; ROBERTSON 1981).

If those features of the social system examined in this study have been selected to adapt to local resource distribution, as is often thought to be true in terrestrial animals (RUBENSTEIN & WRANGLHAM 1986; SLOBODCHIKOFF 1988), then the migratory and nonmigratory variants on our reefs should match differences in resources. The clearest difference in resources between forereef and backreef areas is likely to be availability of food, with most of the zooplankton arriving at the reef front removed by planktivorous fishes before the water approaching the reef is swept over the reef flat or around the edges of the reef into the backreef area (HAMNER et al. 1988).

On our reefs, T. bifasciatum in forereef areas foraged pelagically on zooplankton, while those in backreef areas fed benthically on the substrate. Once the population is separated into different feeding types located on different parts of the reef, differences in water movement between forereef and backreef may influence the mating system. We suggest that backreef areas (where foraging occurs) lie in locations with respect to water movement and other reef structures that make them adequate areas for releasing pelagic eggs (RANDALL & RANDALL 1963; JONES 1968). Forereef areas, where T. bifasciatum feeds on plankton, may be unsuitable for pelagic spawning because surface water from these areas passes over the reef crest (SHAPIRO, HENSLEY & APPELDOORN, unpubl. data). Consequently, selection should produce the ability of individual fish to match their spawning areas with their feeding ecology. The result will be migration from forereef planktivorous areas to locations nearer the lateral edge of the reef, where water containing spawned eggs will not pass over the reef crest. If there is significant concentration of spawning in these areas, then specific sites would become economically defensible and large males would chase intruding males away.

In contrast, fish feeding benthically in backreef areas can remain in place to spawn. These backreef locations are spread over a relatively large area. If there are many possible specific sites for mating, spawning becomes spread over a diffuse area and the potential gains of temporary resource-defense polygyny, as seen in migratory populations, cease to outweigh the costs and territoriality will not develop (EMLEN & ORING 1977).

We do not believe that the proximate cause of migrating or remaining in morning home ranges to spawn is simply a function of current speed, despite the fact that average current velocities may be less in backreef than in forereef areas. If migration were induced simply by current attaining a particular value, then we would expect normally migratory populations not to migrate on days of low current, a result that has not been reported in the literature, and fish in backreef sites to migrate on days of strong current, a result we never observed even when storms resulted in vigorous currents over our sites.

The consequences of the more sedentary and less aggressive social structure in the backreef areas are likely to be theoretically important. T. bifasciatum is a protogynous hermaphrodite and has been used in the past to test hypotheses about sex change (WARNER et al. 1979) and mating systems (ROBERTSON & HOFFMAN 1977; WARNER & ROBERTSON 1978). In these papers, the mating system and sex change itself are assumed to have evolved under conditions of intense
competition for limited spawning sites. As a result of this heavy competition small differences in size are believed to have resulted in disproportionately large gains in male protogynous hermaphroditism (WARNER 1975). In the nonmigratory populations documented here, the relatively large number and wide dispersion of spawning sites and the absence of consistent defense of home ranges or spawning sites leads to reduced competition between males for mates. In this situation, size is probably a less important determinant of male mating success than other factors such as home range location. Since the above explanation for the evolution of protogyny in this species is based on the idea of a size advantage in mating for females, an important new development in the relative proportion of reef populations that employ the migratory, territorial/spawning system vs. the nonmigratory, all-purpose home range mating system documented here.

Acknowledgements

Research was supported by grants from Sigma Xi, the Explorer's Club and Brown University to WTSF and by NIH grant 2 S06 RR063, NSF grant OCE-841079, and grant R/LR-361 from the University of Puerto Rico Sea Grant Program to RTSF and by NIH grant 2


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Received: November 3, 1989
Accepted: April 9, 1990 (G. Barlow)