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Comparative Ecology, Morphology, and Population Genetics of Black Triggerfish, *Melichthys niger*

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COMPARATIVE ECOLOGY, MORPHOLOGY, AND POPULATION GENETICS
OF BLACK TRIGGERFISH, MELICHTHYS NIGER

A Thesis
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
of the Requirements for the Degree of
Master of Arts

by
Kathryn Diane Kavanagh
1991

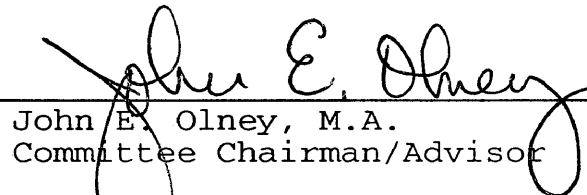
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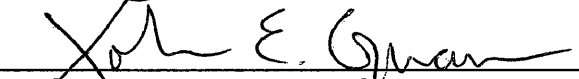


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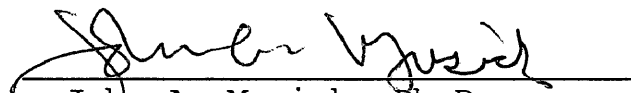
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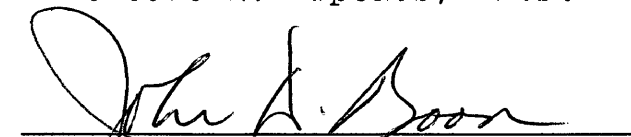
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ABSTRACT

Field measurements of distribution and aggressive behavior were taken from groups of black triggerfish Melichthys niger that exhibited strikingly different densities in two coral reef locations. Triggerfish were found in large swarms of >500 individuals around Johnston Atoll (central Pacific Ocean), while triggerfish around Ambergris Caye, Belize were found in lower abundance and were more dispersed. Intraspecific aggressive behavior was greater in the low-density group, suggesting density-dependent behavior. In the laboratory, analysis of morphology, genetics, diet, condition, and growth factors was performed on specimens collected from Belize, Johnston Atoll, Puerto Rico, Hawaii, and Curacao to look for correlates with the density difference.

Differing population densities and gregarious behavior of widely separated populations of Melichthys niger were apparently not determined by genetic influence. Genetic and morphological results both indicated no within-ocean isolation of populations, but interpretations of between-ocean isolation were contradictory. Morphological analysis indicated similarity in body shape among all groups, but distinct modal differences between Atlantic and Pacific Ocean groups in numbers of pectoral-, anal-, and dorsal-fin rays, with Atlantic specimens tending to have an additional ray. Modes of fin ray counts were consistent between populations within oceans. Vertebral counts were shown to be variable, but they did not show a trend between oceans. Collected specimens from Johnston were generally much smaller than specimens from Belize or the other Caribbean sites. Estimates of growth from annuli deposited on first dorsal spines was estimated to be faster in the Belize group than in the Johnston group, and Belize fish reached a greater maximum size.

Electrophoretic analysis of 36 presumptive gene loci showed no fixed allelic differences between ocean populations, and a very low genetic distance of 0.01 was calculated between ocean groups. While the meristic evidence strongly indicated some evolutionary divergence between ocean groups, the genetic results suggested worldwide gene flow may have occurred relatively recently.

Measurements of diet and condition factors showed variability, but neither was correlated with density of the population. No differences were detectable in the general taxonomic composition and organic content of diets of Johnston and Belize groups, or in condition as measured by relative liver size. However, the high-density Puerto Rico group differed in condition and organic ratio of diet from both low-density Belize and high-density Johnston groups.

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Introduction

A major emphasis of ecological and fisheries research has been to understand the determinants of population size and structure. Variability in abundance and spatial distribution of individuals within populations are the result of a complex series of interactions influenced by the physical environment, the natural history of the species, the genetic makeup of individuals, and community interactions and pressures. Few studies have attempted concurrent examination of a broad range of possible determinants in situations where populations of a species exist at relatively stable but different levels of abundance. This thesis examined aspects of strikingly different population densities of black triggerfish occurring in widely separated locations for correlates with density.

The black triggerfish Melichthys niger Bloch (Balistidae) is a circumtropical coral reef fish found on nearly every tropical reef system in the world (Smith and Heemstra, 1986; Tinker, 1982; Masuda et al, 1984; Randall, 1983), and typically observed as a wary non-schooling fish in groups of 2 to 10 individuals (Aiken, 1975; Walsh, 1984). However, in several locations, M. niger occurs in dense aggregations (Price and John, 1978; Randall et al, 1985;

Lubbock, 1980), and large swarms in these areas dominate the reef community, represent most of the biomass and probably contribute significantly to reef modification (Price and John, 1980). Swarms of M. niger appear to reach their most striking proportions on isolated islands, notably Ascension Island in the Atlantic, where the abundance of black triggerfish have been noted by passing sailors for centuries (Osbeck, 1771; Lubbock, 1980). Similarly, large swarms of black triggerfish have been recorded on Johnston Atoll in the Pacific for at least this century (Randall et al, 1985; Gosline, 1955; Irons et al, 1988). Both islands are extremely isolated and exhibit low ichthyofaunal diversity (Gosline, 1955; Lubbock, 1980; Randall et al, 1985). The difference in population abundance between geographically separated areas is remarkable because of the apparent long-term stability of the high-density populations on the isolated islands, and because of the behavioral difference between individuals occurring in the high- and low-density populations. The natural occurrence of these few isolated high-density populations of black triggerfish presents an unusual opportunity for comparative analysis of the factors which influence population density. A number of parameters may control this situation, ranging from purely genetic factors to the complex elements of community structure.

Although circumtropical distribution is often interpreted as evidence of fairly regular gene flow between

populations, strikingly different behavior (swarming or non-swarming) in geographically isolated populations of M. niger suggests evolutionary divergence in this widespread species. Little information is available on intraspecific variation in balistids, and mechanisms of maintaining gene flow between tropical shorefish populations across oceans are unclear. Furthermore, although most reviews of the genus consider geographically disparate populations of black triggerfish to be conspecific (Berry and Baldwin, 1966; Randall and Klauswitz, 1973), there has been a history of taxonomic confusion within the genus (Randall and Klauswitz, 1973). Thus, the limited information on morphological variation and the total absence of information on genetic variability of black triggerfish does little to resolve the question of whether these geographically isolated populations have diverged evolutionarily.

Natural history observations of black triggerfish have been mainly restricted to observations on settlement, sheltering, and feeding habits, but the result is an overall picture of an omnivorous generalist species with the capacity for long-distance dispersal. From the examination of five specimens ranging from 47-127 mm, Berry and Baldwin (1966) describe a protracted pelagic prejuvenile stage (see Hubbs, 1958:282) for Melichthys niger. Walsh (1984) reported that juvenile recruitment (settlement) of black triggerfish often occurred during new moon periods from

August to October on the Kona coast of Hawaii, and that juveniles were relatively large at settlement (90-140 mm).

Adult black triggerfish appear to be restricted to shore by their requirement for nocturnal shelter. On the Kona coast of Hawaii, black triggerfish ranged widely during the day, sheltered opportunistically when threatened, and returned to the same hole at night to shelter in a loose colony (Walsh, 1984). Inter- and intraspecific agonism increased during the twilight hours as this colony formed, and Walsh (1984) suggested that it was related to social or reproductive functions. Although space is frequently cited as a limiting resource for coral reef fishes (Sale, 1975, 1976, 1977, 1978; Smith and Tyler, 1972, 1973; Johannes, 1978; deBoer, 1978; Fricke, 1980), Walsh determined through experimental manipulation that habitat space was non-limiting in this population of black triggerfish.

Reports on the feeding habits of Melichthys niger indicate general omnivory. Price and John (1978) reported that on Ascension Island "...the fish life is very largely constituted by vast numbers of a single triggerfish, Melichthys niger, the Ascension black-fish," and from a brief gut analysis of the fish, showed "...very clearly that the general diet in the absence of organic refuse in steady supply is highly dependent on algae." However, Aiken (1975) reported a diet consisting mainly of sponges and plankton in black triggerfish from the Caribbean. Randall (1967) found

that 70% of stomach volume in 17 specimens from the Caribbean was algae, either taken as drifting fragments or from the bottom, while the remainder was zooplankton.

Reproductive biology in black triggerfish is not well-known, spawning and nest-building activities are unrecorded, and larvae are undescribed. Wicklund (1969) reported on a possible mating behavior of black triggerfish. Eggs of other genera of balistids are small (0.5-0.6 mm) and demersal, and the larvae are altricial at hatch (Aboussouan and Leis, 1984; Lobel and Johannes, 1980). Thus, we may only infer the reproductive biology and early life history traits of M. niger.

None of the available information on Melichthys niger provides an explanation for the occurrence of these unusual large swarms on the isolated islands. Examining morphological and genetic variability may contribute evidence for evolutionary divergence in the geographically separated populations. By further relating feeding habits, growth rates, inter- and intraspecific agonistic behavior, and potential competitors and predators in the community to the density of the population, an ecological comparison of populations of the species might yield insight into factors that regulate population and community interactions. Thus, the objective of this study was to examine aspects of morphological, genetic, and ecological variability of widely separated populations of Melichthys niger for factors that

could influence the reported difference in abundance and behavior, specifically comparing a high-density population on an isolated island (Johnston Atoll) with a low-density population on a barrier reef (Belize).

Methods

Study sites.-Two primary study sites were used for these comparisons; a high-density site at Johnston Atoll in the central Pacific Ocean, and a low-density site along the northern Belize barrier reef off San Pedro, Ambergris Caye.

Johnston Atoll National Wildlife Refuge is an extremely isolated coral atoll located between the Hawaiian Islands and the Marshall Islands at 16° 45'N, 169° 31'W. The atoll is a broad shallow platform of approximately 50 square miles with a marginal reef emergent only in the northwest (U.S. Dept. of the Interior, 1986). The diversity of fishes on Johnston Atoll (280 total fish species) is less than in Hawaii (680 fish species), and is considered a subset of the Hawaiian fauna (Randall et al, 1985). Seven sampling sites were spread along the marginal reef at depths of 3-10 meters (Fig. 1).

The Belize barrier reef-atoll complex stretches 250 km and is separated from the mainland by a wide (up to 32 km) lagoon. Ambergris Caye (18° 02'N, 87° 34'W) is the most northern of the carbonate islands along the Belize shelf edge. The fish fauna in Belize is more diverse than in the

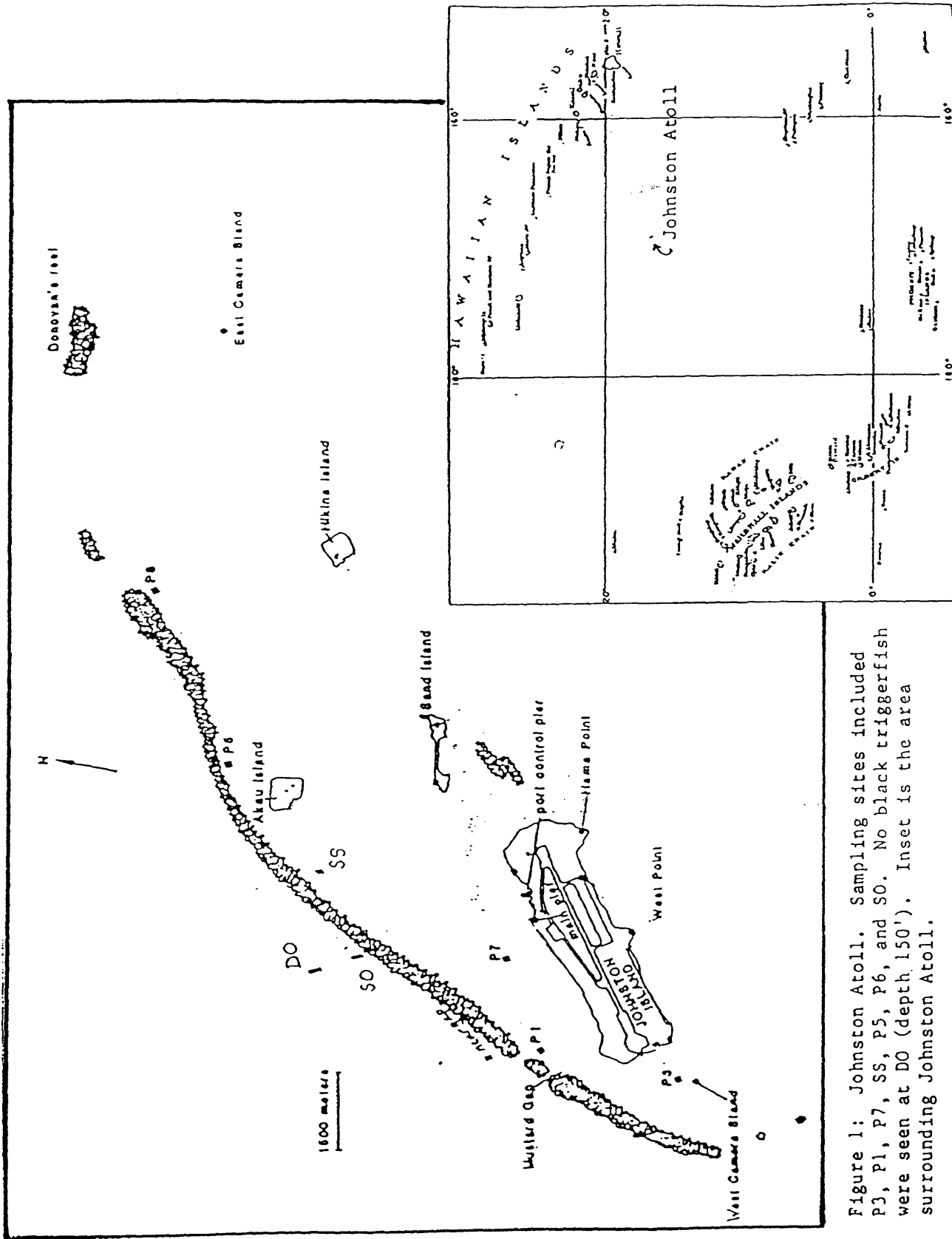


Figure 1: Johnston Atoll. Sampling sites included P3, P1, P7, SS, P5, P6, and SO. No black triggerfish were seen at DO (depth 150'). Inset is the area surrounding Johnston Atoll.

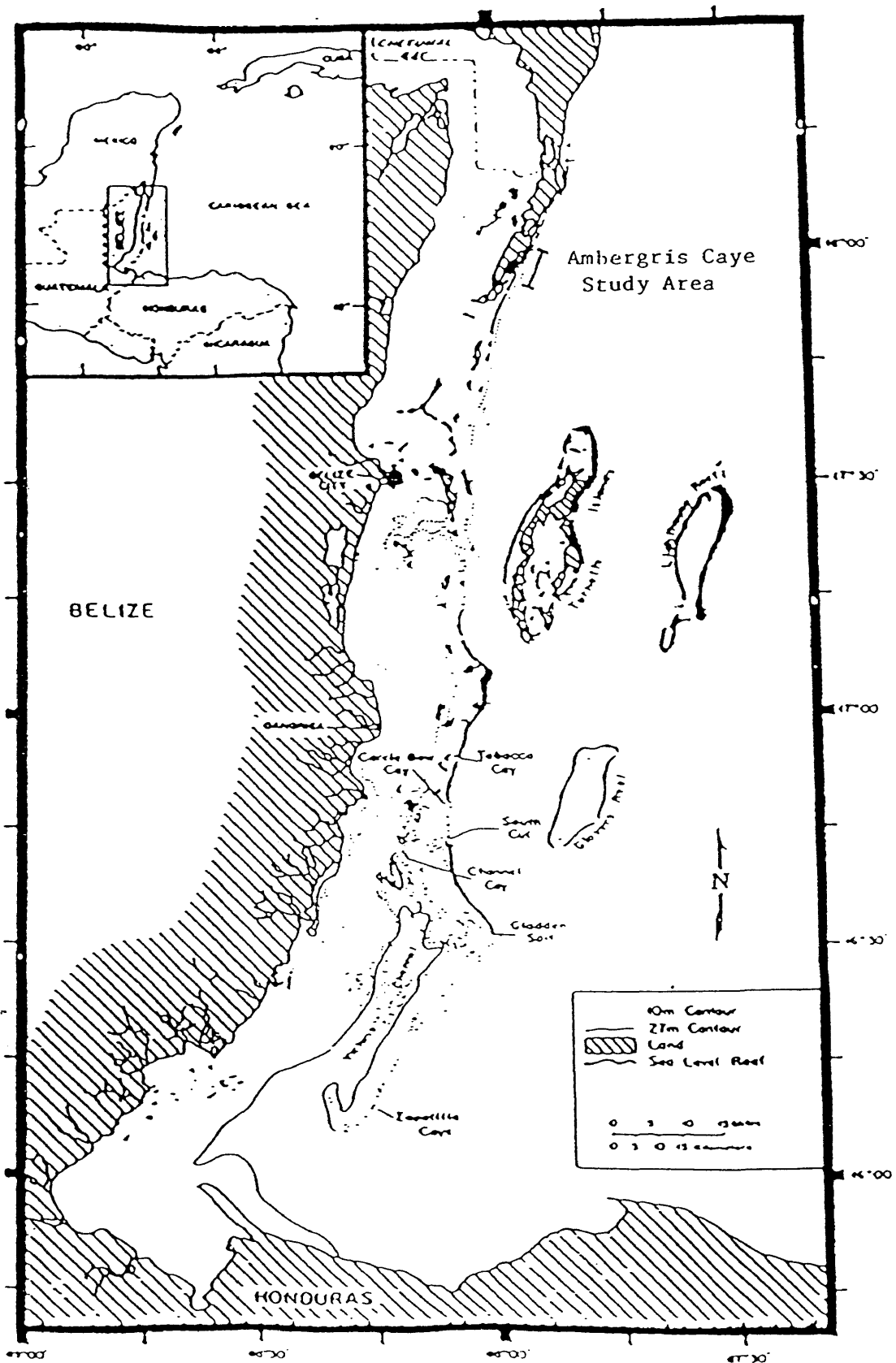
eastern Caribbean, a situation that Greenfield (in Perkins, 1983) attributes to lower disturbance levels. The sampling sites were located along an approximately 10 mile stretch of the barrier reef near San Pedro, Ambergris Caye, and included sites in the Hol Chan Marine Reserve Park (Fig. 2).

Additional localities were visited briefly, mainly for collecting and general observations on between-site variation in behavior and ecology. The other sites included the shelf edge approximately 10 miles off La Parguera, Puerto Rico; on the leeward sides of the islands of Curacao and Bonaire, Netherlands Antilles; and on a few locations on the islands of Hawaii and Maui in the Hawaiian Islands.

Density Estimation, Community Survey, and Behavior

Observation.-A stationary visual census technique developed by Bohnsack and Bannerot (1986) was modified slightly to assess population density of M. niger at several areas within each study site (sites described above). A series of random compass directions and number of swimming kicks from a predetermined anchorage provided the location for each stationary census point. At each location, an imaginary 7.5 m radius cylinder was set up around the diver, and all species seen were recorded for 5 min while the diver slowly rotated. Immediately afterwards all M. niger were counted, and rough abundance of other species present was recorded. This procedure was repeated at each random location within

Figure 2: Belize barrier reef-atoll complex.



the study area for the remainder of the dive (typically 3-5 points). The technique was considered effective for estimating the density of this conspicuous fish because they were not obviously frightened from the diver (as in swimming transects) and were not attracted to the diver (as with species such as yellowtail snapper Ocyurus chrysurus). Each study area was visited for several days throughout the duration of the field effort, and stations were chosen to cover a wide area of reef. Observations were averaged to control for day-to-day temporal bias and to reduce the influence of stochastic interference.

Means and variances of counts of M. niger were calculated using all points, and an F test was used to compare variances between study sites. Observed community species were grouped into taxa, mostly by family.

Using SCUBA for in situ behavioral observation of groups of black triggerfish, aggressive interactions between individuals were quantified by counting number of chases per minute. Rapid and threatening advances of one fish toward another were considered a countable chase. This behavior was quantified only for Johnston Atoll and Belize groups because these were the only sites visited longer than a few days. Groups were chosen subjectively by the diver with the criteria being a defined group which could be seen entirely, such as one milling around the top of a coral head. Number of fish in the observed groups, intraspecific chases, and

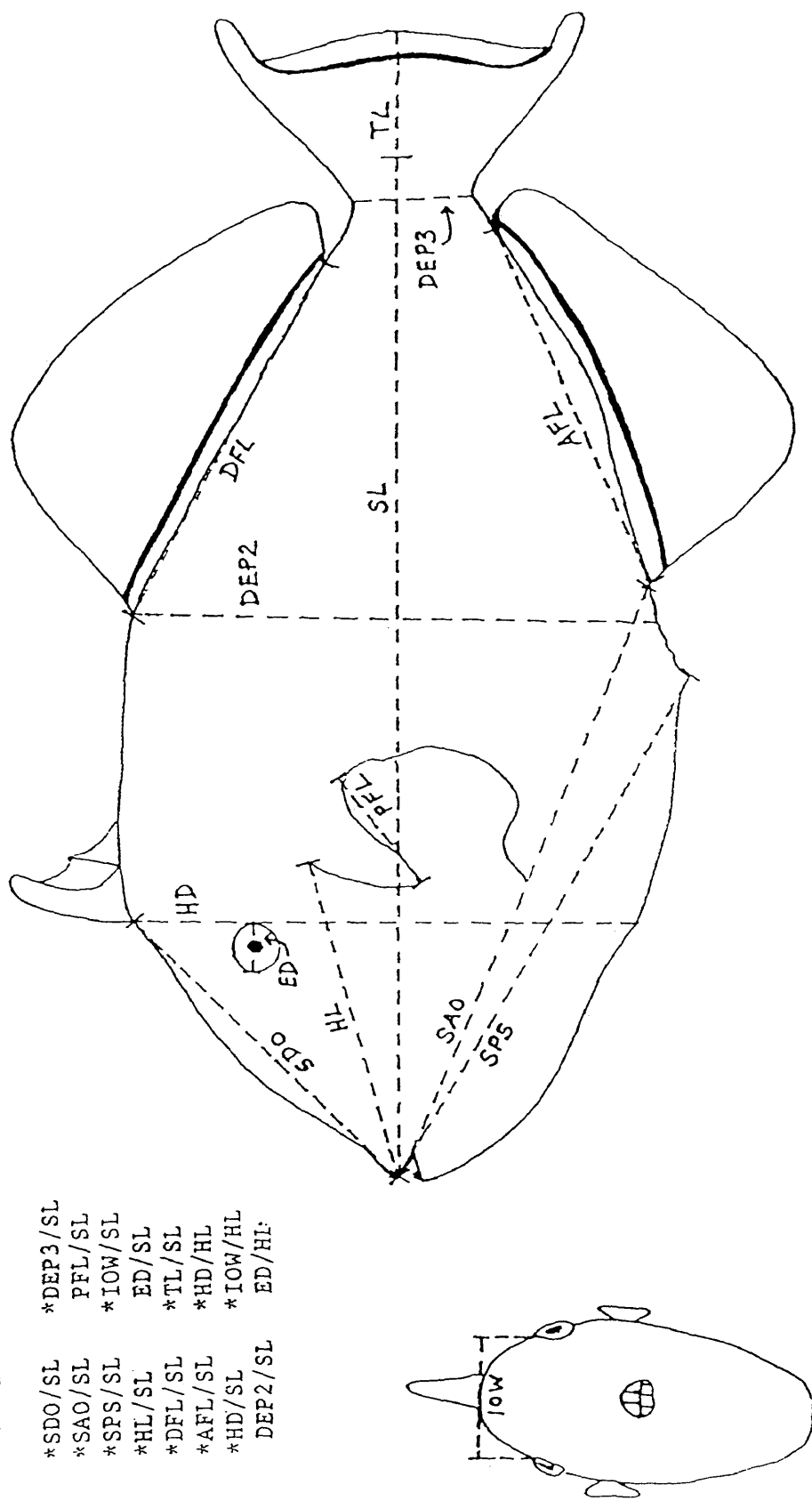
interspecific chases were recorded. Observation periods ranged from a minimum of 10 min to a maximum of 70 min for a single group, and observations were pooled over all times and observation sites along the reef.

Collection and Storage of Specimens.-Black triggerfish were caught by hook-and-line, gill net, or by hand at five sites: Hawaii and Maui (grouped together), Hawaiian Islands; Johnston Atoll; Ambergris Caye, Belize; Curacao, Netherlands Antilles; and La Parguera, Puerto Rico. Whole specimens of Melichthys niger were frozen (approximately -20° C) at the field sites and brought back to the laboratory where they were stored at -70° C (Hawaii and Curacao) or -20° C (all others) for later dissection. Dissected tissues were stored at -70° C.

Morphology.-Meristic counts on black triggerfish specimens included number of pectoral-fin rays (observed in whole specimens) and number of vertebrae, dorsal-fin rays, and anal-fin rays (observed in radiographs). Specimens for morphological analysis not obtained from field sites described above were borrowed from museum collections (Appendix A). Fourteen morphometric variables of identifiable homologous points on 229 black triggerfish were measured (Fig. 3). To assess allometric growth, variables were first plotted against standard length (SL) for visual

Figure 3: Measurements taken from black triggerfish Melichthys niger and ratios used in morphometric analysis. * indicates symmetric growth of that variable for the specimens examined.

- Variable ratios:
- *SDO/SL
 - *SAO/SL
 - *SPS/SL
 - *HL/SL
 - *DFL/SL
 - *AFL/SL
 - *HD/SL
 - DEP2/SL
 - *DEP3/SL
 - PFL/SL
 - *IOW/SL
 - ED/SL
 - *TL/SL
 - *HD/HL
 - *IOW/HL
 - ED/HL



inspection of the scatter. Ratios of variables to SL or head length (HL) were regressed on SL and HL respectively, and the slopes were tested for slope=0. Residuals were visually inspected to look for non-random patterns. Variable ratios that were determined to show allometric growth were not used in further analyses, thus eliminating the need to transform variables.

To determine which variables were the best discriminators between groups, a stepwise discriminant analysis was performed using the SAS procedure PROC STEPDISC (SAS Institute, 1988). This procedure has the potential to increase the power of the following discriminant function tests by eliminating redundancies in variables. The resulting variables from the stepwise discriminant analysis were used in further analyses to quantify the amount of separation of black triggerfish grouped by ocean based on their morphologies. SAS PROC DISCRIM was used to develop a discriminant criterion that classified each observation (morphometric measurement) into one of the two oceanic groups. The analysis also provided output of multivariate statistics for the observations. PROC CANDISC, a dimension-reduction procedure, was used to derive a linear combination of the variables that had the highest possible multiple correlation of the groups, producing a "canonical variable".

Genetics.-Electrophoretic analysis followed the protocols

and recipes described in Murphy et al, 1990. Liver, eye, and white muscle tissues were dissected from 48 triggerfish (22 Pacific and 26 Atlantic) and used immediately for electrophoresis or refrozen at -70° C. Tissues were homogenized in ice-cold Tris-EDTA grinding buffer (Murphy et al, 1990), then centrifuged at 10000xG for 15 minutes at 4° C to separate the cellular debris from water-soluble extracted proteins. The tissue preparations were kept on ice at all times.

Horizontal starch gel electrophoresis was used to separate and identify proteins from tissue homogenates, and gels were histochemically stained for specific enzymes. Table 1 lists the proteins and enzymes surveyed, as well as the tissues and buffers used in the analysis. Interpretations of banding patterns were guided by expectations based on previous allozyme studies on fishes (Waples, 1986)

Allele frequencies, heterozygosity, and Nei's genetic distance (D) (Nei, 1972) were calculated using the software program BIOSYS-1 (Swofford and Selander, 1989). Comparisons were made among populations (Hawaii, Johnston Atoll, Curacao, Belize, and Puerto Rico) and between oceans (Atlantic and Pacific).

Diet and Condition.-Guts from esophagus to anus were dissected from specimens and preserved either directly in

Table 1: Enzymes, loci, tissues, and buffers surveyed in the electrophoretic analysis of 3 populations of Melichthys niger.

Protein	Locus	Tissue	Buffer
Aspartate aminotransferase	AAT-A	M	TCIII
	AAT-B	L	TCIII
Aconitate hydratase	ACOH	L	TCIII
Adenosine deaminase	ADA	M	TCIII
Adenylate kinase	AK-cath	L	TCII
	AK-anod	M	TCII
Alcohol dehydrogenase	ADH-1	L	TCII
	ADH-2	L	TCII
Creatine kinase	CK-A	M	TCIII, II
Esterase	EST	E, L	LiOH
General Proteins	GP	M	LiOH
Glucosephosphate isomerase	GPI-A	M	LiOH, TCII
	GPI-B	L	LiOH, TCII
	GPI-"C"	E	LiOH, TCII
Glucose dehydrogenase	GCDH	L	TCII, III
Glycerol-3-phosphate dehydrogenase	G3PDH-A	M	TCII, III
	G3PDH-B	L	TCII, III
Hexokinase	HK	L	TCII
Iditol dehydrogenase	IDDH	L	TCII, III
Isocitrate dehydrogenase	IDH-m	M	TCII, III
	IDH-s	L	TCII, III
Lactate dehydrogenase	LDH-A	M	TCII, III
	LDH-C	L	TCII, III
	LDH-C4	E	TCII, III
Malate dehydrogenase	MDH-A	L	TCII, III
	MDH-B	M	TCII, III
	MDH-m	M	TCII, III
Phosphoglucomutase	PGM-A	L, M	TCII
	PGM-B	L	TCII
Phosphogluconate dehydrogenase	PGDH	L, E	TCIII
Peptidase (DL-Ala-DL-Met)	PEP-1	E	LiOH
Peptidase (Gly-Leu)	PEP-2	L	LiOH
Superoxide dismutase	SOD-1	L	TCII, III
	SOD-2	E, L, M	TCIII
Xanthine dehydrogenase	XDH	M	TCII, III

Buffers: TCII = Tris-citric acid, pH 8; TCIII = Tris-citric acid, pH 6.9; LiOH = Lithium hydroxide (recipes from Hillis and Moritz, 1990).

Tissues: E = eye; L = liver; M = muscle.

70% ethanol, or first in 5% formalin then transferred after approximately 48 hours to 70% ethanol. Organic and inorganic intake was determined from the contents of ten randomly selected guts from Johnston Atoll, Belize, and Puerto Rico specimens. Contents were carefully removed from the gut wall, weighed, then dried at 60°C for 24 hours and weighed again. To remove organic material, gut contents were ashed in a muffle furnace for 4 hours at 505-550°C, cooled to room temperature, and weighed again. Using the relationship, $\text{dry weight} - \text{ash weight} = \text{ash-free dry weight (afdwt)}$, organic fractions of stomach contents were calculated by $\text{afdwt} / \text{dry weight}$, and two-sample t-tests were used to test population pairs (Johnston and Puerto Rico, Johnston and Belize, and Puerto Rico and Belize) for significance.

Three guts from each study site (Johnston, Belize, and Puerto Rico) were randomly selected for taxonomic analysis. Gut contents were carefully removed and weighed. Contents were examined with a stereo microscope and each type of food item was identified to a general taxonomic group. Accurate quantification of food items was extremely difficult because nearly all of the contents were in a congealed lump of finely macerated bits. Thus, relative importance of an individual food item was assessed only roughly by the number of guts in which it appeared and whether it contributed significantly to the mass. To describe relative importance,

the following categories were used: primary = found in all three guts and constituting a major fraction of the gut contents; common = found in at least two guts but constituting only a small fraction of the gut contents; rare = found only in one gut and constituting a small fraction of the gut contents.

Livers were dissected and weighed from a total of 106 fish from Belize, Johnston Atoll, and Puerto Rico. As a measure of condition of the fish, a liver-somatic index (LSI) (Busacker et al., 1990) was calculated by (liver weight/somatic weight) x 100. A two-sample t-test comparing LSI of population pairs was used to test for significance between the groups.

Age and Growth.-Annual deposition of annuli on first dorsal spines in M. niger was not validated in this study, but was assumed based on the similarity of the annulus formation in confamilial studies (Balistes capriscus, Johnson and Saloman, 1984; Balistes vetula, Manooch and Drennon, 1987) that have validated annuli as annual by marginal increment analysis.

A small subsample of randomly selected fish representative of the range of size of collected fish from Belize (9 fish) and Johnston Atoll (15 fish) were used in the growth analysis for comparison of low- and high-density groups. In Belize, small fish were seen but none were

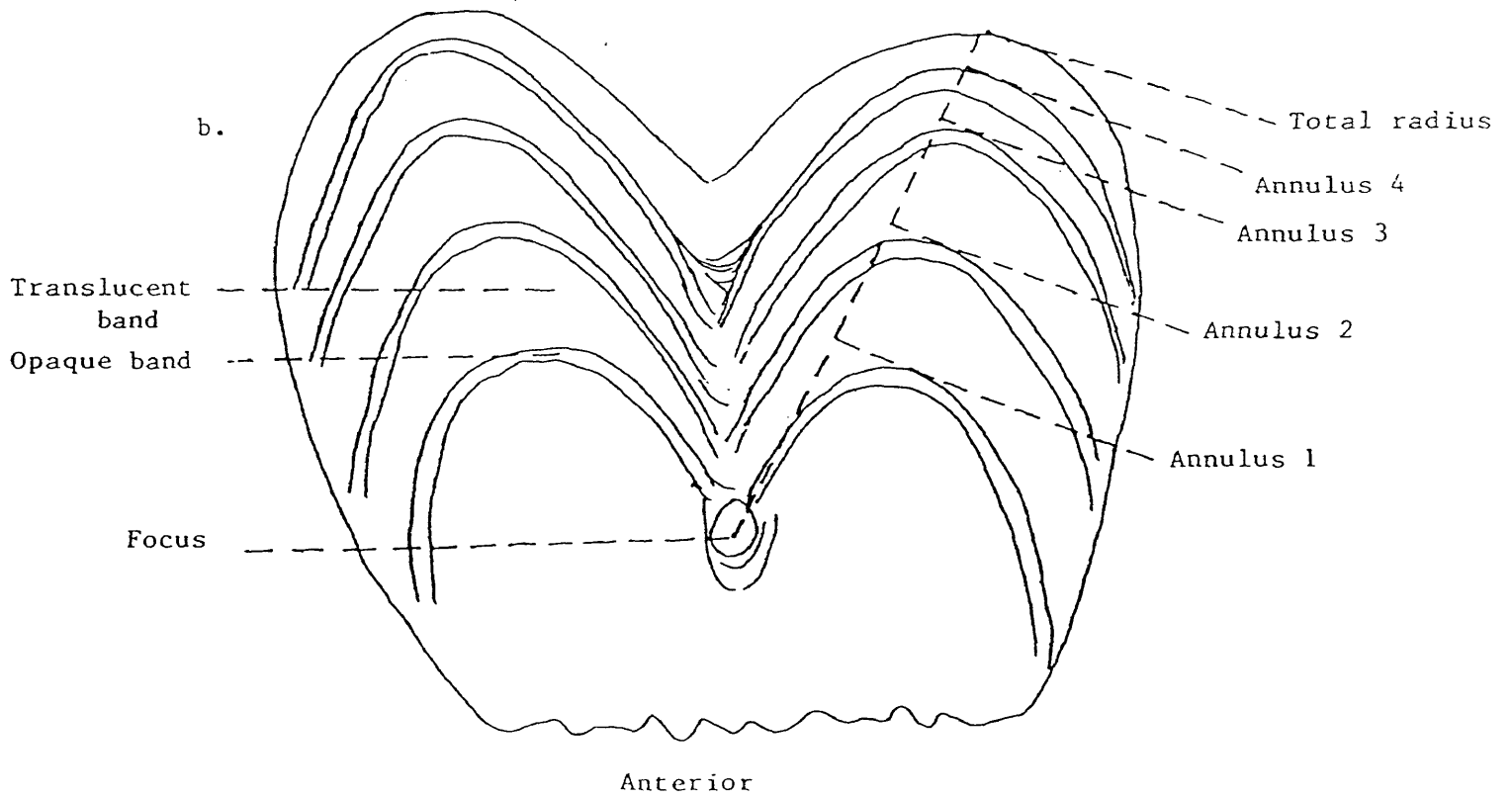
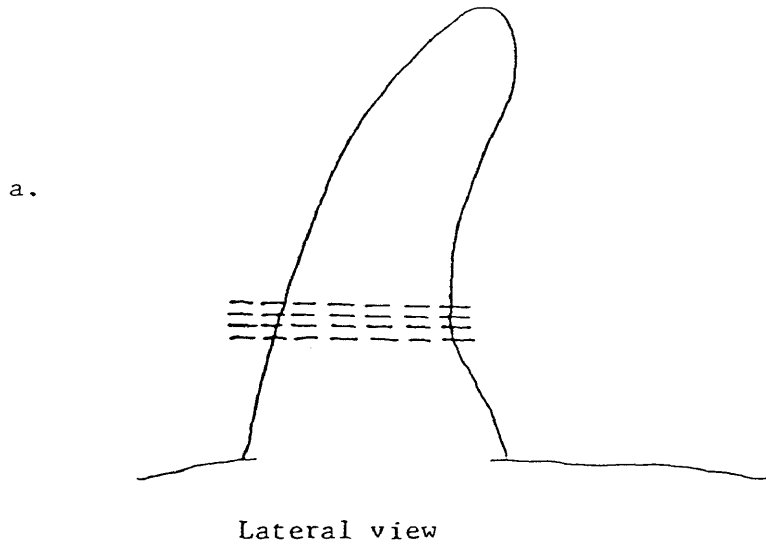
collected. As a result, one juvenile from Curacao was included in the Belize sample to reduce bias that might be caused by lacking data from the early part of the curve where fast growth occurs.

Erect first dorsal-fin spines were removed at the level of the dorsal margin with a coping saw. Each spine was mounted in melted crystalline resin on a cardboard tab. The tab was secured on a platform and lowered onto an 11-1180 Low Speed Isomet Saw with a diamond-edged blade. Three successive 1-mm slices were obtained, the first cut made just above the condyle (the enlarged base of the spine) (Fig. 4a). This position was considered an homologous point on the spines so that measurements of ring widths could be compared among individuals.

The cut sections were removed from the cardboard tab by remelting the resin on a hot plate, and mounted on clear, bubble-free resin on a glass slide. The sections could then be read directly on a dissecting scope with transmitted light. Polishing the surfaces with diamond dust did not improve readability, but occasionally obscured the surface.

Each spine section was read at least four times for total number of annuli, and measurements were taken from the focus to the posterior edge of each translucent ring, as well as a total length for the cross-section (Fig. 4b). Back-calculated lengths-at-age and average annual increments were calculated using the Fraser-Lee equation (Lee, 1920)

Figure 4: First dorsal spine sections from black triggerfish.
a. Placement of cuts in area just above the condyle.
b. Example of measurements from an age 4+ fish.



with the software program DISBCAL (DISBCAL, 1987). To describe theoretical growth, a Von Bertalanffy growth function was applied to these data using the software program FISHPARM (Prager, 1987). The procedure employs the least squares method to fit data. The growth equation (von Bertalanffy 1938, 1957) used was

$$L_t = L_\infty \{1 - \exp^{-K(t-t_0)}\}$$

where L_t is length at age t , L_∞ is asymptotic length, K is the growth coefficient, and t_0 is the time when length would theoretically be zero.

Results

Abundance and Behavior.-Observations of black triggerfish populations on Johnston Atoll and Belize in this study substantiated previous reports of differing population densities and behaviors. Observations were made on Johnston Atoll from July 28 to August 9, 1989. On Johnston Atoll, the black triggerfish were found mainly in the lagoon and outside the reef crest in shallow water (1-5 m) in large, loose groups, the largest consisting of greater than 500 individuals. One fish was observed at 50 m possibly exhibiting a nest-defensive behavior, although no nest was found. Black triggerfish were found at all dive sites except one (Site SS), but large swarms were reported and photographed from Site SS on a previous survey conducted six

months earlier (Kosaki, Univ. of Hawaii, pers. comm.).

Thus, the swarms are apparently ubiquitous in the lagoon and in shallow water just outside the reef crest, seem to range over large areas, but are rarely seen in deeper water. On Johnston Atoll, 30% of groups observed consisted of >100 individuals with a maximum group size of >500 individuals.

Observations from Belize reefs were made from October 26 to November 4, 1989. In Belize, there were rarely more than 10 fish in a group, and the maximum observed was 13 individuals. No black triggerfish were seen below 25 m, which was approximately the depth of the steep drop-off of the outer reef slope. The individuals rarely wandered far off the bottom, but small groups were seen feeding on the surface on sargassum patches.

Results of observations at 80 stationary point samples taken for density estimation are summarized in Table 2. Only six point samples were made in Puerto Rico, while Johnston and Belize had nearly equal sample sizes (36 and 38 respectively). The mean numbers of fish per point sample was highest in Puerto Rico (59), and was similar for Johnston (50). Belize had a much lower average of ~4 fish per sample. Ranges of density in the 7.5 m radius sampling area were 0-310 individuals for Johnston Atoll, 0-13 individuals for Belize, and 3-130 individuals for Puerto Rico observations. Variation in density was high at all sites, with the highest coefficient of variation found in

Table 2: Density estimates of black triggerfish at sampling locations. N=number of point samples, CV= coefficient of variation, Mean and variance numbers in fish/7.5 m radius cylinder.

Site	N	Mean	Variance	CV	Range
Johnston	36	50.22	71.86	143%	0-310
Belize	38	3.98	3.55	89	0-13
Puerto Rico	6	59.00	43.49	74	3-130

data from Johnston Atoll triggerfish (143%), supporting the observation of their contagious spatial distribution.

Observations from the Puerto Rico group were also highly variable, and no significant differences were observed in mean density between Johnston Atoll and Puerto Rico. The variance at Belize was significantly lower than at either Johnston or Puerto Rico, indicating that the fish in Belize were more dispersed and in lower abundance.

The other three sites visited briefly gave evidence of between-site variability in abundance and group size that was not correlated with geographic separation. In Puerto Rico, a localized high-density group that appeared to concentrate only on the top of the steep shelf break at 30 m depth was observed for two days (October 24-25, 1989). The triggerfish remained mostly near the bottom, but local divers said that the groups were often seen swarming high in the water column at midday. The area was also subject to heavy fishing pressure (D. Hensley, Univ. of Puerto Rico, pers. comm.), and the visibility was relatively poor (10 m).

Twelve dives were made on Curacao and three on Bonaire, both leeward islands in the Netherlands Antilles, during the period of 7-16 April 1991. Black triggerfish were rarely seen on dives in the central part of the lee of the island of Curacao, and only in groups of 1 to 3. Near the east point (Awa Blancu), the triggerfish were found consistently in greater abundance in a loose aggregation of ~20 fish. No

black triggerfish were observed below 25 m. At the sites of Karpata and Flamingo Bay on the reefs of Bonaire, black triggerfish were common and seen consistently on all dives in groups of 1-3, and from depths of 3-25 m. No dives were made on the rough windward sides of either Curacao or Bonaire. Two individuals were observed sheltering for the night on Bonaire within minutes of sunset.

Three dives were made off the island of Maui, and two off the island of Hawaii in the Hawaiian Islands. Black triggerfish were common on all dives where there was shelter on Maui and Hawaii, except at Puako, Hawaii, and reached moderate abundance in nearshore areas off Maui, where they were seen in very shallow (1 m) water.

In addition to the difference in grouping behavior, black triggerfish in Johnston Atoll and Belize exhibited differences in intraspecific aggressive interactions (Table 3). A total of 7.6 hrs of observations on intraspecific and interspecific aggressive encounters were made over 12 days during the sampling periods. Interspecific chases were rare, and the calculated interspecific chases/min/fish were similar for Belize and Johnston Atoll (2.8×10^{-5} and 3.0×10^{-5} , respectively). The few observed interspecific encounters were between black triggerfish and Naso lituratus (Acanthuridae) and Sufflamen bursa (Balistidae) on Johnston and with Ocyurus chrysurus (Lutjanidae) on Belize. Intraspecific chases were observed more frequently (n=48),

Table 3: Intraspecific and interspecific aggressive encounters of black triggerfish from Johnston Atoll and Belize.

	Johnston Atoll	Belize
Total observation time (min)	111.0	347.5
Total no. of fish observed	601	82
Intraspecific chases/min	0.09	0.11
Interspecific chases/min	0.018	0.002
Intraspecific chases/min/fish	1.50×10^{-4}	13.41×10^{-4}
Interspecific chases/min/fish	3.00×10^{-5}	2.80×10^{-5}

and calculated chases/min/fish were an order of magnitude larger in the low-density Belize population than in the Johnston Atoll population (13.41×10^{-4} and 1.50×10^{-4} , respectively).

Morphology.-Frequency distributions of paired and median fin-ray counts revealed distinct modal differences in numbers of pectoral-, dorsal-, and anal-fin rays. Pectoral-fin rays ranged from 11-16 in specimens from Pacific localities and from 13-17 in Atlantic specimens. Most (79.1%) of pectoral-fin ray counts from Atlantic specimens were 16, while most (69.4%) of Pacific fishes had 15 pectoral rays. Counts were most variable in the large sample (n=120) from Johnston Atoll. (Table 4)

Modes of second dorsal- and anal-fin ray counts overlapped, but again Atlantic specimens tended to have one more ray than Pacific specimens (Table 5). Most of Atlantic fish had 33 or 34 second dorsal-fin rays (74.5%), while most (76.2%) Pacific fish had 32 or 33 rays. There was similar overlap in anal-fin ray counts; Atlantic and Pacific specimens exhibited modal counts of 30 (49.0%) and 29 (56.5%), respectively. However, many Atlantic fish had 29 and many Pacific specimens had 30.

Vertebral counts were nearly consistently $7+11=18$, as has been previously reported for all balistids (Moore, 1967; Berry and Baldwin, 1966; Randall and Klauswitz, 1973; Leis,

Table 4: Numbers of pectoral-fin rays of black triggerfish collected from study sites or borrowed from museums. Counts of fish from Atlantic and Pacific Oceans are listed by locality below the total from the oceans.

No. of rays	Left Pectoral Rays							Right Pectoral Rays						
	11	12	13	14	15	16	17	12	13	14	15	16	17	
Atlantic			1	1	5	61	4			3	6	45	8	
Pacific	1	1	2	6	68	16		1		5	23	8		
Atlantic (in detail):														
Belize			1		1	27	1				1	16	3	
Puerto Rico				1	3	15				2	3	14		
Ascension					1	12	3			1	2	8	5	
St. Helena						1						1		
Trinidad						6						6		
Pacific (in detail):														
Johnston Atoll	1	1	2	6	64	14		1		5	19	7		
Hawaii					3						2			
Line Islands						2					1	1		
Moluccas Is.					1						1			

Table 5: Numbers of median-fin rays of black triggerfish collected from study sites or borrowed from museums. Counts of fish from Atlantic and Pacific Oceans are listed by locality below the total from the oceans.

No. of rays	Second Dorsal Rays										Anal Rays				
	30	31	32	33	34	35		27	28	29	30	31	32		
Atlantic			5	17	18	7		1	2	13	24	9			
Pacific	2	7	22	26	6			2	10	35	15				
Atlantic (in detail):															
Belize			3	8	8	5		1	1	6	11	6			
Puerto Rico			1	6	3	1			1	3	8		1		
Ascension			1		5					2	1	3			
St. Helena				3						2	1				
Trinidad					2	1					3				
Pacific (in detail):															
Johnston	1	7	20	20	6			1	10	30	13				
Hawaii	1		2	5				1		4	2				
Moluccas Is.				1						1					

1983), but an unusually high occurrence (5%) of anomalous counts, including $7+10=17$, $7+12=19$, and $6+12=18$ (one of each from Johnston Atoll) and $8+11=19$ (one from Belize) was found in this sample of black triggerfish.

Twelve morphometric variable ratios demonstrated symmetric growth and were used in further analysis (Fig. 3, variables used in the analysis are marked with an asterisk). Stepwise discriminant analysis determined that four of the twelve variables [snout-to-pelvic-spine/standard length, snout-to-anal-origin/standard length, interorbital width/head length, and anal-fin length/standard length] were the best discriminators at the significance level of 0.15. However, even these variables were not good discriminators of the oceanic groups, as indicated by the very low values of the individual average squared canonical correlation (0.12-0.22), and the high individual Wilks' Lambda (0.78-0.87) (Klecka, 1980).

Based on a quadratic discriminant function developed from the observations, 86% of the Pacific fish and 61% of the Atlantic fish were correctly classified, yielding an average error of about 23%.

Genetics.-Forty-one presumptive gene loci were surveyed, of which 36 were sufficiently well resolved to score and interpret for comparisons between oceans (Atlantic and Pacific) (Table 1). Eighteen loci were used for comparisons

between all five populations (Johnston Atoll, Hawaii, Belize, Curacao, and Puerto Rico). Sample sizes from populations for each locus are summarized in Table 6.

Mean heterozygosities per locus for triggerfish grouped by ocean were 0.132 (S.E. 0.032) for Atlantic, and 0.141 (S.E. 0.036) for Pacific. These values fall within the range reported for other vertebrates (Avice and Aquadro, 1982). The mean heterozygosities per locus when grouped by population were also within reported values and ranged from 0.097 (S.E. 0.053) to 0.127 (S.E. 0.049). The percentage of polymorphic loci for each group ranged from 16.67 (Belize and Puerto Rico) to 36.11 (Atlantic). Nei's (1978) unbiased genetic distance (D) for fish between oceans was very low, 0.010, and the genetic distances between populations ranged from 0.000 between Johnston and Belize to 0.128 between Puerto Rico and Hawaii (Table 7). Standard error for D can be calculated (Nei and Roychoudhury, 1974) but Swofford (pers. comm.) does not place much confidence in the statistic.

Diet and Condition.-Food items found in the guts of the fish examined are listed in Table 8. The consistent occurrence of a wide range of taxonomic groups in the fish stomachs, including benthic algae, numerous invertebrates, and such diverse planktonic organisms as sargassum, siphonophores and fish eggs supports previous studies illustrating the black

Table 6: Genotypes of individuals for loci surveyed by population, determined from scorable results of allozyme electrophoresis. CU=Curacao; BE=Belize; PR=Puerto Rico; JA=Johnston Atoll; HI=Hawaii; CU, BE, PR grouped as Atlantic; JA, HI grouped as Pacific.

ACOH	ADA-A	AK-1	AK-2	ADH-1	ADH-2
AA	AA	AA AB BB	AA AB BB	AA	AA
CU	6	1 2 2	3 2 -	-	6
BE	-	2 - -	- 3 3	2	2
PR	3	- - -	- - 4	2	2
JA	3	3 - -	1 3 1	3	-
HI	7	- - 5	3 3 -	-	7
AAT-A	AAT-B	CK-A	CK-C	EST-Y	FUM
AA	AA AB BB	AA	AA AB BB	AA	AA
CU	5 0 1	- 2 2	1 - 3	5	6
BE	2 - -	5	- 1 -	2	-
PR	2 - -	3	- 2 -	2	-
JA	1 - -	-	- 2 -	3	-
HI	7 - -	-	- 2 4	6	7
GPI-A	GPI-B	GCDH	G3PDH-A	G3PDH-B	HK-1
AA AB BB	AA AB BB	AA AB BB	AA	AA AB BB	AA
CU	6 - -	- 2 4	6	4 - -	6
BE	- - -	2 1 1	2	2 - -	-
PR	1 1 -	2 - 1	4	3 - 2	-
JA	1 2 -	2 1 -	6	3 3 -	-
HI	7 - 1	2 - 2	7	4 - -	7

Table 6, continued: Genotypes of individuals for loci surveyed by population, determined from scorable results of allozyme electrophoresis. CU=Curacao; BE=Belize; PR=Puerto Rico; JA=Johnston Atoll; HI=Hawaii; CU, BE, PR grouped as Atlantic; JA, HI grouped as Pacific.

HK-2 AA AB BB CU 5 - - BE - - - PR - - 1 JA 1 - 1 HI 2 - 3	IDDH AA 3 4 - 6 4	IDH-M AA 6 4 9 9 6	IDH-S AA 6 4 7 2 7	LDH-A AA 6 6 14 15 7	LDH-C AA 4 2 10 11 6
LDH-C4 AA AB BB CU 1 4 - BE 1 - - PR - - - JA 2 - - HI 1 5 -	MDH-A AA 6 2 10 11 7	MDH-B AA 6 2 10 11 7	MDH-M AA 6 2 10 11 7	PGM-A AA AB BB 5 1 - 2 - - 4 - - 6 1 1 6 1 -	PGDH AA AB BB CC 1 - 1 - 2 - - - 2 - - - 3 - - - - - 1 4
PEP-1 AA CU - BE 3 PR 4 JA 4 HI 4	PEP-2 AA - 2 3 3 -	SOD-1 AA 6 6 5 7 7	SOD-2 AA - 2 2 3 -	GP AA - 2 2 3 -	B-GAL AA AB BB BC 1 - 2 1 - - 4 - - - 4 - - - 4 - - - 6 -

Table 7: Genetic distance coefficients for five populations of black triggerfish.
 Below diagonal: Nei (1978) unbiased genetic distance.
 Above diagonal: Nei (1972) genetic distance.

Population	1	2	3	4	5
1 Curacao	*	.083	.122	.097	.066
2 Belize	.071	*	.014	.013	.094
3 Puerto Rico	.104	.002	*	.021	.128
4 Johnston Atoll	.078	.000	.001	*	.095
5 Hawaii	.049	.084	.111	.077	*

Table 8: Taxonomic composition of stomach contents of black triggerfish from Johnston Atoll, Belize, and Puerto Rico. (x=algae present in stomach contents; p=primary, found in all three guts and constituting a major fraction by volume of the gut contents; c=common, found in at least two guts but constituting only a small fraction of the gut contents; r=rare, found in only one gut and constituting a small fraction of the gut contents).

Item	JA	BE	PR
Algae:	p	p	p
<u>Caulerpa</u> sp.	x	x	x
<u>Padina</u> sp.	x		x
<u>Jania</u> sp.	x	x	x
<u>Sargassum</u> sp.	x	x	x
<u>Dictyota</u> sp.		x	
<u>Corallina</u> sp.		x	x
<u>Ulva</u> sp.		x	
<u>Anadyomene stellata</u>		x	
<u>Styopodium zonale</u>		x	
unidentified	x	x	x
Siphonophores	c	c	c
Sponges	c	p	c
Holothurian spicules	r	r	
Echinoderm spines			r
Coral fragments	c	c	c
Nemotodes	c	c	c
Oligochaetes		r	
Polychaetes		c	
Molluscs		r	
Gastropods	c		c
Decapods	c		c
Pteropods	c	c	p
Isopods		r	
Amphipods		r	
Bryozoans		r	r
Invertebrate egg mass		r	
Fish	r		
Fish eggs	r	r	

triggerfish's omnivory. No striking differences in the taxonomic composition of diet between groups were observed; benthic algae and sponges consistently represented the largest percentage of the gut contents. Siphonophores, pteropods, and nematodes were found in all guts in moderate amounts. One fish had eaten a fairly large crab which constituted a large percent by volume in that individual's stomach.

Percent organic composition of stomach contents, expressed in ash-free-dry-weight/dry weight, ranged from 21 to 32% for Belize, 17 to 38% for Johnston Atoll, and 24 to 43% for Puerto Rico fish (Fig. 5). Means were similar for Belize (0.26, S.D.=0.04) and Johnston Atoll (0.27, S.D.=0.07). Puerto Rico had the highest percent organic composition (0.35, S.D.=0.05). Pooled two-sample t-tests comparing the percent organic compositions could not detect differences between Belize and Johnston Atoll. Differences were detectable between Puerto Rico and Johnston ($P < 0.026$), and Puerto Rico and Belize ($P < 0.001$).

Liver size ranged from less than 1% of body weight to about 8%. Examples of somatic weights, liver weights, and liver-somatic indices (LSI) for some triggerfish of varying sizes are given in Table 9. LSI values for Puerto Rico fish (n=27) were the highest and had the highest range (1.57 to 8.03, \bar{x} =3.88). Belize fish (n=6) had the lowest range (1.17 to 2.19) and relatively low values (\bar{x} =1.75), and Johnston

Figure 5: Food quality and condition measures for black triggerfish *Melichthys niger* from Belize (BE), Johnston Atoll (JA), and Puerto Rico (PR) sites. Bars indicate one standard deviation from the mean. No differences were detectable between BE and JA, but differences were detected between PR and BE, and between PR and JA.

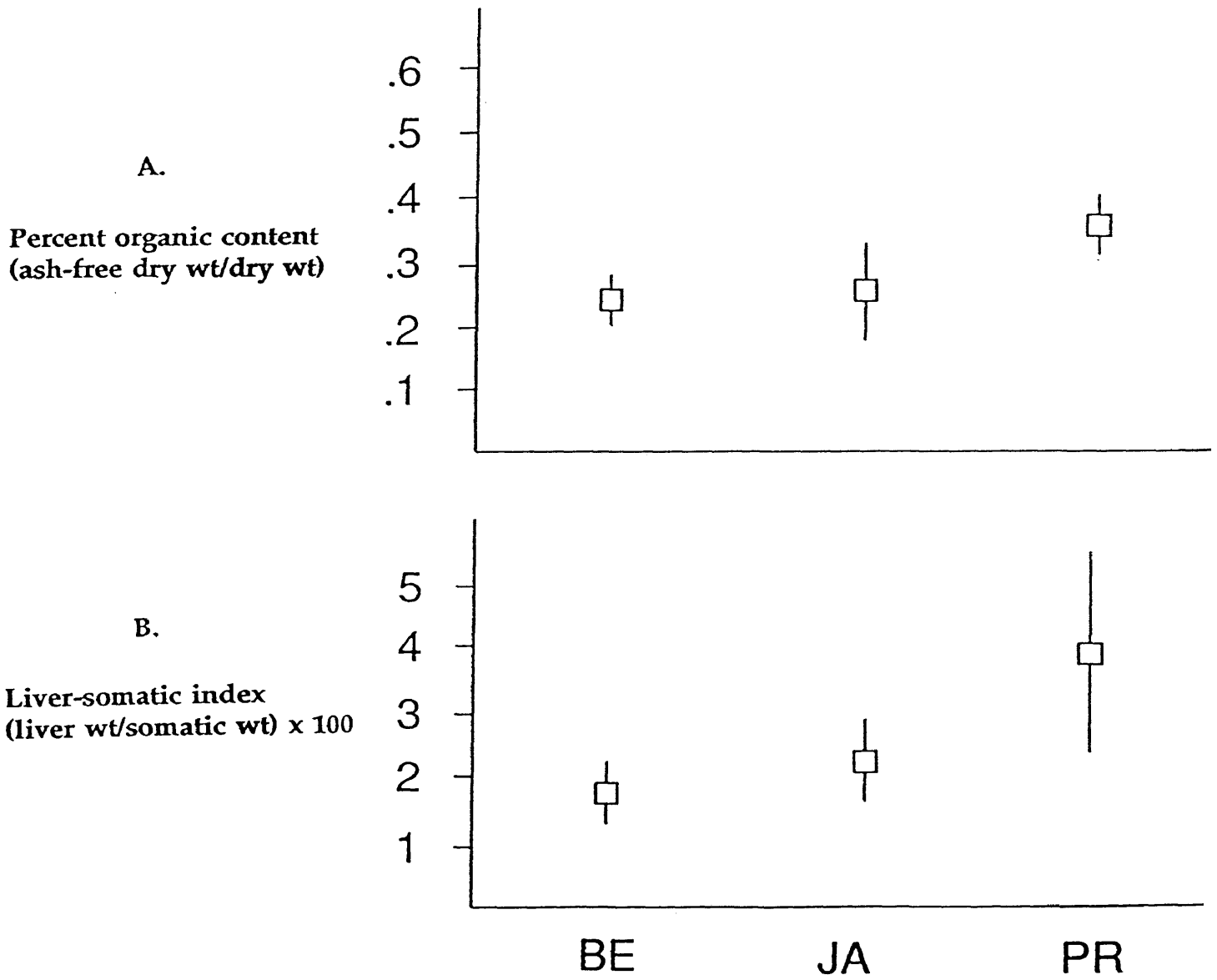


Table 9: Liver weights, somatic weights, and histosomatic indices for selected black triggerfish from Johnston Atoll, Belize, and Puerto Rico.

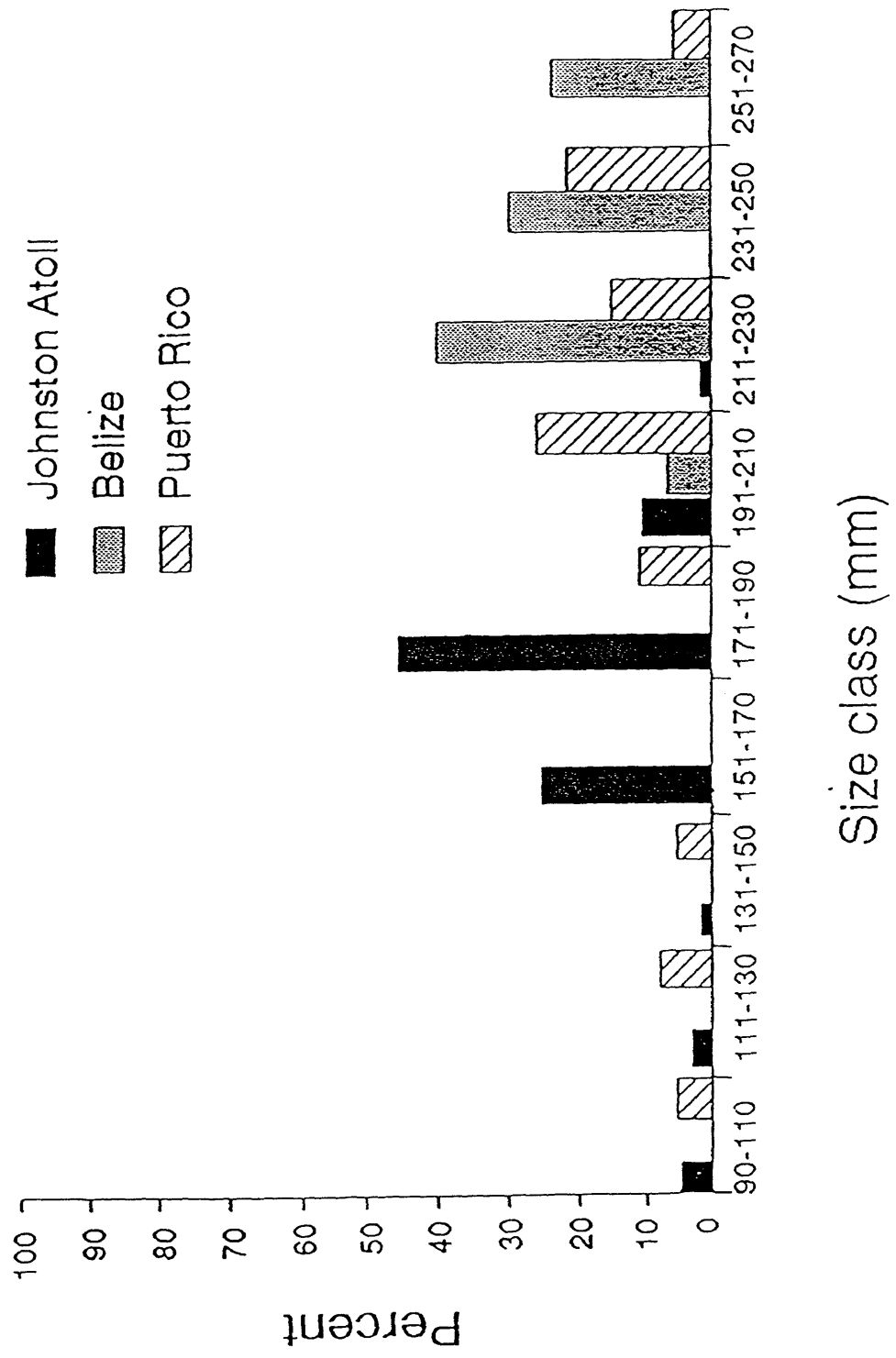
	sl	somatic wt.	liver wt.	HSI
Johnston Atoll	112 mm	57.9 g	1.1 g	1.90
	153	126.2	1.2	0.94
	159	145.5	4.0	2.74
	178	226.6	5.6	2.46
	195	313.0	8.8	2.77
	215	414.1	7.8	1.86
Belize	215	423.7	11.9	2.70
	240	597.8	7.0	1.17
	259	655.9	10.3	1.56
Puerto Rico	104	50.9	0.8	1.57
	123	65.0	2.6	4.00
	180	238.6	6.8	2.83
	214	354.1	14.8	4.11
	240	546.8	44.9	8.03

fish (n=72) had the lowest value and a broad range (0.81 to 5.92, \bar{x} =2.21). Two-sample t-tests comparing the LSI values could not detect differences between Belize and Johnston Atoll, but differences were detected ($p=0.05$) between both Johnston Atoll and Puerto Rico, and Belize and Puerto Rico. Figure 5 illustrates the relative liver-somatic indices for the three populations.

Size, Age Composition, and Growth.-In Belize and Puerto Rico, large fish (>210 mm) were prevalent in the sample, while in Johnston Atoll, fish rarely exceeded 190 mm in length (Fig. 6). The largest fish from Johnston Atoll was 215 mm; the largest from Belize was 263 mm, and the largest from Puerto Rico was 253 mm. Triggerfish under 150 mm were poorly represented in all samples and absent in the Belize sample. The sample from Puerto Rico had no fish between 150 and 170 mm, but included several smaller juveniles.

Dorsal-spine sections were analyzed for Johnston Atoll and Belize triggerfish only. The regression equations $y = 0.038x + 0.662$ (for Johnston Atoll) and $y = 0.031x + 2.037$ (for Belize) describe the positive relationship between the lengths of the first dorsal-spine sections and the standard lengths of the fish. There was generally a positive increase in standard length with number of annuli in all populations. The oldest fish in both groups was estimated to be 11 years. Observed and back-calculated lengths-at-age

Figure 6: Size frequency histogram for collected specimens of black triggerfish *Melichthys niger* from Johnston Atoll, Belize, and Puerto Rico.



varied considerably within age classes, and extremes in length overlapped between age classes, although all age classes were not represented in the sample (Tables 10 and 11). If one assumes that none of the innermost annuli were obscured or resorbed, then it appears that most of the growth occurs in the first year. Based on average back-calculated lengths for fish 1-11 years old, a mean of 40.7% (Johnston) and 35.3% (Belize) of the standard length occurred in the first year. Growth slowed drastically after the first year and, on the average, continued to slow as the fish aged. Average estimated length at age 1 for Belize fish was 163 mm, although the estimates ranged from 137 mm to 189 mm. However, the triggerfish from Curacao estimated to be age 1+ at capture was only 109 mm at the time of first annulus deposition. Johnston triggerfish were estimated to attain an average length of only 119 mm at the time of first annulus deposition, with a range of 97-131 mm.

To describe theoretical growth, Von Bertalanffy growth functions were fit to observed and back-calculated lengths-at-age. The equations describing the growth by population are, for Belize:

$$L_t = 244.4 \{1 - e^{(-.3258(t+1.626))}\}$$

for Johnston Atoll:

$$L_t = 202.1 \{1 - e^{(-.2184(t+3.154))}\}$$

(Fig. 7). Belize fish were found to have a greater K value and a greater asymptotic length than Johnston Atoll fish,

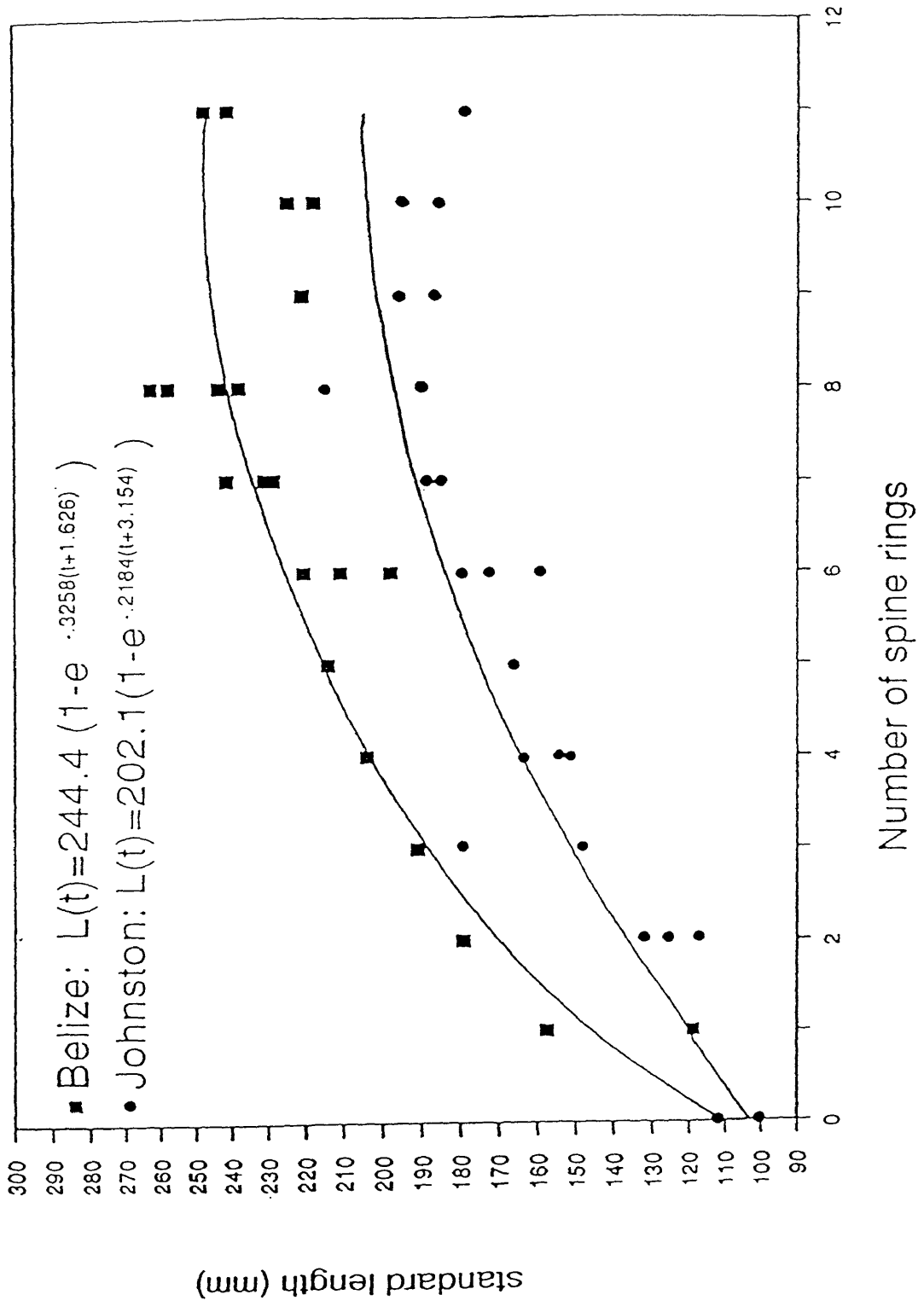
Table 10: Average back-calculated lengths for each age class of black triggerfish from Johnston Atoll.

Year	age	N	1	2	3	4	5	6	7	8	9	10	11
1988	1	0	0.00										
1987	2	2	106.08	115.48									
1986	3	1	130.95	151.28	179.00								
1985	4	2	120.75	134.76	140.66	151.17							
1984	5	0	0.00	0.00	0.00	0.00							
1983	6	2	121.53	130.59	141.23	151.87	161.84	167.40					
1982	7	1	121.84	136.95	148.70	158.78	170.53	180.60	189.00				
1981	8	1	117.60	141.55	154.33	160.71	171.89	178.28	202.23	215.00			
1980	9	1	110.74	130.63	144.84	156.21	167.58	174.68	184.63	188.89	196.00		
1979	10	1	127.32	135.78	147.63	157.78	171.31	181.46	184.85	188.23	191.62	195.00	
1978	11	1	119.07	125.44	138.18	147.74	152.52	157.30	162.07	165.26	170.04	174.81	178.00
all classes			118.69	131.94	147.65	154.14	165.36	172.45	184.56	189.35	185.88	184.91	178.00

Table 11: Average back-calculated lengths for each age class of black triggerfish from Belize.

Year	age	N	1	2	3	4	5	6	7	8	9	10	11
1988	1	1	108.68										
1987	2	0	0.00	0.00									
1986	3	0	0.00	0.00	0.00								
1985	4	0	0.00	0.00	0.00	0.00							
1984	5	0	0.00	0.00	0.00	0.00	0.00						
1983	6	2	144.62	154.33	171.77	183.37	195.24	202.34					
1982	7	2	171.94	193.79	203.98	214.96	222.39	228.95	232.66				
1981	8	3	173.84	193.69	205.75	223.65	233.70	240.21	245.80	252.29			
1980	9	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		
1979	10	1	147.75	161.01	167.63	180.89	194.14	200.77	206.07	210.05	214.02	216.67	
1978	11	1	165.97	175.82	182.38	188.94	197.14	202.07	210.27	225.03	228.31	233.24	241.44
all classes			157.71	179.35	190.97	204.16	214.18	220.67	231.29	238.39	221.17	224.96	241.44

Figure 7: Von Bertalanffy growth functions for Belize and Johnston Atoll black triggerfish Melichthys niger using age data from back-calculations of first dorsal spine annuli.



and thus appear to grow faster and attain a greater length than Johnston fish during the first year and throughout their life.

Community Survey.-The community survey was taken from data obtained at the time of the point sampling for density estimates. Because of the differences in abilities of the observers to identify fishes to species, observed community species were grouped into taxa, mostly by family (Table 12), and the results were examined in terms of cooccurrence with black triggerfish. Several groups were common and abundant at all sites, and appeared to share resources with Melichthys niger in the form of food or space; these included chaetodontids, pomacentrids, labrids, scarids and acanthurids.

During the field work, no predation on black triggerfish was observed, and no published record of predation on black triggerfish is available. The only evidence of predation is anecdotal from fishermen on Ascension Island who reported seeing black triggerfish in the stomachs of sharks. Observations from this study indicated that there were the greatest number of sharks around Johnston Atoll. No sharks were seen during the community surveys in Belize (although some were seen on other dives) and none were seen in the few days of observation in Puerto Rico. Other predators on adults and

Table 12: Cooccurrence of black triggerfish with other fishes in the community. Observations were made during abundance estimation. Groups with >40% cooccurrence and seen in large numbers are marked with an asterisk.

Site	Johnston	Belize	Puerto Rico
Number of observations	36	36	6
% with <u>Melichthys niger</u>	72%	84%	100%
% with cooccurrence of the following species:			
sharks	8	0	0
rays	4	0	0
Synodontidae	4	0	0
Muraenidae	4	0	0
Belonidae	19	3	0
Aulostomidae	19	6	17
Fistulariidae	8	0	0
Sphyraenidae	0	9	0
Serranidae	12	31	50
Lutjanidae	54	81 *	17
Mullidae	54	3	0
Chaetodontidae	61 *	66	67
Carangidae	27	41 *	33
Pomacentridae	42 *	78	83 *
Holocentridae	27	13	83
Pomadasyidae	0	31	67
Sparidae	0	16	0
Kyphosidae	12	13	0
Labridae	100	94 *	83
Scaridae	81 *	78 *	33
Blennioid	8	0	0
Gobiidae	4	13	0
Acanthuridae	100 *	72	67 *
Bothidae	8	0	0
Tetraodontidae	38	6	50
Zanclidae	35	0	0
Balistinae	58	25	17
Monacanthinae	4	6	17
Branchiostegidae	0	6	0
Triglidae	8	0	0

predators on juvenile black triggerfish are unknown, but Graves (pers. comm.) has observed small balistids in the stomachs of marlins (Istiophoridae) in Hawaii.

Discussion

Density observations.-The results of the point-sampling density estimates showed significant differences in abundance and spatial distribution of the surveyed groups for at least the duration of the study period. The study lacks verification of temporal stability of the density differences, however, the combination of historical records, communication with numerous ichthyologists who have explored these reefs, and, in the case of Johnston Atoll, many years of reef surveys made by the University of Hawaii (Irons et al, 1988), provides a basis for the assumption that the large difference in density between these populations is not a recent phenomenon or one that occurs only intermittently. Anecdotal reports of large aggregations of black triggerfish seen in locations other than isolated islands (Cayman Islands; Glover's Reef, Belize; shelf break off La Parguera, Puerto Rico (this study); Mona Island, Puerto Rico (Bohnsack and Harper, 1985); Christmas Island, Indian Ocean; tropical eastern Pacific islands) suggest that conditions for the swarms to form can occur in a variety of reef environments.

Morphology and Genetics. -The examination of genetic similarities among black triggerfish populations through morphological and electrophoretic analyses was intended to determine levels of genetic divergence with which to infer a genetic basis for the strikingly different behaviors of the widely separated groups. Hillis (1987) suggested that studies that combine morphological and molecular techniques could provide a better systematic analysis than either type of study separately. Taxonomic assignments based on traditional methods of morphological analysis have often been shown to have mistakenly treated evolutionarily-divergent taxa as a single taxon. (Grassle and Grassle, 1976; Thorpe et al, 1978; Shaklee and Tamaru, 1981; Waples, 1981). Thus, the combined use of morphology and genetics in this study provided a test case for comparison of traditional systematic methodology with newer molecular techniques.

One interesting result from the morphological examination of black triggerfish was the unusually high percentage of vertebral counts other than the expected $7+11=18$. This observation demonstrated a range of vertebral counts within this species, a condition which has rarely been reported within the family Balistidae (Tyler, 1980).

Though the morphometric analysis found only negligible differences between groups of black triggerfish, the observed modal difference in fin ray counts strongly

indicated divergence between oceans in Melichthys niger. Moore (1967) examined morphologies including dorsal-, anal-, and pectoral-fin ray counts for balistids in the western Atlantic, and the modes and ranges he reported for Melichthys niger correspond with this study's findings for Atlantic fish. Berry and Baldwin (1966) conducted a similar study in the eastern Pacific, and again, the modes and ranges of fin-ray counts of their triggerfish were similar to the Pacific fish analyzed in this study. These reports provided additional evidence that the observed modal differences in fin-ray counts were consistent within oceans and differed between oceans.

The consistent difference in modal fin ray counts between black triggerfish from Atlantic and Pacific Oceans was similar to morphological differences reported for other cross-Panama geminate species (Rosenblatt, 1967; Jordan, 1885) isolated by the closing of the last connection of tropical ocean populations, the Panama isthmus, approximately 3.5 million years ago (Saito 1976; Keigwin 1978, 1982). This divergence has been demonstrated and quantified in numerous genetic studies of conspecifics and paired species of fishes across Panama, and in fact it has been used as a known time of divergence to calibrate "molecular clocks" (Thorpe, 1982; Vawter et al, 1980; Grant, 1987). Electrophoretic analysis of Melichthys niger however, revealed no evidence of divergence on the expected

levels across Panama, in direct contradiction to the strong meristic evidence. The genetic results of this study indicated that Melichthys niger has a cross-Panama genetic distance which is more than an order of magnitude lower than has been reported in previous studies on tropical shorefishes. This result implies that gene flow has occurred within and between Atlantic and Pacific Ocean populations within relatively recent history.

The unexpected results from the electrophoretic analysis immediately cause one to question whether they truly reflect evolutionary history. Because the difference in meristic counts is consistent between widely-separated populations within oceans, it is unlikely that the counts simply reflect ecophenotypes. Another possibility for misleading results may be that fixed allelic differences between the groups were simply missed in the electrophoretic analysis. The probability of missing the expected fixed allelic differences can be estimated based on genetic distances of cross-Panama groups from previous studies (Vawter et al, 1980; Grant, 1987). The average genetic distance between conspecifics or geminate species across Panama is 0.188 (Nei's D without esterases, Vawter et al, 1980) which corresponds to about 15% fixed allelic differences. The probability then, that this study would not find any fixed allelic differences using 36 loci (for analysis by ocean) is $(0.85)^{36}$ or 0.0028. Using 18 loci

(for analysis by population), the probability is near significance at 0.053. Based on these calculations then, it is unlikely that fixed allelic differences were missed. The genetic distances (D) for groups within oceans are uninterpretable because of the presumably large standard error associated with the statistic for such a small number of specimens.

If one supposes that the species has experienced gene flow between oceans relatively recently, one must then speculate on the mechanism of worldwide dispersal ability. The extended pelagic early life history of black triggerfish, very probably on the order of months, gives them the means to travel long distances. The Agulhas Current along the Indian Ocean coast of Africa would carry pelagic pre-juveniles southward. Adult Melichthys niger have been recorded as far south as Durban, South Africa (Smith and Heemstra, 1986). The Benguela Current runs north from the southern tip of the Atlantic coast of Africa up to the equator (Pickard and Emery, 1982) and thus could assist in the transport of pelagic prejuvenile triggerfish to tropical coastal Africa and to St. Helena and Ascension islands. In this way, a major hurdle of cross-ocean dispersal might be completed. Relatively little gene flow is required to maintain a single gene pool between populations. Using the population genetics rule-of-thumb of one individual per local population per generation (Speith,

1974), a few fish would have to get around the south of Africa only every hundred years or so to maintain gene flow within the entire species. Perhaps this set of circumstances has allowed for Melichthys niger to be an exception among the tropical shorefishes.

The contradictory results of the morphological and genetic analyses are, on the one hand, troubling, because if substantiated it suggests the possibility that one or both of the techniques is misleading. But the results are provocative because they beckon further investigation that will undoubtedly lead to a deeper understanding of the relationship of genetics and morphological expression. The possibility of worldwide shorefish dispersal is also cause for further investigation, and perhaps a genetics study designed to detect finer subpopulation differences might give a better picture of the history of the species and increase our understanding of gene flow mechanisms.

Ecology.-Since genetic influence is not likely, ecological influences must be controlling the differing densities and behaviors. Several possibilities are discussed below in light of the results of this study.

Isolation and low diversity on isolated islands create an environment where black triggerfish can readily establish and maintain large populations.

Because of their extreme geographic isolation, some of the islands where black triggerfish are found in great abundance have many environmental characteristics in common, most noticeably low faunal diversity. Low diversity could provide a setting for maintenance of the observed high-density populations by allowing this generalist species to successfully exploit available resources in the absence of competition.

The possibility of individual growth limitation suggests that competition for resources may be occurring in the Johnston Atoll populations, although their abundance indicates that they are successful. Since black triggerfish appear to be nonspecific omnivores, it is difficult to identify a niche in which they are competing for food resources. The results of the community survey provide some clue to the abundances of cooccurring species as a basis for further study of competitive interactions.

Considering coexisting species as potential competitors only in the sense of food availability could be misleading, since community structure in coral reef fishes may be explained simply as an unpredictable event in the "living space lottery", where space is the limiting resource on the reef (Sale, 1978). In this hypothesis, factors that contribute to the establishment of cohorts in the available space determine the community composition, and post-settlement competition for food resources has no

deterministic effect. Is M. niger more successful than other reef fishes in dispersing to isolated islands, colonizing and establishing large populations, and maintaining the large populations? In the living space lottery, space is the limiting factor, however, in at least one study, Walsh (1984) determined that shelter space was non-limiting in a Kona, Hawaii population of black triggerfish. An estimation of the occurrence of coexisting species that require similar shelter space as black triggerfish (balistids, scarids, muraenids, chaetodontids, pomacanthids, acanthurids) indicates that all sites are roughly similar in this respect, but the differential availability of shelter space is unknown. If the black triggerfish's situation is to fit into the living space lottery hypothesis, then the abundance of larvae and settlers must be consistently overwhelming relative to those of other species, regardless of the predictability of factors affecting recruitment of settlers to the isolated island's reef environment. The source of larvae for the population would most likely be the island population itself because of the island's geographic isolation.

High- and low-density populations (e.g. Puerto Rico and Belize in this study) are reportedly found in relatively close proximity, thus this simple explanation of low diversity creating a competitively advantageous environment for black triggerfish is not adequate. Since the few

situations of extreme abundance do seem to be found on isolated islands with low species diversity, e.g. Johnston Atoll and Ascension Island, some other factor which is accentuated by the isolation and low diversity must be the cause.

Disturbed and overfished areas create small scale environments where black triggerfish can flourish.

Black triggerfish are relatively mobile for shorefishes, and could potentially, as adults, move rapidly into areas which have had competitors removed, either by overfishing, or by a shift in food sources. Disturbed areas of coral reefs may have increased macroalgal biomass, especially if algae grazers are reduced (Ogden and Lobel, 1978). The increase in algae-grazing acanthurids after a massive Diadema die-off in the Caribbean was cited as an example of an increase in abundance of one taxonomic group when competitors were reduced (Carpenter, 1990). The reef off Puerto Rico where observations were made in this study was severely overfished (Hensley, Univ. Puerto Rico, pers. comm.), the visibility was relatively poor, and the coral community was poorly developed. Macroalgal abundance was not noted, however the high-density Puerto Rico group was found to have dietary differences from both Johnston and Belize, namely an increase in the ratio of organic content

of their food, such as might happen with increased macroalgal availability.

Perhaps the abundant Puerto Rico fish are in a niche-exploiting situation caused by overfishing of competitors and predators, as was hypothesized of the rapid increase in abundance of another triggerfish, Balistes carolinensis, off the West African coast, where in 20 years it increased from less than 5% of the catches to as much as 50% (Longhurst and Pauly, 1987). It was suggested that the triggerfish was predisposed to proliferate when competitors and predators were removed because it could live through being trawled and rejected at sea. For the black triggerfish, one could hypothesize that low diversity on small spatial scales, due to overfishing or other causes, could explain the proximity of the high-density and low-density groups.

Johnston Atoll black triggerfish are limited in their individual growth rate while Belize fish are limited in population density.

Age-and-growth results showed substantial variation between the two sites and suggest an individual growth limitation in the high-density group from Johnston Atoll. Although the sample size was relatively small, differences in size and growth of the two sampled groups were clear. The data indicating rapid growth in the first year and slow

growth thereafter explains the observation that most of the triggerfish within each population were in a narrow range of sizes (Table 6). Other age-and-growth studies of balistids (Manooch and Drennon, 1987; Johnston and Saloman, 1984) report similar levels of rapid early growth and longevity. Walsh (1984) reported growth data for three black triggerfish (size range 175-217 mm TL) from Hawaii, recaptured and measured after one year. From the mean growth rate of these fish, he calculated that juveniles that recruited in 1979 would have grown to approximately 170-180 mm by 1980. The growth rate estimates from the present study are also in this range (Table 9 and 10). Despite the confirmation of the similar findings from Walsh's study, the capture of a 108 mm juvenile of age 1+ from Curacao casts some suspicion on the age estimates of the Belize fish, which were back-calculated to lengths of 137-189 mm at age 1. Since the largest fishes seem to have the greatest back-calculated lengths-at-age, inner rings may be obscured in the older fish, as suggested by Berkeley and Houde (1983). Thus, patterns of growth of Belize fish (as described in Fig. 8) would require adjustment. Regardless of the accuracy of aging, the difference in size frequency of collected specimens from the different locations suggests either some growth limitation or a higher size-selective mortality rate in the high-density group. A study of relatively undisturbed high- and low-density groups in close

geographic proximity could further test for density-dependent growth limitation.

The environmental cause of the growth limitation is unclear. Competition for food cannot be implied from the limited data. It is interesting to note again that Johnston and Belize triggerfish had no obvious differences in taxonomic composition of diet or condition based on liver size, while the higher LSI value of the Puerto Rico fish suggests a better dietary regime in that area. Observations of gonadal development in Puerto Rico, Belize, and Johnston Atoll fish does not indicate an inverse relationship to liver size; in other words, the difference in liver size is probably not due to a transfer of energy during different times of the year. Certainly further experimental studies would be necessary to conclusively implicate competition as a regulating factor.

Another consideration when comparing growth rates is the assumption that individuals have grown in the same environment (high- or low-density) for the entire portion of their life which is being considered in the growth estimation procedure. Because of the mobility of the adults, and because it is unknown whether individuals stay in groups of similar density during their lifespans, the assumption that growth rates are correlated with density of the groups in which they were observed may be false! Also, it must be allowed that total population abundance, if

measured over a large enough spatial scale, could be similar between the groups, regardless of the difference in swarming behavior, i.e. it is simply the behavior that is different. However, at least on the spatial scales measured in this study, both the variances and means of numbers of triggerfish over the 6-10 mile stretch of reef surveyed were much lower in the Belize group than the Johnston group.

Behavioral cues in different environments affect intraspecific interactions.

The correlation between absolute abundance in the area surveyed and swarming behavior suggests density-dependent swarming. Conspecific abundance has been shown to influence gregarious behavior (Eggleston and Lipcius, 1991). A change in triggerfish behavior with density could change the relationship of the triggerfish to its resources, and thus the density-influenced behaviors themselves could enhance or diminish population growth and/or individual growth by affecting the limiting resource. The difference in intraspecific aggressive encounters may be another aspect of the density-dependent behavior--the fish appear to be more tolerant of close proximity of their conspecifics when population abundance is high. Another possibility for the behavior difference may be that the swarming groups of Johnston and Ascension are exhibiting a protective aggregation response to the large numbers of predators in

the area, as has been demonstrated in other gregarious species (Moyle and Cech, 1988).

Although the question of the swarms is not answered with the results of this study, interesting observations on the natural history of this common coral reef fish illustrate the complexity of the relationship between morphology and genetics, and provide a provocative basis for further investigations on the determinants of population structure. The variability of growth rates, growth maxima, intraspecific behavior, food quality, condition, and habitat among populations of this tropical shorefish demonstrate the importance of conducting detailed comparative population studies before generalizations can be formed about a taxon.

Further studies could include experimental manipulation to test for competitive interactions on several levels (intraspecific and interspecific; and for aspects of food and space resources), and to look for causes of the differences in growth parameters found in this study. Examining the subtleties of nutritional quality of diets and consequential physiological stresses may be insightful. In light of the uncertainty of the readability of the inner rings of the dorsal spine sections, additional growth studies should certainly include validation of settlement mark and annular ring deposition.

APPENDIX A: Museum specimens of Melichthys niger examined.

USNM 267897 (179 mm SL; St. Helena Island)
 USNM 300449 (4 spec.; 200-250 mm SL; Ascension Island)
 USNM 207087 (2 spec.; 210-230 mm SL; Line Islands)
 USNM uncatalogued (7 spec.; 209-248 mm SL; Trinidad Island)
 USNM 210402 (206 mm SL; Moluccas Island)
 USNM uncatalogued, U. of Iowa No. 19248-05052 (168 mm SL; Hawaii)
 USNM uncatalogued, ACC 290319 (2 spec.; 200-202 mm SL; Ascension)
 GMBL 78-17 (167 mm SL; Ascension Island)
 GMBL 78-32 (175 mm SL; Ascension Island)
 GMBL 80-26 (2 spec.; 190-203 mm SL; Ascension Island)
 GMBL 80-32 (2 spec.; 178-180 mm SL; Ascension Island)
 GMBL 80-36 (174 mm SL; Ascension Island)
 GMBL 80-39 (180 mm SL; Ascension Island)
 GMBL 80-41 (192 mm SL; Ascension Island)
 GMBL 80-49 (188 mm SL; Ascension Island)
 BPBM 5035 (235 mm SL; Gardner Island)
 BPBM 5034 (2 spec.; 140-210 mm SL; Hawaii)
 BPBM 2449 (210 mm SL; Marcus Island)
 BPBM 627 (155 mm SL; Hawaiian Islands)
 BPBM 15093 (2 spec.; 69-147 mm SL; Johnston Atoll)
 BPBM 26996 (115 mm SL; Line Islands)
 BPBM 18429 (161 mm SL; Marshall Islands)
 BPBM 5037 (185 mm SL; Johnston Atoll)
 BPBM 7673 (216 mm SL; Fanning Island)
 BPBM 8990 (96 mm SL; Johnston Island)
 BPBM 5038 (191 mm SL; Wake Island)
 BPBM 8944 (161 mm SL; Johnston)
 BPBM 5036 (2 spec.; 157-174 mm SL; French Frigate Shoals)
 BPBM 8391 (196 mm SL; Marcus Island)
 BPBM 7172 (177 mm SL; Marcus Island)

USNM=United States National Museum (Smithsonian Institution)

GMBL=Grice Marine Biological Laboratory, Charleston, S.C.

BPBM=Bernice P. Bishop Museum, Honolulu, Hawaii

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