Heterospecific Fish Schools at the West Back Reef, Discovery Bay, Jamaica: Species Composition, Effects of Damselfish on Feeding Rates, and Possible Resource Partitioning

(with 14 tables and 2 appendices)

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ABSTRACT

144 heterospecific schools were censused on the West Back Reef, Discovery Bay, Jamaica. Twenty-three species engaged in schooling activities; six of them were integral to school structure (Doctorfish, French Grunt, Striped Parrotfish, Princess Parrotfish, Spotted Goatfish, Bluehead Wrasse.)
Princess Parrotfish and Doctorfish together cored over 60% of all schools. The most common associate species were Spotted Goatfish, Doctorfish, and Striped Parrotfish. Bluehead Wrasse were the only common opportunistic species.

Doctorfish and Bluehead Wrasses joined schools indiscriminately. Princess Parrotfish and Striped Parrotfish avoided schools led by the other, while Goatfish avoided French Grunt schools. Reasons for preferential joining of certain types of schools (or the lack of discrimination) are discussed.

Schools of Doctorfish and Striped Parrotfish were generally unsuccessful in swamping damselfish territories, as seen by reduced feeding rates and rapid eviction.
On the other hand, larger schools of larger Princess Parrotfish were sometimes able to swamp damselfish territories and feed for prolonged periods. Therefore the effectiveness of heterospecific school

swamping is probably dependent upon school and individual sizes.

Evidence of resource partitioning within schools is given. Spatial partitioning by species within schools and school movements greater than or equal to school diameter may provide a method of systematic resource harvesting, suggested as being important in mixed species bird flocks. Other comparisons between mixed species flocks and heterospecific schools are made.

INTRODUCTION

A MAJOR CHARACTERISTIC OF THE FISH COMMUNITY OF THE WEST BACK REEF AT DISCOVERY BAY, JAMAICA IS THE COMMON OCCURENCE OF HETEROSPECIFIC SCHOOLS. SUCH A SCHOOL IS SIMPLY A GROUP OF TWO OR MORE FISHES OF TWO OR MORE SPECIES (ITZKOWITZ, 1974).

SEVERAL FACTORS HAVE BEEN SUGGESTED AS THE MAJOR BENEFITS OF SCHOOLING IN FISHES. SHAW (1978) STATES THAT THE INCREASED MECHANICAL EASE OF SWIMMING IN A SCHOOL AND THE REDUCTION OF PREDATION RISK TO AN INDIVIDUAL IN A SCHOOL ARE TWO ADVANTAGES OF SCHOOLING. ALEKSEEVA (1963) DEMONSTRATED A REDUCTION IN PHYSIOLOGICAL STRESS FOR SCHOOLING FISHES. SCHOOLS MAY ALSO ENHANCE THE FEEDING ACTIVITIES OF THE INDIVIDUAL FISH; A PARTICULAR INSTANCE OF SUCH A PHENOMENON WAS ADDRESSED BY ROBERTSON ET AL. (1976) WHEN THEY ADDRESSED THE SWAMPING OF, AND SUBSEQUENT FEEDING IN, DAMSELFISH TERRITORIES BY SCHOOLING PARROTFISHES.

STILL THE QUESTION ARISES: WHY ARE HETEROSPECIFIC SCHOOLS FORMED SO COMMONLY AMONG TROPICAL REEF FISHES? ANY OF THE ABOVE BENEFITS OF SCHOOLING IN GENERAL SHOULD STILL BE APPLICABLE FOR FISHES IN HETEROSPECIFIC SCHOOLS. HETEROSPECIFIC SCHOOLS COULD BE "COMPILED" SCHOOLS OF SPECIES OF FISH WITH POPULATION LEVELS TOO LOW TO FORM UNISPECIFIC SCHOOLS LARGE ENOUGH TO BE ADVANTAGEOUS (SHAW, 1978). HETEROSPECIFIC GROUPS ALSO OCCUR IN AVIAN COMMUNITIES (POWELL, 1979); PERHAPS THE SAME FORCES ARE STRUCTURING HETEROSPECIFIC FISH SCHOOLS. FROM HIS STUDY, POWELL CONCLUDED THAT FEEDING MIGHT BE FACILITATED FOR INDIVIDUALS IN HETEROSPECIFIC GROUPS IN SEVERAL WAYS, INCLUDING THE FOLLOWING:

* FORAGING MAY BE ENHANCED BY FACILITATION OF LOCATION OF FOOD AREAS. FOOD AREAS LOCATED BY AN INDIVIDUAL ARE UTILIZED BY THE ENTIRE GROUP.

* PROXIMAL GROUP MEMBERS MAY FLUSH PREY FOR OTHER MEMBERS.
* THESE GROUPS MIGHT ENABLE A MORE SYSTEMATIC RESOURCE HARVESTING BY LIMITING OVERLAP IN RESOURCE USE.

JUST AS POWELL FOUND VARIOUS BIRD SPECIES PLAYING DIFFERENT ROLES IN HETEROSPECIFIC FLOCKS ("NUCLEAR" VS. "ATTENDANT" SPECIES), DIFFERENT FISH SPECIES PLAY DIFFERENT ROLES IN HETEROSPECIFIC SCHOOLS. ITZKOWITZ (1974) BROKE HETEROSPECIFICALLY SCHOOLING FISHES INTO THREE MAJOR CATEGORIES:

* CORE SPECIES ARE USUALLY IN THE MAJORITY IN THE SCHOOL AND ARE ACTIVE LEADERS OF THE SCHOOL.
* ASSOCIATE SPECIES ARE SUBORDINATE TO THE CORE SPECIES IN DETERMINING THE SCHOOL'S ACTIVITIES. IF A NUMBER OF ASSOCIATE SPECIES ARE PRESENT THEY MAY OUTNUMBER THE CORE SPECIES.
* OPPORTUNISTIC SPECIES GENERALLY JOIN SCHOOLS FOR SHORT TIMES. THIS GROUP ALSO INCLUDES FISH "TRAPPED" IN SCHOOLS SURROUNDING THEIR DAYTIME RESIDENCES, SUCH AS SQUIRRELFISH AND INDIGO HAMLETS.

A SPECIES MAY PLAY ANY ROLE UNDER DIFFERING CONDITIONS; THIS IS NOT UNCOMMON (ITZKOWITZ, 1974).

IN THIS STUDY WE SHALL EXAMINE THE HETEROSPECIFIC FISH SCHOOLS FOUND AT THE WEST BACK REEF, DISCOVERY BAY, JAMAICA. FIRST THE SCHOOLS WILL BE CHARACTERIZED ACCORDING TO SPECIES COMPOSITION. COMPARISONS IN COMPOSITION AND BEHAVIOR WILL BE MADE BETWEEN SCHOOLS LED BY DIFFERENT CORE SPECIES. SECONDLY, THE FEEDING BEHAVIOR, OF FUNDAMENTAL IMPORTANCE TO THESE SCHOOLS (ITZKOWITZ, 1977), OF HETEROSPECIFICALLY SCHOOLING FISHES WILL BE EXAMINED IN VIEW OF THE ABOVE COMMENTS AND SOME MORE SPECIFIC QUESTIONS. IS DAMSELFISH TERRITORY-SWAMPING OF MAJOR IMPORTANCE TO THE FISH IN THESE SCHOOLS? HOW ARE FEEDING

RATES OF HETEROSPECIFICALLY SCHOOLING FISHES AFFECTED BY THE DAMSELFISH AND THEIR TERRITORIES? THE FISH COMPRISING THESE SCHOOLS ARE GENERALLY REGARDED AS GENERALISTS IN THEIR FEEDING BEHAVIOR (SALE, 1980): IS RESOURCE PARTITIONING OCCURING WITHIN THESE SCHOOLS?

SITE DESCRIPTION AND METHODS

The field observations were carried out at the Discovery Bay West Back Reef (UWI Marine Laboratory, Discovery Bay) in an area extending from directly behind the reef flat out approximately 75 m towards the Marine laboratory's dock.

Heterospecific schools were observed regardless of location over the entire area. The study site was a rather homogeneous environment compared to other reefs (Itzkowitz, 1977). It might best be described as composed of numerous patches, each a rock promitory surrounded by *Thalassia* and areas of sand. Though further into the lagoon area the bottom become much more extensively covered by *Thalassia*, the study was concentrated on the area closer to the reef flat itself.

The depth of these study sites ranged from 0.5 to 2.0 metres (approximately) in depth, but was most commonly about 1.5 metres deep.

Data was collected during two sessions a day, from 8:30 to 9:30 AM and from 2:30 to 3:30 PM over the course of seven days, from February 28 to March 6 inclusive. A total of 23 hours was logged.

CHARACTERIZATION OF COMPOSITION DYNAMICS

direction?

Heterospecific schools were located by swimming along a randomly chosen line in the study area. When encountered, the species present, and the numbers of individuals represented were recorded in a plastic underwater notebook. The behaviour was noted to identify the core, associate and opportunistic species, where the core species was defined as the species whose movements were followed by the rest of the group, the associate species those that followed the core and stayed closely in the group, and opportunists those fishes that joined the group ~~but~~ briefly (< 2 minutes).

If any population changes occured over the observation period, the school was treated as a statistically independent group (Itzkowitz, 1977) and the census re-taken as soon as possible. Each school was observed as long as it took to establish composition stability and behaviour, oftentimes up to fifteen minutes for more stable schools, or limited to three minutes for rapidly changing schools.

Where possible, the following characteristics were noted:

a) The overall size of individuals within the school

b) The coherence of each species within the school, and the location of such a sub-group

c) The feeding substrate chosen by each species, and if possible, the food item itself.

Subsequently, different sets of observations described below were made of different schools.

SWAMPING OF DAMSELFISH TERRITORY

Certain schools travel in and out of damselfish territories as they feed. In a number of schools outside ~~of~~ a damselfish territory, an individual was visually selected, and using a diver's digital stopwatch, the number of bites taken over a 30 second bout recorded. This was repeated for a number of different individuals of that species, giving a measure of the overall feeding rate of that group within the school, outside of damselfish territories

If a damselfish was nearby, its species was noted, and it was observed to see how far away from its resting spot it would venture in harrassing fishes feeding close by. This gave an idea of the extent of this territory. Then a heterospecific school in the area (preferably one whose feeding rate had been measured outside the territory) was characterized in terms of size and species composition, and feeding rates for individuals of the species then under study measured and recorded.

Along with qualitative observations of the sucess of lone fish invading damselfish territories, this procedure gave an indication of whether or not feeding rates were higher within the damselfish territories indicating facilitated feeding and effective swamping, or lower, indicating that the damselfish were to some degree sucessful in inhibiting the feeding of the school.

Since schools were often large and fast-moving, it was easy to lose the individual under observation in the mass of fish. Since the schools tend to act as quite coördinated units, if this occured another individual of the same species engaged in the same activity (either searching or biting) was immediately identified and the data collection continued ~~from~~ to the end of that 30 second bout (D.R. Robertson et. al., 1976).

FOOD NICHE OVERLAP

A feeding bout was defined as one where approximately 75% of the individuals in a school were feeding. In a number of trials where a characterized and numbered school was seen to be engaged in a feeding bout, the diameter of the smallest circle enclosing the entire school (the "school diameter") was assesed. The location and substrate on which each species present was feeding was also noted. As the school made a mass movement, we noted whether or not it moved at least the assesed school diameter.

These two measures gave an indication of both food type and actual physical substrate overlap within the school as it fed.

Results

The structure, according to core, associate, and opportunistic species, of all heterospecific schools censused is summarized in tables 1, 2, and 3 respectively. Nine species were observed to lead schools, two species (Princess Parrotfish and Doctorfish) combining to lead over 60% of all schools. Fourteen species acted as associates. Doctorfish and Spotted Goatfish were associates in over half the schools which they did not lead, while Princess Parrotfish (the most common core species) were an associate species in about one third of the schools which they did not core. Fourteen species acted as opportunistic species; of these only the Bluehead Wrasse and Squirrelfish were found in more than 5% of the schools which they did not lead.

In several schools the apparant leader species was not in the majority. In these instances, the core species was defined as the leader species. Table four (4) lists all such cases.

The structures of schools led by the six most common core species (Princess Parrotfish, Doctorfish, Rainbow Wrasse, Striped Parrotfish, French Grunt, and Spotted Goatfish) are summarized in tables 5 through 10 respectively. Doctorfish and Bluehead Wrasses occurred in at least 25% of all schools cored by these six species. Spotted Goatfish occurred in at least 50% of all schools cored by these species with the exception of French Grunt; goatfish occurred in just two of 13 French Grunt schools. Striped Parrotfish were found predominantly in Doctorfish schools, while Princess Parrotfish were found in over one third of French Grunt schools and at least half of Spotted Goatfish

TABLE 1. CORE SPECIES FREQUENCIES

CORE SPECIES	# SCHOOLS LED	% SCHOOLS LED BY THIS CORE SPECIES
PRINCESS PARROTFISH	60	41.4
DOCTORFISH	30	20.7
STRIPED PARROTFISH	14	9.7
FRENCH GRUNT	12	8.3
SPOTTED GOATFISH	9	6.3
RAINBOW WRASSE	8	5.6
BLUEHEAD WRASSE	4	2.8
OCEAN SURGEONS	4	2.8
PUDDINGWIFE WRASSE	3	2.1
	144	

TABLE 2. ASSOCIATE SPECIES FREQUENCIES

ASSOCIATE SPECIES	# SCHOOLS	% SCHOOLS, NOT LED BY THIS SPECIES
DOCTORFISH	76	66.7
SPOTTED GOATFISH	76	56.3
PRINCESS PARROTFISH	30	35.7
STOPLIGHT PARROTFISH	26	18.1
STRIPED PARROTFISH	15	11.5
OCEAN SURGEON	12	8.3
BLUE TANG	6	4.2
RAINBOW WRASSE	4	2.9
FOUR-EYE BUTTERFLY FISH	3	2.1
UNIDENTIFIED BLUESTRIPE PARROT FISH	2	1.4
REDTAIL PARROTFISH	1	0.7
LONGSNOUT BUTTERFLY FISH	1	0.7
THREESPOT DAMSELFISH (JUV.)	1	0.7
UNIDENTIFIED GREEN/WHITE PARROTFISH	1	0.7

TABLE 3. OPPORTUNISTIC SPECIES FREQUENCIES

OPPORTUNISTIC SPECIES	# SCHOOLS	% SCHOOLS, NOT LED BY THIS SPECIES
BLUEHEAD WRASSE	34	24.3
SQUIRREL FISH	8	5.6
UNIDENTIFIED GREEN WRASSE	7	4.7
FRENCH GRUNT	6	4.5
INDIGO HAMLET	6	4.2
PRINCESS PARROTFISH	2	2.4
RAINBOW WRASSE	3	2.2
GOATFISH (SPOTTED)	3	2.2
FOUREYE BUTTERFLYFISH	3	2.1
PUDDINGWIFE WRASSE	2	1.4
DOCTORFISH	1	0.9
STOPLIGHT PARROTFISH	1	0.7
THREE-SPOT DAMSELFISH (JUV.)	1	0.7
YELLOWTAIL SNAPPER	1	0.7

TABLE 4. CASES OBSERVED WHERE SCHOOLS WERE LED BY OTHER THAN THE CORE SPECIES (SPECIES IN MAJORITY).

ACTUAL LEADING SPECIES	#	DESCRIPTION
PRINCESS PARROTFISH	1	INDIVIDUAL LEFT, SCHOOL OF 4 BLUEHEAD WRASSE, 4 DOCTORFISH BROKE UP.
PRINCESS PARROTFISH	1	LED SCHOOL OF 7 DOCTORFISH, 1 SPOTTED GOATFISH, 2 BLUEHEAD WRASSE.
BLUEHEAD WRASSE	4	SCHOOL OF 5 SPOTTED GOATFISH, 3 PRINCESS PARROTFISH DISPERSED WHEN WRASSES LEFT.
STOPLIGHT PARROTFISH	1	LED 5 GOATFISH, 1 PUDDINGWIFE WRASSE UNTIL REACHED EDGE OF TERRITORY. PUDDING-WIFE THEN LED GOATFISH.
RAINBOW WRASSE	1	LED 10 GOATFISH, 1 DOCTORFISH.
SPOTTED EAGLE RAY	1	LED 5 BLUEHEAD WRASSES.
PRINCESS PARROTFISH	5	LED 6 DOCTORFISH.

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TABLE 5. COMPOSITION OF SCHOOLS CORED BY PRINCESS PARROTFISH

SPECIES X	# SCHOOLS LED* (AND CENSUSED)	% TOTAL SCHOOLS LED BY THIS CORE SPECIES	# FISH	$\bar{X}$ WHEN IN SCHOOL (SD)	RANGE
PRINCESS PARROTFISH	60	100.0	650	10.8 (12.4)	1–70
DOCTORFISH	47	78.3	165	3.5 (3.7)	1-21
SPOTTED GOATFISH	41	68.3	123	3.0 (1.6)	1-8
BLUEHEAD WRASSE	16	26.7	32	2.0 (1.6)	1-7
OCEAN SURGEONS	7	11.7	19	2.7 (1.7)	1-6
STOPLIGHT PARROTFISH	7	11.7	11	1.6 (0.5)	1-2
STRIPED PARROTFISH	4	6.7	20	5 (1.7)	4-8
BLUE TANG	2	3.3	3	1.5 (0.5)	1-2
PUDDINGWIFE WRASSE	2	3.3	2	1 (–)	–
FRENCH GRUNT	2	3.3	2	1 (–)	–
INDIGO HAMLET	2	3.3	2	1 (–)	–
RAINBOW WRASSE	1	1.7	2	2 (–)	–
REDTAIL PARROTFISH	1	1.7	2	2 (–)	–
FOUREYE BUTTERFLYFISH	1	1.7	2	2 (–)	–

number of schools in which species X occurs

* BY THIS CORE SPECIES

TABLE 6. COMPOSITION OF SCHOOLS CORED BY DOCTORFISH

SPECIES	IN # SCHOOLS LED* (AND CENSUSED)	% TOTAL SCHOOLS LED BY THIS CORE SPECIES	# FISH	$\bar{X}$ WHEN IN SCHOOL (SD)	RANGE
DOCTORFISH	30	100.0	215	7.2 (4.3)	2-26
BLUEHEAD WRASSE	17	56.7	29	1.7 (1.1)	1-5
PRINCESS PARROT	17	56.7	46	2.7 (1.9)	1-8
SPOTTED GOATFISH	16	53.3	39	2.4 (1.4)	1-5
STRIPED PARROTFISH	9	30.0	24	2.7 (1.2)	1-5
STOPLIGHT PARROTFISH	8	26.7	11	1.4 (0.5)	1-2
SQUIRRELFISH	2	6.7	2	1 (–)	–
BLUE TANG	2	6.7	3	1.5 (.5)	1-2
INDIGO HAMLET	1	3.3	1	1 (–)	–
GREEN UN'ID'd WRASSE	1	3.3	1	1 (–)	–
UN'ID'd PARROTFISH	1	3.3	1	1 (–)	–
FRENCH GRUNT	1	3.3	1	1 (–)	–
THREESPOT DAMSELFISH	1	3.3	1	1 (–)	–
RAINBOW WRASSE	1	3.3	2	2 (–)	–

TABLE 7. COMPOSITION OF SCHOOLS CORED BY RAINBOW WRASSE

SPECIES	IN # SCHOOLS LED* (AND CENSUSED)	% TOTAL SCHOOLS LED BY THIS CORE SPECIES	# FISH	$\bar{X}$ WHEN IN SCHOOL (SD)	RANGE
RAINBOW WRASSE	8	100.0	36	4.5 (2.4)	1-7
DOCTORFISH	6	75.0	11	1.8 (.5)	1-2
SPOTTED GOATFISH	7	87.5	16	2.3 (1.2)	1-4
LONGSNOUT BUTTERFLYFISH	1	12.5	1	1.0 (–)	–
BLUEHEAD WRASSE	2	25.0	2	1.0 (–)	–
UN'ID'd GREEN WRASSE	1	12.5	1	1.0 (–)	–

* BY THIS CORE SPECIES

TABLE 8. COMPOSITION OF SCHOOLS CORED BY STRIPED PARROTFISH

SPECIES	IN # SCHOOLS LED* (AND CENSUSED)	% IN TOTAL SCHOOLS LED BY THIS CORE SPECIES	# FISH	$\bar{X}$ WHEN IN SCHOOL (SD)	RANGE
STRIPED PARROTFISH	13 ~~100.0~~	100.0	98	7.5 (3.9)	3-17
DOCTORFISH	10	76.9	31	3.1 (1.9)	1-6
SPOTTED GOATFISH	7	53.8	45	6.4 (2.8)	3-11
STOPLIGHT PARROTFISH	5	38.5	7	1.4 (0.8)	1-3
UN'ID'd GREEN WRASSE	5	38.5	26	5.2 (1.5)	4-7
BLUEHEAD WRASSE	4	30.8	6	1.5 (0.8)	1-3
BLUESTRIPE PARROTFISH	2	15.4	3	1.5 (0.5)	1-2
FRENCH GRUNT	2	15.4	2	1.0 (-)	-
OCEAN SURGEON	1	7.7	5	5.0 (-)	-
BLUE TANG	1	7.7	2	2.0 (-)	-
SQUIRRELFISH	1	7.7	1	1.0 (-)	-
INDIGO HAMLET	1	7.7	1	1.0 (-)	-
PRINCESS PARROTFISH	1	7.7	1	1.0 (-)	-

TABLE 9. COMPOSITION OF SCHOOLS CORED BY FRENCH GRUNT

SPECIES	IN # SCHOOLS LED* (AND CENSUSED)	% IN TOTAL SCHOOLS LED BY THIS CORE SPECIES	# FISH	$\bar{X}$ WHEN IN SCHOOL (SD)	RANGE
FRENCH GRUNT	13	100.0	480	36.9 (21.7)	6-61
DOCTORFISH	11	84.6	15	1.4 (0.6)	1-3
BLUEHEAD WRASSE	6	46.2	10	1.7 (1.1)	1-4
SQUIRRELFISH	6	46.2	7	1.2 (0.3)	1-2
PRINCESS PARROTFISH	5	38.5	15	3.0 (1.1)	2-5
STOPLIGHT PARROTFISH	3	23.1	5	1.7 (0.5)	1-2
STRIPED PARROTFISH	3	23.1	13	4.3 (1.2)	3-6
SPOTTED GOATFISH	2	15.4	6	3.0 (1)	2-4
INDIGO HAMLET	1	7.7	1	1.0 (-)	-
YELLOWTAIL SNAPPER	1	7.7	1	1.0 (-)	-
FOUREYE BUTTERFLYFISH	3	23.1	3	1.0 (-)	-

* BY THIS CORE SPECIES

TABLE 10. COMPOSITION OF SCHOOLS CORED BY SPOTTED GOATFISH

SPECIES	IN # SCHOOLS LED* (AND CENSUSED)	% TOTAL SCHOOLS LED BY THIS CORE SPECIES	# FISH IN	$\bar{x}$ WHEN IN SCHOOL (SD)	RANGE
SPOTTED GOATFISH	10	100.0	67	6.7 (2.3)	4-12
DOCTORFISH	6	60.0	12	2.0 (1)	1-4
PRINCESS PARROTFISH	5	50.0	13	2.6 (1.0)	1-4
BLUEHEAD WRASSE	3	30.0	10	3.3 (1.7)	1-5
STOPLIGHT PARROTFISH	2	20.0	3	1.5 (0.5)	1-2
BLUE TANG	1	10.0	2	2.0 (-)	-
PUDDINGWIFE WRASSE	1	10.0	1	1.0 (-)	-
RAINBOW WRASSE	1	10.0	1	1.0 (-)	-
FRENCH GRUNT	1	10.0	1	1.0 (-)	-
OCEAN SURGEON	1	10.0	1	1.0 (-)	-

TABLE 11. EXAMINATION FOR PREFERENCE IN SELECTION OF CORE SPECIES BY IMPORTANT ASSOCIATE AND OPPORTUNISTIC SPECIES

SPECIES	DEGREES FREEDOM	χ^2	EXPLANATION OF SIGNIFICANCE ✯
DOCTORFISH	4	2.08	NO DISCRIMINATION, $\alpha = 0.05$
SPOTTED GOATFISH	4	12.52	PREFERENCE, $\alpha = 0.025$
PRINCESS PARROTFISH	4	16.80	PREFERENCE, $\alpha = 0.005$
STRIPED PARROTFISH	4	13.43	PREFERENCE, $\alpha = 0.01$
BLUEHEAD WRASSE	5	9.15	NO DISCRIMINATION, $\alpha = 0.05$

* BY THIS CORE SPECIES

✯ SEE TEXT

AND DOCTORFISH SCHOOLS.

TO DETERMINE IF THE FIVE MOST IMPORTANT ASSOCIATE SPECIES (SPOTTED GOATFISH, DOCTORFISH, BLUEHEAD WRASSE, PRINCESS PARROTFISH, AND STRIPED PARROTFISH) DEMONSTRATED ANY PREFERENCE IN JOINING SCHOOLS CORED BY THE SIX MOST IMPORTANT CORE SPECIES (LISTED ABOVE), CHI-SQUARE ANALYSES (OPPOSING NUMBER OF SCHOOLS CORED BY A PARTICULAR SPECIES WITH A GIVEN ASSOCIATE SPECIES AGAINST THE NUMBER OF SCHOOLS WITHOUT THIS ASSOCIATE SPECIES) WERE PERFORMED. THE RESULTS OF THESE ARE SUMMARIZED IN TABLE 11.

v. good idea

Over the course of the study, successful swamping of territories very rarely appeared to occur. The aggressiveness of the three major damselfish genera represented in the study site (Dusky, Yellowtail and Threespot Damselfish) kept most fish, certainly lone individuals, and also ~~those~~ many of those aggregated in schools of considerable size, out of their territories. Consequently, feeding rate data as expressed by number of bites of selected individuals over a 30 second period were rather more difficult to obtain for the three schooling species of fish studied, (Striped and Princess Parrotfish, and Doctorfish) inside the territories as compared with outside (see appendicies 2a and 2b).

v. good idea

Since we suspected that feeding rates may be affected by the time of day, for the purpose of within- and outside-territory feeding rate comparison, data collected in the morning was analyzed seperately from that collected in the afternoon.

A series of Mann-Whitney U-Tests were used in analyzing this data (see Table 12).

In the cases of the Striped Parrotfish elements, (morning feeding bouts), Doctorfish elements (morning and afternoon) and Princess Parrotfish elements (morning) of heterospecific schools invading such territories, the aggressiveness of the damselfish was successful in reducing the feeding rates of these species to a level significantly lower than that which they attain outside of the territories.

Only in one case of the five that we examined, that of afternoon Princess Parrotfish feeding, did we see no significant overall difference in feeding rates inside and outside of damselfish territories.

AN OBSERVATION CONCERNING FISH IN FEEDING HETEROSPECIFIC SCHOOLS WAS THAT THE VARIOUS SPECIES WOULD GENERALLY SEGREGATE THEMSELVES WITHIN THE SCHOOL. IN OTHER WORDS, SMALL UNISPECIFIC SCHOOLS OCCURRED WITHIN THE HETERO SPECIFIC SCHOOL.

good pt.

SEVERAL FOODS UTILIZED BY STRIPED PARROTFISH AND DOCTORFISH WERE IDENTIFIED. THESE ARE LISTED IN TABLE 13. IT CAN BE SEEN THAT CONSIDERABLE OVERLAP OCCURS IN FOODS USED BY THESE TWO SPECIES.

THE DISTANCES THAT SCHOOLS MOVED BETWEEN FEEDING BOUTS WERE OBSERVED ON THREE OCCASIONS AND COMPARED TO THE SCHOOL DIAMETER. RESULTS ARE SUMMARIZED IN TABLE 14. APPROXIMATELY 80% OF MOVES WERE GREATER THAN OR EQUAL TO THE SCHOOL DIAMETER; THIS DID NOT ~~NOT~~ DIFFER SIGNIFICANTLY AMONG THE THREE OBSERVATIONAL SETS ($X^2 = 0.919$, $\alpha = 0.5$).

TABLE 12 : Comparison of Feeding Rates of Selected Species, Inside and Outside of Damselfish Territories.

SPECIES	SESSION	MEAN FEEDING RATE (NUMBER OF BITES PER 30 SECONDS)		SIGNIFICANCE OF DIFFERENCE –
		INSIDE DAMSELFISH TERRITORY	OUTSIDE DAMSELFISH TERRITORY	MANN – WHITNEY U – TEST
Striped Parrotfish	morning	14 · 9 ± 8 · 0	23 · 5 ± 5 · 5	SIGNIFICANT; $\alpha < 0 \cdot 025$
Doctorfish	morning	0 · 2 ± 0 · 4	7 · 5 ± 7 · 7	SIGNIFICANT; $\alpha = 0 \cdot 05$
	afternoon	9 · 6 ± 9 · 6	19 · 8 ± 9 · 6	SIGNIFICANT; $\alpha = 0 \cdot 01$
Princess Parrotfish	morning	6 · 5 ± 6 · 8	18 · 0 ± 5 · 0	SIGNIFICANT; $\alpha < 0 \cdot 001$
	afternoon	26 · 5 ± 11 · 8	24 · 6 ± 8 · 5	NOT SIGNIFICANT

TABLE 13. FOODS OBSERVED TO BE TAKEN BY PRINCESS PARROTFISH AND DOCTORFISH

FOOD ITEM	PRINCESS PARROTFISH	DOCTORFISH
THALASSIA GRASS	✓	
ENCRUSTING RED ALGAE ON *THALASSIA*	✓	✓
UN'ID FILAMENTOUS BROWN ALGAE	✓	✓
DICTYOTA PARDALIS	✓	✓
DICTYOTA SP.	✓	✓
CERAMIUM SP.	✓	✓
PENICILLUS SP.	✓	✓
CLADOPHOROPSIS SP.		✓

TABLE 14. INTER-FEEDING-BOUT MOVEMENT DISTANCES FOR STRIPED PARROTFISH-CORED SCHOOLS.

	# MOVES ≥ DIAMETER	# MOVES < DIAMETER
OBSERVATION PERIOD 1 (N=29)	24	5
OBSERVATION PERIOD 2 (N=35)	27	8
OBSERVATION PERIOD 3 (N=27)	22	5

DISCUSSION

WE OBSERVED 23 SPECIES PARTICIPATING IN HETEROSPECIFIC SCHOOLING ACTIVITIES. OF THESE, SEVEN SPECIES (DOCTORFISH, FRENCH GRUNT, STRIPED PARROTFISH, PRINCESS PARROTFISH, SPOTTED GOATFISH, AND TO A LESSER EXTENT BLUEHEAD AND RAINBOW WRASSES) WERE COMMON IN SCHOOLS (AND CORRESPONDINGLY SCARCE OUTSIDE SCHOOLS). THESE SPECIES COMBINED IN VARIOUS WAYS TO FORM SCHOOLS OF DIFFERENT BEHAVIOR AND FUNCTION.

SCHOOLS CORED BY PRINCESS AND STRIPED PARROTFISH WERE GENERALLY LARGE (17.3, 17.5 AVERAGE FISH / SCHOOL* RESPECTIVELY) ACTIVELY FEEDING SCHOOLS. SPOTTED GOATFISH AND RAINBOW WRASSE SCHOOLS WERE SMALLER (11.1, 8.4 FISH / SCHOOL), COMPOSED OF FEWER SPECIES, QUICK MOVING AND ACTIVELY FEEDING. FRENCH GRUNT SCHOOLS WERE LARGEST (42.8 FISH / SCHOOL), SEDENTARY, AND NON-FEEDING. FISH WERE SOMETIMES OBSERVED TO LEAVE FRENCH GRUNT SCHOOLS TO FEED, ONLY TO RETURN AND STOP FEEDING.

THUS SCHOOLS OF DIFFERENT TYPES CAN BENEFIT JOINING FISH IN DIFFERENT WAYS DEPENDENT UPON THE CORE SPECIES. SINCE FISH OF DIFFERENT SPECIES MIGHT BE PRESUMED TO HAVE DIFFERENT SCHOOLING NEEDS, IT FOLLOWS THAT FISH SPECIES MIGHT JOIN SCHOOLS PREFERENTIALLY. SUCH PREFERENCES IN SCHOOL TYPE SELECTION WERE DEMONSTRATED (CHI-SQUARE) FOR SPOTTED GOATFISH, PRINCESS PARROTFISH, AND STRIPED PARROTFISH. DOCTORFISH AND BLUEHEAD WRASSES SHOWED NO DISCRIMINATION IN SELECTING SCHOOLS.

DOCTORFISH WERE ASSOCIATE SPECIES IN TWO-THIRDS OF THOSE SCHOOLS WHICH THEY DID NOT LEAD. THEIR LACK OF EXHIBITED PREFERENCE FOR SCHOOL TYPE INDICATES THAT THE MAJOR BENEFITS TO DOCTORFISH OF HETEROSPECIFIC SCHOOLING COULD BE THOSE GENERALLY ATTRIBUTED TO UNISPECIFIC SCHOOLS, SUCH AS REDUCED PREDATION RISK. THE "COMPILED" SCHOOLS REFERRED TO BY SHAW (1978) INTERESTINGLY ENOUGH BENEFITTED AN ACANTHURID; PERHAPS THE CASE IS THE SAME FOR THE

* AVERAGE SCHOOL SIZE DETERMINED BY: $\frac{\text{\# FISH IN SCHOOLS LED BY THIS SPECIES}}{\text{\# SCHOOLS LED BY THIS SPECIES}}$

DOCTORFISH HERE. UNDER SUCH CIRCUMSTANCES THE DOCTORFISH MIGHT EXHIBIT SCHOOLING TENDENCIES WITH WHATEVER SCHOOLS WERE AVAILABLE, AND THUS NO PREFERENCE IN JOINING SCHOOLS OF VARIOUS TYPES.

BLUEHEAD WRASSES ALSO EXHIBITED NO DISCRIMINATION IN CHOOSING AMONG SCHOOLS LED BY VARIOUS CORE SPECIES. OF THE SPECIES EXAMINED, THIS IS THE MOST TYPICAL OPPORTUNISTIC SPECIES. SINCE SCHOOLING ACTIVITIES ARE GENERALLY LESS IMPORTANT TO SUCH SPECIES, IT IS NOT SURPRISING THAT NO PREFERENCE FOR A GIVEN TYPE OF SCHOOL WAS DEMONSTRATED.

THE PREFERENCE FOR PARTICULAR SCHOOL TYPES DEMONSTRATED BY PRINCESS AND STRIPED PARROTFISH CAN BE ATTRIBUTED TO THE SAME FACTOR; BOTH SPECIES SHOWED AN AVERSION TO SCHOOLS LED BY THE OTHER SPECIES OF PARROTFISH. THESE TWO SPECIES HAVE VERY SIMILAR FEEDING HABITS AND MIGHT DO BETTER LEADING THEIR OWN SCHOOLS OR ASSOCIATING WITH NON-PARROTFISH-LED SCHOOLS ~~THAT~~ WHEN THEY CO-OCCUR.

THE PREFERENCE FOR CERTAIN TYPES OF SCHOOLS DEMONSTRATED BY SPOTTED GOATFISH IS DUE TO THIS SPECIES' STRONG AVERSION TO FRENCH GRUNT SCHOOLS. THIS IS CONSISTENT WITH THE IDEA THAT THE GOATFISH'S MAJOR BENEFIT FROM SCHOOLING IS ENHANCED FEEDING, SINCE FRENCH GRUNT SCHOOLS ARE NON-FEEDING. OTHER OBSERVATIONS SUPPORT THIS IDEA; SEVERAL UNISPECIFIC SCHOOLS OF GOATFISH WERE OBSERVED TO COMMENCE FEEDING UPON JOINING A HETEROSPECIFIC SCHOOL. THE ONLY UNISPECIFIC SCHOOL OF GOATFISH OBSERVED FEEDING WAS QUITE LARGE (SEVEN INDIVIDUALS).

Though the degree of food overlap of certain heterospecific school members that attempt to invade damselfish territories is rather small (for example, the

~~opposed to herbivorous Parrotfish~~

sediment - sifting carnivorous goatfish), the degree of overlap with other elements of the same schools such as Doctor-fish (which are close relatives) and parrotfish (~~which are~~ generalist herbivores) can be very high. This may well account for the aggressiveness that damselfish demonstrate towards virtually all approaching schools.

According to Robertson et. al. (1976), schooling functions as a particularly adaptive feeding trait: as a school swarms over a competitor's territory, its members feed on the high concentration of material without being excessively hindered by the resident damselfishes attacks. Since the damsel-fish can only make a limited number of attacks in a given period of time, the attack rate to any particular individual is low, though the attack to the group may be continuous. Furthermore, any individual so attacked can simply change position and lose itself in the milling school.

As Robertson et al (1976) reported, we also observed that individual fishes were consistently and effectively excluded from damselfish territories, regardless of size. However, our further observations and the data previously presented shows that the success of the damselfish in excluding schools ~~from~~ of invaders from their territories is primarily dependent upon three factors; the size of the school itself, the sizes of the individuals within the school, and the aggressiveness of these individuals. Another factor that concerns not the school but the territory holder is the aggressiveness of the damselfish itself, which varies from genus to genus, and individual to individual. In general, Threespot Damselfish are known to be the most aggressive, but we did not obtain a large enough sample size of each of the three species to be able to compare the different effects of each on invader feeding rates.

In the cases of the Striped Parrotfish and Doctorfish components of invading schools, the individuals tended to be small and easily routed by damselfish charges. By directing the attacks towards different areas of the school, the territory holder could usually repel the entire school after three or four charges. It was noted that the schooling fish not immediately under attack would begin biting at their chosen substrate at an extremely high rate (up to 16 bites in 11 seconds), but would be routed so quickly that their rates over the standard 30 second periods were quite low. Otherwise, the school would swim around the territory, apparently evading the damselfish without biting until the core species withdrew, and the rest of the school followed.

In the case of the Princess Parrotfish, these factors are seen to have reduced their feeding rates within damselfish territories during the morning to a level significantly below their feeding rate outside. However, our qualitative field notes indicate that the majority of the heterospecific schools incorporating Princess Parrotfish followed in the afternoon tended to be larger in both numbers and overall individual size. When such schools entered a damselfish territory, the occupant would often retreat until the school had left the territory. In analyzing our records of the behaviour of these schooling fishes, as well as those of smaller, less aggressive schools, we obtained no significant difference in overall feeding rates within and outside of damselfish territories.

In the case of the larger schooling fishes, the mechanism of this swamping is quite different from that described by Robertson et al (1976). However, it should be pointed out that during a dive prior to this study, the swamping Robertson et al (1976) described was in fact noted. That particular dive was made in the fore-reef, where the water is ~~progressively~~ deeper, and fishes tend to be considerably larger than in the backreef. It is conceivable that in such an environment where fishes are larger and possibly more aggressive, Robertson's swamping may be a far more common occurance. Unfortunately, the site description as reported by Robertson et al. (1976) in their study is rather lacking, so comparisons between it and the Discovery Bay site are not possible.

In our own study, we were not able to include a record of the activities of many larger fishes, since they were much faster moving than the smaller fishes, extremely evasive, and difficult to follow. Consequently, our results are for the most part biased towards the behaviour of smaller fishes.

Since this study indicates that a great number of shallow water heterospecific schools enjoy little success in swamping competitor territories, the impact that this mechanism has on the shaping of schooling behaviour is questionable. It is arguable that though the mechanism might be adaptive to a greater extent in larger individuals, it is expressed over the entire population, small and large, becoming truly effective as individuals attain a certain size.

THE FISHES COMPOSING THESE SCHOOLS ARE GENERALLY THOUGHT OF AS GENERALISTS IN THEIR FEEDING HABITS. WE HAVE OBSERVED SIX OF EIGHT FOOD SOURCES BEING USED BY BOTH PRINCESS PARROTFISH AND DOCTORFISH. WHETHER THE RESOURCES USED BY THESE FISHES ARE LIMITING OR NOT IS NOT ADDRESSED HERE; HOWEVER, WE BELIEVE WE HAVE FOUND SOME EVIDENCE OF RESOURCE PARTITIONING AMONG MEMBERS OF THE SAME SCHOOL, BOTH IN THE RESOURCES USED AND WHERE THEY ARE USED.

GENERALLY, DIFFERENT FEEDING GUILDS ARE FOUND WITHIN THE SAME SCHOOL. WRASSES AND GOATFISH ARE INVERTEBRATE CARNIVORES WHILE DOCTORFISH AND PARROTFISH ARE HERBIVORES. MEMBERS OF DIFFERENT GUILDS WITHIN THE SAME SCHOOL ARE NOT COMPETING FOR THE SAME RESOURCES AS MEMBERS OF UNISPECIFIC SCHOOLS MAY. SPATIAL SEGREGATION BY SPECIES WITHIN THE SCHOOL CAN LIMIT COMPETITION WITHIN GUILDS. FOR INSTANCE, WRASSES GENERALLY FORAGED HIGHER IN THE SUBSTRATE THAN DID GOATFISH, WHICH

SIFT SEDIMENTS. DOCTORFISH WERE OBSERVED FEEDING AT THE BASES OF *THALASSIA* WHEREAS PARROTFISH ALWAYS GRAZED NEAR THE BLADE TIP.

SCHOOL MOVEMENTS OF AT LEAST ONE SCHOOL DIAMETER RESULT IN NEW FEEDING TERRITORIES BEING MADE AVAILABLE TO ALL MEMBERS OF THE SCHOOL. WITH THESE MOVEMENTS FISH DO NOT FORAGE/GRAZE IN AREAS PREVIOUSLY USED BY MEMBERS OF THE SAME SCHOOL. THE OBSERVED SPATIAL SEPARATION BY SPECIES WITHIN SCHOOLS, COUPLED WITH SCHOOL MOVEMENTS GREATER THAN OR EQUAL TO THE SCHOOL DIAMETER, MIGHT PROVIDE A MANNER OF SYSTEMATIC RESOURCE HARVESTING AS SUGGESTED FOR BIRD MIXED-SPECIES FLOCKS BY POWELL (1979).

POWELL ALSO SUGGESTED THAT MIXED-SPECIES GROUPS MIGHT ENHANCE FEEDING BY THE FACILITATED LOCATION OF FOOD RESOURCES. THIS IS PROBABLY NOT THE CASE FOR FISHES IN THE BACK REEF, BUT THE DAMSELFISH~~ES~~ TERRITORIES ARE AN INTERESTING PARALLEL. THESE RICH FOOD PATCHES CAN BE EXPLOITED ONLY AS A GROUP, AND NOT INDIVIDUALLY. THUS HETEROSPECIFIC SCHOOLS CAN BE VIEWED AS A MEANS BY WHICH RICH FOOD AREAS ~~CAN~~ ARE IDENTIFIED AND UTILIZED.

POWELL'S THIRD EXPLANATION FOR ENHANCED FEEDING IN MIXED-SPECIES GROUPS WAS THAT FEEDING ACTIVITIES OF PROXIMAL MEMBERS MIGHT FLUSH PREY FOR OTHERS TO CAPTURE. WRASSES APPEARED TO BE FEEDING ON SUCH PREY. DOCTORFISH GRAZED ON ~~FLOATING~~ SUSPENDED *CLADOPHOROPSIS* WHICH HAD BEEN LOOSENED BY THE FEEDING ACTIVITIES OF OTHER SCHOOL MEMBERS (S. LACHANCE, personal observation).

THUS FISH APPEAR TO BE USING HETEROSPECIFIC SCHOOLS IN THE WEST BACK REEF IN SEVERAL WAYS: AS A REFUGE FROM PREDATORS, AS A MEANS OF UTILIZING FAVORABLE FOOD AREAS, AS AN ENHANCER OF FEEDING ACTIVITIES IN GENERAL, AND PERHAPS AS PART OF A SYSTEMATIC RESOURCE HARVESTING SCHEME. THESE HETEROSPECIFIC

FISH SCHOOLS SEEM TO CLOSELY PARALLEL MIXED-SPECIES BIRD FLOCKS IN BOTH STRUCTURE AND FUNCTION.

An excellent, well-focused, and well-written study.

John

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Appendix I : Scientific Names of Fish Species Referred to in Text

Common Name	Scientific Name
Bluehead Wrasse	*Thalassoma bifasciatum*
Blue Tang	*Acanthurus coeruleus*
Doctorfish	*Acanthurus chirurgus*
Four-eye Butterflyfish	*Chaetodon capistratus*
Dusky Damselfish	*Eupomacentrus fuscus*
French Grunt	*Haemulon flavolineatum*
Indigo Hamlet	*Hypoplectrus indigo*
Longsnout Butterflyfish	*Prognathodes aculeatus*
Ocean Surgeon	*Acanthurus bahianus*
Princess Parrotfish	*Scarus taeniopterus*
Puddingwife Wrasse	*Halichoeres radiatus*
Rainbow Wrasse	*Halichoeres pictus*
Redtail Parrotfish	*Sparisoma chrysopterum*
Squirrelfish	*Holocentrus rufus*
Spotted Eagle Ray	*Aetobatus narinari*
Spotted Goatfish	*Pseudopeneus maculatus*
Stoplight Parrotfish	*Sparisoma viride*
Striped Parrotfish	*Scarus croicensis*
Threespot Damselfish.	*Pomacentrus planifrons*
Yellowtail Damselfish	*Microspathodon chrysurus*
Yellowtail Snapper	*Ocyurus chrysurus*
Unidentified Green Wrasse	Family: Labridae
Unidentified Bluestripe Parrotfish	Family: Scaridae
Unidentified Green/white Parrotfish	Family: Scaridae

Appendix 2a: Raw Data of Feeding Rates Inside and Outside of Damselfish Territories – Morning (8:30AM – 9:30AM)

	Feeding Rate (bites per 30 seconds)	
Species	Inside*	Outside*
Striped Parrotfish	2, 19, 14, 9, 10, 25, 21, 25, 21, 25, 9 ($n = 11$, $\bar{x} = 14.9 \pm 8.0$)	27, 18, 21, 21, 21, 33 ($n = 6$, $\bar{x} = 23.5 \pm 5.5$)
Doctorfish	0, 0, 0, 1, 0 ($n = 5$, $\bar{x} = 0.2 \pm 0.4$)	0, 7, 0, 5, 20, 3, 10, 17, 19, 14, 0, 2, 0 ($n = 13$, $\bar{x} = 7.5 \pm 7.7$)
Princess Parrotfish	0, 1, 4, 2, 0, 3, 7, 4, 1, 4, 0, 3, 3, 2, 7, 12, 7, 18, 0, 1, 5, 11, 0, 3, 30, 11, 14, 3, 14, 8, 12, 17 ($n = 32$, $\bar{x} = 6.5 \pm 6.8$)	19, 24, 21, 19, 13, 15, 9, 27, 18, 10, 18, 15, 25, 10, 25, 20, 23, 25, 24, 21, 12, 14, 11, 13, 16, 21, 22, 13, 21, 21, 17, 9, 18, 14, 23, 24, 18, 22, 18, 16, 17, 24, 10, 15 ($n = 44$, $\bar{x} = 18.0 \pm 5.0$)

* damselfish territories

APPENDIX 2b: Raw Data of Feeding Rates Inside and Outside of Damselfish Territories - Afternoon (2:30 PM - 3:30 PM)

	FEEDING RATE (BITES PER 30 seconds)	
SPECIES	INSIDE*	OUTSIDE*
DOCTORFISH	0, 17, 6, 15, 6, 25, 23, 4, 0, 0 (n = 10, $\bar{x}$ = 9.6 ± 9.6)	7, 14, 19, 35, 15, 30, 15, 32, 17, 24, 20, 24, 23, 22, 24, 32, 30, 3, 5, 6 (n = 20, $\bar{x}$ = 19.8 ± 9.6)
PRINCESS PARROTFISH	9, 7, 1, 35, 39, 35, 46, 21, 23, 20, 32, 37, 31, 28, 17, 32, 34, 34, 22, (n = 19, $\bar{x}$ = 26.5 ± 11.8)	10, 18, 15, 25, 10, 25, 23, 20, 25, 24, 32, 20, 33, 25, 13, 10, 20, 16, 22, 14, 22, 32, 43, 26, 30, 35, 37, 38, 38, 42, 31, 30, 41, 29, 30, 30, 20, 32, 19, 28 26, 23, 21, 28, 27, 28, 21, 19, 26, 12, 28, 21, 20, 7, 12 (n = 55, $\bar{x}$ = 24.6 ± 8.8)

* damselfish territories