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Amorphometric and Meristic Study of the Halfbeak, Hyporhamphus unifasciatus (Teleostei: Hemiramphidae) from the Western Atlantic, with the Description of a New Species

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A MORPHOMETRIC AND MERISTIC STUDY OF THE HALFBEAK, *HYPORHAMPHUS UNIFASCIATUS* (TELEOSTEI: HEMIRAMPHIDAE) FROM THE WESTERN ATLANTIC, WITH THE DESCRIPTION OF A NEW SPECIES

A Thesis
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The College of William and Mary in Virginia

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

by
Heidi M. Banford
1993

This thesis is submitted in partial fulfillment of

the requirements for the degree of

Master of Arts

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head and refreshed me for another days work. And finally, I thank Chris Tabit whose support and confidence in me, both in academics and at home, has brought me to realize a confidence in myself to do things I never thought I could.

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ABSTRACT

Hyporhamphus meeki Banford and Collette and *Hy. unifasciatus* (Ranzani) from the western Atlantic are described and compared. *Hyporhamphus meeki* ranges along the Atlantic and Gulf of Mexico coasts of the United States. It has been confused previously with *Hy. unifasciatus* which occurs from Bermuda, southern Florida, the West Indies, and Mexico to southern Brazil. *Hyporhamphus meeki* has more gill rakers, usually 33 to 39 on the first arch and 26 to 29 on the second arch, compared to 28 to 32 on the first arch and 19 to 25 on the second arch in *Hy. unifasciatus*. Pectoral-fin rays are usually 11 or 12 in *Hy. meeki* versus 10 or 11 in *Hy. unifasciatus*. The ratio of preorbital length to orbit diameter is usually greater than 0.70 in *Hy. meeki*, less than 0.70 in *Hy. unifasciatus*.

Intraspecific geographic variation was investigated in both species. Analysis of covariance results indicate morphometric differences between the Atlantic and Gulf of Mexico populations of *Hy. meeki*. Within the Gulf of Mexico morphometric and meristic differences were found between the northwestern and eastern regions. Intraspecific geographic variation within *Hy. unifasciatus* was greatest between all other populations and the Bermudian population. Bermudian *Hy. unifasciatus* have the lowest pectoral-fin ray counts, 9 to 10, with a mean of 10.0, they are thinner at both pectoral and pelvic-fin origins, and have a greater pectoral to pelvic-fin distance than other populations of *Hy. unifasciatus*.

Southern Florida and Yucatan appear to be areas of sympatry between the two species. The species are clearly distinguishable in Florida by a combination of morphometric and meristic characters. In Yucatan hybridization and introgression may be occurring as evidenced by possible character mosaics and intermediacy. Yucatan *Hy. meeki*, or those with high gill raker counts, have a preorbital/orbit ratio typical of *Hy. unifasciatus*.

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INTRODUCTION

Early in the 1960's Frederick Berry and Bruce Collette began studying the halfbeak, *Hyporhamphus unifasciatus* in the western Atlantic and continued making observations and collecting data on the species for the next 25 years. They eventually hypothesized that the name *Hy. unifasciatus* was being applied to populations of what appeared to be more than one species. In 1986 Bruce Collette and I met for the first time to discuss a Masters thesis topic in systematic ichthyology. At that time the *Hy. unifasciatus* problem was presented to me for consideration. After their many years of examining these fishes and recording various morphometric and meristic data, Berry and Collette were convinced they had discovered a new undescribed species of western Atlantic *Hyporhamphus*. Although potential meristic characters for discrminating the putative species had been identified, separation of the two species based upon morphometry had not been established. What was needed was a through morphometric analysis of these fishes. This thesis presents such an analysis.

The beloniform family Hemiramphidae, commonly known as the halfbeaks, is defined on the basis of one synapomorphy, the third pair of upper pharyngeal bones are ankylosed into a plate. Additional diagnostic characters are: a triangular upper jaw; elongate lower jaw, at least in juveniles; parapophyses forked in most adults;

and swimbladder not extending into the haemal canal (Collette et al., 1984). A general description of hemiramphids was given by Collette (1986) and Collette and Parin (1986), as follows:

> Elongate slender bodies, being round to somewhat laterally compressed. The lower jaw is prolonged into a beak in the adults of most species, except for the genera *Chirodorus* and *Oxyporhamphus*. The upper jaw is not prolonged, being short and usually triangular. The teeth are small, in several rows, being either tricuspid or unicuspid. Lower pharyngeal bones are fused into a triangular plate and the third pair of upper pharyngeal bones are also fused into a plate. Gill rakers are well developed on both the first and second gill arches. The nasal organ is a pit with a protruding tentacle. The lateral line begins on the throat, then runs along the ventral margin of the body, with one or two branches to the pectoral fin origin. Scales are moderately large, cycloid, and easily detached. Pectoral fins are placed high on the sides and variable in length. Pelvic fins are in an abdominal position, with 6 soft rays. Both the anal and dorsal fins are posterior and usually opposite. The caudal fin can be emarginate to forked, with the lower lobe being variably longer than the upper lobe. None of the fins have spines.

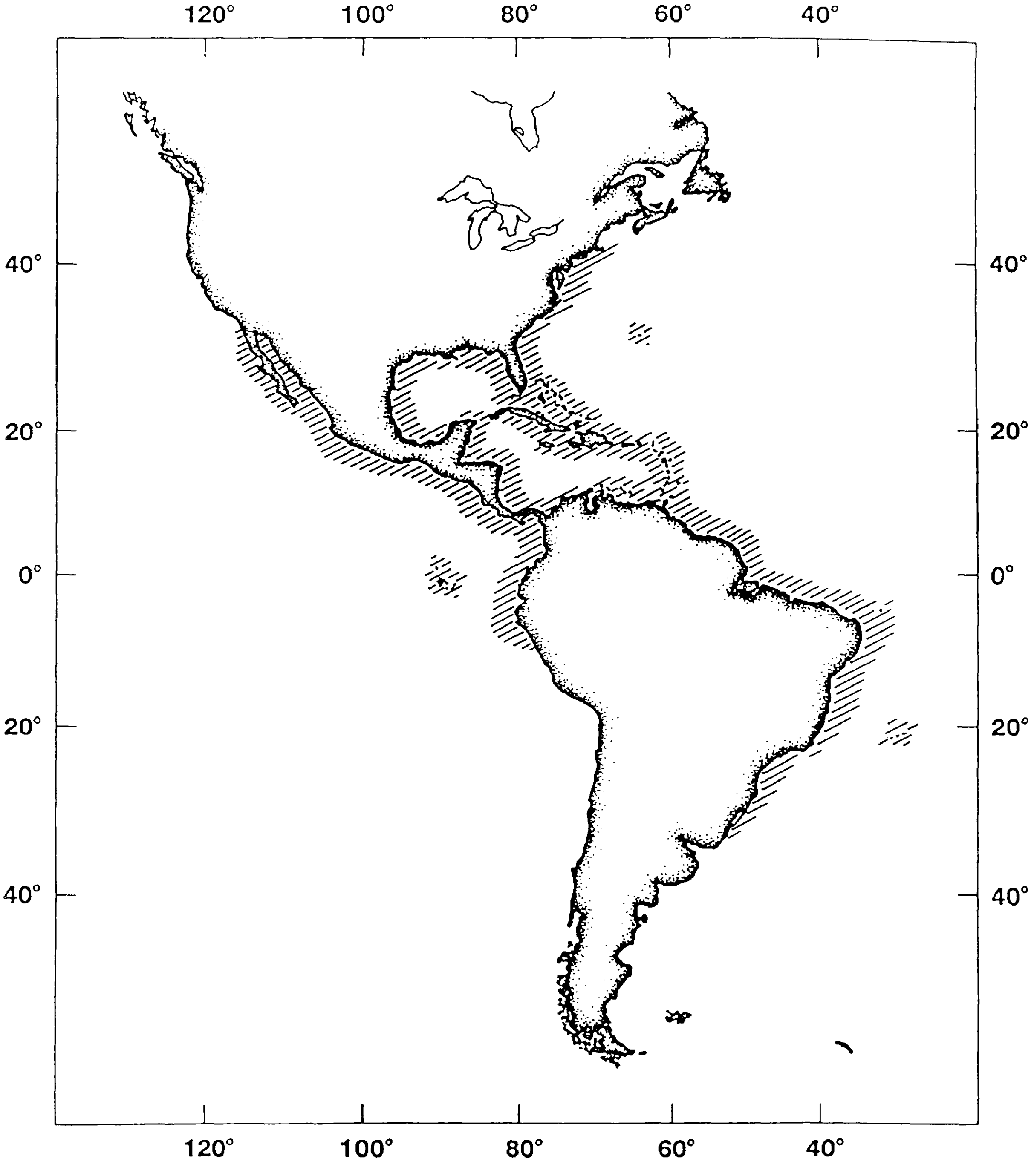
The family is represented in the western Atlantic by nine marine species in five genera (Collette, 1978); *Chirodorus atherinoides* Goode and Bean 1882, *Euleptorhamphus velox* Poey 1868, *Hemiramphus brasiliensis* (Linnaeus 1758), *He. balao* LeSueur 1823, *He. bermudensis* Collette 1962, *Hyporhamphus unifasciatus* (Ranzani 1842), *Hy. roberti* (Valenciennes 1846), *Hy. meeki* Banford and Collette 1993, a new species described herein, and *Oxyporhamphus micropterus similis*

Bruun 1935. Two additional species of *Hyporhamphus*, *Hy. mexicanus* Alvarez 1959, and *Hy. brederi* (Fernandez-Yepez 1948), are found in freshwater drainages of Central America, and the Orinoco and Amazon rivers respectively (Miller, 1966; Collette, 1966, 1974).

Hyporhamphus (Gill, 1859) is the most speciose genus of halfbeaks worldwide. It is composed of two subgenera, *Hyporhamphus* sensu stricto and *Reporhamphus* Whitley (Parin, Collette and Shcherbachev, 1980). The preorbital (lacrimal) canal is unbranched in *Hyporhamphus* but T-shaped in *Reporhamphus*. A full systematic treatment is lacking. However, on this basis and other differences in the acoustico - lateralis system, the two may deserve full generic status (Parin and Ashtakhov, 1982). All New World species of *Hyporhamphus* belong to the subgenus *Hyporhamphus*.

There has been considerable confusion regarding the taxonomy and systematics of the New World halfbeaks (Meek and Goss, 1884; Miller, 1945). Although the status of some species has been clarified, that of *Hyporhamphus unifasciatus* (Ranzani, 1842), the common inshore halfbeak, has been questioned for more than 100 years (Meek and Goss, 1884; Collette, 1978). The name *Hyporhamphus unifasciatus* (Ranzani) has been used for inshore halfbeaks in the western Atlantic, eastern Atlantic, in several parts of the Indo-West Pacific, and the eastern Pacific. The eastern Atlantic *Hyporhamphus* were shown to be *Hy. picarti* (Valenciennes) by Collette (1965); the Indo-West Pacific halfbeaks *Hy. limbatus* (Valenciennes) by

Figure 1. Range of populations currently referred to *Hyporhamphus unifasciatus*.



Range of halfbeaks referred to *Hyporhamphus unifasciatus*

Parin et al. (1980).

Populations referred to *Hy. unifasciatus* range in the western Atlantic (Fig. 1) from Uruguay in the south, northward along the coast of the Americas, through the Caribbean (Jordan and Evermann, 1896), Gulf of Mexico (Hoese and Moore, 1977), and around Bermuda (Beebe and Tee-Van, 1933) to Cape Cod, Massachusetts. Strays have been collected as far north as Chamcook, Passamaquoddy Bay, New Brunswick (Leim and Day, 1959). In the eastern Pacific they range from Peru (Hildebrand, 1946) to Baja California and around the Galapagos Islands (Meek and Hildebrand, 1923). The range of *Hy. unifasciatus* sensu stricto (type locality, Brazil) is from Bermuda and peninsular Florida southward through the Caribbean to Uruguay. Those populations referred to as *Hy. unifasciatus* from outside this range constitute superficially similar undescribed species of *Hyporhamphus* (Collette, 1978).

Meek and Goss (1884) first distinguished between the North American and West Indian southern populations referred to *Hy. unifasciatus*. The North American population was referred to as *Hemiramphus roberti* (=*hildebrandi* Jordan and Evermann), while the southern retained the name *He. unifasciatus*. The distinction between the two was based upon body form, with *He. unifasciatus* being more robust than *He. roberti*.

Gill (1859) described the genus *Hyporhamphus* from the type species *Hy. tricuspidatus* collected at the island of Barbados. Gill based his description on the possession of tricuspid teeth (*Hy. tricuspidatus* is in fact a junior synonym of *unifasciatus*.). He understood Valenciennes (1846) to have described *Hemiramphus* as having simple, unicuspid teeth. Gill (1863) found that tricuspid dentition did not serve to separate *Hyporhamphus* from *Hemiramphus*, and subsequently suggested suppressing the use of the name *Hyporhamphus*. Not until 1945 did Miller clearly show that *Hyporhamphus* was indeed different from *Hemiramphus*. *Hyporhamphus* has an emarginate or slightly forked caudal fin, scales on the upper jaw, presence of a bony preorbital ridge, and a simple preorbital canal. In contrast, *Hemiramphus* has a deeply forked caudal fin, lacks scales on the upper jaw, lacks a preorbital ridge, and has a branched preorbital canal (Miller, 1945; Collette, 1977).

My hypothesis is that there are at least two species of *Hy. unifasciatus* in the western Atlantic, in agreement with both Meek and Goss', and Collette and Berry's observations. The northern form is undescribed, deserves full species status and should be described accordingly. The southern form retains the name *Hy. unifasciatus*. However the designation of the North American form as *Hy. roberti* was found to be in error (Miller, 1945). The northern population was provisionally distinguished from the southern form by having a greater number of gill rakers and pectoral fin rays, and a longer beak (B. Collette pers. comm.). However, available morphometric and meristic data have not permitted a clear separation of the two species.

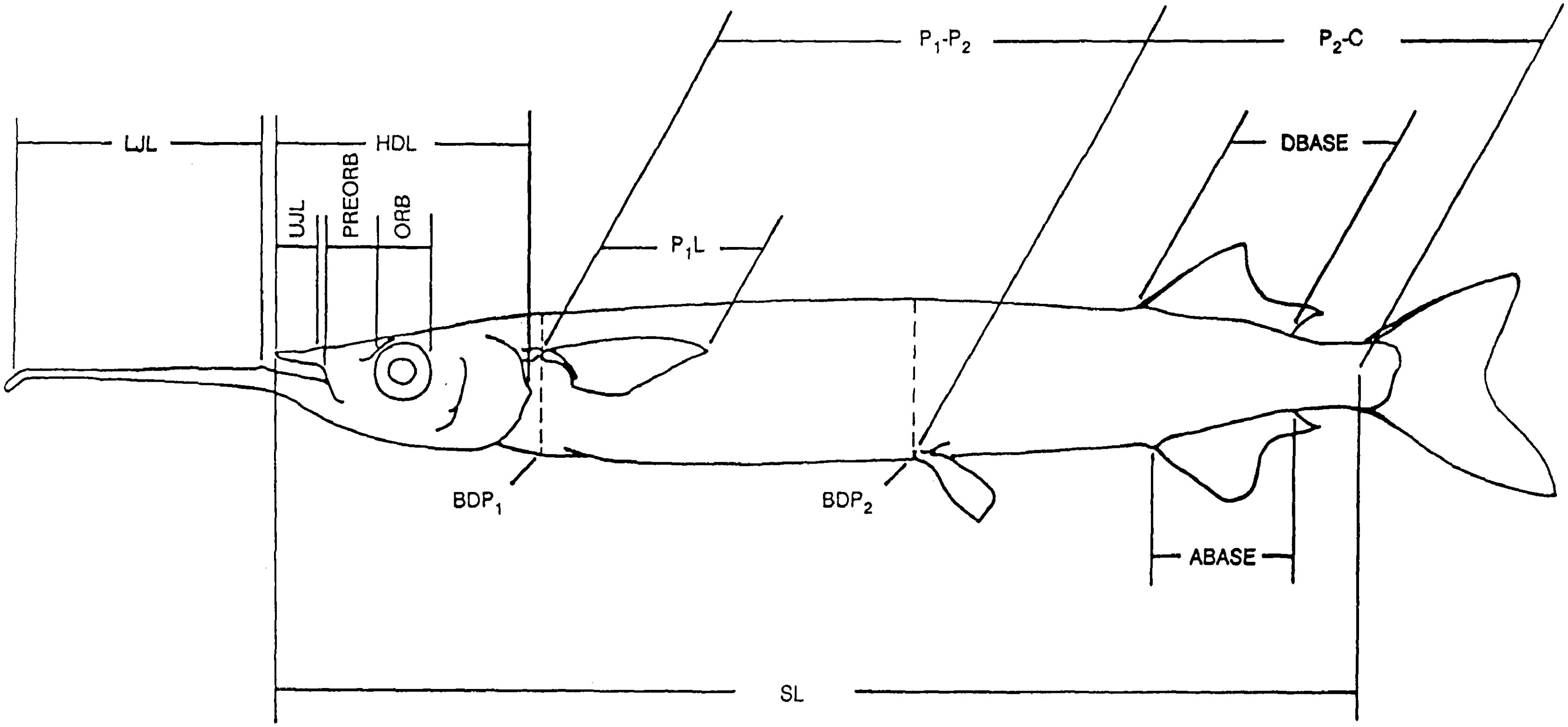
My objective is to present a morphometric and meristic analysis of western Atlantic populations of halfbeaks referred to *Hy. unifasciatus*, with the description of a new species. This new species of *Hyporhamphus* is to be compared with the true western Atlantic *Hy. unifasciatus* (Ranzani, 1842; type locality Brazil). The eastern Pacific populations, also referred to as *Hy. unifasciatus*, will not be discussed in this study. Some intraspecific geographic variation will be presented and discussed. The limited life history literature on this group of fishes will be reviewed and summarized, with the objective of thoroughly presenting the known biological information pertaining to these species of fish. Additionally, zoogeographic information will be presented and potential implications discussed as it addresses the observed geographic variation.

MATERIALS AND METHODS

A total of 568 specimens of western Atlantic *Hyporhamphus* was examined for 24 morphometric and meristic characters. An additional 1088 specimens were examined only for meristic characters, mostly by Bruce Collette. He has generously allowed me access to this data for the purposes of this study. The number of specimens examined for each character varies due to the condition of material. Due to the poor condition of some specimens not all characters could be reliably observed. Material was chosen to represent the entire geographical range of what has been considered *Hy. unifasciatus* in the western Atlantic. The majority of material examined was obtained from the following institutions (abbreviations from Leviton et al., 1985): AMNH, ANSP, CBL (Chesapeake Biological Laboratory, specimens now at VIMS), CAS, MCZ, MZUSP, SIO, UF, VIMS, UMMZ, USNM. I collected additional material in the York River at Gloucester Pt., VA that is housed at VIMS. Sampling was done both on the VIMS beach (shore facing southwest, adjacent to the boat basin), and from the VIMS Ferry Pier. Beach sampling was done with a 100 ft. beach seine with 1/4 in. mesh, during both daylight and nighttime hours, semi-regularly from the months of May through October, 1988-92. Sampling from the VIMS Ferry Pier was accomplished with dipnet and night-light. This involved hanging a light, at night, from the pier, 3 to 6 feet above the water surface (elevation above surface of the water was dependent upon tide height). Some fish and invertebrates in the water were attracted into the area of the light, and schooled about in the lighted area. This afforded an opportunity to capture organisms near the surface of the water. This capture strategy worked well with halfbeaks for they were both attracted into the light and are surface dwellers. The light was usually set up two hours prior to maximum flood tide and sampling continued until slack before ebb. The timing was important for two reasons: One, during this tide stage a maximum volume of water, and most likely small water borne organisms, will pass under the sampling location on the pier; and two, the accuracy of using a dipnet is increased when the distance from the pier deck to the water surface is an easy reach, thus when this distance is at a minimum. Specimens were preserved by one of the following methods: 1) frozen at -80°C for use in allozyme electrophoresis; 2) measured fresh then placed in 95% ethanol (EtOH) for future examination of otoliths; or 3) measured fresh then fixed in 10% formalin and transferred to 70% EtOH.

Most morphological characters examined follow Collette (1965) and Parin et al. (1980). Measurements were made to the nearest 0.1 mm. with dial calipers. Abbreviations and descriptions of characters (Fig. 2) examined are as follows: SL (standard length); LJL (lower jaw length, tip of upper jaw to tip of lower jaw); HDL (head length, from tip of upper jaw to posterior margin of opercle membrane); UJL (upper jaw length, from tip of upper jaw to where upper jaw bends); UJW (upper jaw width, where upper jaw bends); P_1-P_2 (distance from base of upper most pectoral ray to base of anteriormost pelvic ray); P_2-C (distance from base of anteriormost

Figure 2. Morphometrics on *Hyporhamphus unifasciatus*. Measurements are straight-line distances from point to point, not the distance between the perpendiculars.


LJL
HDL
UJL
PREORB
ORB
P_1L
P_1-P_2
P_2-C
DBASE
BDP_1
BDP_2
ABASE
SL

pelvic ray to caudal base); P_2-CX (P_2-C distance extended anteriorly from base of anteriormost pelvic ray to a point on the body or head); BD P_1 (body depth at origin of pectoral fin); BD P_2 (body depth at origin of pelvic fin); ABASE (length of anal fin base); DBASE (length of dorsal fin base); P_1L (pectoral fin length, distance from base of uppermost pectoral ray to tip of longest ray); ORB (soft orbit diameter); PREORB (preorbital length, from the corner of the mouth to anterior margin of orbit); ANA (number of anal-fin rays); DOR (number of dorsal-fin rays); P_1 (L,R, number of pectoral-fin rays); PRED (number of predorsal scales in median row in front of dorsal fin); RGR_1 (number of gill rakers on first arch (upper + lower = total); RGR_2 (number of gill rakers on second arch (upper + lower = total); VERT (number of precaudal plus caudal vertebrae, including the hypural plate = total number of vertebrae). All VERT data were received from Dr. Collette.

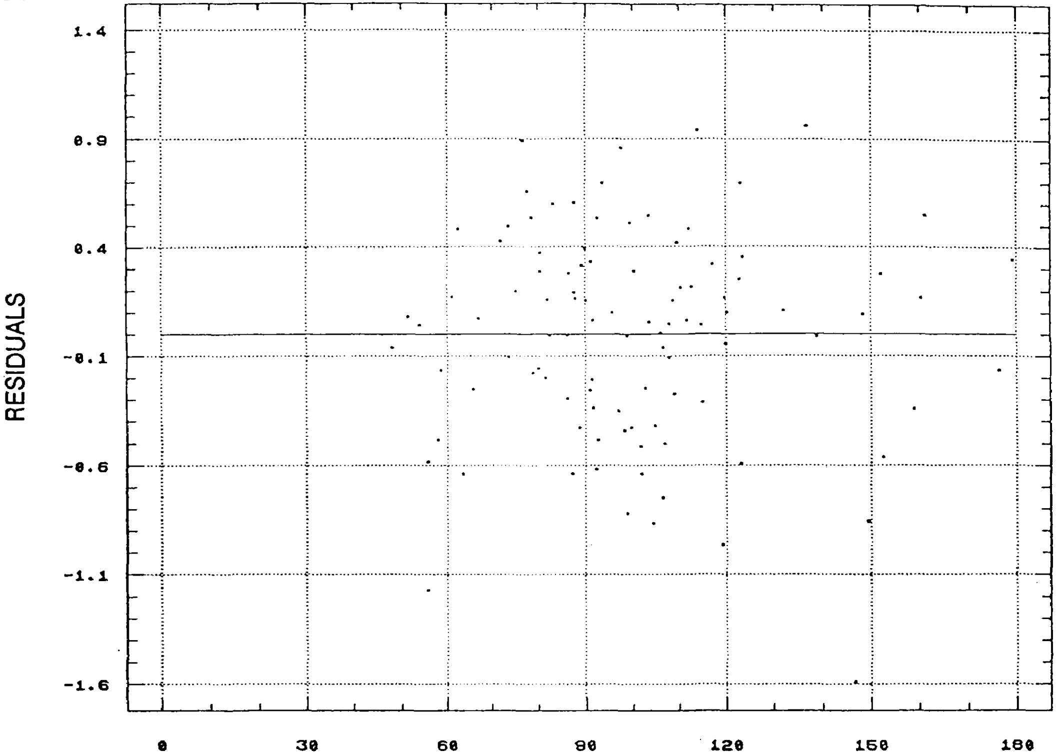
Statistical analyses utilized SAS software (SAS Institute Inc. 1985). Frequency distributions of counts were compared between geographic populations and are presented in summary tables. If two populations in close geographic proximity were found not to have significantly different counts, counts were combined to form a single population in subsequent statistical analysis. Analysis of variance (ANOVA) was performed on five data sets of meristic characters. If the F value for an ANOVA was significant ($P<.05$), Tukey's Studentized Range Test (Tukey-Kramer method) (SAS, 1985) was performed to determine which means were significantly different from the others. The Tukey-Kramer method is a modification, for unequal cell sizes, of Tukey's test for equal cell sizes (the "honestly significant difference" test), and is recommended (Chittenden pers. comm.; SAS, 1985).

Values of morphometric characters were first plotted against SL, and then plotted against one another to visually inspect for separation between populations. Only those that were found to be diagnostic for the species are presented. Residual plots were inspected for homogeneity of variance. To assume homogeneity of variance the residuals plotted should form an ellipse along the x axis (Fig. 3), whereas in the heteroscedastic case (Fig. 4), the scatter of the residuals increases with increase of SL. Due to heteroscedasticity of variance, all morphometric data were log transformed for analysis of covariance (ANCOVA) (Sokal and Rohlf, 1981). To test for differences between populations, ANCOVA was performed on the regressions of body part against SL for each morphometric character. If the assumption of homogeneity of slopes for ANCOVA (Sokal and Rohlf, 1981) was not met in some cases, no further analysis could be carried out, unless there were more than two treatments (geographic populations) in the analysis (see below). If the slopes were homogeneous, the least squares means adjusted for the covariate, SL, were compared with the GLM SAS procedure. This was done rather than compare the intercepts which fall well outside of the observed data.

When more than two treatments were considered in ANCOVA, as in the intraspecific analysis of geographic variation within both *Hy. meeki* and *Hy. unifasciatus*, analysis could be continued beyond the initial slopes and means tests. If slopes or means were found not to be homogeneous, apriori contrasts (SAS CONTRAST statement) were done between pairs of treatments. These are pre-planned comparisons and the number of treatments minus one is the number of allowable comparisons of pairs.

Figure 3. Homogeneity of variance as shown by homoscedastic residual plots of morphometric characters. A) Residuals from regression of BDP_1 on SL for the Massachusetts to Georgia population (NOF); B) Residuals from regression of BDP_2 on SL for the Bermudian population (BERM).

A


RESIDUALS
1.4
0.9
0.4
-0.1
-0.6
-1.1
-1.6
0
30
60
90
120
150
180

B

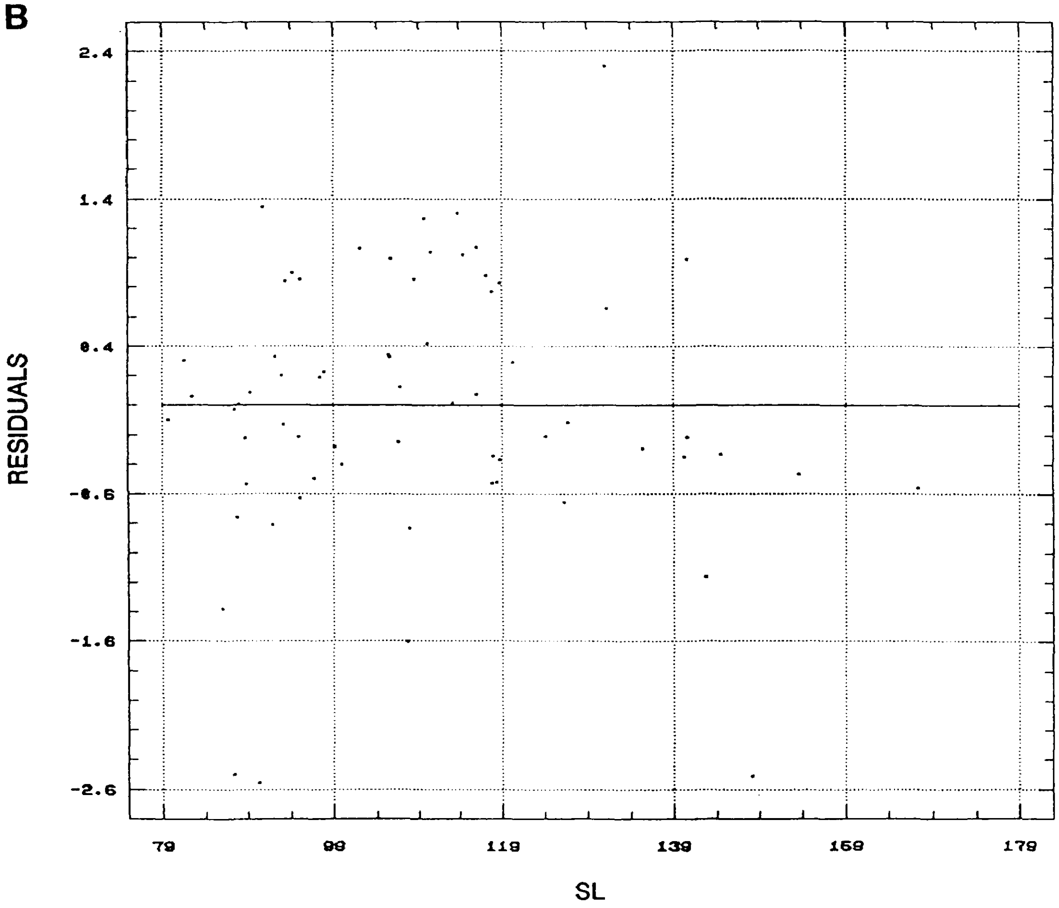
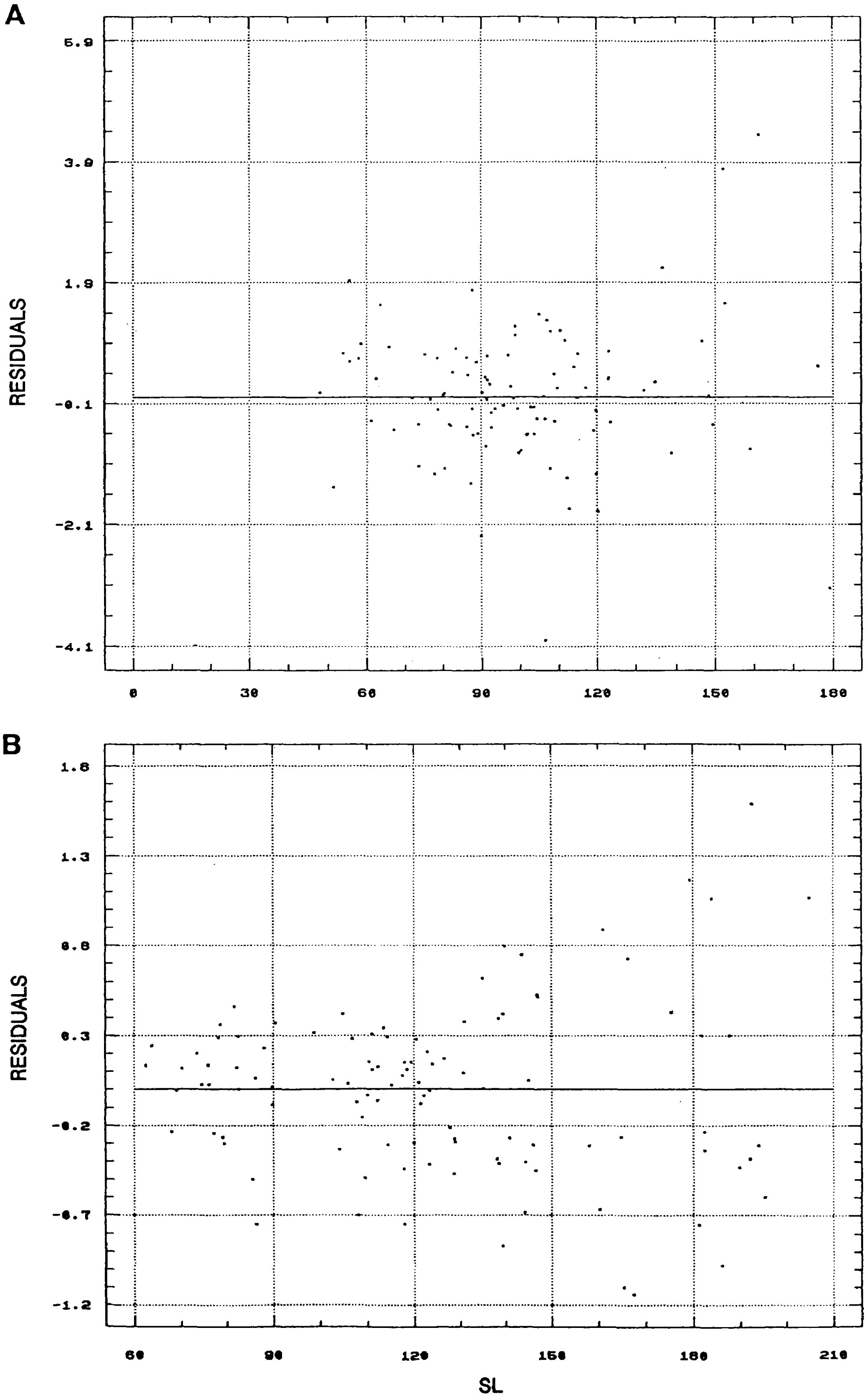

RESIDUALS
2.4
1.4
0.4
-0.6
-1.6
-2.6
79
99
119
139
159
179
SL

Figure 4. Heterogeneity of variance as shown by heteroscedastic residual plots of morphometric characters. A) Residuals from regression of P_2-C on SL for the Massachusetts to Georgia population (NOF); B) Residuals from regression of UJW on SL for the West Indies population (WI).


A
RESIDUALS
5.9
3.9
1.9
-0.1
-2.1
-4.1
0
30
60
90
120
150
180
B
RESIDUALS
1.8
1.3
0.8
0.3
-0.2
-0.7
-1.2
60
90
120
150
180
210
SL

Throughout the ANCOVA's alpha was held at 0.01. It was found that an alpha of 0.05 was too sensitive. This alpha level, of 0.01, was arrived upon by examining the results of ANCOVA's of morphometric characters at both alpha levels of 0.01 and 0.05. Scatter plots and regressions of the morphometric characters against SL found to be significantly different between populations were inspected visually to see if any separation was observable. In this way, it became apparent that an alpha of 0.05 was not useful in this study. This consideration of alpha level was most important in intraspecific comparisons in the analysis of geographic variation. In interspecific comparisons results were more clear cut and obvious. There were few instances of marginal significance between the levels of 0.05 and 0.01.

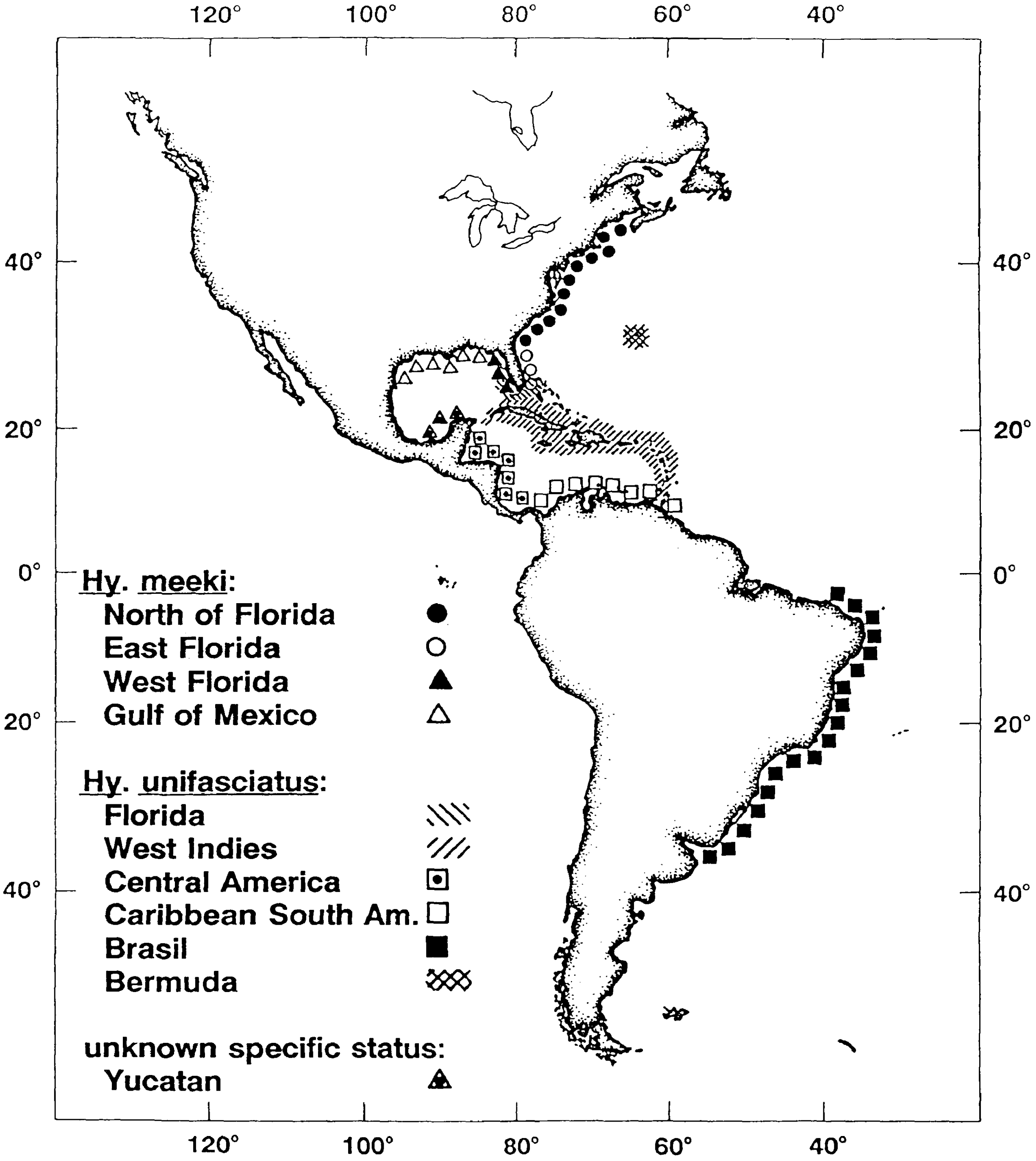
The following abbreviations for geographic areas are used (Fig. 5):

NOF (North of Florida) *Hy. meeki* Massachusetts to Georgia
EFLA (East Florida) *Hy. meeki* Atlantic coast peninsular Florida
WFLA (West Florida) *Hy. meeki* West coast peninsular Florida
GULF (Gulf of Mexico) *Hy. meeki* Florida panhandle through Texas
YUC (Yucatan) uncertain specific status, Yucatan peninsula
UFLA (Florida) *Hy. unifasciatus*, both coasts of peninsular Florida
WI (West Indies) *Hy. unifasciatus*, insular
CAM (Central America) *Hy. unifasciatus*, coastal
CSA (Caribbean South America) *Hy. unifasciatus*, north coast of South America

SAM (South America) *Hy. unifasciatus*, Brazil

BERM (Bermuda) uncertain specific status, at this time referred to as *Hy. unifasciatus*.

Figure 5. Geographic areas used in statistical analyses.



Geographic areas used in statistical analyses

RESULTS

Hyporhamphus meeki Banford and Collette

Plate 1A

Synonymy.--A partial nomenclature of this species is listed here, citing a number of the usages. More combinations and spellings exist. A complete synonymy will be included in the halfbeak section of "Fishes of the western North Atlantic" (Collette pers. comm.).

Hyporhamphus roberti (non Valenciennes, 1846) Jordan and Evermann, 1896 (Newport, RI, Longport and Beesleys Pt., NJ, Beaufort, NC, Charleston, NC, Pensacola, San Sebastian R., and Cedar Keys, FL, New Orleans, LA); Smith, 1907 (Beaufort, NC; common along our Atlantic and Gulf coasts); Jordan et al., 1930 (north to RI).

Hemirhamphus unifasciatius (non Ranzani, 1842) Cope, 1870 (Newport, RI); Jordan and Gilbert, 1878 (Beaufort, NC); Jordan, 1880 (San Sebastian R. FL); Jordan, 1880 (St. John's R., FL); Jordan and Gilbert, 1882 (Charleston, SC); Jordan and Gilbert, 1882 (Pensacola, FL); Goode and Bean, 1882 (Gulf of Mexico).

Plate 1. A) *Hyporhamphus meeki* Banford and Collette, holotype, USNM 294369 (160 mm SL); B) *Hyporhamphus unifasciatus* (Ranzani), USNM 206658 (161 mm SL).

USNM 294369
Hy. meeki
USNM 206658
Hy. unifasciatus
Clay Adams
INCHES
METRIC

Hyporhamphus hildebrandi (non Jordan and Evermann, 1927) Perlmutter, 1961 (W.I. species which occasionally drifts as far north as Cape Cod).

Hyporhamphus unifasciatus (non Ranzani, 1842) Jordan, 1907 (Atlantic coast); Meek and Hildebrand, 1923 (material from Atlantic coast in USNM does not include specimens of *Hy. roberti*); Hildebrand and Schroeder, 1928 (Chesapeake Bay); Jordan et al., 1930 (north to RI and NJ); Miller, 1945 (characters of genus *Hyporhamphus*, species ranges from Uruguay to Cape Cod); Baughman, 1950 (TX); Fowler, 1952 (Longport, Ocean City, Cape May, NJ); Springer and Bullis, 1956 (Gulf of Mexico) Hoese, 1958 (Texas); Leim and Day, 1959 (Chamcook, N.B.); Tagatz and Dudley, 1961 (near Beaufort, NC); Perlmutter, 1961 (Gulf and Atlantic, Brazil to Cape Cod, straggler to ME); Böhlke and Chaplin, 1968 (more species of *Hyporhamphus* than previously thought, follow current usage of name for both populations from east coast of U.S. and West Indies); Musick, 1972 (composite species pending revision by B.B. Collette); Lipson and Moran, 1974 (larvae and juveniles in Chesapeake Bay); Hardy, 1978 (description of eggs, larvae and juveniles from Mid-Atlantic Bight); Houde et al., 1979 (larvae collected in <30m water in eastern Gulf of Mexico); Bruce, 1986 (infested with parasitic isopod *Mothocya nana*, from MD, GA, and FL).

Hemirhamphus roberti (non Valenciennes, 1846) Commissioners of Fisheries, 1876

(Maryland); Meek and Goss, 1884 (Atlantic coast of the U.S. north of the Florida Keys, original statement cited in hypothesis of two species in Introduction of this thesis).

Hyporhamphus meeki, nomen nudem. Bruce, 1986 (infested with *Mothocya nana* from Duval and Levy counties, FL).

Hyporhamphus sp. Schwartz, 1962 (Maryland); Hardy and Johnson, 1974 (larvae and prejuveniles described from Chesapeake Bay); Collette, 1978 (superficially similar with *Hy. unifasciatus*, W. Atlantic along the Gulf and Atlantic coasts of U.S.); Olney and Boehlert, 1988 (eggs and juveniles collected in seagrass (*Zostera* and *Ruppia*) beds in Chesapeake Bay).

Hyporhamphus meeki Banford and Collette 1993 (original description).

Diagnosis.--A member of the subgenus *Hyporhamphus* distinguished from *Hy. roberti* (Valenciennes) by having the dorsal and anal fins covered with scales. This species is distinguished from *Hy. unifasciatus* by the following combination of characters: gill rakers on the first arch 31-40 (Table 1); gill rakers on the second arch 20-30 (Table 2); ratio of preorbital length to orbit diameter is usually greater than 0.70 (>0.70 in 92% of 265 specimens examined).

Table 1. Numbers of total first arch gill rakers on first arch in populations of *Hyporhamphus meeki* and *Hy. unifasciatus*.

Population	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	N	mean
Hy. meeki																	
NOF						2	7	43	64	77	43	13	1	1		251	34.5
EFLA							3	10	15	39	19	9	4	2		101	35.1
WFLA						5	31	61	54	28	12	3				194	33.6
GULF						2	14	28	23	51	32	32	21	3	1	207	35.3
YUC									8	6	9	3	1			27	35.3
Species total						9	55	142	164	198	115	60	27	6	1	780	34.6
Hy. unifasciatus																	
BERM	1	3	13	39	43	11	3									113	29.5
UFLA		1	4	15	30	11	4		1							66	30.0
WI		1	7	16	41	35	44	14	7	5						170	31.1
YUC				3	6	3										12	30.0
CAM			2	9	17	14	6	4	1							53	30.5
CSA			1	17	26	34	20	12	6	3						119	31.1
SAM		3	3	15	26	40	28	8	1							124	30.8
Species total	1	8	30	114	189	148	105	38	16	8						657	30.6

Table 2. Numbers of total gill rakers on second arch in populations of *Hyporhamphus meeki* and *Hy. unifasciatus*.

Population	19	20	21	22	23	24	25	26	27	28	29	30	N	mean
Hy. meeki														
NOF		2				2	11	53	80	33	8		189	26.8
EFLA		2	4	8	2	2	11	29	40	10	6		114	25.9
WFLA						12	50	60	40	14	1		177	26.0
GULF				1	4	11	26	44	53	10	5	2	156	26.2
YUC					1	3	6	10	5	2			27	25.5
Species total														
Hy. unifasciatus														
BERM		5	34	37	17	5	2						100	23.5
UFLA		2	7	10	18	17	5						59	22.9
WI	2		3	11	25	46	37	11	5	1			141	24.1
YUC			1	1	5	4	1						12	23.3
CAM			2	5	10	11	6		1				35	23.5
CSA				6	27	33	23	24	1				114	24.3
SAM			5	16	31	33	21	2	1				109	23.5
Species total	2	7	52	86	133	149	95	37	8	1			570	23.5

Description.--Gill rakers on upper limb of first arch 8 to 12, usually 9 to 11, mean 9.8; lower limb 20 to 29, usually 24 to 27, mean 25.1; total of upper and lower limbs 31 to 40, usually 33 to 37, mean 34.6 (Table 1). Gill rakers on upper limb of second arch 2 to 6, usually 4 or 5, mean 4.3; lower limb 20 to 26, usually 22 or 23, mean 22.3; total 20 to 30, usually 25 to 28, mean 26.2 (Table 2). Dorsal-fin rays 12 to 17, usually 14 or 15, mean 14.5 (Table 3); anal-fin rays 14 to 18, usually 15 to 17, mean 15.9 (Table 4); and pectoral-fin rays 10 to 13, usually 11 or 12, mean 11.4 (Table 5). Predorsal scales (N = 87) 34 to 39, usually 35 to 37, mean 36.1 (Table 6). Vertebrae (N = 88) 31-35 precaudal + 16-19 caudal = 49-53 total (Table 7).

Morphometric data for *Hy. meeki* are summarized in Table 8. Ratio of lower jaw length to head length is 0.79 to 1.54 with 83% of 240 specimens greater than or equal to 1.0. Ratio of LJL to SL 0.20 to 0.35 with 95% of 240 specimens 0.22 to 0.30. PREORB to ORB ratio 0.61 to 1.0, usually 0.70 to 0.90 (92% of 265 specimens). Distance from base of anteriormost pelvic ray to caudal base extends anteriorly to mid-eye, usually between posterior portion of eye and posterior margin of opercular membrane. Dorsal and anal-fin bases about equal, ratio of ABASE to DBASE 0.83 to 1.07, mean 0.96 for 265 specimens. Origin of dorsal-fin over that of anal-fin. Bases of dorsal and anal-fins covered with scales. Distance from anteriormost pectoral ray to origin of pelvic-fin less than the distance from the pelvic-fin origin to the caudal base. Median pore of preorbital canal usually posterior, sometimes medial.

Table 3. Numbers of dorsal-fin rays in populations of *Hyporhamphus meeki* and *Hy. unfasciatus*.

Population	12	13	14	15	16	17	N	mean
Hy. meeki								
NOF		2	100	56	1	1	160	14.4
EFLA		8	40	34	3		85	14.4
WFLA			52	95	10		157	14.7
GULF	1	5	90	65	4		165	14.4
YUC			15	12			27	14.5
Species total	1	15	297	262	18	1	594	14.5
Hy. unifasciatus								
BERM		5	48	27	2		82	14.3
UFLA			14	28	6		48	14.8
WI		1	42	77	7		127	14.7
YUC			1	9	2		12	15.1
CAM			6	35	3		44	14.9
CSA			16	92	10		118	14.9
SAM		1	32	76	11		120	14.8
Species total		7	159	344	41		551	14.8

Table 4. Numbers of anal-fin rays in populations of *Hyporhamphus meeki* and *Hy. unifasciatus*.

Population	14	15	16	17	18	N	mean
Hy. meeki							
NOF	1	18	107	36	1	163	16.1
EFLA	1	31	43	10		85	15.7
WFLA		13	98	45	1	157	16.2
GULF	10	59	80	16		165	15.6
YUC		3	21	3		27	16.0
Species total	12	124	349	110	2	597	15.9
Hy. unifascitus							
BERM		2	21	46	12	81	16.8
UFLA			25	22	1	48	16.5
WI		15	83	29	1	128	16.1
YUC			10	2		12	16.2
CAM		4	27	13		44	16.2
CSA		8	63	47		118	16.3
SAM	1	9	63	45	1	119	16.3
Species total	1	38	292	204	15	550	16.4

Table 5. Numbers of pectoral-fin rays in populations of Hyporhamphus meeki and Hy. unifasciatus.

Population	9	10	11	12	13	N	mean
Hy. meeki							
NOF		2	75	59	3	158	11.4
EFLA		19	70	17		106	11.0
WFLA			49	98		147	11.7
GULF		1	77	41	1	120	11.4
YUC			18	9		27	11.3
Species total		22	289	224	4	558	11.4
Hy. unifascitus							
BERM	3	104				107	10.0
UFLA		19	45	5		69	10.8
WI		39	94	3		136	10.7
YUC			11	1		12	11.1
CAM	2	2	35	2		41	10.9
CSA		9	108	3		120	11.0
SAM		14	104	4		122	10.9
Species total	5	187	397	18		607	10.7

Table 6. Numbers of predorsal scales in populations of Hyporhamphus meeki and Hy. unifasciatus.

Population	33	34	35	36	37	38	39	N	mean
Hy. meeki									
NOF		1	6	13	10			30	36.1
EFLA			1	2	1			4	36.0
WFLA	no counts								
GULF			3	9	5	2	1	20	36.5
YUC		2	5	19	7			33	35.9
Species total		3	15	43	23	2	1	87	36.1
Hy. unifasciatus									
BERM	no counts								
UFLA			1	1	1	1		4	36.5
WI	2	3	9	5	1	1		21	35.1
YUC	no counts								
CAM	no counts								
CSA			6	4	1			11	35.6
SAM				3	6	3		12	37.0
Species total	2	3	16	13	9	5		48	35.8

Table 7. Numbers of pre-caudal, caudal and total vertebrae for populations of *Hyporhamphus meeki* and *Hy. unifasciatus*.

PRE-CAUDAL	32	33	34	35	N	MEAN
Hy. meeki						
EFLA		4	4		8	33.5
YUC	1	8	28	3	40	33.8
Hy. unifasciatus						
WI	2	10			12	32.8
CSA	3	35	9		47	33.1

CAUDAL	17	18	19	N	MEAN
Hy. meeki					
EFLA	3	5		8	17.6
YUC	17	23		40	17.8
Hy. unifasciatus					
WI	3	9		12	17.8
CSA	12	31	4	47	17.8

TOTAL	50	51	52	53	N	MEAN
Hy. meeki						
EFLA	1	5	2		8	51.1
YUC	2	22	14	2	40	51.4
Hy. unifasciatus						
WI	5	7			12	50.6
CSA	6	37	4		47	51.0

Table 8. Summary of morphometric data in percent standard length in populations of _Hyporhamphus_ _meeki_, except for SL in mm.

CHARACTER % SL	ATLANTIC						GULF OF MEXICO					
	N	MIN	MAX	MEAN	SD	SE	N	MIN	MAX	MEAN	SD	SE
SL	169	48.1	179	96.7	27.16	2.09	124	63.6	176	128.9	23.81	2.14
P1-P2	169	31.8	37.8	34.5	1.01	0.08	124	31.7	38.1	34.6	1.09	0.10
P2-C	169	39.2	46.2	43.0	1.04	0.08	124	41.3	45.7	43.6	0.91	0.08
LJL	161	20.6	35.1	27.0	2.32	0.18	107	20.5	29.8	23.9	1.88	0.18
HDL	169	19.1	34.4	24.4	1.27	0.10	124	21.9	26.0	23.7	0.76	0.07
UJL	169	2.2	4.8	4.2	0.32	0.02	124	3.7	4.8	4.3	0.23	0.02
UJW	169	4.3	6.2	5.2	0.32	0.02	124	4.7	5.8	5.2	0.21	0.02
BDP1O	169	8.6	13.1	11.7	0.79	0.06	124	10.1	13.3	11.9	0.62	0.06
BDP2O	169	7.2	15.9	11.4	1.62	0.12	124	9.0	15.3	12.9	1.20	0.11
ABASE	169	12.3	17.3	14.4	0.79	0.06	124	12.5	16.0	13.9	0.72	0.06
DBASE	169	13.3	16.9	14.8	0.67	0.05	124	13.2	16.4	14.6	0.67	0.06
P1L	161	12.3	16.4	14.6	0.72	0.06	109	13.1	16.3	14.5	0.64	0.06
ORB	169	4.8	7.1	5.9	0.41	0.03	124	5.0	6.9	5.7	0.39	0.03
PREORB	169	3.4	6.1	4.5	0.28	0.02	124	3.4	5.2	4.2	0.30	0.03

Color.--Coloration in life is a silvery light tan-green. The fleshy tip of the lower jaw is a bright orange red.

Size.--Adults attain a maximum size of 179 mm SL (USNM 90798, Cape Charles, VA).

Habitat.--All specimens observed were collected at the surface of inshore or estuarine waters. I collected specimens in the Chesapeake Bay and the Gulf of Mexico (Florida) in areas with a sandy substrate and in proximity of submerged aquatic vegetation (eel grass, *Zostera*; and turtle grass, *Thallassia*). As is often the case in estuarine conditions, the water inhabited by Hy. meeki is generally turbid.

Biology and Early Life History.--Larvae of *Hy. meeki* have been described (as *Hyporhamphus* sp.) from Chesapeake Bay, which may indicate utilization of estuarine waters as nursery areas (Hardy and Johnson, 1974). Larvae were collected along the Gulf coast of Florida most frequently during spring and summer in less than 30 m of water (Houde et al., 1979). The specifics of spawning are unknown. Eggs with adhesive filaments have been found on floating *Zostera* over vegetated habitats during summer months in Chesapeake Bay (Olney and Boehlert, 1988).

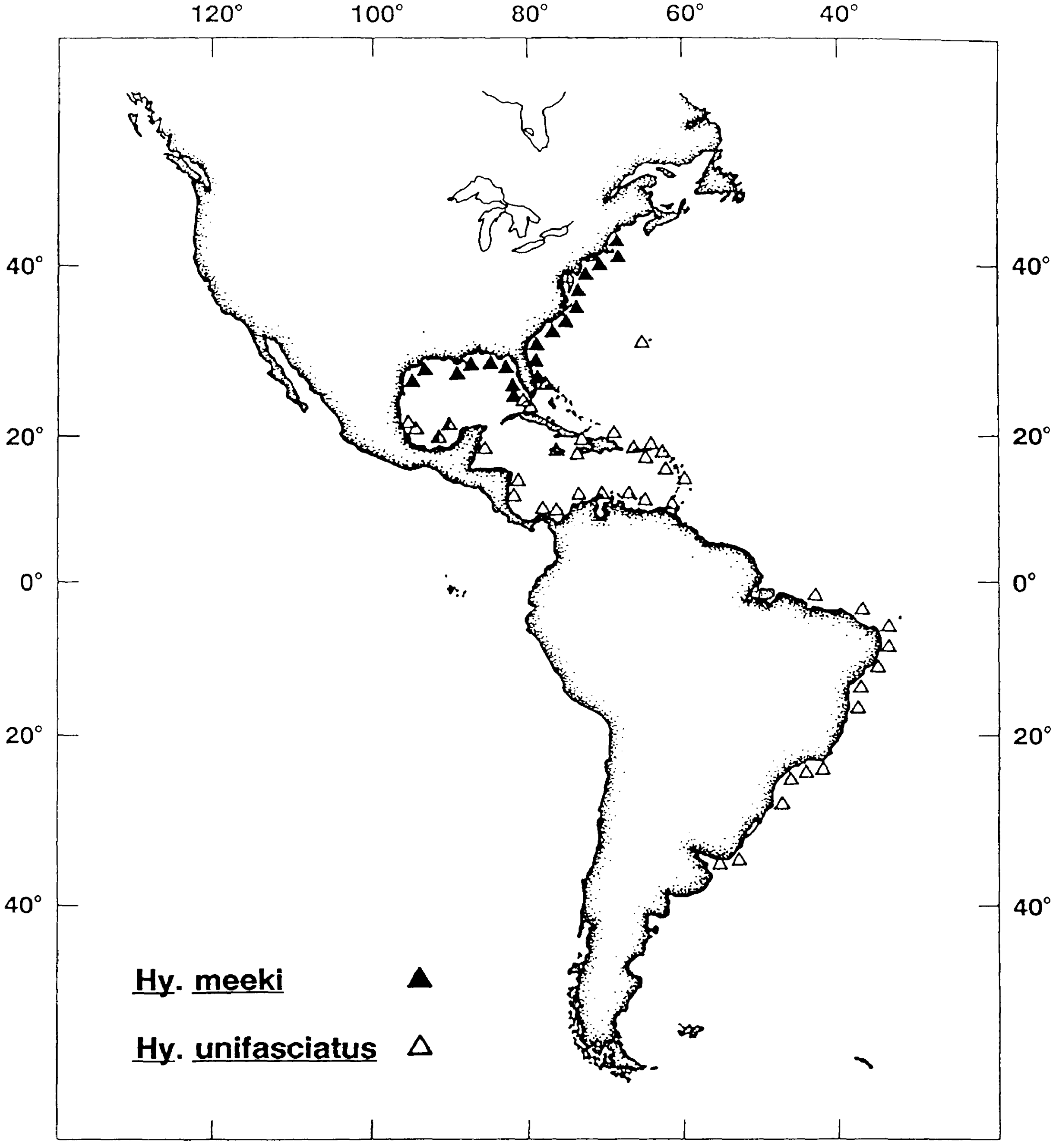
Stomachs of adults contained small crustaceans, mollusks and vegetable matter (Hildebrand and Schroeder, 1928). In a study of feeding habits of fishes in seagrass beds near Crystal River, Florida, adult *Hyporhamphus* stomachs contained fresh seagrass, epiphytic algae and detritus (Carr and Adams, 1973). A stomach of a single juvenile specimen contained crab megalope and veligers, copepods and insect remains. Based on behavioral observations of these fish they (Carr and Adams) suggest that seagrass is gathered and ingested at the surface, along with associated epiphytes and detritus. It is uncertain as to which species, *Hy. meeki* or *Hy. unifasciatus*, were analyzed in the above study by Carr and Adams, for the collections were made throughout the year (Oct. 1970 - Aug. 1971) and *Hy. unifasciatus* may stray that far north during the summer months.

Distribution.--Atlantic coast of the United States from Miami, FL to Cape Cod, MA, and rarely north to Chamcook, New Brunswick (Leim and Day, 1959) and in the Gulf of Mexico from the Everglades to Galveston, TX (Fig. 6). Also occurs in Yucatan. The observed water temperature range is 13.7 to 34.9° C, so *Hy. meeki* has a subtropical to temperate distribution. Sympatric with *Hy. unifasciatus* on the east coast of Florida from St. Lucie Inlet south to Miami and on the west coast from the Everglades to Tampa Bay.

Etymology.--Named after Seth E. Meek who first separated the two species (Meek and Goss, 1884)..."all specimens taken off the Atlantic coast of the U.S. north of the Florida Keys belong to a species different from the West Indian *unifasciatus* in slenderness of body and greater length of the lower jaw" but mis-applied the name *Hy. roberti* to the northern species.

Comparisons.--Meristic characters allow for the statistical separation of *Hy. meeki* from *Hy. unifasciatus* (alpha = 0.05; Tables 9-13), though intraspecific variation exists within populations of both species. *Hyporhamphus meeki* is discernable from the southern species *Hy. unifasciatus* in usually having more gill rakers on both the first and second arches (Tables 1 and 2). Ninety two percent of the 780 *Hy. meeki* specimens examined have total RGR_1 counts from 33 to 40, while in *Hy. unifasciatus* 91% of 657 specimens examined have total RGR_1 counts from 26 to 32.

Figure 6. Distribution of *Hyporhamphus meeki* (closed triangles), *Hy. unifasciatus* (open triangles), and area of potential hybridization and introgression (partial open closed triangles), based on material examined.



Ranges of Hyporhamphus meeki and Hyporhamphus unifasciatus

Table 9. Comparison of means for dorsal-fin ray counts for populations of *Hyporhamphus meeki* and *Hy. unifasciatus*, and between *Hy. meeki* and *Hy. unifasciatus*. Populations joined by the same line are not significantly different by the Tukey-Kramer method, alpha = 0.05.

Population	N	MEAN	TK		
Hy. meeki					
West peninsula of FL	157	14.7		│	
Yucatan	26	14.5		│	│
FL panhandle to TX	165	14.4			│
Atlantic coast of FL	85	14.4			│
MA to GA	160	14.4			│
Hy. unifasciatus					
Yucatan	12	15.1	│		
Caribbean South America	118	14.9	│	│	
Central America	44	14.9	│	│	
Florida	48	14.8	│	│	
South America (Brazil)	120	14.8	│	│	
West Indies	127	14.7		│	
Bermuda	82	14.3			│
Hy. meeki	594	14.5	│		
Hy. unifasciatus	551	14.8		│	

Table 10. Comparison of means for anal-fin raycounts for populations of *Hyporhamphus meeki* and *Hy. unifasciatus*, and between *Hy. meeki* and *Hy. unifasciatus*. Populations joined by the same line are not significantly different by the Tukey-Kramer method, alpha = 0.05.

Population	N	MEAN	TK		
Hy. meeki					
West peninsula of FL	157	16.2	│		
MA to GA	163	16.1	│		
Yucatan	26	16.0	│		│
Atlantic coast of FL	85	15.7		│	│
FL panhandle to TX	165	15.6		│	
Hy. unifasciatus					
Bermuda	81	16.8	│		
Florida	48	16.5	│	│	
Caribbean South America	118	16.3		│	
South America (Brazil)	119	16.3		│	
Central America	44	16.2		│	
Yucatan	12	16.2		│	
West Indies	128	16.1		│	
Hy. meeki	597	15.9	│		
Hy. unifasciatus	550	16.4		│	

Table 11. Comparison of means for pectoral-fin ray counts for populations of *Hyporhamphus meeki* and *Hy. unifasciatus*, and between *Hy. meeki* and *Hy. unifasciatus*. Populations joined by the same line are not significantly different by the Tukey-Kramer method, alpha = 0.05.

Population	N	MEAN	TK		
Hy. meeki					
West peninsula of FL	147	11.7	│		
MA to GA	158	11.4	│	│	
FL panhandle to Texas	120	11.4		│	
Yucatan	26	11.3		│	
Atlantic coast of FL	106	11.0			│
Hy. unifasciatus					
Yucatan	12	11.1	│		
Caribbean South America	120	11.0	│	│	
South America (Brazil)	122	10.9	│	│	
Central America	41	10.9	│	│	
Florida	69	10.8		│	
West Indies	136	10.7		│	
Bermuda	107	10.0			│
Hy. meeki	558	11.4	│		
Hy. unifasciatus	607	10.7		│	

Table 12. Comparison of means for total first arch gill raker counts for populations of *Hyporhamphus meeki* and *Hy. unifasciatus*, and between *Hy. meeki* and *Hy. unifasciatus*. Populations joined by the same line are not significantly different by the Tukey-Kramer method, alpha = 0.05.

Population	N	MEAN	TK		
Hy. meeki					
Yucatan	26	35.3	│		
FL panhandle to TX	207	35.2	│		
Atlantic coast of FL	101	35.1	│	│	
MA to GA	255	34.5		│	
West peninsula of FL	194	33.6			│
Hy. unifasciatus					
Caribbean South America	119	31.1	│		
West Indies	170	31.1	│		
South America (Brazil)	124	30.6	│	│	
Central America	53	30.5	│	│	
Yucatan	12	30.0		│	│
Florida	66	30.0		│	│
Bermuda	113	29.5			│
Hy. meeki	780	34.6	│		
Hy. unifasciatus	657	30.6		│	

Table 13. Comparison of means for total second arch gill raker counts for populations of *Hyporhamphus meeki* and *Hy. unifasciatus*, and between *Hy. meeki* and *Hy. unifasciatus*. Populations joined by the same line are not significantly different by the Tukey-Kramer method, alpha = 0.05.

Population	N	MEAN	TK		
Hy. meeki					
MA to GA	189	26.8	|		
FL panhandle to TX	156	26.2		|	
West peninsula of FL	177	26.0		|	
Atlantic coast of FL	114	25.9		|	
Yucatan	38	25.5			|
Hy. unifasciatus					
Caribbean South America	114	24.3	|		
West Indies	141	24.1	|		
South America (Brazil)	109	23.5	|	|	
Central America	35	23.5	|	|	
Yucatan	12	23.3		|	
Florida	59	22.9		|	
Bermuda	100	21.9			|
Hy. meeki	662	26.2	|		
Hy. unifasciatus	570	23.5		|	

Second arch gill rakers in 76% of 662 specimens of *Hy. meeki* range from 26 to 30, whereas 92% of 570 specimens of *Hy. unifasciatus* range from 19 to 25. Pectoral fin usually with 11 or 12 rays, mean 11.4, 10 or 11, mean 10.7 in *Hy. unifasciatus* (Tables 3-5). Though only of a statistical nature and not useful in separating the two species, dorsal and anal fin ray counts are significantly different. Mean dorsal fin ray counts are 14.5 in *Hy. meeki*, 14.8 in *Hy. unifasciatus* (Table 3). Mean anal fin ray counts are 15.9 in *Hy. meeki*, 16.4 in *Hy. unifasciatus* (Table 4).

Regressions of morphometrics also allow distinguishing the two species. This is best illustrated in the preorbital on orbit relationship (Fig. 7). The slopes of the regressions are significantly different (prob>F > .001). Ratio of preorbital length to orbit diameter is usually greater than 0.70 in *Hy. meeki* (92% of 265 specimens examined), but less than 0.70 in *Hy. unifasciatus* (75% of 224 specimens). Lower jaw length on standard length tends to be greater in *Hy. meeki* (Fig. 8). However, there is considerable intraspecific variation within populations of the two species especially in *Hy. unifasciatus* (see Geographic Variation within *Hy. unifasciatus*).

Regressions of morphometric characters on SL were compared between species of *Hy. meeki* and *Hy. unifasciatus* with ANCOVA. Due to high levels of intraspecific variation, populations from Yucatan and Bermuda were omitted from this analysis (see Geographic Variation). Eleven of thirteen morphometric characters were found to have either significantly different slopes or means for the two species (Table 14). Only P_2-C and DBASE were found not to have significantly different adjusted least squares means for the two species.

Figure 7. Relationship of preorbital length to orbit length in *Hyporhamphus meeki* (squares) and *Hyporhamphus unifasciatus* (triangles).

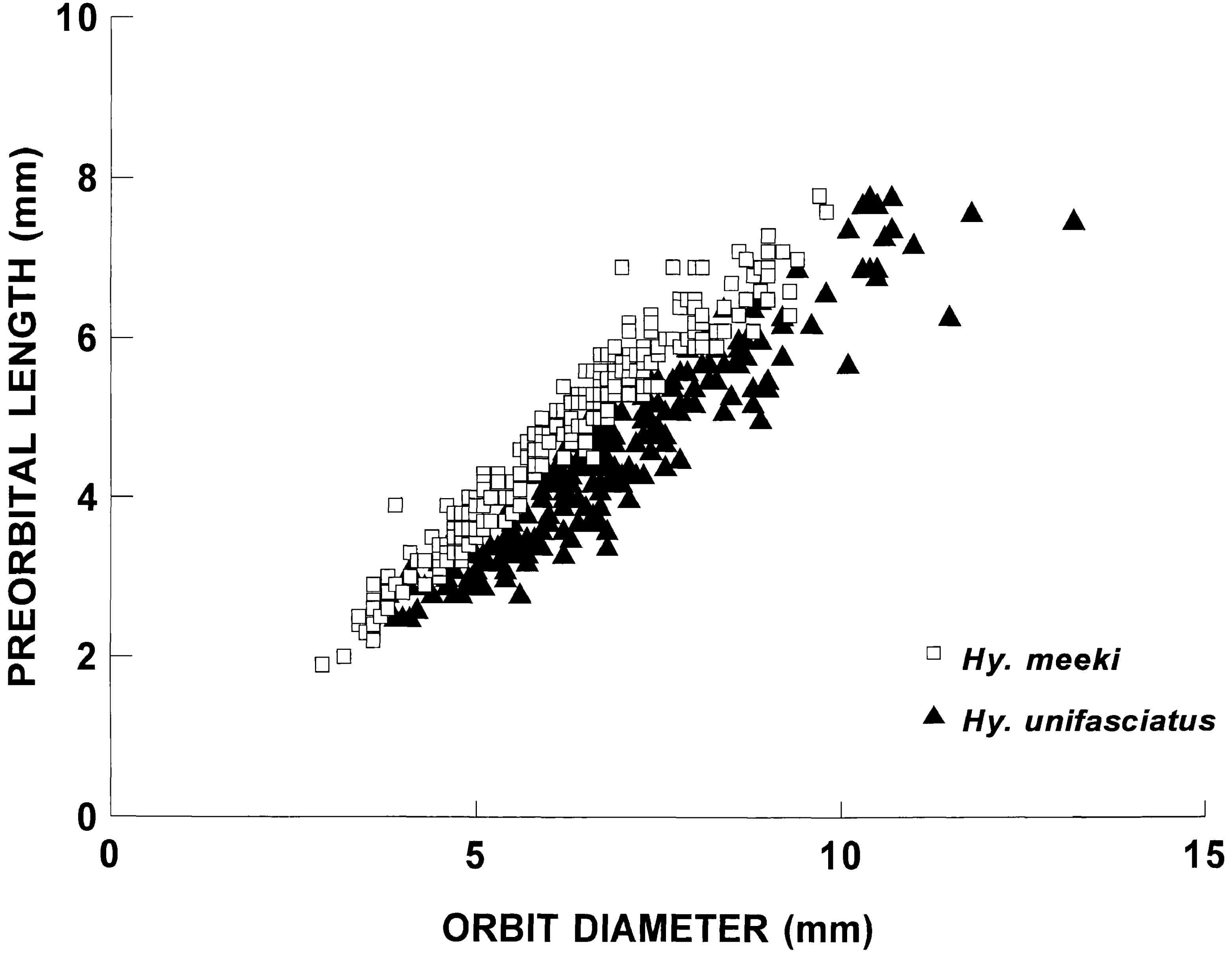

PREORBITAL LENGTH (mm)
0
2
4
6
8
10
ORBIT DIAMETER (mm)
0
5
10
15
□ Hy. meeki
▲ Hy. unifasciatus

Figure 8. Relationship of lower jaw length to standard length in *Hyporhamphus meeki* (squares) and two populations of *Hyporhamphus unifasciatus* Central and South America (triangles) and West Indies (diamonds).

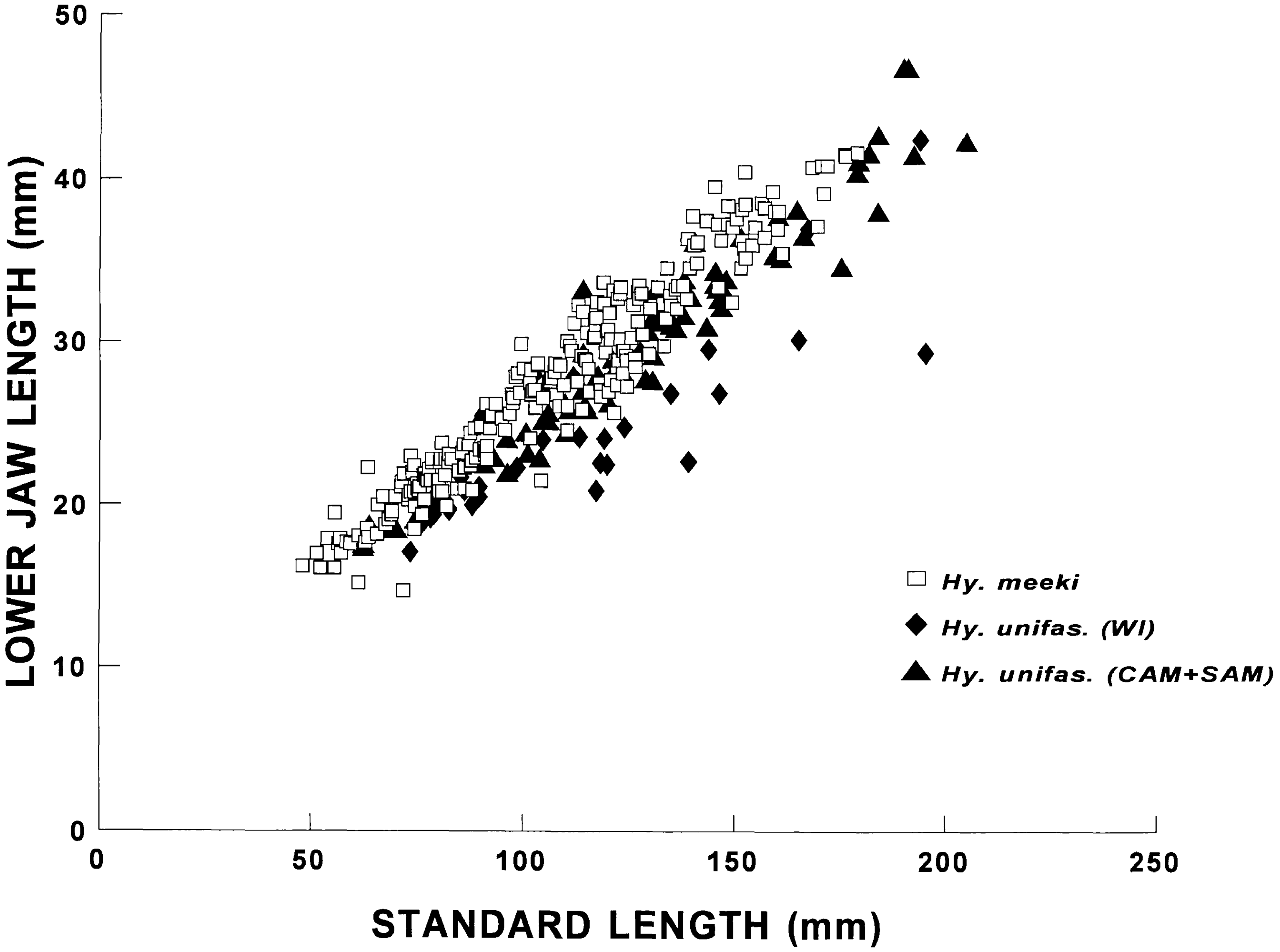

LOWER JAW LENGTH (mm)
0
10
20
30
40
50
STANDARD LENGTH (mm)
0
50
100
150
200
250
□ Hy. meeki
◆ Hy. unifas. (WI)
▲ Hy. unifas. (CAM+SAM)

Table 14. Analysis of covariance with two treatments, *Hyporhamphus meeki* (M) and *Hy. unifasciatus* (U). No Yucatan nor Bermudian specimens included.

CHARACTER	SPECIES	Y=	R-SQUARED	N		F	P
P1-P2	U	1.034x-0.523	0.984	155	REGRESSION	18875.21	<.001**
	M	1.037x-0.537	0.991	265	SLOPES	5.84	0.016
					MEANS	35.23	<.001**
P2-C	U	0.983x-0.327	0.989	155	REGRESSION	13115.31	<.001**
	M	1.005x-0.375	0.994	265	SLOPES	0.07	0.787
					MEANS	3.50	0.062
LJL	U	0.771x-0.158	0.872	133	REGRESSION	1188.46	<.001**
	M	0.770x-0.122	0.925	240	SLOPES	0.00	0.978
					MEANS	98.27	<.001**
HDL	U	1.018x-0.680	0.976	155	REGRESSION	5758.59	<.001**
	M	0.959x-0.534	0.976	265	SLOPES	14.04	<.001**
					MEANS		
UJL	U	1.122x-1.658	0.948	155	REGRESSION	2749.33	<.001**
	M	1.082x-1.543	0.953	265	SLOPES	2.53	0.112
					MEANS	87.73	<.001**
UJW	U	1.199x-1.685	0.959	155	REGRESSION	4650.46	<.001**
	M	1.075x-1.431	0.976	265	SLOPES	36.62	<.001**
					MEANS		
BDP1O	U	1.297x-1.544	0.957	155	REGRESSION	4811.29	<.001**
	M	1.144x-1.218	0.980	265	SLOPES	50.65	<.001**
					MEANS		
BDP2O	U	1.574x-2.115	0.934	155	REGRESSION	2787.64	<.001**
	M	1.400x-1.732	0.963	265	SLOPES	25.86	<.001**
					MEANS		
ABASE	U	0.827x-0.493	0.951	154	REGRESSION	3982.44	<.001**
	M	0.887x-0.619	0.971	265	SLOPES	11.78	<.001**
					MEANS		
DBASE	U	0.926x-0.679	0.976	155	REGRESSION	6780.90	<.001**
	M	0.934x-0.697	0.980	265	SLOPES	0.25	0.614
					MEANS	3.31	0.070
P1L	U	1.078x-1.002	0.961	134	REGRESSION	4371.13	<.001**
	M	1.009x-0.854	0.975	254	SLOPES	12.64	<.001**
					MEANS		
ORB	U	0.919x-1.069	0.947	155	REGRESSION	2970.26	<.001**
	M	0.827x-0.888	0.956	265	SLOPES	21.44	<.001**
					MEANS		
PREORB	U	0.976x-1.365	0.946	155	REGRESSION	2986.54	<.001**
	M	0.936x-1.222	0.961	265	SLOPES	3.57	0.060
					MEANS	500.02	<.001**

Material examined.-- 338 specimens of *Hy. meeki* (48.1-179 mm SL) from 50 collections, with almost complete morphometric and meristic data, are listed. Data from additional specimens used mainly for meristics are in Bruce Collette's files.

Holotype - USNM 294369 (1, 160) Morehead City, NC; 5 Sept 1964.

ATLANTIC U.S. (paratypes): 71 specimens (51.5-179) from 20 collections. USNM 132257 (4, 55.7-115) Woods Hole, MA; 2 Sept 1876. USNM 68368 (5, 54-65.8) Great South Bay, NY; 1898. USNM 187214 (2, 73.6-98.9) Deep Cove, Indian R., DE; 7 Sept 1956. VIMS-CBL 173 (2, 123-108) CBL Pier, MD; 21 Jul 1936. VIMS-CBL 1523 (11, 73.6-91.1) Broomes I., Patuxent R., MD; 13 Aug 1958. USNM 90798 (1, 179) Cape Charles, VA. VIMS 00061 (21, 87.6-123) Lynnhaven Inlet, Broad Bay, VA; 29 Sept 1954. VIMS 607 (7, 78.5-159) York R., VA; 18 Jul 1970. USNM 131146 (1, 147) Cape Charles, VA. USNM 131146 (4, 102-117) Morehead City, NC; 5 Sept 1964; taken with the holotype. VIMS-CBL 3571 (1, 51.5) Morehead City, NC; 9 Jul 1967. USNM 51878 (1, 153) Beaufort, NC. VIMS 7873 (3, 71.9-115) Carteret Co., Atlantic Ocean beach, NC; 12 Sept 1976. USNM 294396 (1, 150) SC, 32°26' N, 79°50'W; 6 Aug 1953. USNM 149969 (1, 107) Georgia coast. USNM 294377 (2, 99.7-104) St. Simons I., GA; 15 Mar 1956. USNM 294426 (1, 119) St. Simons I., GA; 14 Apr 1960. USNM 294427 (1, 105) St. Simons I., GA; 16 Nov 1955. USNM 294441 (1, 160) St. Simons I., GA; 11 Nov 1956. USNM 294435 (1, 55.6) off Savannah, GA, 31° 41'N, 80°35'W; 21 Oct 1953.

Other material examined: ATLANTIC U.S.: VIMS uncat. (56, 48.1-146), Gloucester Pt., York R., VA; 19 Jul 1989 to 17 Sept 1989.

ATLANTIC FLORIDA: 62 specimens (52.3-145) from 6 collections. UF 62140 (1, 125) 4.5 miles N. of Jupiter Inlet; 21 Aug 1964. UF 77037 (2, 111-127) Matheson Hammock; 11 Jul 1970. UF 83999 (20, 59.4-97.8) Indian R., Brevard Co.; 16 Aug 1976. USNM 294365 (4, 55.8-141) Off New Smyrna Bch., 29°00'N, 80°32'W; 14 Oct 1953. USNM 294397 (19, 52.3-119) 29°40'N, 81°06'W; 15 Oct 1953. USNM 294494 (16, 91.4-145) 27°52'N, 80°26'W; 20 Jan 1961.

GULF COAST FLORIDA: 82 specimens (50.1-171) from 10 collections. UF 1010 (9, 63.6-88.1) Cedar Key; 24 Jul 1948. UF 51083 (5, 71.8-135) Alligator Harbor; 7 Sept 1954. UF 52066 (5, 146-170) Alligator Harbor; 16 May 1954. UF 68483 (6, 114-148) St. Andrew's Bay, Panama City; 8 Oct 1968. UF 76904 (24, 50.1-74.2) 1 mile N of Lee-Collier Co. line; 18 Jun 1966. USNM 125446 (2, 139-153) Tarpon Springs; 5 Nov 1896. USNM 184268 (4, 133-146) Johns Pass, Madeira Bch.; 29 Sept 1958. USNM 294431 (5, 103-136) Sarasota; 24 Aug 1967. USNM 294452 (16, 119-134) Sanibel I., FL; 11 Aug 1959. USNM 294489 (6, 149-171) Sanibel I.; 8 Aug 1964.

GULF COAST U.S., ALABAMA - TEXAS: 39 specimens (69.1-176) from 10 collections. USNM 187122 (2, 151-152) S Mobile, AL; 7 Jul 1960. VIMS 5095 (1, 113) Pelican Bay, Dauphin I., AL; 29 Aug 1974. USNM 147781 (1, 176) Mississippi Gulf coast; 1948. USNM 187120(2, 123-128) inside Chandeleur Sound, LA; 19 Aug 1959. USNM 187123 (1, 73.9) Grande Isle, LA; 21 Jul 1930. USNM 94546 (1, 141) Corpus Christi, TX. USNM 103390 (1, 69.1) near Corpus Christi, TX; 1937. USNM 120056 (2, 128-155) Galveston, TX; 1941. USNM 187119 (2, 168-172) Corpus Christi, Shamrock Cove, TX; 7 Apr 1927. USNM 294440 (26, 100.5-152) Aransas Pass, Institute of Marine Science pier, TX; ~4 Mar 1959.

YUCATAN: 46 specimens (64.2-183) in 3 collections. UMMZ 143085 (28, 94.2-145) west of Progreso; 28 Mar to 1 Apr 1936. UMMZ 143087 (15, 64.2-152) Chicxulub, near Progreso; 1 Apr 1936. MCZ 32881 (3, 142-183) Yucatan; 1906.

Geographic Variation within *Hyporhamphus meeki*

Inspection of meristic frequency tables and comparisons of meristic means by the Tukey-Kramer method indicate some geographic variability in populations of *Hy. meeki* (Tables 9-13). Specimens from the west coast of the Florida peninsula have the highest mean dorsal, anal and pectoral fin ray counts with 14.7, 16.2 and 11.7 respectively (Tables 9-11). Yucatan has intermediate counts for these meristic characters, with a mean dorsal fin ray count of 14.5, a mean anal fin ray count of 16.0, and a mean pectoral fin ray count of 11.3. The Atlantic coast of Florida usually exhibits low mean dorsal, anal, and pectoral fin ray counts, with 14.4, 15.7, and 11.0 respectively. The Florida panhandle to Texas has intermediate mean counts for both dorsal and pectoral fin rays, with 14.4 and 11.4 respectively; but drops to the lowest for the anal fin ray counts with a mean of 15.6. Massachusetts to Georgia shows no consistent trend, with its dorsal mean the lowest at 14.4, anal mean second highest at 16.1, and pectoral mean second highest at 11.4.

In both RGR_1 and RGR_2 (Tables 1 and 2) counts there appears to be no trend. One interesting point to be made is that Yucatan's mean RGR_1 count is the highest with a mean of 35.3, while for RGR_2 it is the lowest with a mean of 25.5. The potential for hybridization and introgression in Yucatan is included in the discussion.

Meristic clinal variation with latitude (i.e. water temperature) is not strongly indicated. Though along the Atlantic coast of the U.S. from Massachusetts to Florida, the Massachusetts to Georgia population (NOF) usually has higher mean meristic counts then the East coast of Florida population (EFLA). However in two of five cases this difference is not significant (RGR_1 and DOR). In the Gulf of Mexico traversing from Texas eastward, only RGR_1 counts are significantly greater in the northern Gulf (GULF, mean of 35.2) than along the west coast of peninsular Florida (WFLA, mean of 33.6). The other meristic character means are either not significant or show the reverse trend.

One way analysis of covariance of four geographic populations (treatments) of *Hy. meeki* indicated some intraspecific variability on a geographic scale (Table 15). The four populations are those used in the meristic analysis, NOF, EFLA, WFLA, GULF (Fig. 5). Slopes of morphometric character regressions found to be significantly different (alpha = 0.01) are, lower jaw length (LJL), head length (HDL), upper jaw length (UJW), and pectoral fin length (P_1L). In all other morphometric characters ANCOVA was continued to test for differences in means. The means were significantly different except for pectoral to pelvic distance (P_1-P_2), pectoral fin length (P_1L), and orbit diameter (ORB).

Table 15. Analysis of covariance with four treatments, populations of *Hyporhamphus meeki* (NOF, EFLA, WFLA, and GULF).

CHARACTER	POP.	Y=	R-SQUARED	N		F	P
P1-P2	NOF	1.057x-0.575	0.991	107	REGRESSION	4785.80	<.001**
	EFLA	1.021x-0.505	0.993	62	SLOPES	2.33	0.075
	WFLA	1.026x-0.523	0.985	42	MEANS	74.08	<.001**
	GULF	1.064x-0.593	0.981	54			
P2-C	NOF	0.997x-0.361	0.991	107	REGRESSION	6477.16	<.001**
	EFLA	0.982x-0.329	0.994	62	SLOPES	1.66	0.177
	WFLA	1.014x-0.387	0.994	42	MEANS	8.57	<.001**
	GULF	1.019x-0.402	0.988	54			
LJL	NOF	0.737x-0.051	0.919	101	REGRESSION	533.86	<.001**
	EFLA	0.847x-0.264	0.958	60	SLOPES	6.91	<.001**
	WFLA	0.847x-0.305	0.953	38	MEANS		
	GULF	0.922x-0.443	0.870	41			
HDL	NOF	0.995x-0.606	0.957	107	REGRESSION	1652.07	<.001**
	EFLA	0.999x-0.610	0.986	62	SLOPES	4.25	0.006**
	WFLA	0.917x-0.446	0.985	42	MEANS		
	GULF	0.903x-0.424	0.980	54			
UJL	NOF	1.154x-1.694	0.934	107	REGRESSION	852.64	<.001**
	EFLA	1.078x-1.525	0.964	62	SLOPES	6.76	<.001**
	WFLA	0.982x-1.341	0.954	42	MEANS		
	GULF	0.961x-1.281	0.935	54			
UJW	NOF	1.108x-1.496	0.967	107	REGRESSION	1686.23	<.001**
	EFLA	1.143x-1.558	0.980	62	SLOPES	3.98	0.009**
	WFLA	1.025x-1.326	0.984	42	MEANS		
	GULF	1.045x-1.376	0.958	54			
BDP1O	NOF	1.163x-1.250	0.978	107	REGRESSION	2072.18	<.001**
	EFLA	1.148x-1.232	0.972	62	SLOPES	1.27	0.284
	WFLA	1.122x-1.166	0.978	42	MEANS	10.75	<.001**
	GULF	1.098x-1.129	0.974	54			
BDP2O	NOF	1.391x-1.708	0.958	107	REGRESSION	1116.14	<.001**
	EFLA	1.399x-1.746	0.952	62	SLOPES	0.95	0.415**
	WFLA	1.358x-1.625	0.971	42	MEANS	13.47	<.001**
	GULF	1.298x-1.524	0.927	54			
ABASE	NOF	0.864x-0.575	0.963	107	REGRESSION	1424.04	<.001**
	EFLA	0.924x-0.690	0.979	62	SLOPES	2.37	0.072
	WFLA	0.915x-0.665	0.954	42	MEANS	11.72	<.001**
	GULF	0.914x-0.686	0.961	54			
DBASE	NOF	0.897x-0.628	0.981	107	REGRESSION	2129.56	<.001**
	EFLA	0.911x-0.656	0.977	62	SLOPES	3.04	0.309**
	WFLA	0.980x-0.782	0.970	42	MEANS	11.23	<.001**
	GULF	0.925x-0.678	0.960	54			
P1L	NOF	1.001x-0.839	0.964	100	REGRESSION	1512.79	<.001**
	EFLA	1.089x-1.007	0.984	61	SLOPES	1.78	0.152
	WFLA	0.997x-0.826	0.960	42	MEANS		
	GULF	0.955x-0.745	0.958	51			
ORB	NOF	0.826x-0.890	0.937	107	REGRESSION	871.22	<.001**
	EFLA	0.901x-1.026	0.973	62	SLOPES	4.82	0.003**
	WFLA	0.752x-0.726	0.926	42	MEANS		
	GULF	0.801x-0.835	0.922	54			
PREORB	NOF	0.976x-1.298	0.942	107	REGRESSION	986.81	<.001**
	EFLA	0.993x-1.329	0.967	62	SLOPES	2.86	0.037
	WFLA	0.890x-1.130	0.957	42	MEANS	4.62	0.004**
	GULF	0.898x-1.150	0.963	54			

To ascertain what specific geographic populations differed in slopes or least squares means adjusted for the covariate standard length, a priori contrasts were run (Table 16). With three contrasts allowable between geographic areas, the following were chosen, NOF versus EFLA, EFLA versus WFLA, and WFLA versus GULF. The contrast of geographic areas NOF versus EFLA showed upper jaw length and both body depth (P_1O and P_2O) means to be significantly different. Additionally, lower jaw length (LJL), and pectoral fin length (P_1L) regression slopes are significantly different. The contrasts of geographic areas EFLA versus WFLA and WFLA versus GULF show the greatest amount of intraspecific difference. In EFLA versus WFLA contrast, upper jaw width (UJW) and orbit (ORB) slopes were significantly different. The following means were significantly different: pectoral to pelvic (P_1-P_2), pelvic to caudal (P_2-C), lower jaw length (LJL), body depth at both pectoral and pelvic fin origins (P_1O,P_2O), anal fin base (ABA), and dorsal fin base (DBA). A similar amount of intraspecific difference was found between WFLA and GULF, where pectoral to pelvic (P_1-P_2), lower jaw length (LJL), head length (HDL), upper jaw width (UJW), body depth at both pectoral and pelvic fin origins (P_1O and P_2O), and dorsal fin base (DBASE), means are significantly different.

Subsequently, with the adjustment of degrees of freedom for previous analysis, ANCOVA was performed on Atlantic (NOF+EFLA) versus Gulf (WFLA+GULF) populations of *Hy. meeki* (Table 17). All regressions were highly significant, (>.95). Again, intraspecific variation is present between populations. The least squares adjusted means of P_2-C, HDL, UJW, DBASE, and PREORL; and slopes of the LJL regressions are significantly different.

Table 16. Slopes and least squares means contrasts between four populations of *Hyporhamphus meeki*.

CHARACTER	POP.	F	SLOPES P	LSMEANS P
P1-P2	NOF v EFLA	4.93	0.027	0.831
	EFLA v WFLA	0.06	0.811	<.001**
	WFLA v GULF	2.05	0.153	<.001**
P2-C	NOF v EFLA	1.26	0.262	0.042
	EFLA v WFLA	2.97	0.086	0.006**
	WFLA v GULF	0.05	0.830	0.033
LJL	NOF v EFLA	9.58	0.002**	
	EFLA v WFLA	0.00	0.997	<.001**
	WFLA v GULF	1.54	0.216	<.001**
HDL	NOF v EFLA	0.02	0.891	0.970
	EFLA v WFLA	5.40	0.021	0.690
	WFLA v GULF	0.11	0.736	0.009**
UJL	NOF v EFLA	3.63	0.058	0.001**
	EFLA v WFLA	3.00	0.084	0.012
	WFLA v GULF	0.10	0.748	0.089
UJW	NOF v EFLA	1.51	0.220	0.120
	EFLA v WFLA	9.08	0.003**	
	WFLA v GULF	0.17	0.677	0.005**
BDP1O	NOF v EFLA	0.32	0.575	<.001**
	EFLA v WFLA	0.45	0.501	0.001**
	WFLA v GULF	0.29	0.590	<.001**
BDP2O	NOF v EFLA	0.03	0.868	<.001**
	EFLA v WFLA	0.41	0.522	<.001**
	WFLA v GULF	0.66	0.416	<.001**
ABASE	NOF v EFLA	5.62	0.019	0.335
	EFLA v WFLA	0.06	0.799	0.006**
	WFLA v GULF	0.00	0.979	<.001**
DBASE	NOF v EFLA	0.45	0.504	0.537
	EFLA v WFLA	5.14	0.024	<.001**
	WFLA v GULF	2.33	0.128	0.005**
P1L	NOF v EFLA	10.02	0.002**	
	EFLA v WFLA	5.94	0.016	0.765
	WFLA v GULF	0.85	0.357	0.064
ORB	NOF v EFLA	6.13	0.014	0.011
	EFLA v WFLA	12.77	0.004**	
	WFLA v GULF	0.97	0.325	0.075
PREORB	NOF v EFLA	0.25	0.616	0.785
	EFLA v WFLA	5.29	0.022	0.120
	WFLA v GULF	0.02	0.886	0.193

Table 17. Analysis of covariance with two treatments within Hyporhamphus meeki, Atlantic (A) and Gulf of Mexico (G).

CHARACTER	SPECIES	Y=	R-SQUARED	N		F	P
P1-P2	A	1.050x-0.560	0.991	174	REGRESSION	11315.26	<.001 **
	G	1.034x-0.532	0.991	124	SLOPES	1.68	0.197
					MEANS	5.00	0.026
P2-C	A	0.995x-0.355	0.993	174	REGRESSION	18627.52	<.001 **
	G	0.990x-0.340	0.996	124	SLOPES	0.14	0.709
					MEANS	28.69	<.001 **
LJL	A	0.762x-0.102	0.928	166	REGRESSION	1403.86	<.001 **
	G	0.852x-0.302	0.956	94	SLOPES	12.64	<.001 **
					MEANS		
HDL	A	0.979x-0.575	0.964	174	REGRESSION	3732.66	<.001 **
	G	0.972x-0.569	0.982	124	SLOPES	0.06	0.809
					MEANS	8.99	0.003**
UJL	A	1.096x-1.574	0.937	174	REGRESSION	2386.85	<.001 **
	G	1.085x-1.553	0.970	124	SLOPES	0.19	0.662
					MEANS	0.07	0.793**
UJW	A	1.106x-1.491	0.971	174	REGRESSION	4360.42	<.001 **
	G	1.094x-1.479	0.983	124	SLOPES	0.01	0.912
					MEANS	11.52	<.001 **
BDP1O	A	1.159x-1.247	0.976	174	REGRESSION	3847.96	<.001 **
	G	1.167x-1.271	0.970	124	SLOPES	0.44	0.510
					MEANS	3.97	0.047
BDP2O	A	1.410x-1.755	0.957	174	REGRESSION	2365.64	<.001 **
	G	1.439x-1.816	0.957	124	SLOPES	1.11	0.292
					MEANS	0.13	0.719
ABASE	A	0.893x-0.631	0.971	174	REGRESSION	3400.82	<.001 **
	G	0.846x-0.531	0.970	124	SLOPES	6.11	0.014
					MEANS	5.29	0.022
DBASE	A	0.908x-0.650	0.980	174	REGRESSION	5606.66	<.001 **
	G	0.907x-0.634	0.983	124	SLOPES	0.04	0.836
					MEANS	44.48	<.001 **
P1L	A	1.019x-0.876	0.970	174	REGRESSION	4078.24	<.001 **
	G	1.011x-0.862	0.982	120	SLOPES	0.05	0.817
					MEANS	0.75	0.388
ORB	A	0.834x-0.903	0.946	174	REGRESSION	2339.06	<.001 **
	G	0.814x-0.861	0.969	124	SLOPES	0.26	0.265
					MEANS	0.96	<.001 **
PREORB	A	0.959x-1.268	0.939	174	REGRESSION	2344.67	<.001 **
	G	0.976x-1.316	0.972	124	SLOPES	1.25	0.265
					MEANS	14.12	<.001 **

Hyporhamphus unifasciatus (Ranzani, 1842)

Plate 1B

Synonymy.--Listed here is a partial nomenclature of this species, citing a number of the usages. More combinations and spellings exist. A complete synonymy will be included in the halfbeak section of "Fishes of the western North Atlantic" (Collette pers. comm.).

Hemirhamphus unifasciatus Ranzani, 1842 (original description; Brazil). Meek and Goss, 1884 ("more robust, shorter and thicker ... than *Hy. roberti*"; Havana, Cuba and Key West, FL)(*Hy. roberti* = *Hy. meeki*).

Hemiramphus richardi Valenciennes in Cuvier and Valenciennes, 1846 (original description; St. Croix, Cayenne, Bahia, Rio de Janeiro).

Hyporhamphus tricuspidatus Gill, 1859 (original description; Barbados).

Hemirhamphus fasciatus Poey, 1860 (original description; Cuba).

Hemirhamphus poeyi Günther, 1866 (replacement name for *He. fasciatus* Poey, preoccupied by *He. fasciatus* Bleeker).

Hemiramphus unifasciatus Jordan, 1889 (Port Castries, St. Lucia).

Hyporhamphus unifasciatus Jordan and Evermann, 1896 (Key West to Rio de Janeiro). Meek and Hildebrand, 1923 (Colon, Panama). Beebe and Tee-Van, 1928 (Port-au-Prince, Haiti). Beebe and Tee-Van, 1933 (Bermuda). Miller, 1945 (diagnosis of *Hyporhamphus*). Collette, 1965 (*Hy. unifasciatus* compared to *Hy. picarti*). Böhlke and Chaplin, 1968 (Bahamas). Austin, 1971 (in mangroves, collected only during fall; La Parguera, Puerto Rico). Collette, 1977 (FAO ID sheet, range). Figueiredo and Menezes, 1978 (Southeast Brazil). Chao et al, 1985 (Dos Patos Lagoon. Brazil). Yáñez-Arancibia et al., 1985 (occasional visitor; Terminos Lagoon, Mexico). Leon and Racedo, 1985 (Cartagena Bay and Cienaga Grande Santa Maria, Colombia). Bruce, 1986 (infested with parasitic isopods, *Mothocya argenosa, M. bermudensis, M. nana, and M. omidaptria*).

Hyporhamphus hildebrandi (not of Jordan and Evernamm) Beebe and Tee-Van, 1933 (Bermuda, confused with *Hy. unifasciatus*).

Diagnosis.--A member of the subgenus *Hyporhamphus* distinguished from *Hy. roberti* by having the dorsal and anal fins covered with scales, and median pore of preorbital canal usually posterior in *Hy. unifasciatus* while anterior in *Hy. roberti.* This species is distinguished from *Hy. meeki* by the following combination of characters: gill rakers on the first arch 26-35 (Table 1); gill rakers on the second arch 19-28 (Table 2); ratio of preorbital length to orbit diameter is usually less than 0.70 (<0.70 in 75% of 224 specimens examined).

Description.--Gill rakers on the upper limb of the first arch 7 to 10, usually 8 to

10, mean 8.7; lower limb 19 to 25, usually 20 to 23, mean 21.7; total of upper and lower limbs 26 to 35, usually 28 to 33, mean 30.6 (Table 1). Gill rakers on upper limb of second arch 2 to 6, usually 3 to 5, mean 3.9; lower limb 16 to 23, usually 17 to 21, mean 19.2; total 19 to 28, usually 21 to 26, mean 23.5 (Table 2). Dorsal-fin rays 13 to 16, usually 14 to 16, mean 14.8 (Table 3); anal-fin rays 14 to 18, usually 16 or 17, mean 16.4 (Table 4); and pectoral-fin rays 9 to 12, usually 10 or 11, mean 10.7 (Table 5). Predorsal scales (N = 48) 34 to 38, usually 35 to 37, mean 35 (Table 6). Vertebrae (N = 59) 32 to 34 precaudal + 17 to 19 caudal = 50 to 52 total (Table 7).

Morphometric data for *Hy. unifasciatus* are summarized in Table 18. The ratio of LJL to HDL is 0.67 to 1.58 with 93% of 183 specimens 0.70 to 1.29. Ratio of LJL to SL 0.15 to 0.31 with 94% of the specimens 0.17 to 0.28. PREORB to ORB ratio 0.50 to 0.77, usually 0.50 to 0.70 (75% of 224 specimens). Distance from base of anteriormost pelvic ray to caudal base extends anteriorly to mid-eye, usually between posterior portion of eye (posterior to pupil) and posterior margin of opercular membrane. Dorsal and anal-fin bases about equal, ratio of ABASE to DBASE 0.85 to 1.13, mean 0.98 for 223 specimens. Origin of dorsal-fin over that of anal-fin. Distance from anteriormost pectoral ray to origin of pelvic-fin less than distance from the pelvic-fin origin to the caudal base. Median pore of preorbitalcanal usually posterior, rarely medial.

Color.--Coloration in life is a silvery light tan-green. Specimens observed and collected along a low energy beach in San Blas, Panama were cryptically colored against the sandy substrate. The fleshy tip of the lower jaw is a bright orange red,

Table 18. Summary of morphometric data in percent standard length in populations of Hyporhamphus unifasciatus, except for SL in mm.

CHARACTER % SL	WEST INDIES AND FLORIDA						CENTRAL AND SOUTH AMERICA						BERMUDA					
	N	MIN	MAX	MEAN	SD	SE	N	MIN	MAX	MEAN	SD	SE	N	MIN	MAX	MEAN	SD	SE
SL	76	73.5	195.0	119.4	32.55	3.73	86	62.4	205.0	129.4	33.62	3.63	69	79.70	168.0	109.3	19.57	2.36
P1-P2	76	30.8	38.2	35.4	1.50	0.17	86	32.6	40.6	35.4	1.20	0.13	69	34.7	39.0	35.7	0.86	0.10
P2-C	76	40.1	47.2	43.7	1.33	0.15	86	38.9	45.8	43.2	1.11	0.12	69	39.5	44.7	41.7	0.91	0.11
LJL	59	15.0	31.0	23.0	3.03	0.39	81	19.8	29.5	23.8	1.86	0.21	50	19.7	30.9	25.3	2.72	0.39
HDL	76	19.6	26.0	22.6	1.06	0.12	86	21.0	25.6	23.1	0.96	0.10	69	19.5	24.7	22.8	0.86	0.10
UJL	76	2.9	4.6	3.8	0.31	0.04	86	3.4	4.9	4.1	0.27	0.03	69	3.1	4.5	3.8	0.27	0.03
UJW	76	4.2	5.8	5.3	0.40	0.05	86	4.4	6.8	5.5	0.53	0.06	69	4.0	5.8	5.1	0.37	0.04
BDP1O	76	7.9	13.8	11.6	1.22	0.14	86	9.4	15.6	12.2	1.31	0.14	69	8.4	11.6	10.3	0.71	0.09
BDP2O	76	6.5	15.3	12.0	2.05	0.24	86	7.6	17.2	12.5	2.41	0.26	69	5.7	12.7	9.9	1.38	0.17
ABASE	76	12.0	17.1	14.3	1.01	0.12	85	12.1	16.8	13.9	0.99	0.11	69	11.9	16.4	14.8	0.78	0.09
DBASE	76	13.4	16.3	14.7	0.65	0.07	86	13.1	17.6	14.7	0.77	0.08	69	12.7	16.8	14.5	0.78	0.09
P1L	58	11.9	16.5	14.4	0.94	0.12	82	11.9	16.1	14.7	0.91	0.01	64	12.4	15.6	14.4	0.52	0.07
ORB	76	5.1	6.7	5.8	0.39	0.04	86	4.9	7.0	5.8	0.37	0.04	69	5.0	6.7	5.8	0.39	0.05
PREORB	76	3.1	4.2	3.8	0.22	0.03	85	2.9	4.5	3.9	0.24	0.03	69	3.2	4.3	3.7	0.19	0.02

this is often seen protruding out of the water as they swim along the surface.

Size.--Largest specimen at 240 mm SL from Brazil (MCZ 4684; Collette pers. comm.). Adults do not usually attain a size greater than 200 mm SL.

Habitat.--This is an inshore coastal and estuarine species. They usually inhabit waters in the vicinity of seagrass beds (see feeding habits below). Austin (1971) reported collecting numerous individuals in a mangrove lined canal and lagoon in La Parguera, Puerto Rico. The substrate was marl and mud with nearby *Thalassia* meadows. In Brazil this species has been collected in the surf zone with a sand substrate and detached algae abundant in the area (R. Teixeira pers. comm.). In Panama collections were made along a sand beach adjacent to extensive seagrass beds behind a barrier reef (El Porvenir, San Blas).

Biology and Early Life History.--In a study of feeding habits, *Hy. unifasciatus* were collected in the surf zone near Maceio in northeastern Brazil (R. Teixeira pers. comm.). The stomachs contained remains of the following: unidentified fish, a sygnathid, crustaceans, bivalve molluscs, cnidarians, insects, sediments, and algae, the largest single constituent at 62 percent. Juveniles were reported to feed on vegetation, whereas adults, in addition to vegetation, were feeding on crustaceans and mollusks (Figueiredo and Menezes, 1978). Remains of algal cells were reported from the stomach of a specimen from Port-au-Prince, Haiti (Beebe and Tee-Van, 1928). They have been observed in Bermuda to feed on fresh broken off pieces of seagrass (Collette pers. comm.).

Distribution.--Bermuda and peninsular Florida south through the Caribbean, along the South American coast to Uruguay (Collette, 1977). Also from Yucatan, ranging into the Gulf of Mexico as far north as Vera Cruz, Mocambo, Mexico (UMMZ 143085). Sympatric with *Hy. meeki* in Yucatan and along the Florida peninsula (see sections on the distribution of *Hy. meeki* and on sympatry of the two species) (Fig. 6).

Etymology.--The name *unifasciatus* is from the Latin *uni*, one and *fascia*, band, referring to the single plumbeous band running along the mid body from pectoral fin to caudal fin.

Comparisons.--For comparisons with *Hy. meeki* see *Hy. meeki* section.

Material examined.--230 specimens of *Hy. unifasciatus* (62.4-205) from 54 collections, with almost complete morphometric and meristic data are listed. Additional specimens used mainly for meristic data are in Bruce Collette's files.

FLORIDA: 26 specimens (75-192) from 5 collections. UF 56209 (1, 143) Virginia Key; 26 Nov 1959. UF 62140 (11, 108-134) N. of Jupiter Inlet; 21 Aug 1964. USNM 34999 (4, 182-192) Key West; Dec 1883. USNM 158069 (3, 108-129) Snipe and Content Keys; June 1956. USNM 38544 (3, 138-144) Key West; 15-27 Apr 1884. USNM 187121 (4, 75.0-79.9) St. Joseph's Bay; 2 Feb 1959.

WEST INDIES: 52 specimens (77.2-194) from 16 collections. USNM 10730 (2, 79.5-89.9) Bahia Honda, Cuba. USNM 107428 (2, 135-165) Bahia Honda Anchorage, Cuba; 5 Apr 1937. USNM 82366 (3, 77.2-86.3) Los Arroyos, Cuba; 19 May 1914. USNM 130652 (1, 195) Cuba. USNM 5847 (1, 103) Jamaica. USNM 8803 (1, 111) Jamaica. USNM 38537 (2, 120-127) Jamaica; 1-11 Mar 1884. USNM 94077 (4, 112-139) Jamaica. USNM 294493 (6, 78.6-119) Jobes Harbor, Greater Antilles; 20 Feb 1966. USNM 132524 (3, 109-147) Port-au-Prince, Haiti; 22 Oct

1945. USNM 50111 (1, 194) San Juan Mkt., Puerto Rico; 14 Jan 1899. USNM 294515 (11, 81.9-167) 17°56'30"N lat. 66°13'12"W long.; 18 Feb 1966. USNM 34938 (2, 118-123) St. Thomas. USNM 294364 (5, 90.5-129) Sable Bay, Dominica; 13 Nov 1964. USNM 5802 (2, 146-186) Barbados. USNM 38601 (6, 119-158) Curacao; 10-18 Feb 1884.

BERMUDA: 69 specimens (79.7-168) from 16 collections. AMNH 18711 (2, 87.3-90.2) Bermuda. ANSP 96626 (2, 114-117) Somerset, Bermuda; 12 Jun 1952. ANSP 109562 (15, 82.5-135) Somerset, Bermuda; 4 Jun 1952. ANSP 123715 (4, 100-141) Bermuda; Jun 1930. MCZ 34890 (5, 110-168) Bermuda. MCZ 40757 (6, 106-118) Bermuda; 1872. UMMZ 172321 (3, 99.2-154) Reach at Bio. Sta., Bermuda; 31 May 1951. UMMZ 172369 (3, 81.6-97.9) St. George's I.; 5 Jun 1951. UMMZ 172418 (13, 87.9-145) St. George's I., Bermuda; 8 Jun 1951. UMMZ 175957 (2, 85.9-108) Reach at Bio. Sta., Bermuda. UMMZ 175967 (3, 124-140) Jetty at Bio. Sta., Bermuda; 19 Mar 1957. UMMZ 175974 (1, 105) Ferry Reach at Bio. Sta., Bermuda; 21 Mar 1957. UMMZ 175981 (1, 79.7) Ferry Reach at Bio. Sta., Bermuda; 24 Mar 1957. UMMZ 176014 (1, 148) Ferry Reach at Bio. Sta., Bermuda; 14 Apr 1957. UMMZ 176154 (1, 114) Ferry Reach at Bio. Sta., Bermuda; 4 Jun 1957. USNM 294439 (7, 87.7-110) Bermuda Harbor, Bermuda; 9 Mar 1963.

MEXICO AND CENTRAL AMERICA: 24 specimens (62.4-183) from 6 collections. UF 7107 (2, 165-181) Veracruz, Mocambo, Mexico; 20 Jan 1958. MCZ 32881 (1, 183) Yucatan, Mexico; 1906. UMMZ 143085 (10, 94.2-140) W. of Progreso, Yucatan, Mexico; 28 Mar - 1 Apr 1936. UMMZ 143087 (1, 71)

Chicxulub, Yucatan, Mexico; 1 Apr 1936. USNM 187843 (9, 62.4-85.5) Off Bluefields, Nicaragua; 3-4 Jun 1962. USNM 79658 (1, 160) Colon Mkt., Panama; 23 Jan 1912.

SOUTH AMERICA: 59 specimens (86.1-205) from 10 collections. USNM 203826 (11, 104-121) Gulf of Uraba, Colombia; 11 Jul 1966. USNM 206658 (17, 121-205) Baru I., Colombia; 26 Sept 1969. USNM 38574 (1, 135) Sabanilla, Colombia; 16-22 Mar 1884. USNM 94764 (1, 188) near Puerto Colombia, Barranquillas, Colombia. USNM 128286 (3, 121-129) Gulf of Venezuela, Venezuela; 5 Apr 1925. USNM 198404 (3, 86.1-108) Off French Guiana; 30 Jul 1956. USNM 107220 (1, 151) Recife, Brazil; 1932. MZUSP 41094 (12, 131-179) Pontal, Ilheus, Brazil; 25 Oct 1971. MZUSP 5206 (7, 131-148) Ubatuba, Brazil; 1967. MZUSP 41092 (3, 184-191) Praia de Itapenia, Brazil; Jul 1965.

Geographic variation within *Hyporhamphus unifasciatus*

As in *Hy. meeki*, meristic frequency tables and comparisons of meristic means by the Tukey-Kramer method indicate some geographic variability in populations of *Hy. unifasciatus* (Tables 9-13). The West Indies (WI) population tends to have low dorsal, anal and pectoral fin ray counts, means 14.7, 16.1, 10.7 respectively (Tables 3-5 and 9-11). Caribbean South America (CSA), Central America (CAM) and Florida (UFLA) populations all have intermediate counts for these same meristic characters. The Caribbean South American population has a mean dorsal fin ray count of 14.9, a mean anal fin ray count of 16.3, and a mean pectoral fin ray count of 11.0. The Central American population has the following mean fin ray counts; dorsal, 14.9; anal, 16.2; and pectoral,10.9. The Florida population has the following mean fin ray counts: dorsal, 14.8; anal, 16.5; and pectoral, 10.8. The Yucatan population has the highest dorsal and pectoral fin ray counts with means of 15.1 and 11.1 respectively. However, anal fin ray counts are one of the lower with a mean of 16.2. The other population of interest is Bermuda with very low pectoral fin ray counts, ranging from 9 - 10, with a mean of 10.0. The Bermudan population also has the lowest dorsal counts with a mean of 14.3. However, anal fin ray counts are the highest with a mean of 16.8. In both pectoral and dorsal counts the population most similar to Bermuda is the West Indian, though statistically they are significantly different.

Populations of *Hy. unifasciatus* exhibit the same trends in RGR_1 and RGR_2 counts (Tables 1, 2, 12 and 13), here listed in descending order; Caribbean South America, West Indies, Brasil, Central America, Yucatan, Florida and Bermuda.

As with *Hy. meeki*, ANCOVA was performed on *Hy. unifasciatus* intraspecifically to ascertain levels of geographic variation. A one way ANCOVA of three geographic populations (treatments) of *Hy. unifasciatus* indicated some intraspecific variability (Table 19). The three populations or geographic regions are: AREA 1, which encompasses WI and UFLA; AREA 2, encompassing CAM, CSA, and SAM; and BERM. These regions were constructed on zoogeographic information (Briggs, 1974; Acero, 1984) and from the results of a preliminary

Table 19. Analysis of covariance with three treatments, populations of Hyporhamphus unifasciatus; Area 1 = WI and UFLA; Area 2 = CAM, CSA and SAM; and BERM.

CHARACTER	POP.	Y =	R-SQUARED	N		F	P
P1-P2	AREA1	1.044x-0.543	0.979	76	REGRESSION	2698.44	<.001**
	AREA2	1.027x-0.508	0.988	79	SLOPES	0.40	0.670
	BERM	1.029x-0.494	0.984	69	MEANS	35.27	<.001**
P2-C	AREA1	0.995x-0.350	0.987	76	REGRESSION	4228.34	<.001**
	AREA2	0.978x-0.318	0.992	79	SLOPES	1.09	0.339
	BERM	0.967x-0.313	0.985	69	MEANS	63.54	<.001**
LJL	AREA1	0.671x-0.032	0.791	59	REGRESSION	226.54	<.001**
	AREA2	0.815x-0.238	0.964	74	SLOPES	5.70	0.004**
	BERM	0.629x-0.154	0.612	50	MEANS		
HDL	AREA1	1.006x-0.659	0.970	76	REGRESSION	1738.09	<.001**
	AREA2	1.019x-0.679	0.981	79	SLOPES	1.63	0.199
	BERM	1.068x-0.782	0.962	69	MEANS	3.46	0.033
UJL	AREA1	1.144x-1.714	0.947	76	REGRESSION	850.36	<.001**
	AREA2	1.077x-1.549	0.961	79	SLOPES	2.25	0.108
	BERM	1.172x-1.773	0.904	69	MEANS	18.62	<.001**
UJW	AREA1	1.162x-1.610	0.957	76	REGRESSION	1016.61	<.001**
	AREA2	1.227x-1.741	0.960	79	SLOPES	2.60	0.077
	BERM	1.275x-1.851	0.940	69	MEANS	4.61	0.011
BDP1OB	AREA1	1.294x-1.542	0.948	76	REGRESSION	1111.22	<.001**
	AREA2	1.289x-1.524	0.964	79	SLOPES	0.02	0.978
	BERM	1.301x-1.601	0.955	69	MEANS	60.03	<.001**
BDP2O	AREA1	1.561 2.080	0.935	76	REGRESSION	624.31	<.001**
	AREA2	1.594 2.160	0.933	79	SLOPES	0.42	0.654
	BERM	1.646 2.323	0.885	69	MEANS	35.62	<.001**
ABASE	AREA1	0.852x-0.540	0.942	76	REGRESSION	792.03	<.001**
	AREA2	0.814x-0.469	0.960	78	SLOPES	1.10	0.334
	BERM	0.805x-0.434	0.916	69	MEANS	8.79	<.001**
DBASE	AREA1	0.957x-0.743	0.974	76	REGRESSION	1478.64	<.001**
	AREA2	0.899x-0.621	0.979	79	SLOPES	8.40	<.001**
	BERM	0.821x-0.477	0.917	69	MEANS		
P1L	AREA1	1.022x-0.887	0.946	58	REGRESSION	1016.95	<.001**
	AREA2	1.110x-1.067	0.970	76	SLOPES	6.26	0.002**
	BERM	0.973x-0.787	0.957	64	MEANS		
ORB	AREA1	0.893x-1.015	0.942	76	REGRESSION	684.11	<.001**
	AREA2	0.939x-1.108	0.949	69	SLOPES	6.09	0.003**
	BERM	0.772x-0.772	0.862	69	MEANS		
PREORB	AREA1	0.962x-1.345	0.950	76	REGRESSION	892.95	<.001**
	AREA2	0.965x-1.333	0.950	79	SLOPES	3.85	0.023
	BERM	1.087x-1.610	0.936	69	MEANS	23.88	<.001**

ANCOVA of all geographic populations of *Hy. unifasciatus*. Slopes were found to be significantly different (alpha>.01) between the three treatments in LJL, DBASE, P_1L, and ORB. To ascertain what specific geographic regions differed in slopes, apriori contrasts were run (Table 20). With two contrasts allowable between treatments, the following were chosen, AREA1 versus AREA2, and AREA1 versus BERM. These contrasts indicate that for LJL, AREA1 versus AREA2 are significantly different, and for DBASE, AREA1 versus BERM are significantly different. Morphometric characters P_1L and ORB were not found to have significantly different slopes for the contrasts carried out. Thus, by process of elimination it is likely that their slopes differ for the contrast not carried out, AREA2 versus BERM. Least squares means for each morphometric character were compared between regions if the slopes were found to be homogeneous (Table 16). For AREA1 versus AREA2 least squares means are significantly different for UJL and PREORL. For AREA1 versus BERM, P_1-P_2, P_2-C, LJL, P_1O, and P_2O are significantly different.

Bermuda is shown to be morphologically different from the remainder of *Hy. unifasciatus* (AREA1 and AREA2) when morphometric characters P_1-P_2, P_1O, and P_2O are plotted against SL (Figs. 9-11). From these plots it is obvious that Bermudan *Hyporhamphus* are thinner (P_1O and P_2O) and have a somewhat greater P_1-P_2 than other populations of *Hy. unifasciatus*.

Table 20. Slopes and least squares means contrasts between three populations of *Hyporhamphus unifasciatus*.

CHARACTER	POP.	F	SLOPES P	MEANS P
P1-P2	AREA1 v AREA2	0.75	0.387	0.816
	AREA1 v BERM	0.29	0.588	<.001**
P2-C	AREA1 v AREA2	1.30	0.256	0.042
	AREA1 v BERM	1.70	0.194	<.001**
LJL	AREA1 v AREA2	8.43	0.004**	
	AREA1 v BERM	0.30	0.586	<.001**
HDL	AREA1 v AREA2	0.30	0.584	0.010
	AREA1 v BERM	3.23	0.074	0.111
UJL	AREA1 v AREA2	2.92	0.089	<.001**
	AREA1 v BERM	0.25	0.617	0.577
UJW	AREA1 v AREA2	2.82	0.094	0.574
	AREA1 v BERM	4.27	0.040	0.019
BDP1O	AREA1 v AREA2	0.01	0.912	0.074
	AREA1 v BERM	0.02	0.901	<.001**
BDP2O	AREA1 v AREA2	0.25	0.619	0.318
	AREA1 v BERM	0.82	0.365	<.001**
ABASE	AREA1 v AREA2	1.69	0.195	0.049
	AREA1 v BERM	1.35	0.247	0.020
DBASE	AREA1 v AREA2	5.79	0.017	0.449
	AREA1 v BERM	15.91	<.001**	
P1L	AREA1 v AREA2	6.68	0.011	0.274
	AREA1 v BERM	1.05	0.306	0.635
ORB	AREA1 v AREA2	1.76	0.186	0.457
	AREA1 v BERM	6.09	0.014	0.746
PREORB	AREA1 v AREA2	0.01	0.916	<.001**
	AREA1 v BERM	6.75	0.010**	

Figure 9. Relationship of pectoral to pelvic distance to standard length in Bermudian (triangles) and West Indian (squares) populations of *Hyporhamphus unifasciatus*.

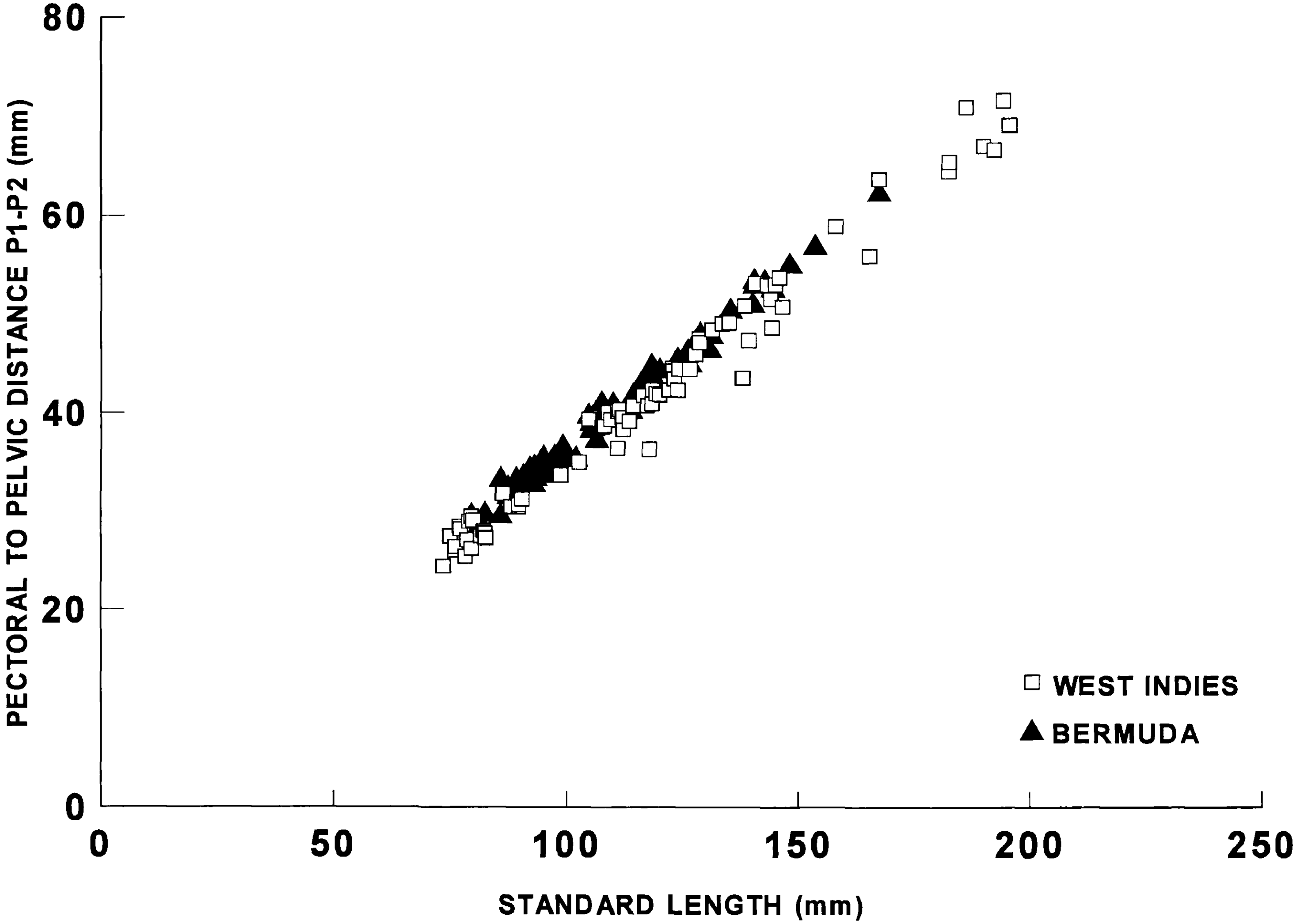

80
60
40
20
0
PECTORAL TO PELVIC DISTANCE P1-P2 (mm)
0
50
100
150
200
250
STANDARD LENGTH (mm)
□ WEST INDIES
▲ BERMUDA

Figure 10. Relationship of body depth at pectoral-fin origin to standard length in Bermudian (triangles) and West Indian (squares) populations of *Hyporhamphus unifasciatus*.

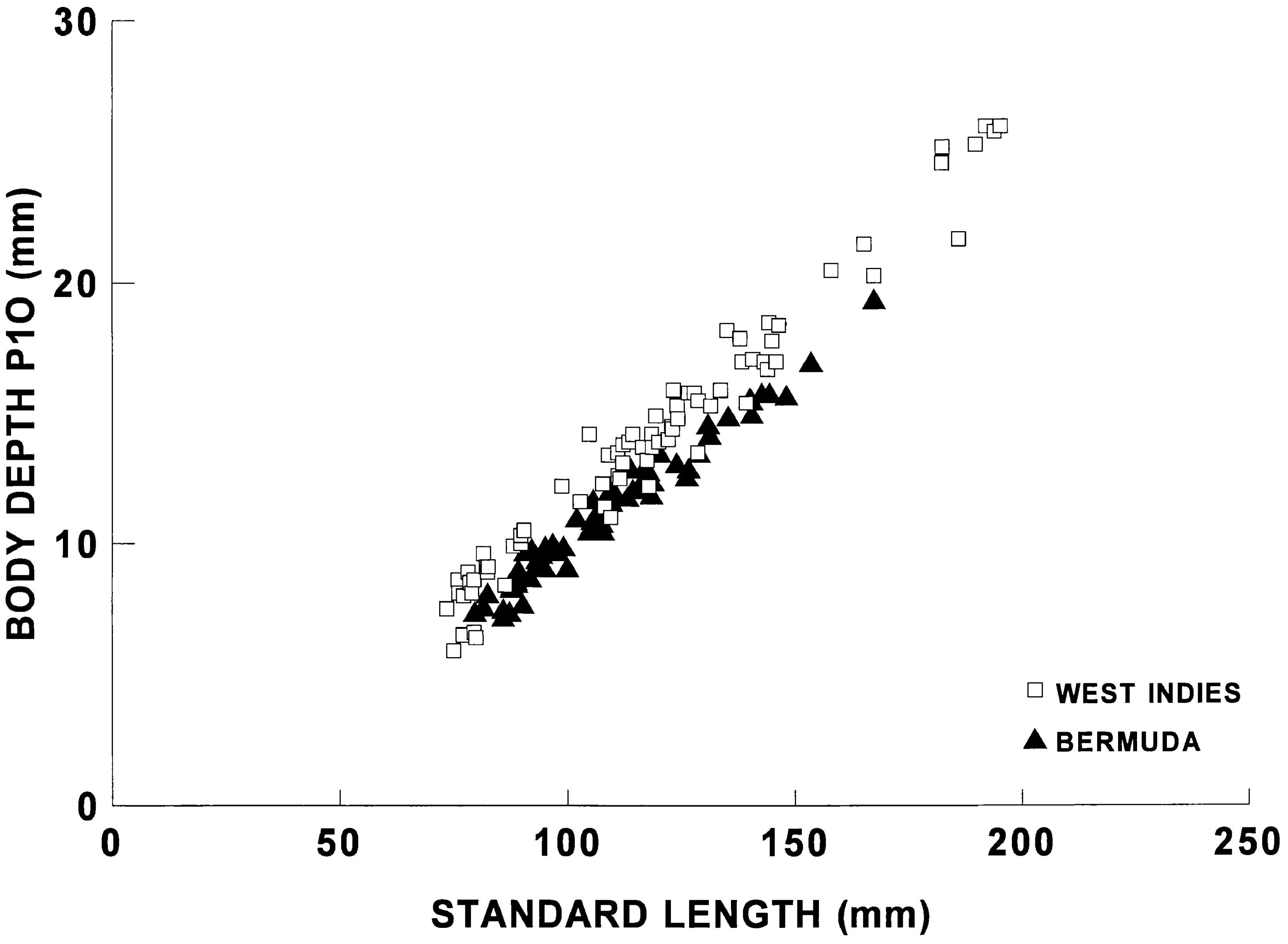
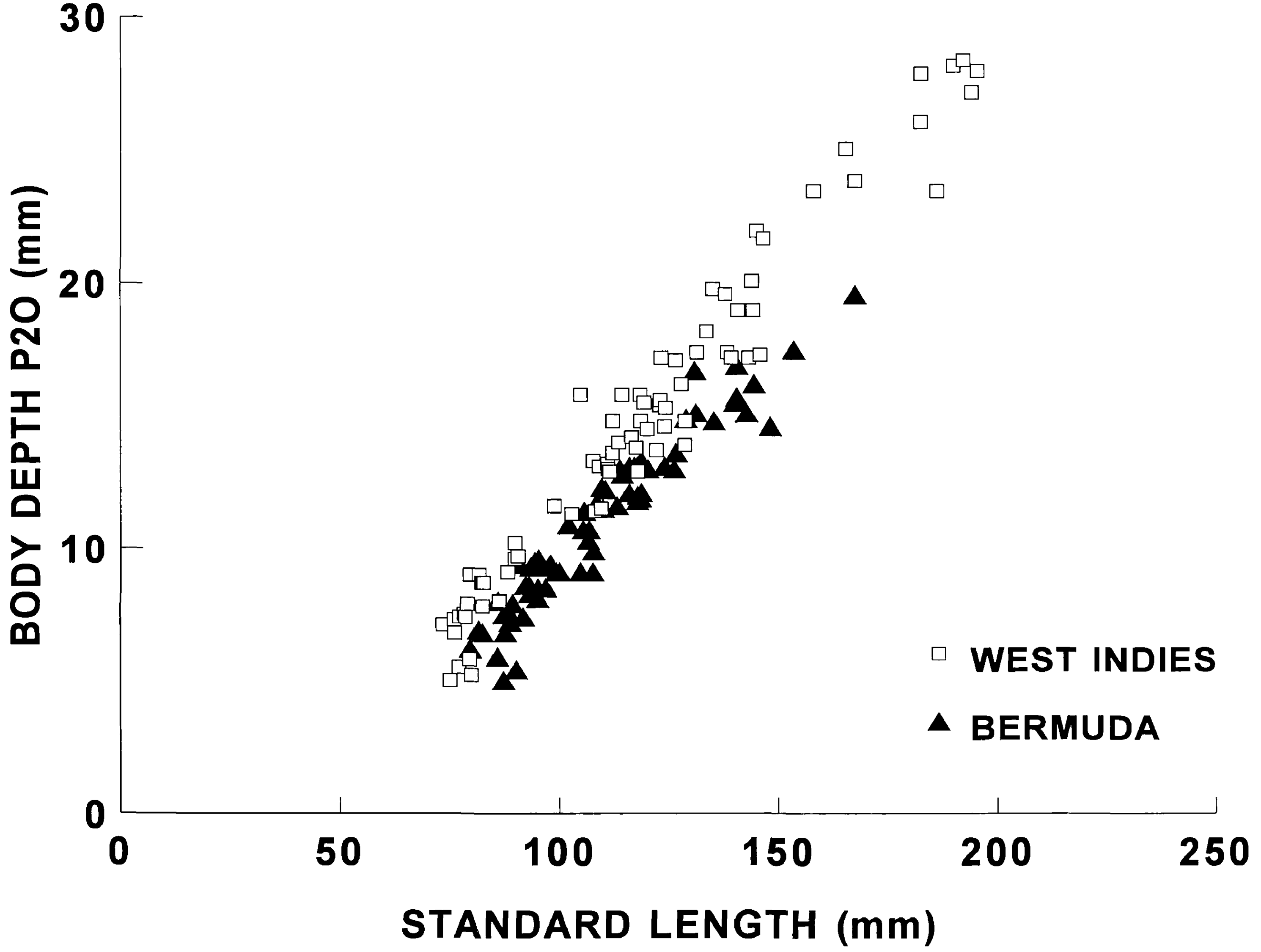

30
20
10
0
BODY DEPTH P1O (mm)
0
50
100
150
200
250
STANDARD LENGTH (mm)
□ WEST INDIES
▲ BERMUDA

Figure 11. Relationship of body depth at pelvic-fin origin to standard length in Bermudian (triangles) and West Indian (squares) populations of *Hyporhamphus unifasciatus*.


BODY DEPTH P2O (mm)
30
20
10
0
0
50
100
150
200
250
STANDARD LENGTH (mm)
□ WEST INDIES
▲ BERMUDA

Comparisons of sympatric populations of *Hy. meeki* and *Hy. unifasciatus.*

Southern Florida and Yucatan appear to be areas of sympatry between the two species. In the meristic frequency tables, Yucatan specimens are divided into *Hy. meeki* and *Hy. unifasciatus*. This was done on the basis of gill raker counts, *Hy. meeki* having 33 or greater and *Hy. unifasciatus* having 32 or fewer. This division of specimens may be in error, for they appear to possess a mosaic of or intermediate morphologic characters typified by hybridization and introgression (Hubbs and Kuronuma, 1942; Smith, 1992). Additionally, individual collections from Yucatan (UMMZ 143085 and MCZ 32881) contain both species based on the above criteria. However, Yucatan *Hy. meeki*, or those with high gill raker counts, have a preorbital/orbit ratio typical of *Hy. unifasciatus*. To date, not enough data have been collected on these species from this area, and preserved material is not abundant (N = 39 from only 3 individual samples). Analysis of covariance was performed onYUC, CAM, and GULF, the area of sympatry and adjacent areas (Tables 21 and 22). YUC versus CAM yielded significant differences in LJL and UJL slopes, and HDL, P_2O, and ORB means (Table 21). YUC versus GULF showed significant differences once again in LJL and UJL slopes, and P_1O, DBASE, ORB, and PREORL means (Table 22).

The dynamics of the two species' sympatry in Yucatan is probably different than in peninsular Florida. Collection data indicate that sympatry of the two species in Florida may be largely avoided temporally, because both species migrate northward up the Florida coasts when the waters warm during summer and autumn.

Table 21. Analysis of covariance with two treatments, sympatric and adjacent populations of *Hyporhamphus meeki* and *Hy. unifasciatus*; Yucatan (YUC) and Central America (CAM).

CHARACTER	SPECIES	Y=	R-SQUARED	N		F	P
P1-P2	YUC	1.033x-0.529	0.990	12	REGRESSION	2955.01	<.001**
	CAM	1.017x-0.487	0.997	12	SLOPES	0.35	0.556
					MEANS	6.12	0.018
P2-C	YUC	1.040x-0.444	0.992	28	REGRESSION	2031.01	<.001**
	CAM	1.002x-0.487	0.992	12	SLOPES	1.38	0.248
					MEANS	0.49	0.486
LJL	YUC	0.643x-0.108	0.920	28	REGRESSION	483.64	<.001**
	CAM	0.816x-0.229	0.988	11	SLOPES	12.40	0.001**
					MEANS		
HDL	YUC	0.939x-0.499	0.993	28	REGRESSION	2996.70	<.001**
	CAM	0.969x-0.589	0.994	12	SLOPES	1.30	0.261
					MEANS	55.36	<.001**
UJL	YUC	1.186x-1.758	0.964	28	REGRESSION	870.75	<.001**
	CAM	0.990x-1.389	0.992	12	SLOPES	13.02	0.001**
					MEANS		
UJW	YUC	1.097x-1.493	0.980	28	REGRESSION	1284.88	<.001**
	CAM	1.151x-1.596	0.991	12	SLOPES	1.47	0.233
					MEANS	1.46	0.235
BDP1O	YUC	1.098x-1.150	0.972	28	REGRESSION	960.16	<.001**
	CAM	1.201x-1.357	0.988	12	SLOPES	3.79	0.059
					MEANS	0.37	0.546
BDP2O	YUC	1.441x-1.827	0.963	28	REGRESSION	808.15	<.001**
	CAM	1.509x-2.003	0.985	12	SLOPES	0.76	0.389
					MEANS	10.81	0.002**
ABASE	YUC	0.875x-0.602	0.977	28	REGRESSION	1135.96	<.001**
	CAM	0.799x-0.441	0.992	12	SLOPES	4.86	0.034
					MEANS	1.26	0.269
DBASE	YUC	0.865x-0.565	0.960	28	REGRESSION	822.60	<.001**
	CAM	0.922x-0.664	0.992	12	SLOPES	1.68	0.203
					MEANS	6.28	0.017
P1L	YUC	0.811x-0.442	0.833	16	REGRESSION	787.27	<.001**
	CAM	1.058x-0.967	0.994	12	SLOPES	6.48	0.018
					MEANS	0.20	0.660
ORB	YUC	0.830x-0.878	0.969	28	REGRESSION	826.82	<.001**
	CAM	0.862x-0.966	0.983	12	SLOPES	0.50	0.485
					MEANS	13.94	<.001**
PREORB	YUC	0.955x-1.325	0.936	28	REGRESSION	497.04	<.001**
	CAM	0.912x-1.226	0.989	12	SLOPES	0.54	0.467
					MEANS	1.90	0.177

Table 22. Analysis of covariance with two treatments, sympatric and adjacent populations of Hyporhamphus meeki and Hy. unifasciatus; Yucatan (YUC) and the Gulf of Mexico (GULF)

CHARACTER	SPECIES	Y=	R-SQUARED	N		F	P
P1-P2	YUC	1.033x-0.529	0.990	12	REGRESSION	1628.69	<.001**
	GULF	1.064x-0.593	0.981	54	SLOPES	0.94	0.335
					MEANS	0.32	0.571
P2-C	YUC	1.040x-0.444	0.992	28	REGRESSION	2423.79	<.001**
	GULF	1.019x-0.402	0.988	54	SLOPES	0.71	0.402
					MEANS	2.52	0.116
LJL	YUC	0.643x-0.108	0.920	28	REGRESSION	178.57	<.001**
	GULF	0.922x-0.443	0.870	41	SLOPES	12.39	<.001**
					MEANS		
HDL	YUC	0.939x-0.499	0.993	28	REGRESSION	1687.71	<.001**
	GULF	0.903x-0.424	0.980	54	SLOPES	1.76	0.189
					MEANS	0.15	0.699
UJL	YUC	1.186x-1.758	0.964	28	REGRESSION	476.19	<.001**
	GULF	0.961x-1.281	0.935	54	SLOPES	14.75	<.001**
					MEANS		
UJW	YUC	1.097x-1.493	0.980	28	REGRESSION	751.50	<.001**
	GULF	1.045x-1.376	0.958	54	SLOPES	1.21	0.274
					MEANS	2.29	0.135
BDP1O	YUC	1.098x-1.150	0.972	28	REGRESSION	990.50	<.001**
	GULF	1.098x-1.129	0.974	54	SLOPES	0.00	0.989
					MEANS	38.36	<.001**
BDP2O	YUC	1.441x-1.827	0.963	28	REGRESSION	417.01	<.001**
	GULF	1.298x-1.524	0.927	54	SLOPES	3.14	0.081
					MEANS	0.09	0.763
ABASE	YUC	0.875x-0.602	0.977	28	REGRESSION	739.80	<.001**
	GULF	0.914x-0.686	0.961	54	SLOPES	0.92	0.340
					MEANS	0.33	0..567
DBASE	YUC	0.865x-0.565	0.960	28	REGRESSION	642.54	<.001**
	GULF	0.925x-0.678	0.960	54	SLOPES	1.81	0.183
					MEANS	11.02	0.001**
P1L	YUC	0.811x-0.442	0.833	16	REGRESSION	392.44	<.001**
	GULF	0.955x-0.745	0.958	51	SLOPES	2.05	0.157
					MEANS	0.38	0.541
ORB	YUC	0.830x-0.878	0.969	28	REGRESSION	393.61	<.001**
	GULF	0.801x-0.835	0.922	54	SLOPES	0.35	0.559
					MEANS	20.67	<.001**
PREORB	YUC	0.955x-1.325	0.936	28	REGRESSION	634.33	<.001**
	GULF	0.898x-1.150	0.963	54	SLOPES	1.38	0.244
					MEANS	181.69	<.001**

Consequently, *Hy. unifasciatus* moves into areas occupied by *Hy. meeki* in the winter. As with Yucatan fish, specimens from Florida were specifically identified on the basis of gill raker counts. Inspection of meristic frequencies (Tables 1-5 and 9-13) indicate that Florida *Hy. unifasciatus* means are consistent with other *Hy. unifasciatus* population means. Analysis of covariance was performed on EFLA, WFLA, and UFLA. EFLA versus UFLA yielded significant differences in either slopes or means of every morphologic character observed (Table 23). The level of significant difference is similar when WFLA and UFLA are compared (Table 24), with only P_2-C and DBASE significantly different in neither slopes nor means. Thus, identification to the specific status is clear and discernable in Florida, whereas in Yucatan character intermediacy causes confusion.

Table 23. Analysis of covariance with two treatments, sympatric populations of *Hyporhamphus meeki* (EFLA) and *Hy. unifasciatus* (UFLA) in Florida.

CHARACTER	SPECIES	Y=	R-SQUARED	N		F	P
P1-P2	EFLA	1.021x-0.505	0.993	62	REGRESSION	5986.90	<.001**
	UFLA	0.964x-0.366	0.993	25	SLOPES	7.70	0.007**
					MEANS		
P2-C	EFLA	0.982x-0.329	0.994	62	REGRESSION	6048.09	<.001**
	UFLA	1.017x-0.393	0.992	25	SLOPES	3.25	0.075
					MEANS	9.72	0.003**
LJL	EFLA	0.847x-0.264	0.958	60	REGRESSION	637.34	<.001**
	UFLA	0.622x-0.163	0.937	22	SLOPES	26.97	<.001**
					MEANS		
HDL	EFLA	0.999x-0.610	0.986	62	REGRESSION	2373.32	<.001**
	UFLA	1.137x-0.943	0.987	25	SLOPES	21.35	<.001**
					MEANS		
UJL	EFLA	1.078x-1.525	0.964	62	REGRESSION	868.28	<.001**
	UFLA	1.172x-1.777	0.965	25	SLOPES	3.30	0.073
					MEANS	63.22	<.001**
UJW	EFLA	1.143x-1.558	0.980	62	REGRESSION	2120.74	<.001**
	UFLA	1.332x-1.983	0.992	25	SLOPES	25.59	<.001**
					MEANS		
BDP1O	EFLA	1.148x-1.232	0.972	62	REGRESSION	1375.02	<.001**
	UFLA	1.568x-2.138	0.982	25	SLOPES	73.23	<.001**
					MEANS		
BDP2O	EFLA	1.399x-1.746	0.952	62	REGRESSION	724.89	<.001**
	UFLA	1.847x-2.709	0.959	25	SLOPES	29.88	<.001**
					MEANS		
ABASE	EFLA	0.924x-0.690	0.979	62	REGRESSION	1634.04	<.001**
	UFLA	0.771x-0.354	0.961	25	SLOPES	19.25	<.001**
					MEANS		
DBASE	EFLA	0.911x-0.656	0.977	62	REGRESSION	2029.87	<.001**
	UFLA	0.941x-0.703	0.988	25	SLOPES	0.89	0.348
					MEANS	10.62	0.002**
P1L	EFLA	1.089x-1.007	0.984	61	REGRESSION	1580.84	<.001**
	UFLA	1.095x-1.050	0.969	19	SLOPES	0.02	0.900
					MEANS	32.13	<.001**
ORB	EFLA	0.901x-1.026	0.973	62	REGRESSION	1436.70	<.001**
	UFLA	1.022x-1.304	0.984	25	SLOPES	11.61	0.001**
					MEANS		
PREORB	EFLA	0.993x-1.329	0.967	62	REGRESSION	966.03	<.001**
	UFLA	1.041x-1.505	0.975	25	SLOPES	1.21	0.274
					MEANS	168.38	<.001**

Table 24. Analysis of covariance with two treatments, sympatric populations of *Hyporhamphus meeki* (WFLA) and *Hy. unifasciatus* (UFLA) in Florida.

CHARACTER	SPECIES	Y=	R-SQUARED	N		F	P
P1-P2	WFLA	1.026x-0.523	0.985	42	REGRESSION	1782.26	<.001 **
	UFLA	0.964x-0.366	0.993	25	SLOPES	4.91	0.030
					MEANS	74.08	<.001 **
P2-C	WFLA	1.014x-0.387	0.994	42	REGRESSION	3044.80	<.001 **
	UFLA	1.017x-0.393	0.992	25	SLOPES	0.02	0.8803
					MEANS	0.26	0.6146
LJL	WFLA	0.847x-0.305	0.953	38	REGRESSION	338.52	<.001 **
	UFLA	0.622x-0.163	0.937	22	SLOPES	22.89	<.001 **
					MEANS		
HDL	WFLA	0.917x-0.446	0.985	42	REGRESSION	1523.92	<.001 **
	UFLA	1.137x-0.943	0.987	25	SLOPES	51.62	<.001 **
					MEANS		
UJL	WFLA	0.982x-1.341	0.954	42	REGRESSION	506.82	<.001 **
	UFLA	1.172x-1.777	0.965	25	SLOPES	11.76	0.001 **
					MEANS		
UJW	WFLA	1.025x-1.326	0.984	42	REGRESSION	1809.94	<.001 **
	UFLA	1.332x-1.983	0.992	25	SLOPES	91.76	<.001 **
					MEANS		
BDP1O	WFLA	1.122x-1.166	0.978	42	REGRESSION	1069.66	<.001 **
	UFLA	1.568x-2.138	0.982	25	SLOPES	87.17	<.001 **
					MEANS		
BDP2O	WFLA	1.358x-1.625	0.971	42	REGRESSION	572.07	<.001 **
	UFLA	1.847x-2.709	0.959	25	SLOPES	39.07	<.001 **
					MEANS		
ABASE	WFLA	0.915x-0.665	0.954	42	REGRESSION	467.31	<.001 **
	UFLA	0.771x-0.354	0.961	25	SLOPES	9.55	0.003**
					MEANS		
DBASE	WFLA	0.980x-0.782	0.970	42	REGRESSION	898.34	<.001 **
	UFLA	0.941x-0.703	0.988	25	SLOPES	1.05	0.310
					MEANS	0.19	0.662
P1L	WFLA	0.997x-0.826	0.960	42	REGRESSION	510.64	<.001 **
	UFLA	1.095x-1.050	0.969	19	SLOPES	3.22	0.078
					MEANS	9.33	0.003**
ORB	WFLA	0.752x-0.726	0.926	42	REGRESSION	486.97	<.001 **
	UFLA	1.022x-1.304	0.984	25	SLOPES	33.84	<.001 **
					MEANS		
PREORB	WFLA	0.890x-1.130	0.957	42	REGRESSION	624.65	<.001 **
	UFLA	1.041x-1.505	0.975	25	SLOPES	10.70	0.002**
					MEANS		

Observations of *Hyporhamphus meeki* in the York River

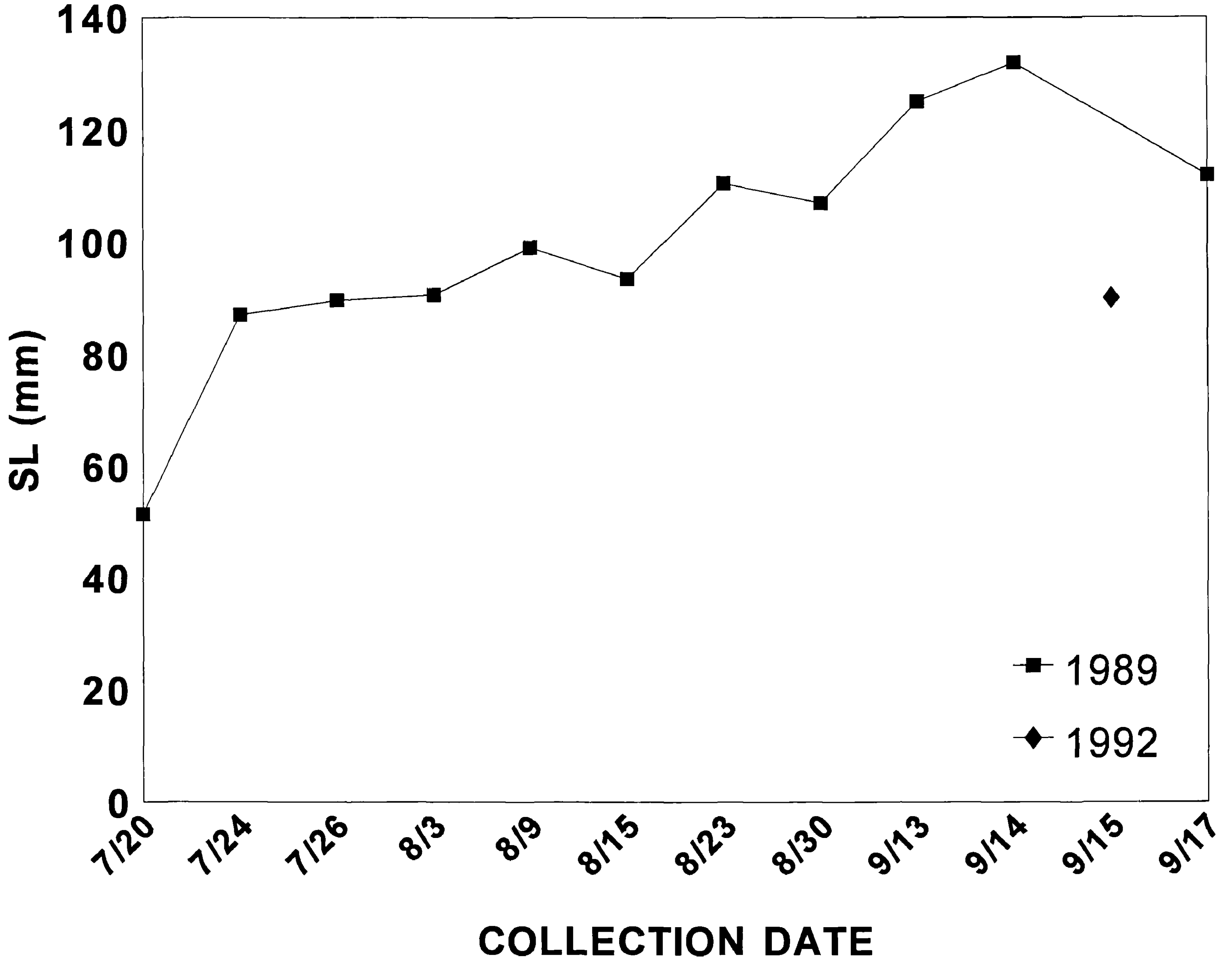
A rigorous sampling design was not employed for the capture of halfbeaks, as it was not pertinant to the objectives of this study. However some useful information was collected during the course of my halfbeak sampling. This information is not intended for critical analysis, but it does offer some insights into the biology of *Hy. meeki*. It is hoped that in the future this information can be of use in designing a thorough study of halfbeak biology and life history.

The most comprehensive sampling in the York River, VA for fresh specimens of halfbeaks was accomplished in 1989. Positive collections were made on the following dates: July 19, 20, 24, and 26; August 2, 3, 9, 14, 15, 23, 28, and 30; and September 13, 14, and 17 (Table 25). There is a general increase in size with time (Fig. 12). Prior to and during this time period a fellow graduate student (J. Luo) was sampling nightly under a light hung from the VIMS Ferry Pier. We observed large adult halfbeaks (SL estimated, > 100 mm) only during May and early June. In mid-July we observed the appearance of small juveniles (30-50 mm SL). These observations are consistent with: Olney and Boehlert's (1988), of eggs and juveniles taken in Chesapeake Bay from May to August; Hardy's (1978) of a recently hatched specimen taken from the Chesapeake on July 8th; larval, juvenile and adult material examined by Hardy and Johnson (1974); and collection dates (May - Oct.) of USNM material from Chesepeake Bay. From this data I hypothesize that mature adult *Hy. meeki* arrive in Chesapeake Bay in about May. They then spawn in eel-

Table 25. Hyporhamphus meeki collected in the York River, VA.

COLLECTION DATE	N	SIZE RANGE SL (mm)	MEAN
20 JUL 89	8	36.4-77.1	51.4
24 JUL 89	11	78.1-106.8	87.1
26 JUL 89	11	78.6-106.8	89.7
3 AUG 89	10	80.9-99.2	90.7
9 AUG 89	7	84.3-109.3	99.1
15 AUG 89	18	61.3-115.4	93.5
23 AUG 89	4	105.8-120.9	110.5
30 AUG 89	12	97.0-124.6	107.0
13 SEPT 89	4	116.3-135.1	125.1
14 SEPT 89	9	102.6-140.1	111.9
17 SEPT 89	4	121.8-146.2	132.0
15 SEPT 92	5	83.2-96.8	90.1

Figure 12. Mean standard length of *Hyporhamphus meeki* collected in the York River, VA during 1989 and 1992.


140
120
100
80
60
40
20
0
SL (mm)
7/20
7/24
7/26
8/3
8/9
8/15
8/23
8/30
9/13
9/14
9/15
9/17
COLLECTION DATE
1989
1992

grass beds (*Zostera*), the filamentous eggs attaching to the blades of grass. The subsequent time of hatching and larval period are unknown. However juveniles are susceptible to the sampling gear at >30 mm SL, which occurs during July. While dipnetting during July, small juveniles were observed to pass through the net mesh. Likwise, few individuals < 30 mm SL have been captured while seining. Young of the year *Hy. meeki* grow during the summer months in the Chesapeake Bay, departing and migrating south during October. The exact timing of these events in the Chesapeake vary from year to year with environmental conditions (i.e. water temperature). For example, seining and dipnetting efforts in July 1992 yielded a single specimen. Specimens collected Sept. 15, 1992 (Fig. 12) were smaller than those collected during the same period in 1989. The spring and summer of 1992 were cooler than the previous few years and water temperatures remained depressed well into the summer. Slow development of juvenile alosines and striped bass was also noted this same year (B. Hill and D. Seaver pers. comm.).

DISCUSSION

Zoogeography

United States Gulf and Atlantic coasts-- The results of the morphometric and meristic comparisons of Gulf and Atlantic populations of *Hy. meeki* indicated some differences between these populations, implying some degree of isolation. These findings are in agreement with the conclusions of other studies of marine taxa with populations along the U.S. east coast and the Gulf of Mexico (e.g. *Opsanus*, Avise et al., 1987; *Ammodramus*, Avise and Nelson, 1989; Avise and Ball, 1990; *Microgobius*, Birdsong, 1981; Briggs, 1974; sciaenids, Ditty, 1989; *Microgobius*, Ginsburg, 1934; *Crassostrea*, Reeb and Avise, 1990; Retzer, 1990; *Limulus*, Saunders et al, 1986; *Sphoeroides*, Ship and Yerger, 1969; *Hypsoblennius*, Smith-Vaniz, 1980; *Chasmodes*, Williams, 1983; and *Menidia*, Johnson, 1975 and Mickevich and Johnson, 1976).

The similarity of these patterns of differentiation among diverse taxa may be indicative of a common causal process; geologic history. The obvious geographic barrier between Atlantic and Gulf of Mexico populations is the Florida peninsula. Its northern shores are temperate while the southern tip extends into the tropics, isolating two warm temperate faunas; one in the Gulf of Mexico, and the other on the east coast of the U.S. Over the course of its geologic history the Florida peninsula has not always existed as such. It has been repeatedly inundated by rising sea levels, and has reemerged with lowered sea levels. During Quaternary and even Pliocene interglacial periods high sea level stands formed marine terraces and beach ridges (Kennet, 1982). Burgess and Franz (1978) reviewed the work of many geologists concerning the zoogeography of the aquatic fauna of the St. Johns River. Alt (1968) dates the earliest and most extensive stands during the late Miocene and Pliocene. The highest of these stands probably occurred during the late Pliocene (1.85-5 mya) reducing the Florida peninsula to a relatively minor protuberance between the Gulf and Atlantic coasts. It is hypothesized that during this high stand ("Wicomico"), continuous distributions of the predecessors of now disjunct taxa, existed through the Gulf, accross the submerged Florida peninsula, and northward along the Atlantic coast (Springer, 1959; Shipp and Yerger, 1969). During these interglacial high stands gene flow was unimpeded between the Gulf and Atlantic (Avise, 1989; Reeb and Avise, 1989). In contrast, during glacial periods of low sea level, vast expanses of the continental margins were exposed isolating the Gulf of Mexico faunas. During the high stands, when the Florida peninsula was submerged, parts of the Peninsula remained above the sea as offshore islands between the mainland and Caribbean landmasses (Cooke, 1945). Springer (1959) hypothesized that *Chasmodes saburrae* developed in isolation around the offshore islands, then displaced *C. bosquinanus* when the peninsula formed. Whereas *C. saburrae*, the species occupying the region about the southern Florida peninsula between the two disjunct Gulf and Atlantic populations (subspecies Williams, 1983), does not extend into the tropical Caribbean. Other taxa occupying this void around the tip of

Florida, do have Caribbean distributions. The Florida peninsula is thought to be transitional between the Carolinian province to the north and the Caribbean to the south (Woodring, 1966).

The distribution patterns described above are similar to those found for *Hy. meeki* and *Hy. unifasciatus*. *Hyporhamphus meeki* extends down the U.S. east coast to the faunal break midway down the Florida peninsula, in the area of St. Lucie's Inlet. The range is disjunct around the southern tip of Florida, where *Hy. meeki* is replaced by the tropical species *Hy. unifasciatus*. The range of *Hy. meeki* resumes on the Gulf coast of Florida in the vicinity of Sanibel Island and continues through the Texas Gulf shore. *Hyporhamphus unifasciatus* extends into the warm temperate northern Gulf coast of Florida when the waters warm to tropical temperatures. Similarly its range up the Atlantic coast is extended during seasonal warmings. These distribution patterns are most likely the result of a combination of historical temperature (Walters and Robbins, 1961; Smith-Vaniz, 1980) and sea level fluctuations (see others cited above) since the late Miocene. However, without phylogenetic data and analysis a mechanism for the distribution of *Hyporhamphus* in the western Atlantic is merely speculative. This work does provide a hypothesis for future study of the relationships and zoogeography of *Hyporhamphus* in the western Atlantic.

Within *Hy. meeki* variation was found between the northwestern and eastern Gulf of Mexico (WFLA) populations. The results of my statistical analysis (ANOVA and ANCOVA) between the west Florida population (WFLA) and other populations of *Hy. meeki* (EFLA, GULF, NOF) show greater differences between

WFLA and other populations of *Hy. meeki* (ie. WFLA vs EFLA; WFLA vs GULF), than those found between these other populations (ie. NOF vs EFLA; EFLA vs GULF). Once again this pattern of variation within the Gulf of Mexico is found in other taxa, including differentiation at the species level (*Sphoeroides parvus* and *S. nephelus*, Shipp and Yerger, 1969; *Chasmodes bosquianus longimaxilla* and *C. b. bosquianus*, Williams, 1983), and population level (*Gymnachirus texae*, Dawson, 1964; *Menidia peninsulae*, Johnson, 1975). Some researchers have attributed these differences to past physical barriers in the northern Gulf, such as the Mississippi River plume (Baughman, 1950) or a peninsula (Ginsburg, 1952; see Briggs, 1974 for a summary of this information). Others have pointed to ecological differences in the northwestern and eastern Gulf of Mexico (Hedgepeth, 1954; and Briggs, 1974). Finally, Dahlberg (1970) attributed east-west disjunctions to lowered sea temperatures in the northwestern Gulf.

Bermuda-- The status of the Bermudian population of *Hy. unifasciatus* is still in question. The results of the morphometric and meristic analysis indicate differences in the Bermudian population from the remainder of *Hy. unifasciatus*. The Bermudian population has the lowest RGR_1, RGR_2, DOR, and P_1 counts, and the highest ANA counts. They also are thinner in body depth at both P_1O and P_2O, and their P_2-CX extends to a point the most posterior (never anterior to the preopercle, usually on the opercle) of any population. Additionally, Bermudian *Hy. unifasciatus* may not attain as great a length (SL) as individuals in other populations. The largest specimen was 168 mm and the mean SL of specimens examined was 109 mm (Table 7). The other populations of *Hy. unifasciatus* attain a greater size as indicated by morphometric maximums and means. However, this discrepancy in size may be an artifact of sampling.

The above differences in morphometry may be indicative of some degree of isolation of this population. Bermuda, an oceanic island, approximately 900 mi. distant from the West Indies has been included in the West Indian faunal province (Briggs, 1974) due to the similarities of their faunas. The Caribbean nature of the Bermudian fauna has been attributed to the effects of the Gulf Stream (Beebe and Tee Van, 1933), which was thought to be a continual source of faunal elements to Bermudian waters, thus maintaining gene flow between these populations. Collette (1962) in his survey of Bermudian shore fishes reported a low level of endemism, only 5 percent. Briggs (1974) also theorized that the tropical fauna of Bermuda was extinguished during the Wisconsin glaciation, a mere 11,000 ybp. Thus the recolonization of Bermuda has occurred over a relatively recent period of time, not allowing the evolutionary effects of isolation to be more pronounced.

In formally recognizing populations within a species, the assignment of subspecific status is a matter of some taxonomic debate. The differences observed in the Bermudian *Hy. unifasciatus* morphometry could be the result of one of two possible scenarios. First, that the characters observed to differ are ecophenotypic expression due to ecological and environmental parameters. Secondly, that they could reflect actual phylogenetic histories. If the latter is the case, the Bermudian population deserves formal taxonomic recognition as a subspecies. Avise and Ball (1990) outline the methods of concordance principals useful in correctly assigning subspecific status to taxa. They prescribe the use of multiple, independent genetic characters, and specifically have employed mtDNA gene genealogies.

Collette (1966) noted that some Bermudian endemics, *Harengula callolepis, Jenkinsia viridis* and *Hemiramphus bermudensis* all have greater numbers of gill rakers than the taxa from which they may be derived. He also noted that *H. callolepis, He. bermudensis* and *Haemulon aurolineatum angustum* are thinner and have a greater SL than the taxa from which they were derived. Collette invoked the possible role of ecological and environmental stresses, resulting in these character differences, specifically the paucity of food in the nutrient poor Sargasso Sea surrounding Bermuda. My morphological findings in Bermudian *Hy. unifasciatus* are somewhat different, in that they have fewer gill rakers and though they are thinner they attain a smaller size (SL). Therefore, the characters distinguishing the Bermudian population from other populations may be due to ecophenotypic plasticity. Though there is a possible extrinsic barrier, open ocean distance, isolating the Bermudian population, the Gulf Stream may provide means of penetrating this barrier for some species. However, since *Hyporhamphus* are inshore species, it is unlikely that they would be entrained and transported by the Gulf Stream. Interestingly, Collette (1962) also described a species of *Hemiramphus* as an island endemic, *He. bermudensis* in Bermuda, although the other two members of this genus in the Atlantic Ocean are wide ranging pelagics. It is therefore surprising that *Hyporhamphus*, being a coastal inshore species with limited dispersal capabilities, has not speciated in Bermuda. One would expect the opposite, based on concepts of isolation and the biology of the species involved. Thus, at this time, the taxonomic status of *Hyporhamphus* in Bermuda, with only the morphologic data at hand remains in question. In the future a molecular genetic analysis of these populations (or taxa) may clarify the status of Bermudian *Hy. unifasciatus.*

Hy. meeki and *Hy. unifasciatus*, species comparisons

Morphological differences between *Hy. meeki* and *Hy. unifasciatus* are not as pronounced as between some species of the genus. A combination of meristic characters, number of gill rakers on the first and second arches, and morphometric characters, preorbital/orbit ratio, are best for diagnosing these species. The underlying question in species recognition is one of reproductive isolation and therefore a lack of gene flow. Allozyme electrophoretic data (Banford, unpublished data) indicate lack of gene flow between the species recognized above. In a survey of 29 presumptive loci, 10 potential fixed allelic differences were observed between specimens of *Hy. meeki* from Chesapeake Bay, VA and *Hy. unifasciatus* from the San Blas Arch., Panama. The unbiased minimum genetic distance (Nei, 1978) between the two species was found to be 0.383. This agrees with the results of a comparison of *Hy. unifasciatus* and *Hy. synderi* in the eastern Pacific. The two species are morphologically distinct from one another, with *Hy. synderi* lacking or having only a few scales on the dorsal and anal fins of adults, and having 45-55 gill rakers on the first arch (B. Collette pers. comm.). These two eastern Pacific species were found to have an unbiased minimun genetic distance of 0.393 (Banford, unpublished), similar to the level of genetic distance found between the western

Atlantic species of *Hyporhamphus* compared to date.

Hybridization and introgression

Hybridization between *Hy. meeki* and *Hy. unifasciatus* may be occurring in the Yucatan, as evidenced by possible character mosaics and intermediacy between the two species. Hybridogenesis can result in first generation (F_1) gene combinations. However, due to frequent sterility in this generation, these combinations are not typically passed on to subsequent generations. This type of hybridization can continue between the two hybridizing species without passing beyond the first generation. However, through introgression, where the F_1 generations are fertile (fertile hybrid backcrossing), genes are segregated or recombined in subsequent generations. In this way genetically independent morphological characters will result in a mosaic of characters from the original crossing lineages (species),(Smith, 1992). There are multivariate morphometric techniques for discerning hybridization and introgression (see citations in Smith, 1992). However the certainty of hybridization and introgression is still in question, due to the unknown genetic nature and ecophenotypic plasticity of morphologic characters. Additionally, morphology may not allow hybrids (F_1) to be easily discerned from backcrossed (F_2) individuals. Molecular genetic methods would be the most appropriate and expediant means of answering the question of hybridization and introgression in Yucatan. Thus, once again, more study both in multivariate morphometrics and molecular genetics is needed to clarify the situation in Yucatan.

SUMMARY

In summary, it has been clearly shown that the hypothesis of Meek and Goss (1884), and Collette and Berry was correct. *Hyporhamphus unifasciatus* sensu stricto occurs in southern peninsular Florida, around Bermuda, in the Yucatan and southward to southern Brazil, occasionally to Uruguay. The newly described species, *Hy. meeki* Banford and Collette, constitutes the northern form of Meek and Goss (1884), and Collette and Berry (Collette pers. comm.). *Hyporhamphus meeki* occurs on the Atlantic coast from Cape Cod, MA to St. Lucie's Inlet, FL and on the Gulf coast from the vicinity of Tampa Bay, FL to the U.S. Mexico border and also in Yucatan.

Areas of sympatry of the species are peninsular Florida and Yucatan. Temporal avoidance may be occurring in Florida. In Yucatan hybridization and introgression may be occurring as evidenced by possible character mosaics and intermediacy. More work is required in both of these regions; specifically multivariate morphometric and molecular genetic analyses.

Geographic variation has been explored on a preliminary level with univariate statistics. Once again further work is needed and anticipated. Multivariate statistical techniques (principal components analysis) may be more sensitive in exploring overall shape changes from one population to another and offer more insight into the actual geographic limits of these populations.

Also, preliminary zoogeographic implications of this study have been explored. This area of investigation will benefit from a rigorous phylogenetic analysis of both morphologic and genetic aspects of *Hyporhamphus* in the New World.

Finally, I would like to reiterate that this problem was first hypothesized in 1884 over 100 years ago. This is but one example of many more systematic problems of this nature at the alpha-taxonomic level. The alpha-taxonomy of the New World *Hyporhamphus* needs to be completed before a phylogenetic analysis can be undertaken. Most work on the status of species of *Hyporhamphus* has been accomplished (B. Collette pers. comm.), however, the status of *Hy. unifasciatus* in the eastern Pacific, and the populations at Bermuda and the Galapagos are still in question. These problems need to be addressed before we can gain a thorough understanding of ecological, evolutionary and phylogenetic relationships and processes.

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