Territoriality, community structure and coexistance in three species of the genus Eupomacentrus (Pisces:Pomacentridae).

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Bob:
Good study and excellent discussion of [illegible]
John

Abstract. The territorial systems of three damselfish species were studied at Discovery Bay, Jamaica. Structural parameters of defended algal lawns were measured and aggressive behavior which maintains the territory was quantified. Three-spot Damselfish defend a smaller territory than either the Dusky or the Beaugregory. Estimated algal volume was greatest for Beaugregories, followed by Three-spots and Duskies. The results of the study are discussed with reference to previous models of interspecific territoriality, competition and community structure. The factors permitting the coexistance of the three damselfish species remain to be fully explained.

Introduction

Territoriality in reef fishes, including especially the damselfishes (Pomacentridae) has attracted the attention of behavioral biologists and ecologists for many years. Interesting questions remain unanswered despite this coverage, and perhaps the most interesting of these focus on the adaptive significance of the interspecific territoriality of the damselfishes, and on territoriality as a mechanism of niche seperation and resource partitioning permitting the coexistance of closely related species in coral reef habitats. Niche overlap may be considerable in the damselfish (Itzkowitz, 1977), yet the factors allowing coexistance are not clear at present (Sale, 1974;1975). The situation is intriguing when compared to the model proposed by Murray (1971) in which, for birds, interspecific territoriality was considered a non-adaptive and evolutionarily unstable strategy. According to Murray, interspecific territoriality will be the temporary result of contact between formerly allopatric, closely related species, and is maintained primarily by misdirected intraspecific aggression until, over evolutionary time, the species diverge in habitat, behavior, morphology or other niche parameters. Myrberg and Thresher (1974) and Ebersole (1977) have shown that damselfish exhibit fine species discrimination, as both the area of defended space and the intensity of aggression elicited vary with intruder identity.

At Discovery Bay, Jamaica, three species of territorial damselfish of the genus Eupomacentrus are common and easily studied. These are the Three-spot Damselfish (E. planifrons (Cuvier and Valenciennes)), the Dusky Damselfish (E. fuscus (Cuvier and Valenciennes)), and the Beaugregory (E. leucostictus (Miller and Troschel)). Each species -

defends a Type A territory (sensu Wilson, 1975:265) which are used for courtship, mating, shelter and feeding activities. The primary resource defended is the algal lawn, consisting of lush algal growth on the surface of coral rubble or loose substrate, and defense involves attacks and displays toward conspecifics and other species. General observations at Discovery Bay and descriptions in the literature (including 1978 Dartmouth F.S.P. Advanced Marine Biology projects) indicated that while these congeneric species are similar in many respects, they differ in the structure of the algal lawn itself and in their aggressive territorial behavior.

The purpose of this study was to quantifiably test the hypothesis that the three Eupomacentrus species defend resources that differ in certain respects. I predicted that the morphology of the algal lawns varied in both gross dimensions (area, cover) and in subtle characteristics. The former were approached directly through physical measurements. Differences in the fine details of resources present were investigated indirectly by observing the behavior of each damselfish toward intruders. This approach was based on the conclusions of Myrberg and Thresher (1974) that the response by territory residents parallels the competetive threat posed by each species of trespasser which in turn is a function of niche overlap. Thus variation between the damselfish in terms of resourses used should be reflected in differences between the aggressive hierarchies maintained toward invaders. By investigating the interaction between territorial resources and their defense, I hoped to clarify the factors which underly the structure of the damselfish community and to deal with the role of interspecific territoriality as a coexistance mechanism in coral reef habitats.

Methods

Two study sites on the Discovery Bay reef were chosen for the presence of territorial damselfish and ease of observation. Three-spot and Dusky Damselfish are abundant in the *Acropora cervicornis* zone of the fore reef. The site in this zone was located at 15m depth on the western edge of Kinzie Gorges reef. Observations at this site (hereafter referred to as West Fore Reef or WFR) were made using SCUBA. The second site was situated in a pool, 1-2m deep, cutting through the *Acropora palmata* area of the back reef crest. Beaugregories, Duskies and Three-spots were all present here (West Back Reef or WBR) and were observed using mask and snorkel.

Observations were made over a five day period (Feb.26-Mar.2, 1979), with data recorded on a plexiglas slate with pencil. Each site was visited once each day, and a total of roughly 300 minutes of behavioral data were collected. 29 territories were observed and measured as follows:

Three-spot: WBR 5, WFR 5
Dusky : WBR 5, WFR 9
Beaugregory: WBR 5

I observed each territory for at least ten minutes to determine its general location, center and borders. A center reference point was then chosen from which intrusion distances were measured. When appropriate, this point coincided with the center of the defended algal lawn or with the refuge crevice used by the resident fish. After familiarization with the territory, a ten minute observation period was completed (shortened to eight minutes in two cases due to insufficient air supply). During this interval, the following data were recorded:

1. Number of intrusions within 1.5m of the territory center.

2. Species of intruder

3. Elapsed time of each intrusion (mental estimate to nearest five seconds for short trespasses). "Neighbor" Eupomacentrus species were assumed to be present for entire interval when on territory.

4. Distance of deepest penetration of trespass (from territory center) and/or distance of attack by resident, especially for "intrusions" of greater than 1.5m.

5. Number of aggressive responses to intruder by resident damselfish.

To aid in estimating attack and intrusion distances, a meter stick ruled to 0.1m was placed in the territory several minutes before the start of the observation period. I detected no disruption of resident behavior caused by this introduction. Distances for intrusion/attacks were approximated and grouped as follows: 0.25, 0.5, 0.75, 1.0, 1.5, and greater than 1.5m.

After completion of the behavioral observations, the size of each resident damselfish was recorded (±1cm) and the structure of the algal lawn was measured. I recorded:

1. Area of the algal patch, estimated as length by width, each ± 0.1cm.

2. For 5 randomly selected points:
   a. % algal cover, ± 10%, using a small ring to aid estimation.
   b. Depth of algal cover, ±0.05cm, using a plastic centimeter rule.

3. Nature of substrate and general notes.

I had hoped to carry out obsevations at a third site in the lagoon area, where Beaugregories and Three-spots are common, but was limited to the two areas above by time constraints.

Results

As noted in Methods, a total of 29 territories were observed and measured at the two sites. Table 1 gives the mean size of

Species	n	size (cm)	range (cm)
Three-spot	10	12.6 + 1.0	10 - 14
Dusky	14	11.1 + 0.9	10 - 13
Beaugregory	5	11.0 + 0.6	10 - 12

Table 1. Mean Size for Resident Damselfish on Territories Observed

each Eupomacentrus species. As these means are not significantly different (Student's t-test, all $p>0.05$), size of individual fish will be taken to be relativelt constant and will not be included in further analysis.

1. Parameters of the Algal Lawn

Table 2 gives the mean and deviation for each of the measurements made on the algal lawns defended by residents by species and subdivided by site for the Three-spot and Dusky. Comparing the total means (WFR and WBR combined), the Three-spots defend lawns significantly smaller than Duskies (t-test, $p<0.001$) and Beaugregories ($p<0.001$), which themselves are not significantly different ($0.1<p<0.2$). At the same time, mean algal cover (calculated as the mean % cover over the five sample points multiplied by the mean depth of cover for the same points) was significantly smaller for the Dusky than for the other damselfish (both $p<0.001$), which were not different ($0.1<p<0.2$). Multiplying the mean cover and area parameters yields an estimate of the volume of algae present on the territories; the means of this measure are significantly different for all damselfish species pairs ($p<0.001$).[1] These results are represented graphically in Fig. 2, and the seperation of territory morphology by species is readily apparent.

It is interesting to note that for both the Three-spot and the Dusky, the mean values for lawn area, cover and volume are not

1. BEAUGREGORY > THREE-SPOT > DUSKY (m^3 algae $\times 10^{-2}$ / territory)

significantly different between sites, but they are arranged similarly about the combined mean for each species. The West Fore Reef territories in both cases are slightly larger and more sparsly covered than in the West Back Reef area, which may reflect a difference in habitat quality (such as light intensity) between the sites.

2. Interactions between Congeneric Damselfish

All aggressive interactions between Eupomacentrus damselfish were recorded, and intruders and neighbors were lumped for analysis, since I was unable, in most cases, to be sure of the status of trespassers. Table 3 lists the aggressive acts recorded for each species toward congenerics and the number of acts per minute of total observation time. The sample size obtained is regrettably small and not suitable for full statistical analysis. However, it does appear that while most resident-intruder pairs demonstrated similar rates of aggression, the Beaugregory may be more aggressive toward conspecifics. I have not controlled for damselfish densities (though they appeared to be roughly equal for all species) or for the distinction between neighbors and "floaters", both of which should directly influence the rates of aggression observed. More careful work is called for in this area.

Table 4 lists the distance from the resident's territory center that each intruding congeneric was allowed to approach. The same data are depicted graphically as percentages in Fig. 2. None of the damselfish residents responded differently to the various intruding congenerics, though larger sample sizes might substantiate trends seen in the figures (2a-c). The responses of the three residents to congenerics taken as a whole does show significant

variation (X^2=25.4,10 dgf,p<0.01); the Three-spot will allow congenerics to approach its territory center more closely than will Beaugregories or Duskies. (Fig. 2d).

3. Response to All Intruders

Aggression and intrusions involving fish outside the genus Eupomacentrus are presented in Table 5. As with congenerics, aggressive acts include attacks and displays, and the same procedure of intrusion measurement was employed, though all fish in this section were considered intruders. Few of the other fish on the reef are strongly territorial, so the "neighbor" category was not involved.

The number of intrusions for each species varied widely, and the total sample size is small for any one invader. As a result, the data are not well suited to statistical analysis. I calculated the mean and deviation of aggressive acts per minute for the Bluehead Wrasse (adult and immature), the Yellowhead Wrasse, and the Striped Parrotfish. In each case, the deviation exceeded the mean and comparisons between resident species were not significant. The most visible general trend, shown in Fig. 3, is that the Three-spot defends a smaller area than the Dusky or the Beaugregory (X^2=37.9, 10 dgf, p<0.005). The latter two species respond almost identically to intruders as a whole in terms of defended area.

Where sufficient samples allow comparison in terms of aggressive intensity (acts per minute trespass time), all the damselfish are quite variable with an overall range of 0 to 9 aggressive acts per minute toward various intruders. Different responses by the three Eupomacentrus species to a single intruder should indicate a varying degree of competetive threat, i.e. niche overlap, to the res-

ident. An example is the Striped Parrotfish, which elicited responses of 2.3, 1.2, and 0.6 aggressive acts per minute from Duskies, Three-spots, and Beaugregories respectively. Unfortunately, further interpretation of the results is restricted by the inadequate distribution and number of observations. The general result seen that the aggression exhibited varies with the identity of the intruding species does agree with the observations of previous researchers (Myrberg and Thresher, 1974; Ebersole, 1977).

Discussion

The results of this study indicate that in the ways measured, the Three-spot, Dusky and Beaugregory damselfish differ in the nature of the resources they defend and in the behavior employed to defend them. The algal lawn of the Three-spot is small and lush while that of the Dusky is large and sparsly covered. The Beaugregory lawn covers as large an area as the Dusky's, but may be as rich as the Three-spot's. I suspect, however, that the presence of calcareous algal forms on most Beaugregory territories acts to inflate the estimate of algal volume present. These non-filamentous algal types are probably not avaliable to the damselfish as a food resource, and the value for usable algal volume for the Beaugregory may be effectively lower, and closer to the values for the Three-spot and Dusky.

I predicted that these differences in the gross morphology of the defended resource would be reflected in the aggressive behavior used by the three species to defend their territories. The results indicate that the factor responsible for the most obvious variation in defense is the area of the algal lawn. The Three-spot defends an area coinciding with its very small and

compact algal lawn; intruding individuals are often allowed to approach just to the edge of the patch, 0.25m or less from the center of the territory. The Dusky and Beaugregory, whose lawns do not significantly differ in area, exhibit nearly identical patterns of defense in terms of intrusion distance allowed. This similarity exists despite the wide gap in algal volume present, as measured.

After lawn area, factors further influencing variation in defense behavior are difficult to pinpoint from the results of this study. The Beaugregory territory may, in fact, be richer in terms of volume of algae avaliable; the relatively high degree of intra-specific aggression exhibited by Beaugregories may reflect large demands for algal resources. In contrast, Three-spots and Duskies appear to be relatively tolerant of conspecifics. This situation could coincide with the stability of the territorial communities on the whole rather than a difference in resource levels. Beau-gregories appeared to wander more regularly than the other damsel-fish species, and they may pose a greater threat to conspecifics as a result.

The variation in area defended with the area of the lawn is supported by the data on both responses to congenerics and to intruders in general. I am unable to reach strong conclusions concerning the variation of aggressive response to different tres-passing species between the three damselfish. As is often the case with behavioral studies of this kind, a very large sample size would be required to clearly elucidate the responses of the different Eupomacentrus residents. As mentioned above, species discrimination is apparent in the responses of the damselfish,

and the defensive hierarchy, maintained due to the range of competetive threat of intruders, could be clearly determined for each resident species with further study. I still feel that differences between the hierarchies of the Eupomacentrus species would be useful in determining the degree of niche overlap within the genus and would aid in the clarification of the structure of the damselfish community, but my results are inadequate for this analysis.

The most important question to be asked in interpreting these results is whether the factors measuered are in fact important in permitting the coexistance of the three damselfish species on the reef. Cody (1974) reviewed the mechanisms underlying ecological isolation and coexistance in birds, and I will use his study as an outline for this discussion, as the processes involved should be largely similar for both birds and fishes.

A. Segregation by Habitat

1. Segregation on a geographic scale. This factor is not involved, since the species are coexistant over a broad geographic range (Randall, 1968).

2. Segregation by Altitude. Depth may influence the community in this sense. As noted above, the Beaugregory is not found in the deeper reef zones. Still, some mechanism must explain the coexistance of the three species inthe back reef area, and of two species in most other areas of the reef system.

3. Local or Between-habitat Segregation. As with depth, habitat preferences may be an important factor, especially in accounting for the coexistance of the Beaugregory and the Dusky. Beaugregories are not found in the fore-reef habitat, and Duskies are present but rare in the lagoon area, in shallow water. The

back-reef area, then, appears to represent a narrow zone of over lap between these two species, and to some degree, the close similarity of the territorial behavior of the Beaugregory and the Dusky may be indicative of niche overlap too extensive to allow extensive coexistance. Again, the back reef community appears to be a fairly stable system with all three species present. Factors other than habitat selection alone must permit the coexistance of three species in small areas, and two species over large zones of the reef complex.

4. Within-habitat Segregation. This mechanism, which includes specializations to both structural and biological aspects of the environment, is apparently involved to a considerable degree in the damselfish community. Three-spots tend to defend lawns growing on Acropora cervicornis, Duskies defend large rubble and Montastraea annularis mounds, and Beaugregories are usually found near flat coral rubble (personal observations). Overlap in these preferences is extensive, though I have not quantified this character of the damselfish community. It is difficult to see how substrate choice alone would permit extensive coexistance in the damselfish community, and this segregation fails to account for the persistence of interspecific territoriality.

B. Vertical Stratification of Feeding Zones. Though this factor is the most important in determining the structure of bird communities in tall habitats (Cody, 1974), there probably exists little opportunity for vertical stratification among benthic reef fishes such as the damselfishes. In this sense, the coral reef represents a structurally simple habitat in which other isolating mechanisms must predominate.

C. Differences in Food and Feeding Behavior. Normally, the combination of body morphology and feeding behavior, which determines the food resources exploited by a species, will be sufficiently adaptable to enable closely related species to coexist through charater divergence and reduced niche overlap. In birds, bill morphology and feeding behavior alone are sufficient to characterize the food aspects of ecological isolation (Cody, 1974:35), but the situation is less clear in the damselfishes. The three species in question show little divergence in body size, or feeding adaptations, and, unlike most bird species, they do not overlap in the location of feeding activity due to the interspecifically territorial system. Randall (1967) desribed the gut contents of the three species and found wide overlap in types of food taken. Food preferences alone do not appear to account for niche seperation between these generalist species.

D. Time. Cody's final mechanism concerns segregation due to timing of breeding seasons or to differences in diurnal activity patterns, resulting in seperation of resources exploited. This mechanism is probably not involved here, since the damselfish are territorial throughout the year and exhibit similar diel behavior.

Even when taken in combination, Cody's coexistence mechanisms are unable to completely account for the structure of the Eupomacentrus community, and additional factors must be involved to explain the persistence of interspecific territoriality and the similarity of the three damselfish species. Wilson (1975:262) outlined five ways by which an animal can gain exclusive use of terrain:

1. Overt Defense
2. Repulsion by Advertisement
3. Selection of different living quarters by different life forms (i.e. complete habitat segregation)

4. Random effects of dispersal
5. Some combination of these effects

The damselfish community structure is probably best explained by the distribution of individuals due to random effects coupled with exclusive resource use resulting from interspecific territoriality. Sale (1974;1975) and Itzkowitz (1977) found that dispersal of juvenile damselfish played an important role in the establishment of damselfish territories. The random aspect of this process may to a large degree account for the coexistence in the Eupomacentrus by continually introducing individuals of all three species into vacancies in the community.

Territory size has been shown to vary with the number of competitors coexisting with territorial birds (Yeaton and Cody, 1974). Where more competitors are present, territory size increases to compensate for resources lost due to the numerous niche overlaps. That territory size varied little in the Dusky and Three-spot when the Beaugregory was present (in fact the territories of both were smaller with the Beaugregory present on the back reef) implies that the damselfish do not respond to fluctuations in competetive pressure by adjusting territory size. Rather, it appears that, as omnivores in the diverse reef fish community, damselfish are subjected to niche overlap from so many competitors that a unique strategy has replaced area compensation. Unable to increase territory size in the face of extreme competition, probably due to the logistics and mechanics of defense over large areas of reef, the damselfish have resorted to complete defenseof small, rich territories, excluding all intruders which pose a competetive threat. If this is the case, then the situation in these reef fish would be a strong example of interspecific territoriality as an adaptive strategy. The random

effects of juvenile dispersal and the intense competetive environment of the coral reef may set damselfish territoriality apart from Murray's (1971) model for interspecific territoriality in birds.

As a final point, the similarity of territorial systems of the three Eupomacentrus species may in fact be as important as the differences I investigated. Cody (1974;163) lists three factors which will promote similarity in appearance: a. common ancestry; b. common niche characteristics; and c. selection for common signals used in territorial defense. These similarities can exist either as a result of convergent evolution or a lack of divergence. All aspects of this phenomenon may be involved in the structure of the damselfish community.

In conclusion, the mechanisms which permit the coexistance of the three Eupomacentrus species on the coral reef appear to be complex and subtle. Though I have shown that the species do vary in the morphology of the algal lawns defended and in the aggressive behavior by which the territory is maintained, it is not yet clear how the parameters ofthe territories themselves are involved in the structure of the community as a whole. The damselfish are a unique and fascinating component of the coral reef fauna, and further study concerning the niche parameters and competetive interactions which underly the coexistance ofthese interspecifically territorial species should be fruitful and have important implications for the evolution of territoriality and community structure.

These differences in algal lawns may simply reflect the harvesting or maintenance behavior of the species and may not imply a selection in the area to be defended. JJS

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Species & Site	n	Area of Algal Lawn (m^2)	Mean Height of Algae (cm)	Mean % Algal Cover	Mean Cover (cm)	Mean Algal Volume ($m^3 \times 10^{-2}$)
Dusky Damselfish						
WBR	5	0.85 ± 0.18	0.28 ± 0.11	49.2 ± 13.0	0.14 ± 0.08	0.14 ± 0.10
WFR	9	1.15 ± 0.36	0.23 ± 0.12	29.4 ± 16.1	0.08 ± 0.07	0.08 ± 0.05
TOTAL	14	1.06 ± 0.33	0.25 ± 0.11	36.5 ± 17.6	0.10 ± 0.07	0.10 ± 0.07
3-Spot Damselfish						
WBR	5	0.18 ± 0.04	1.41 ± 0.37	86.0 ± 6.8	1.22 ± 0.37	0.21 ± 0.05
WFR	5	0.31 ± 0.08	1.24 ± 0.30	81.6 ± 12.4	1.00 ± 0.23	0.32 ± 0.13
TOTAL	10	0.24 ± 0.09	1.33 ± 0.33	83.8 ± 9.7	1.11 ± 0.30	0.26 ± 0.11
Beaugregory						
WBR	5	0.86 ± 0.24	1.38 ± 0.15	62.6 ± 14.3	0.86 ± 0.24	0.76 ± 0.31

TABLE 2. ALGAL LAWN PARAMETERS FOR THREE <u>EUPOMACENTRUS</u> SPECIES
(mean values ± one s.d.)

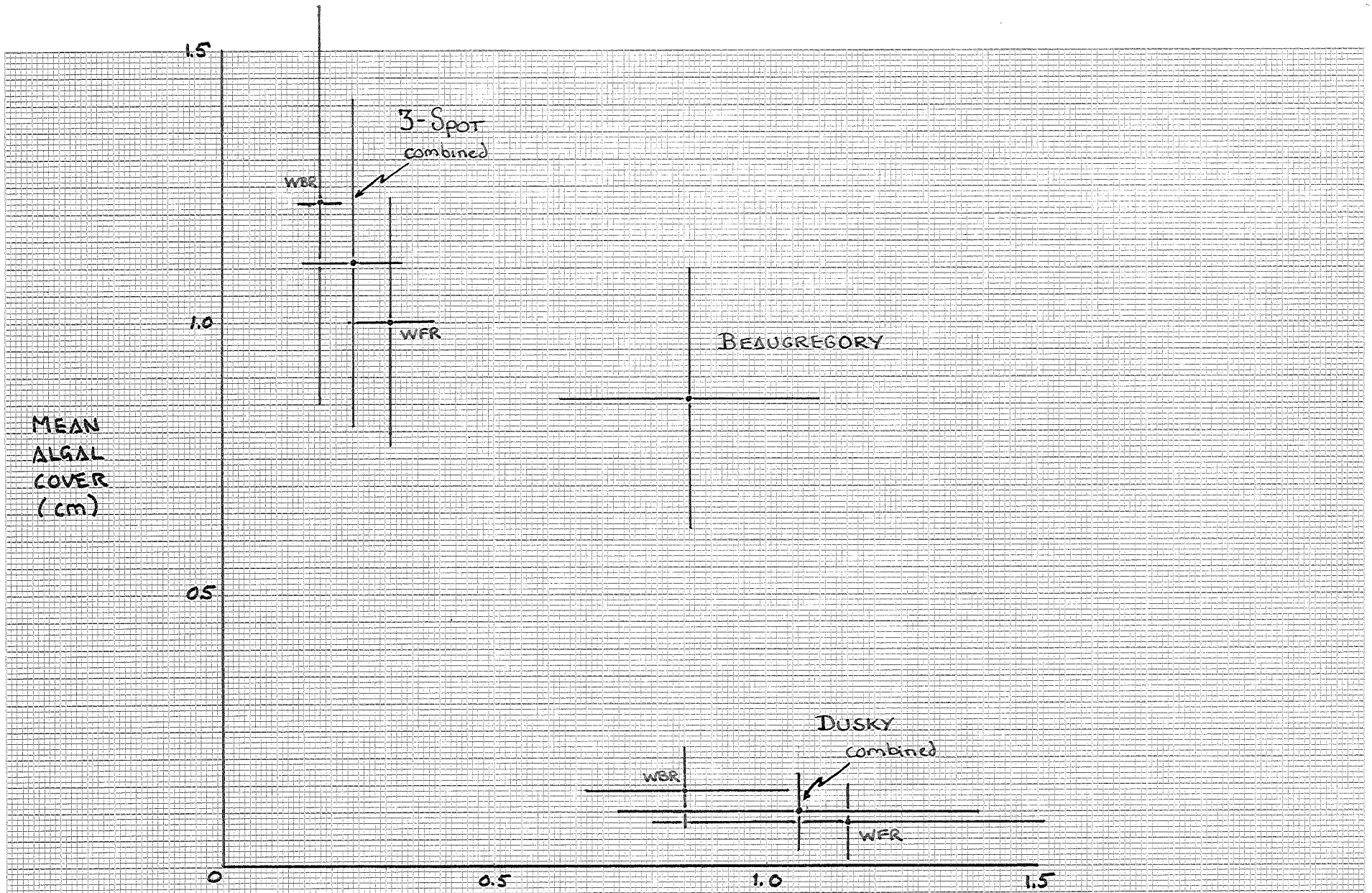

FIG. 1. ALGAL LAWN MORPHOLOGY FOR THREE *EUPOMACENTRUS* DAMSELFISH

Vertical and horizontal bars depict one standard deviation on each side of the mean.

10 Millimeters to the Centimeter

Intruder/ Neighbor		Resident: 3S (total obs. time = 116 min)	DD (140 min)	BG (50 min)	
	3S	17	6	1	← TOTAL # INTRUSIONS
		10	4	2	← Aggressive Acts (Total)
		0.09	0.03	0.04	← A.A. per minute of total observation time
	DD	8	7	3	
		8	5	9	
		0.07	0.04	0.18	
(present for 50 mins. of DD & 3S observations)	BG	5	5	#12	
		6	5	23	
		0.12	0.10	0.46	

TABLE 3. AGGRESSION TOWARD CONGENERICS (*Eupomacentrus* spp.)

RESIDENT	NEIGHBOR/ INTRUDER	DISTANCE FROM TERR. CENTER (m) 0.25	0.5	0.75	1.0	1.5	>1.5	Total
3SPOT	3S	2	10	2	0	3	0	17
	DD	2	2	1	1	1	1	8
	BG	0	3	0	1	0	1	5
	ALL	4	15	3	2	4	2	30
DUSKY	3S	0	1	1	2	1	1	6
	DD	0	1	1	1	0	3	#6
	BG	0	~~0~~ 1	0	4	0	0	5
	ALL	0	3	2	7	1	4	17
BEAUGREGORY	3S	0	0	0	1	0	0	1
	DD	0	0	1	1	0	1	3
	BG	0	0	1	4	4	3	12
	ALL	0	0	2	6	4	4	16

TABLE 4. NEIGHBOR/ INTRUDER DISTANCES (*Eupomacentrus* spp.)
(number of intrusions for each distance/ square cell)

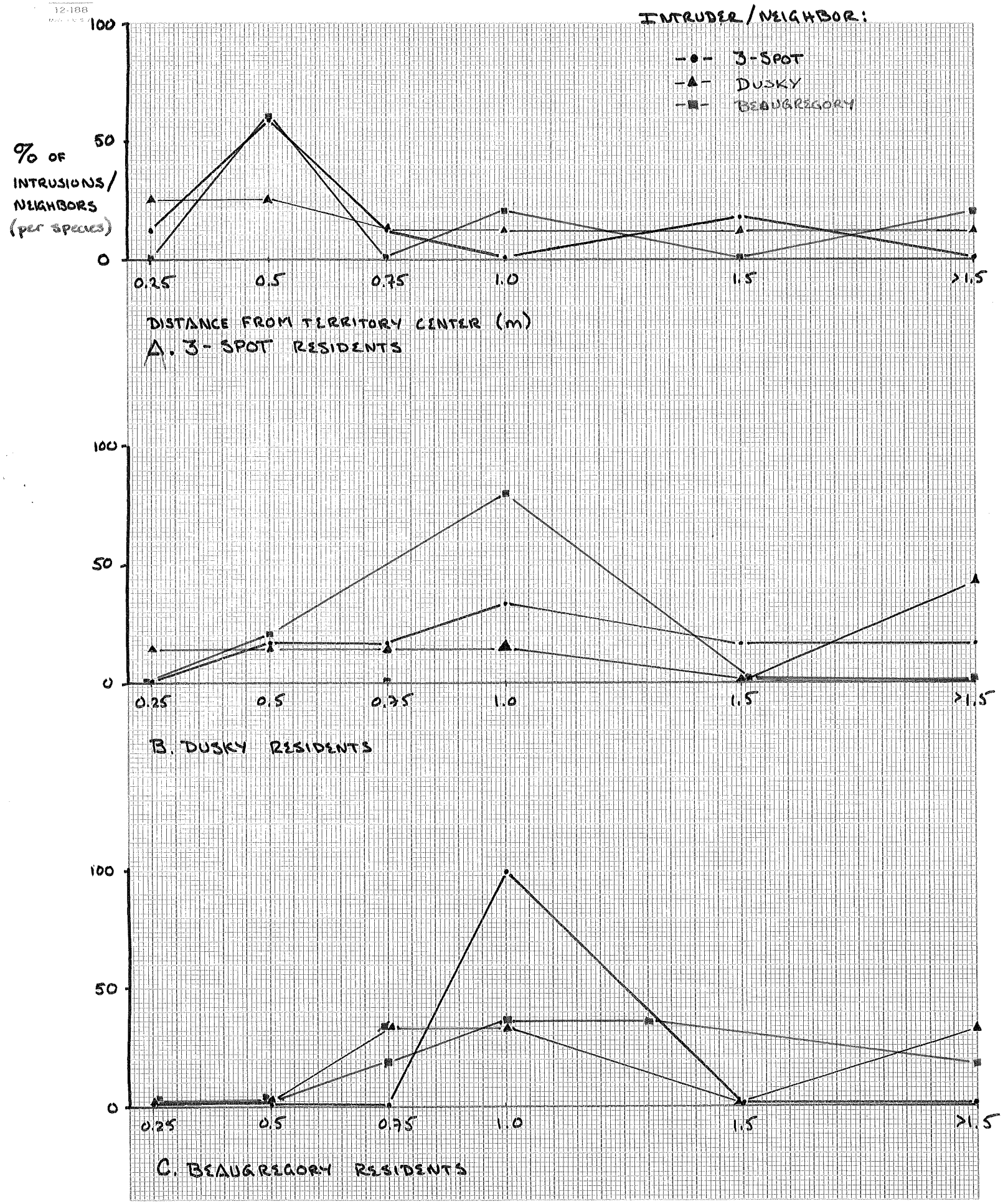

FIG. 2. NEIGHBOR/INTRUDER DISTANCES (*Eupomacentrus* spp.)

NATIONAL 12-188 10 Millimeters to the Centimeter

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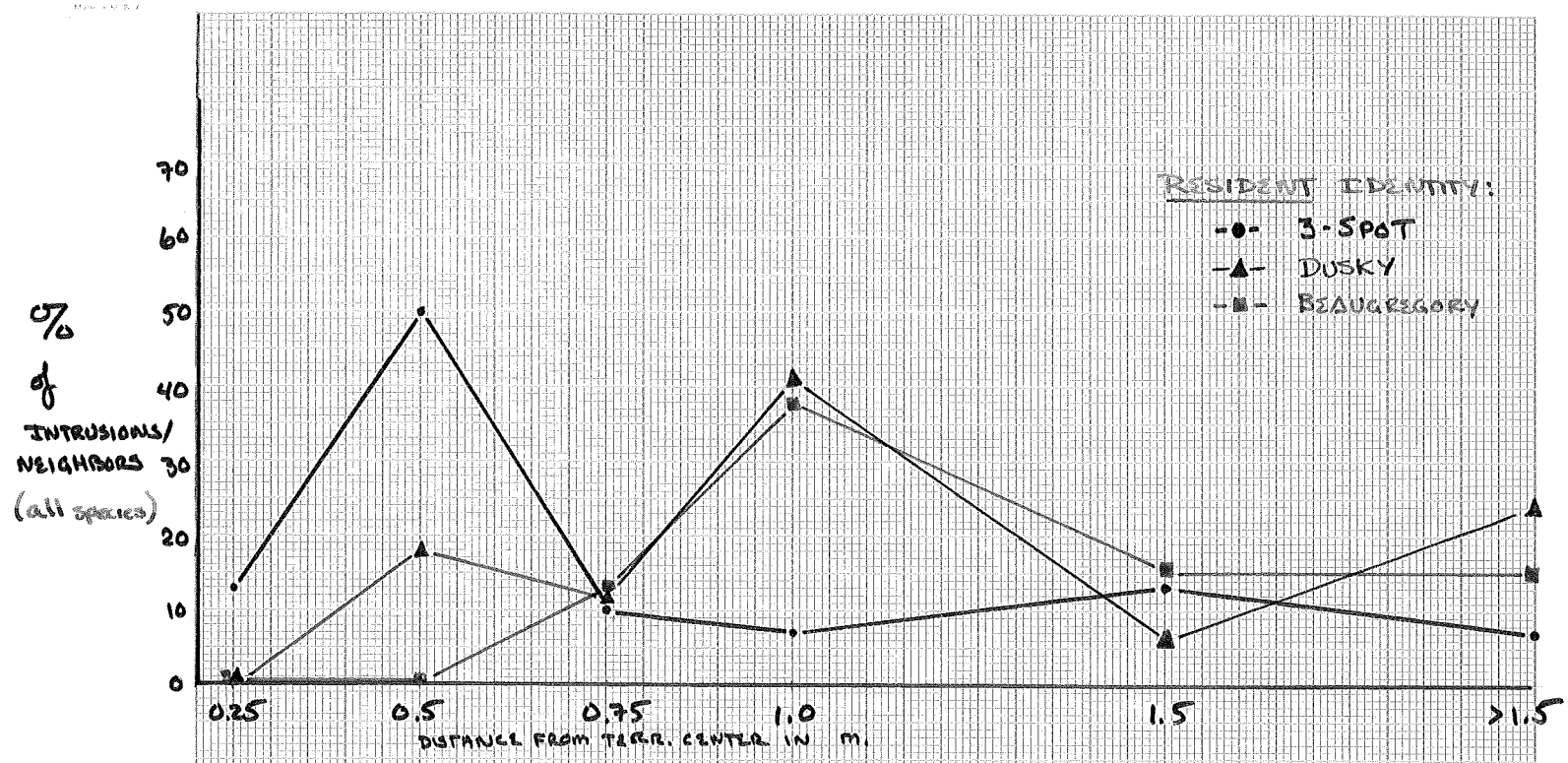

FIG. 2 D. ALL NEIGHBORS/INTRUDERS OF GENUS EUPOMACENTRUS
(ie RESPONSE OF EACH DAMSELFISH TO CONGENERICS AS A WHOLE)

10 Millimeters to the Centimeter

Intruding Species	Resident: 3-Spot # Trespass	# Aggress. Acts	Total Trespass Time (seconds)	Agg. Acts/min. Trespass	Mean Trespass Distance (meters)	Dusky #T	# AA	TTT	AA/min	Distance	Beaugregory #T	# AA	TTT	AA/min	Distance
Bluehead Wrasse (adult)	1	1	15	4.0	0.25	2	1	30	2.0	1.1	3	3	20	9.0	1.33
Bluehead Wrasse (imm)	3	0	55	0	0.83	19	8	420	1.1	0.92	7	5	215	1.4	0.93
Yellowhead Wrasse	3	3	25	4.8	0.67	15	14	105	8.0	1.2	0	—	—	—	—
Striped Parrot	42	16	800	1.2	0.53	19	11	290	2.3	0.92	18	3	315	0.60	0.88
Stoplight Parrot	2	3	25	4.8	0.67	2	0	75	0	1.0	5	0	260	0	1.0
Redband Parrot	4	4	60	4.0	0.63	3	2	30	6.0	0.83	0	—	—	—	—
Blue Chromis	9	2	225	0.5	0.61	8	2	100	1.2	0.78	0	—	—	—	—
Yellowtail Damselfish	1	1	10	6.0	1.0	3	2	160	1.1	0.92	0	—	—	—	—
Bandtail Puffer	0	—	—	—	—	4	2	100	1.2	0.88	0	—	—	—	—
Sharpnose Puffer	1	1	60	1.0	1.5	0	—	—	—	—	0	—	—	—	—
Indigo Hamlet	6	2	275	0.44	0.46	0	—	—	—	—	0	—	—	—	—
Conez	4	0	110	0	0.50	0	—	—	—	—	2	0	20	0	0.75
Rock Hind	2	0	50	0	0.32	2	0	40	0	0.50	0	—	—	—	—
3-Spotted Goatfish	0	—	—	—	—	1	1	20	3.0	1.0	1	0	10	0	0.5
Yellow Goatfish	3	2	90	1.$\bar{3}$3	0.75	0	—	—	—	—	0	—	—	—	—

TABLE 5. DAMSELFISH TERRITORIAL DEFENSE TOWARDS INTRUDERS OTHER THAN CONGENERICS

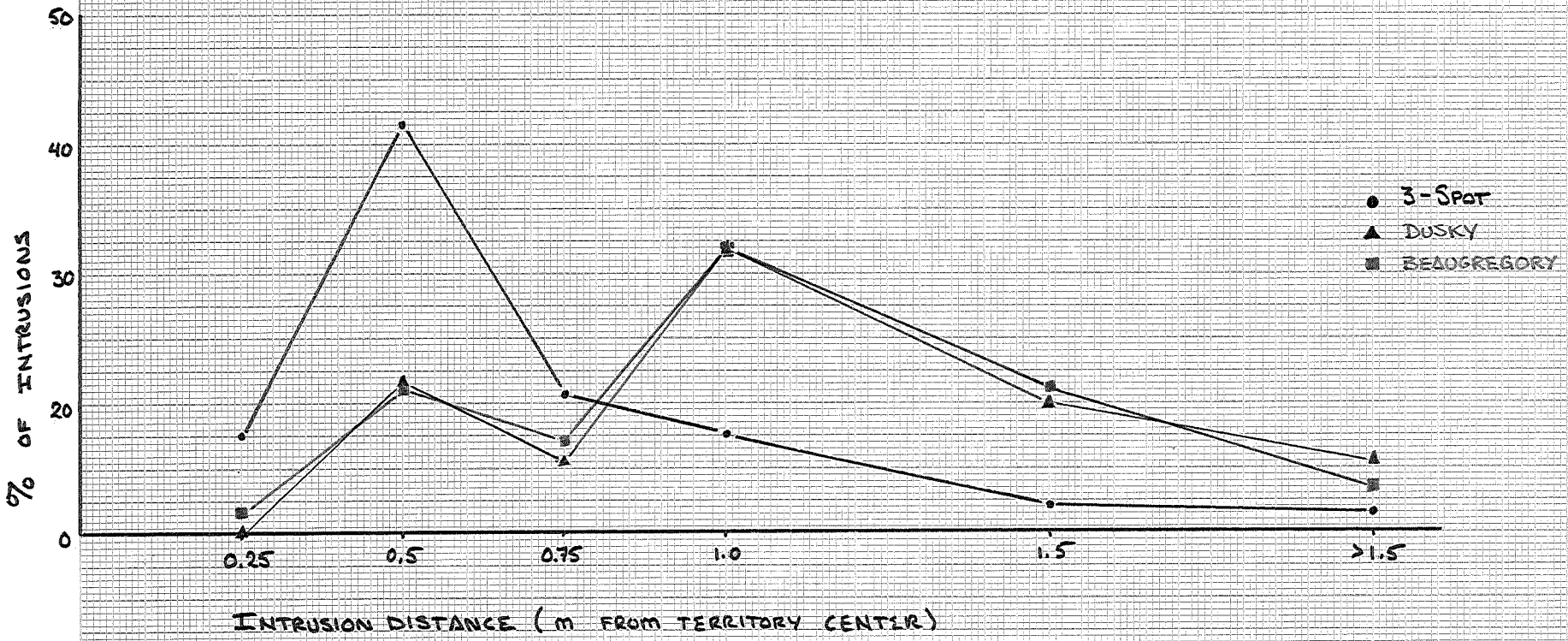

FIG. 3. RESPONSE OF *Eupomacentrus* damselfish to INTRUDERS AS A WHOLE

10 Millimeters to the Centimeter
12-188