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Title: A Contribution to the Comparative Ecology of *Pomacentrus lividus* and *Pomacentrus albofasciatus* (Pisces: Pomacentridae) Tumon Bay, Guam

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R. S. JONES, Chairman, Thesis Committee

Two species of *Pomacentrus*, *P. lividus* and *P. albofasciatus*, from Tumon Bay, Guam, were investigated for factors that might provide potential ecological separation of the species. Specific factors investigated were habitat and community structure, behavior, size differences, feeding habits, and reproduction.

The fishes are sympatric in the coral zone of the inner reef flat where each lives in a different habitat; *P. lividus* is usually found in *Acropora* colonies and *P. albofasciatus* in the spaces between these coral colonies. Both pomacentrids are browsing herbivores that generally eat the same algal species but the proportions vary. This variance appears to be a function of the differences in habitat. *Pomacentrus lividus* is a highly territorial species. The slightly larger size of *P. lividus* appears to aid it in excluding *P. albofasciatus* from the coral colonies.

A CONTRIBUTION TO THE COMPARATIVE ECOLOGY OF *POMACENTRUS LIVIDUS* AND *POMACENTRUS ALBOFASCIATUS* (PISCES: POMACENTRIDAE) TUMON BAY, GUAM

by

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I would like to thank R. H. Randall for identifying the corals from Tumon Bay and H. W. Larson for identifying the fish taken in the poison station. I am most indebted to my husband for his assistance in spearing fish, critical reading of the manuscript and many sacrifices made during the preparation of this thesis.

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Section 1

INTRODUCTION

This study considers two species of *Pomacentrus*, *P. lividus* (Bloch and Schneider) and *P. albofasciatus* Schlegal and Müller, that inhabit Tumon Bay, Guam, Mariana Islands. These species are distributed from the Western Indian Ocean to the Western and Central Pacific Ocean. The available literature is descriptive (Bloch and Schneider, 1801; Schlegel and Müller, 1839; and Woods and Schultz, 1960) and distributional (De Beaufort, 1940; and Smith and Smith, 1963) in nature.

The study was undertaken between March and December 1970 and deals with the comparative ecology of these two morphologically similar fishes. The species are sympatric in Tumon Bay and appear to occupy overlapping niches, which raises the question of possible competition between them. The possibility of competition as a factor in their spatial distribution is considered in relation to the competitive exclusion principle (Gause, 1934). Ecological factors such as food habits, behavior, size differences, and habitat division were used to analyze the niches and identify specific factors that would tend to reduce niche overlap and consequently, competition.

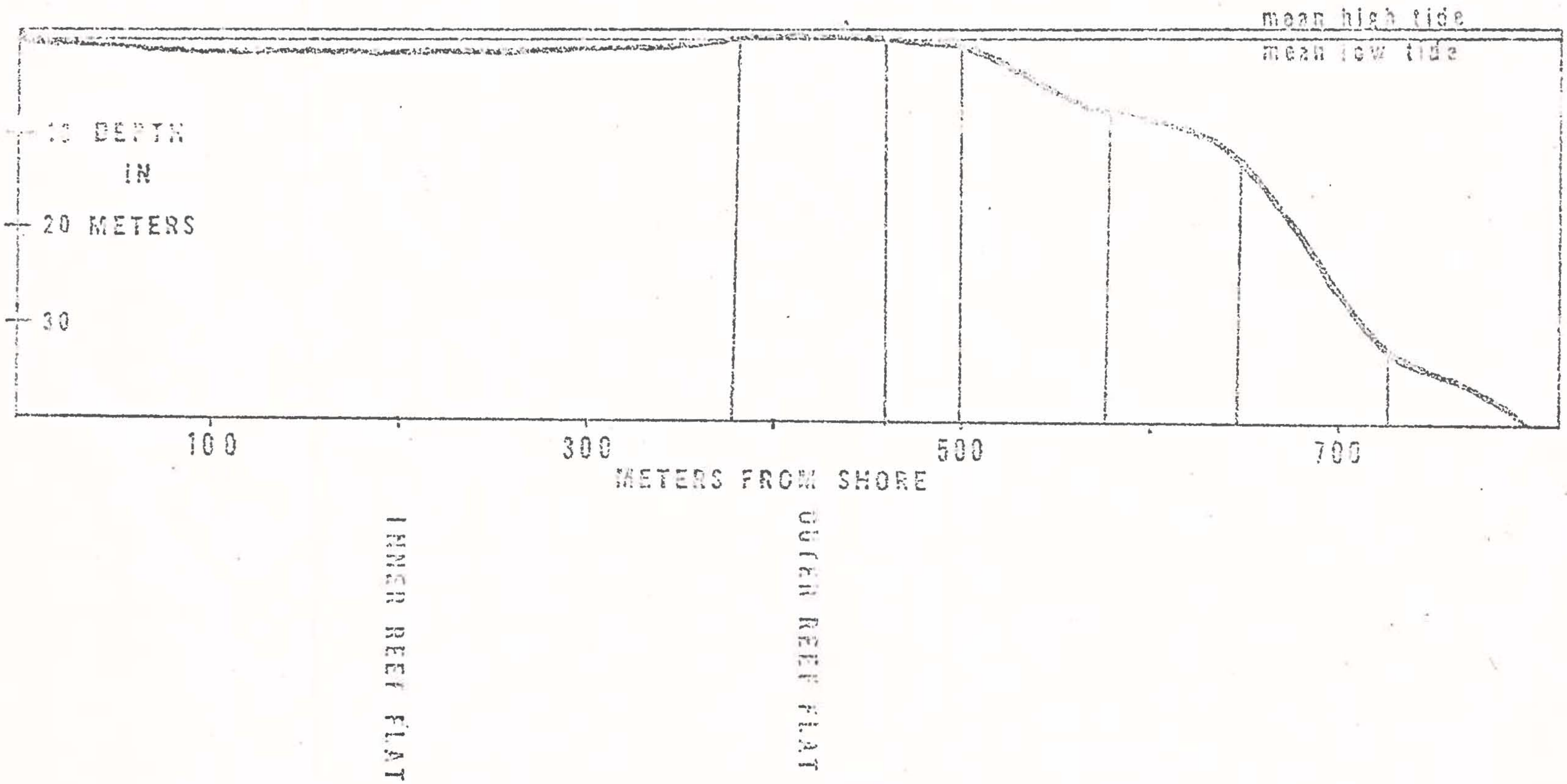
Section 2

DESCRIPTION OF STUDY AREA

Tumon Bay is on the southwest side of Guam's limestone plateau, close to the Island's narrowest point. Tracey et al. (1964) divide Tumon Bay from the beach seaward into inner reef flat, outer reef flat, reef margin, reef front, and submarine terrace (Figure 1). The inner reef flat is further subdivided into sand zone, coral zone and boulder zone. The sand zone typically has a sandy bottom with scattered living corals. The coral zone typically has a bottom of sand and coral rubble with many _Acropora_ spp., _Pavona_ spp., and _Pocillopora_ spp. growing in it. _Porites_ spp. are found on the outer edge of the coral zone. The boulder zone is composed of rubble and boulders over truncated pavement. The first half of the outer reef flat is "barren irregular rock pavement"; the seaward side is covered with algae and many corals. The reef margin is a constantly awash, low algal crest cut by several channels that extend through the reef front. The reef front contains many algal buttresses and slopes seaward to the submarine terrace which is about five to seven meters deep at the reef, descending to greater depths as it progresses seaward.

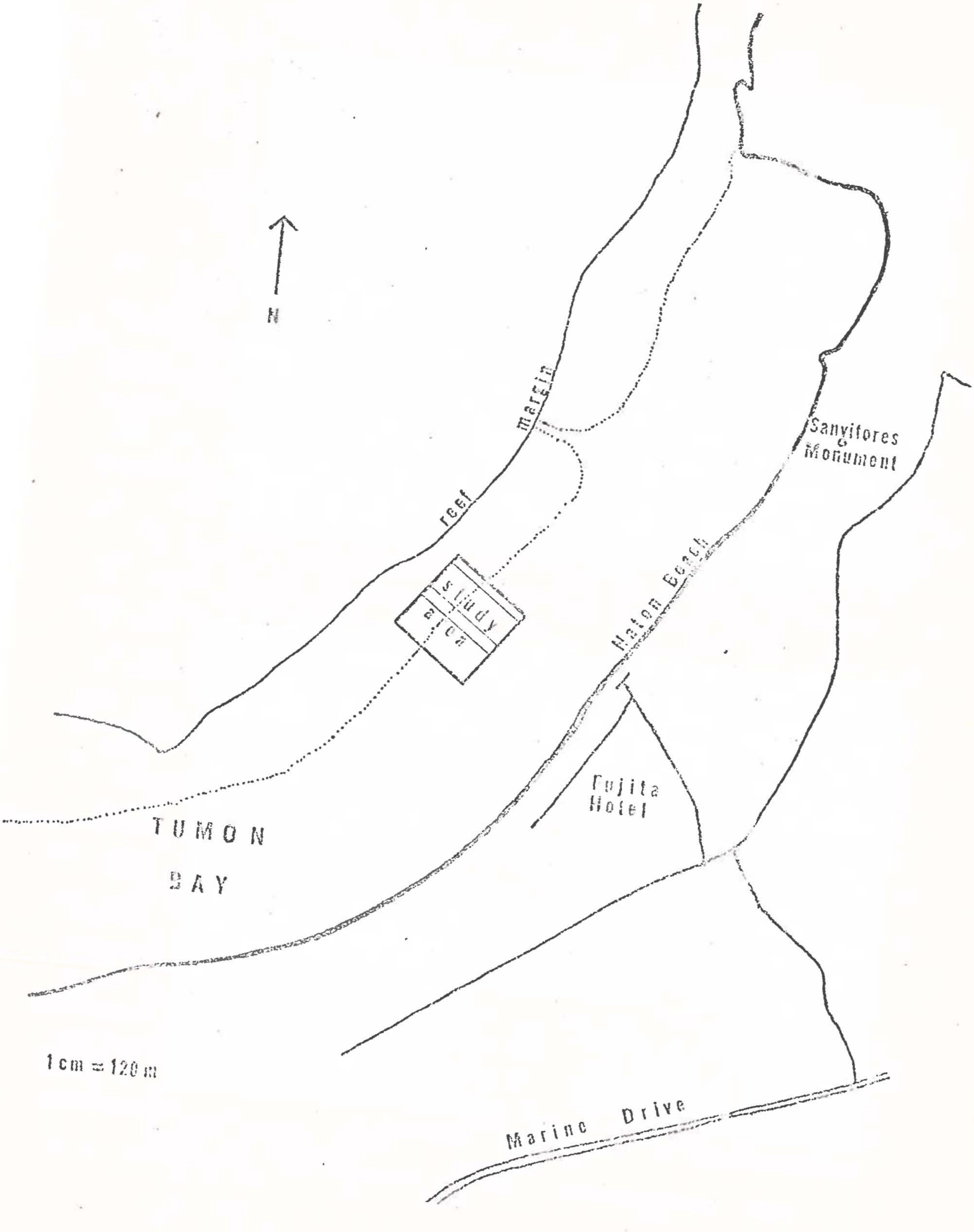
The study area centers around a 150 meter long section of coral zone in front of the Fujita Tumon Beach Hotel (Figure 2). The area contains large colonies of *Acropora aspera* (Dana) separated by patches of sand and rubble (Figure 3). Colonies of *Acropora acuminata* Verrill are also present but much less common than the former. The boulder zone in the study area is reduced to a few small boulders and some scattered coral rubble. It grades quickly into the outer reef flat and thus, for purposes of this study, the outer reef flat is considered contiguous with the coral zone of the inner reef flat.

Fig. 1. Reef profile, Tumon Bay, Guam. Vertical exaggeration X5.



mean high tide
mean low tide
10 DEPTH
IN
20 METERS
30
100
300
500
700
METERS FROM SHORE
INNER REEF FLAT
OUTER REEF FLAT

Fig. 2. Map of Tumon Bay, Guam, showing the study area and approximations of the transects.



N
reef margin
study area
Sanvitores Monument
Naton Beach
Fujita Hotel
TUMON BAY
1 cm = 120 m
Marine Drive

Fig. 3. A. and B. Typical *Acropora* colonies and sand patches found in the coral zone of Tumon Bay, Guam.

Section 3

METHODS

Field Procedures

I observed the feeding and both inter- and intra-specific behavior of *Pomacentrus lividus* and *P. albofasciatus* in the coral zone of the inner reef flat in Tumon Bay. Snorkeling equipment, an underwater slate, a camera, and a watch were used. Observations were made by staying as still as possible in the water and never over two meters away from the subjects. I appeared to cause little disturbance among the fishes if no spears were carried. Observation times ranged from 30 minutes to one hour when no spearing was involved and between three and four hours when specimens were collected.

From March to December 1970, 304 fishes, including 189 *P. lividus* and 115 *P. albofasciatus*, were collected. One hundred eighty-one were speared with Hawaiian slings and the others were poisoned using rotenone. The poison station was divided into two parts, one, a small screened enclosure and the other, the rest of the poisoned reef. Poison was placed inside the screen wire enclosure but was quickly carried out by a northerly current which spread the kill over an area 33 meters long by 10 meters wide. The screened enclosure yielded data on the fish community of a single *Acropora aspera* colony 1.5 meters long, 1.2 meters wide and 0.7 meters high. Approximately 0.2 meters of water covered the coral.

Three transects were run perpendicularly across the coral zone and onto the outer reef flat in order to quantify the number of *P. lividus* and *P. albofasciatus* in each habitat. The one meter wide transects were 126.6 m, 106.6 m and 123.3 m long. The transects were divided into 3.3 m subunits for ease of counting.

In order to further study the habitat of these sympatric fishes, I sampled 60 quadrats, 30 on coral colonies (mostly *Acropora aspera*) and 30 in the sandy, rocky spaces between coral colonies. As I moved through the coral zone parallel to the beach, I placed the square meter quadrat on the nearest coral colony with an area greater than the quadrat size. All *Pomacentrus lividus* and *P. albofasciatus* were counted after waiting two minutes for the fishes to recover after being disturbed. I used the same procedure to count 30 quadrats between the coral colonies.

Laboratory Procedures

The majority of the fishes were frozen prior to processing, labeling and preserving in 10% formalin. The fishes were checked closely for accurate identification (see p.38). Data recorded on all specimens included standard length, sex, and condition of gonads if observable. Juvenile refers to fishes below the size of the normally sexable adults. All fishes are cataloged in the University of Guam Natural History Collection (catalog numbers 5638-5673).

I collected and quantified stomach and/or intestine samples from 70 P. lividus and 51 P. albofasciatus. Preparation of samples for quantitative gut analysis included stripping the contents from the intestinal membranes, dissolving any sand with 10% HCl and completely mixing the sample during the dissolution process. I then placed one drop of the liquid mixture on each end of a standard glass slide and placed a cover glass on each drop. The relative abundance value for each algal species was quantified using a modification of the point method used by Jones (1968). Both preparations were scanned to record all algal species. Next, five positions on each sample were selected at random and the number of ocular grid points touching any one species of algae recorded. The central 81 points of a 100 unit ocular grid were used giving a total of 810 available points. The relative abundance of each algal species was calculated by dividing its total number of grid point intersections by the total points enumerated for all algae in all guts sampled from P. lividus. The same procedure was used for P. albofasciatus.

I collected 10 pieces of algal covered Acropora (2.5-3.5 cm long) from typical P. lividus territories. The algae were cut off at their bases with scissors, treated with 10% HCl to remove sand and quantified in the same manner as were the gut contents. Also samples were collected from the spaces between the *Acropora* colonies and all algal species recorded. The latter area was not quantified.

Student's t-test was used for all analyses.

Section 4

RESULTS

Habitat and Community Structure

In order to define the limits of the habitat in which P. lividus and P. albofasciatus are found sympatrically, three transects and sixty quadrats were run.

From the three transects I calculated a mean of 3.64 P. lividus per transect subunit (N=233) in the coral zone and a mean of 0.48 per transect subunit (N=21) on the outer reef flat. The number of P. lividus in the coral zone is significantly greater (P<.001) than the number on the outer reef flat. The 21 P. lividus observed on the outer reef flat were in small Acropora heads which were growing in depressions.

I calculated, from the same three transects, a mean of 1.60 P. albofasciatus per transect subunit (N=103) in the coral zone and a mean of 1.53 per transect subunit (N=66) on the outer reef flat. There was no significant difference (P>.05) in the number of P. albofasciatus from either reef area. Most of the 103 P. albofasciatus observed in the coral zone were in the spaces between coral colonies.

The three transects narrowed the area of sympatry to the coral zone. Sixty quadrats were then run to delineate quantitatively which part of the coral zone each species occupied.

One hundred eighteen *P. lividus* and 16 *P. albofasciatus* were counted in 30 quadrats containing 100% coral. Six *P. lividus* and 42 *P. albofasciatus* were observed in 30 quadrats between coral colonies. The six *P. lividus* were transient when observed and did not appear to occupy territories in the spaces between coral colonies. There were a significantly greater ($P<.001$) number of *P. lividus* in the *Acropora* than in the sand spaces and a significantly greater ($P<.001$) number of *P. albofasciatus* in the sand spaces than in the coral.

An enclosed coral head was poisoned to find out which species of fishes lived with *P. lividus* in the coral and which ones might be potential interspecific competitors for the benthic algae available within the coral colony. Twenty-five juveniles made up the majority (83%) of a *P. lividus* population collected by poisoning a single enclosed coral colony (1.8 m^2). Five adults, one male, one female, and three that were unsexable made up the remaining 17%. The 30 *P. lividus* constituted 21% of the total fish population of 141 individuals. Table 1 is a checklist of species found within the poisoned coral colony and includes those found outside the enclosure in the rest of the affected reef. The collection outside the

TABLE 1

Members of the coral zone fish community collected by poisoning. Food preferences (C-carnivore, H-herbivore, O-omnivore, D-detritus). The number of each species collected inside the enclosure is shown.

Species	Inside Enclosure	Outside Enclosure	Food Preference
Abudefduf biocellatus (Quoy & Gaimard)	1	-	O
Abudefduf glaucus (Cuvier & Valenciennes)	2	x	O
Apogon [illegible] (Jordan & Seale)	-	x	C
Apogon novemfasciatus (Cuvier & Valenciennes)	10	x	C
Apogon nubilus (Garman)	46	x	C
Asterropteryx semipunctatus (Rüppell)	4	x	C
Aulostomus chinensis (Linnaeus)	-	x	C
Chaetodon ephippium (Cuvier)	-	x	D
Chromis caeruleus (Cuvier & Valenciennes)	3	x	C
Corythoichthys intestinalis (Jordan & Seale)	-	x	C
Dascyllus aruanus (Linnaeus)	11	x	O
Enchelyurus sp.	1	x	H
Epibulus insidiator (Pallas)	-	x	C
Epinephelus merra (Bloch)	-	x	C
Fusigobius neophytus (Günther)	1	x	C
Gnatholepis deltoides (Seale)	-	x	C
Gymnothorax fimbriatus (Bennett)	-	x	C
Gymnothorax thyrsoideus (Richardson)	-	x	C
Gymnothorax undulatus (Lacepède)	1	x	C
Halichoeres trimaculatus (Quoy & Gaimard)	-	x	C
Holocentrus microstomus (Günther)	-	x	C
Holocentrus sammara (Forskål)	5	-	C
Holocentrus spinifer (Forskål)	2	x	C
Megaprotodon strigangulus (Gmelin)	-	x	H
Myrichthys elaps (Fowler)	-	x	C
Myripristis murdjan (Forskål)	1	-	C
Paramia quinquelineata (Cuvier & Valenciennes)	-	x	C
Plesiops corallicola (Bleeker)	1	-	C
Pomacentrus albofasciatus (Schlegel & Müller)	-	x	H
Pomacentrus lividus (Bloch & Schneider)	30	x	H
Pomacentrus nigricans (Lacepède)	-	x	H
Scorpaenodes guamensis (Quoy & Gaimard)	12	x	C
Siganus spinus (Linnaeus)	-	x	H
Stethojulis axillaris (Quoy & Gaimard)	1	x	C

enclosure is probably not completely representative of the coral zone fish community. The food preference of each species is included.

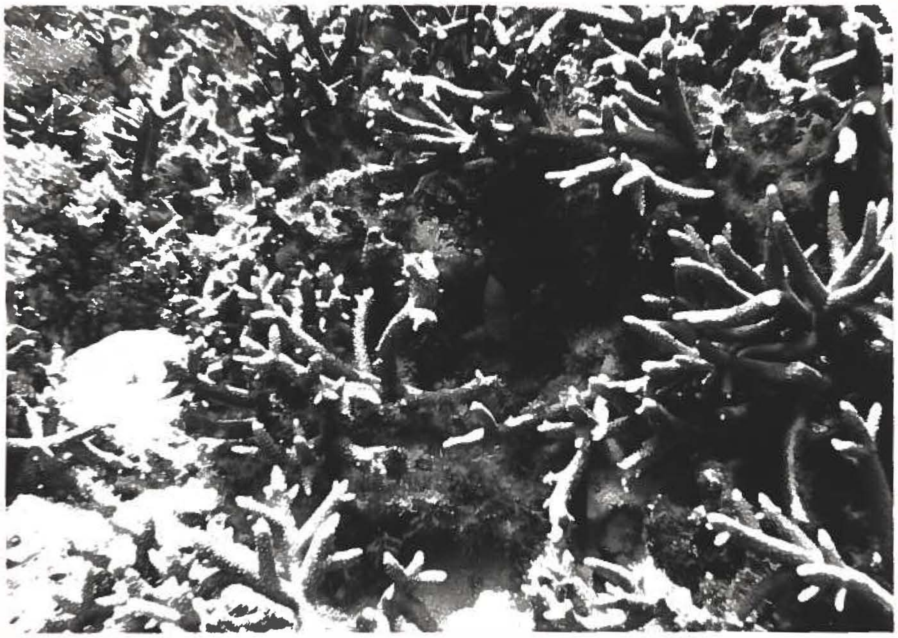
Territorial Behavior

The apparent strong territoriality of P. lividus indicated a possible area of separation between the two species. The obvious activity P. albofasciatus engages in is feeding. Territorial defense is much less pronounced in this species. The following are observations made on territoriality.

Normal territorial behavior for P. lividus involves stopping whatever it is doing and emerging to observe any animal moving in its direction (Figure 4). If another species of fish enters its territory P. lividus erects the dorsal fin and chases the intruder out. Pomacentrus lividus then resumes activities, such as feeding, unless the intruder still threatens to invade its territory.

Pomacentrus lividus react strongly to some interspecific conflicts. When a school of intruders such as rabbitfishes (Siganidae) threatens a colony, territorial owners emerge from the coral and pause just above it, nose down with fins spread. If the school continues to advance towards the P. lividus territories, the defender dashes toward the intruders scattering them. The species appears to form a united front to threaten potential intruders but acts individually to repel trespassers entering a particular

Fig. 4. A. *Pomacentrus lividus* in the center of its territory "observing" the photographer. B. *Pomacentrus lividus* in its territory.



territory. The nose down position is a behavioral stance used under extreme circumstances.

"Jaw fighting" and "fin-batting" were observed when two *P. lividus* battled over territorial ownership or boundary lines. When such activity occurred, the other *P. lividus* nearby evidenced "interest" in the struggle suggesting that the outcome might affect territorial boundaries of other fish in the immediate area. Juveniles sometimes fought in this manner but were ignored by larger fish. Severe intra-specific conflict was not typical and was rarely seen; normally only threatening gestures, such as dorsal fin erection and short advances, were exchanged.

Pomacentrus lividus, a light brown fish, may display irregular pink markings on the head and body which brightened when the fish engaged in jaw fighting. The pink color is subdued, almost non-existent at other times. At night *P. lividus* displays two light bars, edged in gray, on a pinkish-white background. One bar extends through the mouth and past the base of the pectoral fin; the second extends from the base of the first few soft dorsal rays vertically to the underside. During the day only one individual was observed displaying bars which were pinkish-white on a brown background.

Pomacentrus albofasciatus is black during the day (I could not find them at night) and may display two white bars located in the same position as those described for *P. lividus*.

The presence of the barred pattern and its intensity seemed to be dependent on the fish's state of excitation. Individuals that were feeding and intermittently struggling with other fishes usually displayed the vertical white bar. Both bars were displayed by individuals that were not feeding and appeared to be constantly engaged in inter- or intraspecific aggressive activity.

On a few occasions P. albofasciatus were observed guarding small fragmented pieces of Acropora, rocks, or crevices (Figure 5). These territories were defended against other species more vigorously than against other P. albofasciatus.

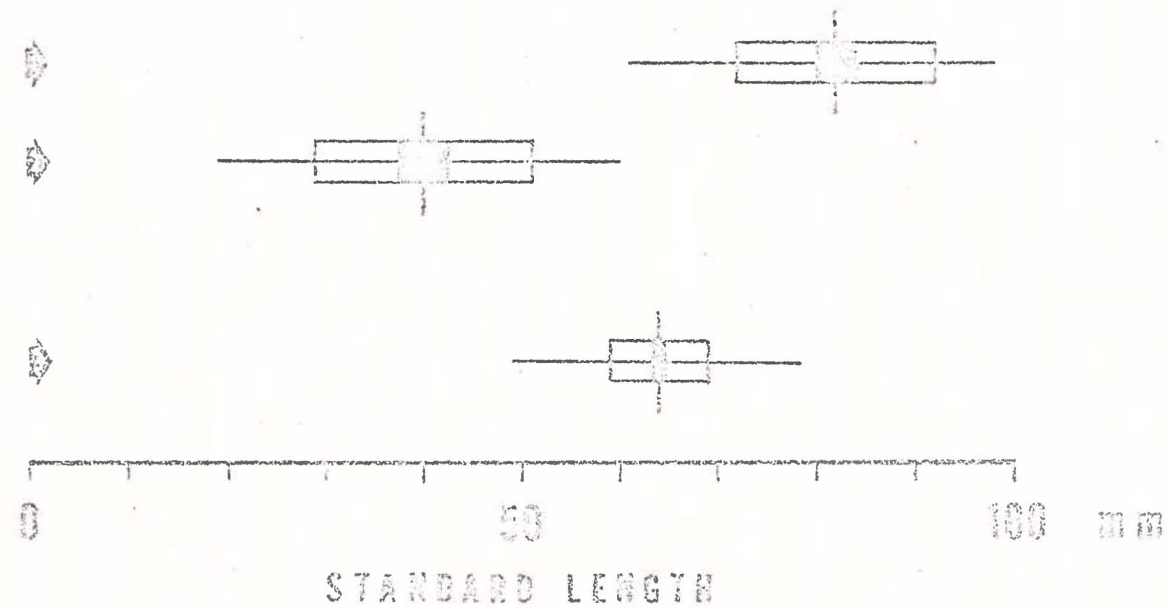
Size

Preliminary observations in the field indicated that a larger size might be ecologically important to P. lividus in excluding P. albofasciatus from the territory of the former. Pomacentrus lividus did prove to be larger than P. albofasciatus. Standard lengths of both male and female P. lividus are significantly larger ($P<.001$) than male and female P. albofasciatus (Figure 6).

I collected only one small (36 mm) P. albofasciatus and none were taken in the poison station. Possibly the young were in holes where I could not find them but most likely they inhabit a different part of the reef or ocean. I observed numerous small (19-60 mm) P. lividus in the

Fig. 5. *Pomacentrus albofasciatus* guarding a small branch of *Acropora*.

Fig. 6. Comparison of standard lengths in 1. adult *Pomacentrus lividus* 2. juvenile *Pomacentrus lividus* and 3. adult *Pomacentrus albofasciatus*. The horizontal line represents the range and the vertical line represents the mean. The light rectangle represents one standard deviation while the dark rectangle represents two standard errors on either side of the mean.


0
50
100 mm
STANDARD LENGTH

field and collected 75 in the poison station. Apparently these small fish stay within the depths of the coral colony, tolerated by the territorial adults.

Feeding

Foraging methods, food eaten, and food present in the habitat were studied in an attempt to further differentiate the niches of P. lividus and P. albofasciatus.

Pomacentrus lividus and P. albofasciatus are generally browsers. To obtain food they move up to the algae, take it in their mouths and then sever the filaments by jerking the head to one side. When the fishes feed slowly this behavior is quite evident but when they feed rapidly they appear to peck the surface on which the algae is growing. I also observed several P. albofasciatus eating from sand patches. They engulfed large amounts of sand, sifted some out through the gills, and swallowed the rest. A sample of the sand substratum yielded fragments of algae most of which are common in the guts of P. albofasciatus. Ingestion of sand plus the fact that sand is often found on stands of algae help explain the consistent presence of sand in the intestines of these fishes. P. lividus were never seen feeding in sand patches and this may indicate potential niche separation.

A checklist of algal species found in the guts and habitats is presented in Table 2. Pomacentrus albofasciatus,

TABLE 2

Checklist of the algae found in *Acropora*, sandy spaces and the guts of *Pomacentrus lividus* and *Pomacentrus albofasciatus*. An asterisk (*) indicates primary foods.

Algal Species	*Pomacentrus lividus*	*Pomacentrus albofasciatus*	*Acropora*	Sandy Spaces
Blue-greens				
Calothrix confervicola B. & F.	x	x	x	x
Calothrix pilosa B. & F.	x	x	x	x
Hormothamnion solutum B. & F.	x			x
Microcoleus lyngbyaceus (Crouan) Ag.	x	x	x	x
Schizothrix mexicana Gomont	x	x		x
Greens				
Bryopsis pennata Lamx.		x	x	
Chaetomorpha indica Kutz.		x	x	
Cladophoropsis membranacea (Ag.) Boerg.	x	x	x	
**Enteromorpha clathrata* (Roth) J. Ag.	x	x	x	x
Halimeda sp.		x		
Neomeris sp.		x		
**Pseudochlorodesmis furcellata* (Zanard.) Boerg.	x	x	x	x
Browns				
Dictyopteris repens (Okam.) Boerg.		x		
Dictyota divaricata Lamx.	x	x	x	x
Ectocarpus indicus Sonder	x	x	x	x
Lobophora variegata (Lamx.) Womersley		x		x
Padina spp.		x		x
Sargassum polycystum C. Ag.	x	x		x
**Sphacelaria furcigera* Kutz.	x	x	x	x
Reds				
Acrochaetium sp.	x	x	x	x
**Centroceras minutum* Yamada	x	x	x	
Ceramium gracillimum Griffiths & Harv.	x	x	x	
Ceramium huysmansii W. v. Bosse	x	x	x	
Ceramium vagabunde Dawson	x	x	x	x
**Champia compressa* Harv.	x	x		x
Galaxaura filamentosa Chou		x		
**Hypnea esperi* Bory	x	x		x
**Hypnea pannosa* J. Ag.	x	x	x	x
**Jania capillacea* Harv.	x	x	x	x
Laurencia majuscula (Harv.) Lucas		x		x
Laurencia sp.			x	
Mastophora lamourouxii (Dcne.) Harv.				x

TABLE 2 -- Continued

Algal Species	Pomacentrus lividus	Pomacentrus albofasciatus	Acropora	Sandy Spaces
Reds -- continued				
Peyssonelia sp.	x	x		x
*Polysiphonia scopulorum Harv.	x	x	x	x
*Polysiphonia sp.	x	x	x	
*Pterocladia parva Dawson	x	x	x	x
Spyridia filamentosa (Wulf.) Harv.	x	x		
Taenioma perpusillum (J. Ag.) J. Ag.		x		
Tolypiocladia glomerulata (Ag.) Schmitz		x		

the wider ranging species, eats a greater variety of food than *P. lividus*, the species confined to the coral colonies. The similarity in overall food habits can be seen qualitatively from the checklist. *Pomacentrus albofasciatus* shares 96% of the algal species eaten by *P. lividus*, while the latter eats only 71% of the species consumed by *P. albofasciatus*.

Grouping the gut analysis data for each fish species allowed identification of primary and secondary foods. Algae with five percent or greater relative abundance were considered primary food and species with less than five percent were called secondary food. Primary foods for *P. lividus* and *P. albofasciatus* are presented in Table 3. The first three species of algae, *Pterocladia parva*, *Polysiphonia scopulorum*, and *Sphacelaria furcigera*, are the

TABLE 3

Relative abundance of primary foods for *Pomacentrus lividus* and *Pomacentrus albofasciatus*. Relative abundance of secondary foods appear in parentheses where necessary for comparison.

Algal Species	*P. lividus*	*P. albofasciatus*
Pterocladia parva	17.6	8.6
Polysiphonia scopulorum	15.2	12.6
Sphacelaria furcigera	5.6	8.8
Pseudochlorodesmis furcellata	11.1	(.6)
Hypnea cenomyce	6.7	(1.7)
Enteromorpha clathrata	15.0	(2.0)
Polysiphonia sp.	5.0	(2.0)
Jania capillacea	(1.4)	15.3
Hypnea pannosa	(3.6)	11.2
Champia compressa	(3.7)	8.8
Centroceras minutum	(1.2)	7.6

only ones serving both fishes as primary foods, other algae being primary food for one species and secondary food for the other. From these data a percent overlap in primary foods, which takes into account differences in quantities of primary algae consumed by each of the fishes, may be calculated according to the following formula:

$$\frac{\Sigma\% \text{ overlapped primary food}}{\Sigma\% \text{ primary food for } P.\ lividus \text{ (or } P.\ albofasciatus\text{)}} \times 100 = \% \text{ overlap}$$

Overlap of primary foods for *P. lividus* on *P. albofasciatus* was 35.2% and for *P. albofasciatus* on *P. lividus* the overlap was 36.8%.

The checklist (Table 2) also shows the similarity between algal species in guts of *P. lividus* and those growing on the coral; 73% of algal species eaten by P. lividus grow on the base of Acropora. The overlap of primary foods eaten by P. lividus on primary algal species found on Acropora is 52.5%. The relative abundance of primary algal species for both P. lividus and coral are presented in Table 4. The first four species, Pterocladia parva, Polysiphonia scopulorum, Polysiphonia sp., and Sphacelaria furcigera are primary species both in P. lividus guts and on the Acropora. Dawson, Aleem, and Halstead (1955) noted that fishes appear to be better algal collectors than are researchers. This statement plus the fact that no collections were taken from other places on the coral probably account for the remaining few algae not officially recorded from the coral.

TABLE 4

Relative abundance of primary foods for Pomacentrus lividus and primary algal species growing on Acropora. Relative abundance of secondary species appear in parentheses where necessary for comparison.

Algal Species	P. lividus	Acropora
Pterocladia parva	17.6	33.4
Polysiphonia scopulorum	15.2	12.5
Polysiphonia sp.	5.0	7.8
Sphacelaria furcigera	5.6	5.0
Hypnea esperi	6.7	(0)
Enteromorpha clathrata	15.0	(.4)
Pseudochlorodesmis furcellata	11.1	(.3)
Microcoleus lyngbyaceus	(3.6)	17.9

The species of algae eaten by P. lividus and P. albofasciatus are basically the same when viewed qualititively but differences exist in the relative abundance of each algal species consumed. For example *Pterocladia parva* the most abundent alga on the coral is eaten in significantly greater amounts (P<.01) by *P. lividus* than by *P. albofasciatus* (Table 3). Also *Jania capillacea* the species with the highest relative abundance in *P. albofasciatus* guts is consumed at a significantly lower rate (P<.01) by *P. lividus* and is even less abundant on the coral. The similarities between *P. lividus* gut contents and the algae growing on the *Acropora* indicates that the differences in feeding are probably due to subhabitat differences. Fryer (1959) found that herbivorous fishes ate the algal species available to them in their habitats during his study of Lake Nyasa cichlids. No quantification of algae in the sandy rubble filled spaces between the coral colonies was undertaken due to the diversity of the area.

Seven *P. lividus* and four *P. albofasciatus* ingested sponge. Because of the low number of fishes eating this material it was thought to be incidental. Emery (1968) indicated that it is typical for pomacentrids to clean encrusting animals from nesting substrate. This may be a partial explanation for the presence of sponge.

Reproduction

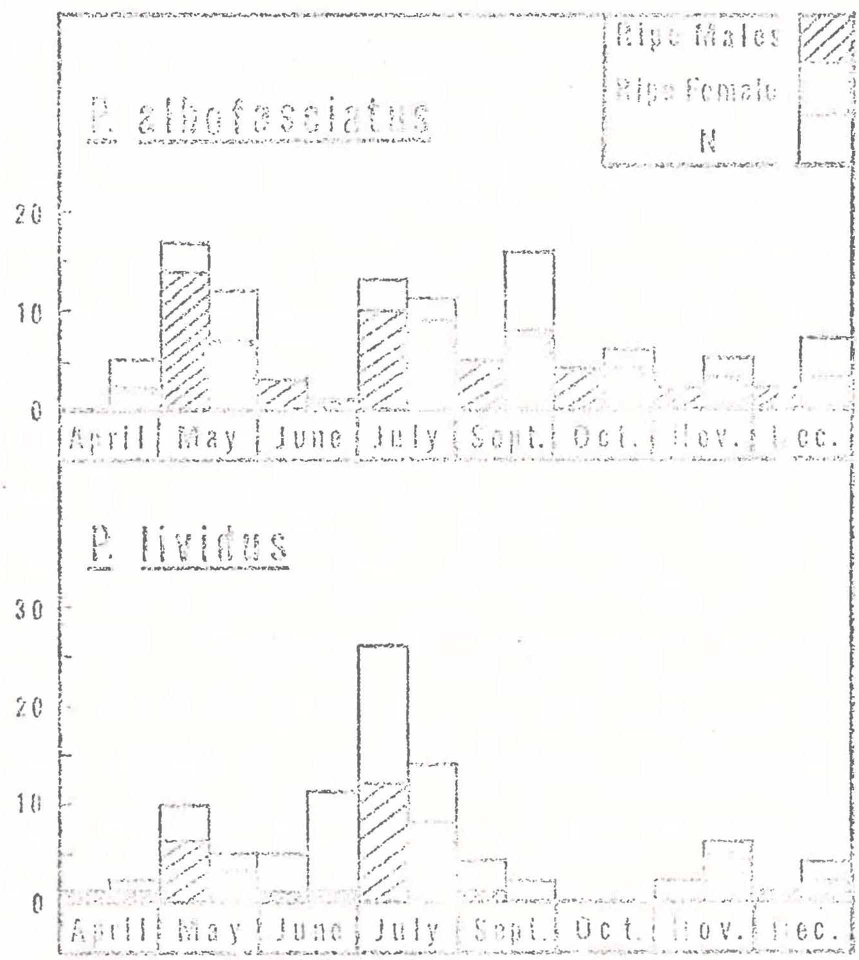
Reproduction and breeding cycle are often useful tools in differentiating the niches of two similar organisms. Ideal separation would involve no overlap of reproductive cycles. However, examination of gonads indicated that both

P. lividus and *P. albofasciatus* are protentially reproductive all year (Figure 7). No peak spawning periods were found but this may be indicative of the small monthly sample size. No nests were found and only one possible example of courtship or spawning behavior was observed.

Two *P. albofasciatus* opposite one another were observed displaying both white bars. The fish dipped from midwater to the sand in fast succession. The white was intensified as the fish descended and became less intense as the fish regained their original midwater positions. Such dipping was associated with reproductive behavior in the pomacentrid *Dascyllus aruanus* (Fischelson in Emery, 1968).

The data allows calculation of a sex ratio for each species. There are 1.1 male *P. lividus* per female and 1.3 female *P. albofasciatus* per male.

Fig. 7. The number of ripe male and female *Pomacentrus albofasciatus* and *Pomacentrus lividus* collected in 1970. No collections were made in January, February, March or August.



Ripe Males
Ripe Female
N
P. albofasciatus
20
10
0
April
May
June
July
Sept.
Oct.
Nov.
Dec.
P. lividus
30
20
10
0
April
May
June
July
Sept.
Oct.
Nov.
Dec.

Section 5

DISCUSSION

The competitive exclusion principle (Gause, 1934) states that no two species can occupy the same niche. The purpose of this paper has been to point out the niche differences between *P. lividus* and *P. albofasciatus*, to show that the overlap of niches is insignificant and that these fishes are not in direct competition for a limited resource.

Pomacentrus albofasciatus lives on the outer reef flat and in part of the coral zone. On the outer reef flat these fish lived in holes and crevices in the rock pavement but were also found in small scattered *Acropora* heads when no *P. lividus* were present. In the coral zone *P. albofasciatus* lived in the sandy, rubble filled spaces between the *Acropora* colonies. Here too, holes and crevices were utilized for cover and possibly reproduction. Several individuals I observed lived at the edge of coral colonies usually in rocks but sometimes in coral. These fish often took cover in the coral occupied by *P. lividus* but were quickly chased out.

Pomacentrus lividus lives in the *Acropora* colonies of the coral zone. The fish seldom leave the protective cover of the coral which is never completely exposed even during extreme minus tides. Large adult *P. lividus* established territories 0.3 m^3 while small adults had territories half that size as roughly measured with a ruler. Both sexes held territories but juveniles did not; rather they ranged freely throughout the coral colony tolerated by the larger fish. The territories are probably for feeding and protective cover since both sexes hold them.

Pomacentrus lividus is larger than P. albofasciatus and this may be an important factor in the spatial distribution of these fishes. Pomacentrus lividus excludes P. albofasciatus from its territories in the Acropora colonies. Another important difference between the species is that apparently no juvenile P. albofasciatus live in the coral zone of Tumon Bay. The juvenile P. lividus are found deep in the coral colonies and receive protection owing to the territorial behavior of the adults. Therefore, the juveniles of the two species are not in competition as far as was discerned.

Qualitatively these two fishes eat the same species of algae but a good deal of difference exists in the proportion of each algal species consumed. Apparently the difference is a result of the fishes feeding in different subhabitats.

Brown and Orians (1970), in a review of ecological literature, showed that in territorial species there are often large numbers of potentially reproductive individuals unable to breed due to lack of breeding sites or mates. Clarke (1970) studying the pomacentrid Hypsypops rubicunda found that removal of individuals resulted in appearance of new individuals of the same species from outside the territory. Population density was high enough to create pressure for repopulation of vacated territories. My observations made during the poison station study suggest that there is a larger supply of potentially reproductive _P. lividus_ than there are vacant territories. When the small _Acropora_ colony was poisoned and the original occupants removed, I observed other _P. lividus_ occupying territories in the same coral within an hour. The immigrants were large enough to be sexually mature but were smaller than the original adults.

The poison station was also used to find out which fishes shared the coral colonies with _P. lividus_ and which might be competing for the benthic algae found on the base of the _Acropora_ branches. Most species were carnivores, a few were omnivores but only one other in the enclosure was a herbivore; therefore it is doubtful that there is any great amount of competition for food between any of these species and _P. lividus_.

Brown and Orians (1970) define an "all-purpose territory" as a territory that is "identical in extent with home range". They further state that no such territory has yet been demonstrated for fishes. _Pomacentrus lividus_ appears to meet these requirements and may establish an all-purpose territory.

During this study a taxonomic problem came to light which is presently being examined. Pomacentrus albofasciatus and P. nigricans, a third Pomacentrus in Tumon Bay, were found to be indistinguishable in the field. Based on collected specimens a 10% error is possible for observational data. With microscopic examination P. nigricans can be distinguished from P. albofasciatus by the presence of scales on the lower preopercular margin. This area is naked on P. albofasciatus. Although Woods and Schultz (1960) give several other characters, such as scales anterior to nostrils and dorsal and anal fin ray counts, to differentiate the species, I found these characters too variable or too overlapping to be relied upon. Until further work is done to prove conclusively that these fishes are good species, I must agree with De Beaufort (1940) and Fowler (1956) that their status is questionable. Doubt definitely exists when one collects a specimen (as I did) with one naked margin and one scaled margin.

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