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A MORPHOLOGICAL AND ALLOZYMIC ANALYSIS OF SPECIES IN THE *GOBIONELLUS OCEANICUS* COMPLEX (PISCES: GOBIIDAE)

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ABSTRACT

Morphological and allozymic investigations were conducted on the three nominal species *Gobionellus gracillimus, G. hastatus* and *G. oceanicus,* termed here the *Gobionellus oceanicus* complex. Gulf of Mexico samples of the complex differed in lateral scale row number from Caribbean and South Atlantic samples, while samples from the eastern coast of the United States included both forms and many specimens with intermediate values as well. No fixed differences were found between the two morphotypes at 21 presumptive gene loci. Allelic frequencies for specimens of the two forms from a syntopic collection suggested limited genetic divergence between northern and southern populations with south to north introgression. *Gobionellus gracillimus* was not distinguishable using the diagnostic characters offered in its original description. A single species, *Gobionellus oceanicus,* is recognized, of which *G. gracillimus* and *G. hastatus* are junior synonyms.

Species of the genus *Gobionellus* are a familiar component of fish communities of the estuaries and coastal waters of the eastern United States south of Virginia, especially along southeastern Florida and the northern Gulf of Mexico. As many as 12 speices of *Gobionellus* have been recognized from this region (Robins et al., 1980). Taxa allotted to this genus range from small, large-scaled species such as *Gobionellus boleosoma* to elongate, small-scaled forms like *G. gracillimus*. Along with *G. gracillimus,* two other nominal species of long-bodied *Gobionellus* with small scales frequent U.S. estuaries, *G. hastatus* and *G. oceanicus*. *Gobionellus gracillimus* and *G. hastatus* are found in the Gulf of Mexico and along the southeastern Atlantic coast of the United States. *Gobionellus oceanicus* is known from North Carolina to southern Brazil, including the Greater and Lesser Antilles. The only other elongate species of *Gobionellus* found in estuaries of the western Atlantic is *G. stomatus,* which is limited to Brazil.

Gobionellus stomatus is readily distinguished from *G. gracillimus, G. hastatus* and *G. oceanicus* by: reduced ctenoid scales, smooth to the touch, covering the entire trunk; a combination of 13 rays in the second dorsal fin and 14 anal fin rays; elongate jaws in males that may reach to the preopercular margin of the cheek; pronounced vertical bars on the trunk; and a large suborbital bar running from the eye to the jaw. The other three species have reduced ctenoid scales limited to the anterior portion of the body with ctenoid scales covering the bulk of the trunk, and have 14 second dorsal fin rays and 15 anal fin rays. They also lack the distinctive pigmentation of *G. stomatus,* with the most prominent markings usually being a large anterolateral splotch on the trunk beneath the pectoral fin and a basicaudal spot. In some individuals, a row of midlateral spots and irregularly spaced and formed bars may also be found. These markings are generally limited to juveniles but appear occasionally in some adult specimens over 120 mm SL.

Gobionellus gracillimus, G. hastatus and *G. oceanicus* are not easily separated. Ginsburg (1932) distinguished *Gobionellus hastatus* and *G. oceanicus* by the number of scale rows in a lateral series on the trunk. He also discerned a correlation

between the number of scale rows and geographic locality for the few specimens available to him. A southern form (*G. oceanicus*), represented by specimens from Puerto Rico, Panama, Cuba and Key West, Florida, was shown to have 60 to 76 scales in a series, whereas a northern form (*G. hastatus*), described from specimens from the northern Gulf of Mexico (Pensacola, Florida and Louisiana), had 76 to 89 scales in series. Hildebrand and Cable (1938) later found both species along the North Carolina coast.

Ginsburg (1953) later reported that the ranges of scale counts for the species *G. hastatus* and *G. oceanicus* were not strictly contiguous, but overlapped. He also described a third species that had previously been confused with *G. hastatus*. This new form, *G. gracillimus,* was distinguished from *G. hastatus* by a longer caudal fin, a more slender body, longer dorsal spines and finer scales (more in a lateral series). Each character seemed to have a bimodal distribution. Ginsburg (1953) noted, however, that there was broad overlap between *G. hastatus* and *G. gracillimus* for all characters and that individual specimens could not always be confidently referred to one taxon or another. He suggested that these forms either represented "ecological subspecies" or were simply two species not sharply distinguishable by the taxonomic methods available at that time. The geographic range of *Gobionellus gracillimus* was said to be basically the same as for *G. hastatus,* although most specimens of *G. gracillimus* were from the vicinity of Pensacola, Florida. Robins and Ray (1986: 246–247) considered *G. gracillimus* to be indistinguishable from *G. hastatus,* and suggested that *G. hastatus* and *G. oceanicus* might be one variable species.

The purpose of this study is to clarify the taxonomic confusion surrounding the three nominal species (*G. gracillimus, G. hastatus* and *G. oceanicus*) comprising the *Gobionellus oceanicus* complex. We present morphological and allozymic data indicating that *Gobionellus hastatus* and *G. gracillimus* should be recognized as junior synonyms of *G. oceanicus*.

Materials and Methods

Meristic and Morphometric Analyses.—Measurements of standard length, caudal peduncle length, pectoral fin length (=length of longest pectoral ray), head width and interorbital width (least fleshy width) were done using standard methods (Hubbs and Lagler, 1958). Jaw length was measured as the distance from the tip of the upper jaw to the corner of the jaw. Head length was measured from the tip of the snout to the bony edge of the opercle at its upper angle. Orbit length was measured as the horizontal diameter at the level of the anterior otic pore. Eye to origin of the first dorsal fin (D_1) was measured from the orbit margin at the anterior otic pore to the dorsal origin. Snout length was measured from the tip of the snout to the anterior orbit margin in a line through the posterior nares. Anal fin terminus to D_2 terminus was measured from the base of the last ray of the second dorsal to the base of the last ray of the anal fin. Anal fin origin to D_2 origin was the distance from the base of the spine of the second dorsal fin to the base of the spine of the anal fin. Pelvic fin length was taken as the length of the innermost (longest) rays. Caudal fin length was the length of the longest caudal ray.

Lateral scale rows were counted as described by Ginsburg (1932). Predorsal scales were the number of rows counted forward from the first dorsal origin on the side of the nape and occipital region along a furrow formed between the low midnape muscular ridge and the sides of the nape.

Principal component analysis was used to describe and assess multivariate morphological variation. Graphical depictions of specimen positions along vectors were surveyed for discrete groups. This method was chosen because it required no a priori assumptions of taxonomic identity of specimens (Reyment et al., 1984). Morphometric variables used in the principal component analyses were transformed with natural logarithms. Variables were standardized in analyses incorporating both meristic and morphometric characters. A correlation matrix was used in analyses of combined meristic and morphometric characters. Analyses using only morphometric variables were based on covariance matrices and the variables were not standardized. Separate analyses were performed on males and females to eliminate sexual dimorphism as a confounding factor in the interpretation of morphometric variation. Analyses were done using programs published by the SAS Institute (1982).

Material Examined.—Museum acronyms follow Leviton et al. (1985) except where noted. NORTH CAROLINA: CPL (Carolina Power and Light) BN 338(1); CPL BR4 1833(2); UNC 8100(1); UNC 10363(1); UNC 10419(1); UNC 10477(1); UNC 10587(2); UNC 11414(1); UNC 11594(1); UNC 13135(1); UNC 15376(4); UNC 15555(1); USNM 123211(1); USNM 123213(1). SOUTH CAROLINA: ANSP 149615(1); ANSP 149724(2); GMBL 65-8(10). FLORIDA (east coast): ANSP 79475(1); IRCZM 107:3515(1); IRCZM 107:5422(2); MSU uncat. (5), FP-189; MSU uncat. (1), FP-185; MSU uncat. (1), FP-188; TNHC 10702(1); TNHC 10885(8); UF 30511(4); UF 31224(1); UF 100229(3); USNM 53340(1); USNM 62702(1), paratype, *Gobionellus gracillimus*; USNM 123228(2), paratypes, *G. gracillimus*; USNM 174954(1). FLORIDA (Keys): USNM 35155(5). FLORIDA (west coast): ANSP 73083(1); ANSP 79026(1); ANSP 146432(2); ANSP 146435(4); ANSP 146437(2); ANSP 146441(12); UF 8954(1); UF 14222(1); UF 18980(1); UF 38040(1); USNM uncat. (1), BOC, Pensacola; USNM 123225(1), paratype, *G. gracillimus*; USNM 123227(1), holotype, *G. gracillimus*. ALABAMA: AMNH 52029(1); USNM 186172(1); USNM 197651(1). MISSISSIPPI: ANSP 31627(1); USNM uncat. (1), acc. no. 231485, U60-16; USNM uncat. (3), U60-7; USNM uncat. (3), U60-2; USNM 263260(1). LOUISIANA: FMNH 32998(3); MSU uncat. (1), FP-82; MSU uncat. (1), FP-77; MSU uncat. (2), FP-70; USNM 123224(1), paratype, *G. gracillimus*; UNO (University of New Orleans) 3386(1). TEXAS: ANSP 70903(4); ANSP 74060(3); ANSP 96787(1); ANSP 99077(1); ANSP 99136(1); ANSP 115784(1); FMNH 38685(2); FMNH 40237(2); MSU uncat. (1), A-1-10; MSU uncat. (1), Hockaday et al.; MSU uncat. (10), FP-177; TCWC 0746.8(1); TCWC 0921.3(4); TCWC 0929.8(13); TCWC 0936.6(3); TCWC 1619.1(1); TCWC 2049.2(1); TCWC 2194.1(1); TNHC 10470(3); USNM 123226(1), paratype, *G. gracillimus*; UTMSI (University of Texas Marine Science Institute) 371(7); UTMSI 1336(5); UTMSI 2340(2). MEXICO: UTMSI 372(17). GULF OF MEXICO: FMNH 45604(1). CUBA: ANSP 55901(1); ANSP 70767-73(7); ANSP 83497(2); AMNH 11416(5); FMNH 2629(3); USNM 164933(1). JAMAICA: ANSP 95631(10); USNM BOC 3377(9). HAITI: ANSP 81860(1); ANSP 83498(5); USNM 132119(1); USNM 178719(2). DOMINICAN REPUBLIC: ANSP 77296(1). PUERTO RICO: ANSP 144493(4); AMNH 2069(1); LACM 7725(6); USNM 49365(1), holotype, *Gobius bayamonensis*; USNM 205203(1); USNM BOC 2746(1). GUADELOUPE: ANSP 142989(1). BARBADOS: USNM uncat. (12), Long Pond, BZ-69-4, ref. no. 549. PANAMA: FMNH 32189(1); FMNH 32235(2); FMNH 32237(1); FMNH 32238(2); USNM 81880(3); USNM 81882(2). VENEZUELA: FMNH 3753(1). SURINAM: MNHN A.1262(1), syntype, *Gobius bacalaus*; FRENCH GUIANA: MNHN A.1505(1); MNHN A.8016(5); MNHN 2523(6); USNM 226246(1). BRAZIL: ANSP 86872(1); ANSP 121230(2); ANSP 121231(3); ANSP 121243(6); AMNH 20722(3); MNHN A.1260(2), syntypes, *G. bacalaus*; MNHN 1360(2), syntypes, *G. bacalaus*; USNM 87751(2); UF 19256(3).

Allozymic Analysis.—Specimens of the *Gobionellus oceanicus* complex were obtained from the Indian River, FL, Bayou Choupique, LA, and the mouths of the Rio Grande, TX, and Rio Tonala, MX. Skeletal muscle, eye, and liver tissue samples from each specimen were mechanically homogenized in an approximately equivalent volume of buffer consisting of 0.001 M Tris-HCl, 0.001 M EDTA, and 0.0001 M beta-mercaptoethanol (pH 7.1). Resultant homogenates were centrifuged at 5,300 G for 20 min at 4°C. Supernatant fractions were subjected to horizontal starch gel electrophoresis at 4°C. All gels were prepared with 12% Sigma starch.

Thirteen enzyme systems encoded for by 21 presumptive gene loci were assayed. Enzyme systems examined, locus abbreviations, tissue specificity and electrophoretic conditions are described in Table 1. Enzyme nomenclature and locus abbreviations follow recommendations of Buth (1984) except for malic enzyme and superoxide dismutase for which no intracellular designations were made.

RESULTS

Morphological Analyses.—Counts of lateral scale rows of 195 specimens from the western Atlantic revealed a bimodal distribution with modes of 65 and 82 scales in a series (Fig. 1) and a trough in the vicinity of 75 or 76 scales. Consequently, only two forms were distinguishable by scale counts, not three. As Ginsburg (1932) noted, the irregular placement of the small, reduced ctenoid scales on the anterior portion of the body introduces a potential source of error in counting, and different values may be obtained even when one repeats counts for a single specimen. To reduce the variation observed due to counting precision, lateral scale rows were also counted from an imaginary line running vertically from the anal fin origin to the second dorsal fin, midlaterally, in a straight line to the base of the caudal fin. When these counts (A–C lateral scales) were listed for localities of sufficient sample size a strong coincidence between lateral scale count and geography was demonstrated (Table 2). A Student-Newman-Keuls test (Sokal and Rohlf, 1969)

Table 1. Enzyme systems examined, locus abbreviations, tissue sources and electrophoretic procedures employed

Enzyme	E.C. number	Locus	Tissue source	Electrophoretic buffers
Adenylate kinase	2.7.4.3	Ak-A	muscle	A
		Ak-B	muscle	A
Aspartate aminotransferase				
(mitochondrial)	2.6.1.1	M-Aat-A	muscle	A, B
(supernatant)		S-Aat-A	muscle	A, B
Creatine kinase	2.7.3.2	Ck-A	muscle	A, B
Glucosephosphateisomerase	5.3.1.9	Gpi-A	muscle	A
		Gpi-B	muscle	A
Glycerol-3-phosphate dehydrogenase	1.1.1.8	G-3-pdh-A	muscle	A
Isocitrate dehydrogenase				
(mitochondrial)	1.1.1.42	M-Icdh-A	muscle	A
(supernatant)		S-Icdh-A	liver	A
Lactate dehydrogenase	1.1.1.27	Ldh-A	muscle	A
		Ldh-B	liver	A
		Ldh-C	eye	A
Malate dehydrogenase				
(mitochondrial)	1.1.1.37	M-Mdh-A	muscle	A
(supernatant)		S-Mdh-A	muscle	A
(supernatant)		S-Mdh-B	muscle	A
Malic enzyme	1.1.1.40	Me-A	muscle	A
Leucine aminopeptidase		Lap	muscle	B
Phosphoglucomutase	2.7.5.1	Pgm-A	muscle	A
Phosphogluconate dehydrogenase	1.1.1.44	Pgdh-A	muscle	A
Superoxide dismutase	1.15.1.1	Sod-A	muscle	A, B

A, Tris-citrate pH 7.5 (Stein et al., 1985); B, Poulik (Selander et al., 1971).

showed that means of samples from Gulf of Mexico localities did not differ significantly from one another (Table 3). Means for samples from the Greater Antilles, Panama and Brazil were not significantly different from one another either. Member samples of each of these two sets did have significantly different means from samples of the other set, however. The mean for the sample from southeast Florida differed significantly from all other population samples (Table 3) due to the presence of both southern (*G. oceanicus*) and northern (*G. hastatus*) forms in approximately equal frequency.

Frequencies of A–C lateral scale counts were graphed for all specimens except for those from the eastern coast of the United States where both the northern (*G. hastatus*) and southern forms (*G. oceanicus*) are known to occur and intergrades might be expected (Fig. 2). The distribution of counts again indicated that only two different forms could be recognized from scale counts, with no suggestion of another peak at the higher end of the total range (representing *G. gracillimus*).

Several individuals demonstrating scale counts typical of the southern form were observed in Gulf of Mexico samples (Fig. 2, Table 2). These specimens, assignable to *G. oceanicus,* were from east Texas at Port Arthur and the Houston Ship Channel. Ninety-five percent confidence intervals were calculated for the two A–C lateral scale number distributions in Figure 2, with these Texas specimens being included in the Caribbean/Brazilian group. Specimens identified as *G. oceanicus* had a 95% C.I. of 30–37 scales from the anal fin origin to the caudal

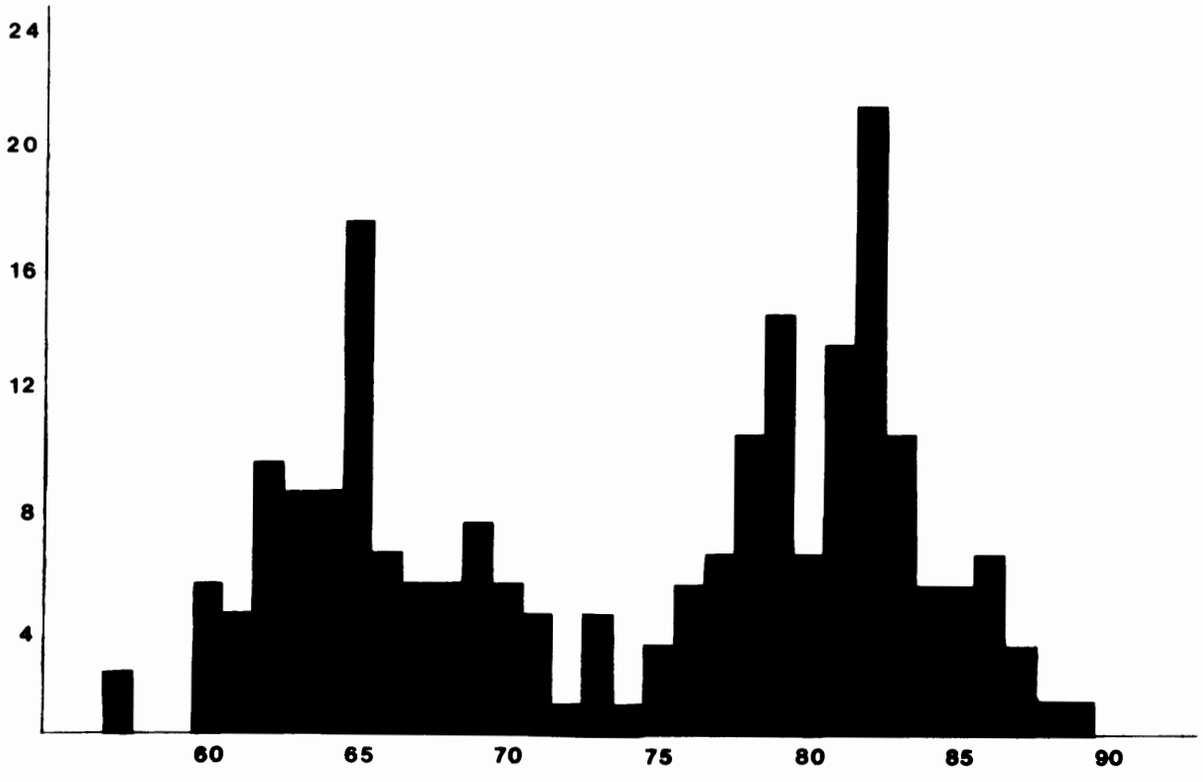

Figure 1. Frequency distribution of lateral scale row counts of specimens of the *Gobionellus oceanicus* complex.

fin, while the *G. hastatus* sample had a 95% C.I. of 41–48 scales in that series. Applying these confidence intervals to the samples in Table 3, it can be seen that specimens from southeast Florida not only span much of the range for counts, but that 5 specimens (19%) fall between the two confidence intervals. Only one specimen from Pensacola (where Caribbean fish species are frequently carried by the Loop Current) and one specimen from east Texas fall between the two confidence limits. Although both forms can be recognized using these scale counts, there is no bimodality evident where their ranges overlap in southeastern Florida.

Ginsburg's (1953) description of *G. gracillimus* was based on bimodality in four different characters, caudal fin length, body depth, dorsal spine length and the number of lateral scales, in specimens identified as *G. hastatus*. Despite evidence of intergradation, Ginsburg stated that males 120 mm SL or larger were easily distinguished. Twenty-four males 120 mm SL or longer with scale counts at the higher end of the range for the species complex were graphed for the four diagnostic characters, as well as the number of lateral scales from the anal origin to the caudal fin (Fig. 3). Only the total lateral scale number distribution could possibly be considered bimodal.

The statistic g_2 was calculated for the sample of total lateral scale counts to test for kurtosis (Sokal and Rohlf, 1969). Kurtosis is the manner and degree to which a distribution is peaked. A distribution can depart from normality by being more sharply peaked than normal (a leptokurtic curve) or by being flatter than normal (a platykurtic curve). A bimodal distribution represents an extreme platykurtic condition in which very few observations are found at the mean or in the tails, but many are found in the intervening regions. A negative g_2 signifies platykurtosis, while a positive g_2 denotes leptokurtosis. For this sample ($N = 23$), $g_2 = 0.184$.

Table 2. The distribution of lateral scale row counts from anal fin origin to base of caudal fin of *Gobionellus oceanicus* complex specimens by region

	N	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50
Tampico	(16)												1	2	4	3	3	3				
Rio Grande	(12)												1		3	6	1		1			
Port Aransas	(20)												1	3	3	3	3	4	2	1		
East Texas	(28)	2					1				1		1	2	4	5	4	5	3			
Pensacola	(22)											1	2		3	5	5	4	2			
SE Florida	(26)				1	4	2	2	2	2	1	2	3	1	1	1	2		1	1		
Cuba	(12)	3		1	3	2		1	2													
Jamaica	(19)			3	5	9	1	1														
Puerto Rico/Hispaniola	(15)	2	1	2	7	1		2														
Panama	(11)			2	3	1	3	1	1													
Rio de Janeiro	(14)		1	1	3	1	3	1	3		1											

Table 3. Results of Student-Newman-Keuls tests between population sample means for A–C lateral scale row number. * signifies a significant difference ($P < 0.01$). Sample means that do not significantly differ are underlined

			Port Aransas	Pensacola	Tampico	Rio Grande	East Texas	SE Florida	Rio de Janeiro	Panama	Jamaica	Cuba	PR/Hisp
	$\bar{x}$		44.45	44.27	43.88	43.83	42.93	39.12	34.79	34.09	33.58	33.25	32.8
	$\bar{x}$	(N)	(20)	(22)	(16)	(12)	(28)	(26)	(14)	(11)	(19)	(12)	(15)
Port Aransas	44.45	(20)	—										
Pensacola	44.27	(22)	0.18	—									
Tampico	43.88	(16)	0.57	0.39	—								
Rio Grande	43.83	(12)	0.62	0.44	0.05	—							
East Texas	42.93	(28)	1.52	1.34	0.95	0.90	—						
SE Florida	39.12	(26)	*5.33	*5.15	*4.76	*4.71	*3.81	—					
Rio de Janeiro	34.79	(14)	*9.66	*9.48	*9.09	*9.04	*8.14	*4.33	—				
Panama	34.09	(11)	*10.36	*10.18	*9.79	*9.74	*8.84	*5.03	0.70	—			
Jamaica	33.58	(19)	*10.87	*10.69	*10.30	*10.25	*9.35	*5.54	1.21	0.51	—		
Cuba	33.25	(12)	*11.20	*11.02	*10.63	*10.58	*9.68	*5.87	1.54	0.84	0.33	—	
PR/Hisp	32.8	(15)	*11.65	*11.47	*11.08	*11.03	*10.13	*6.32	1.99	1.29	0.78	0.45	—

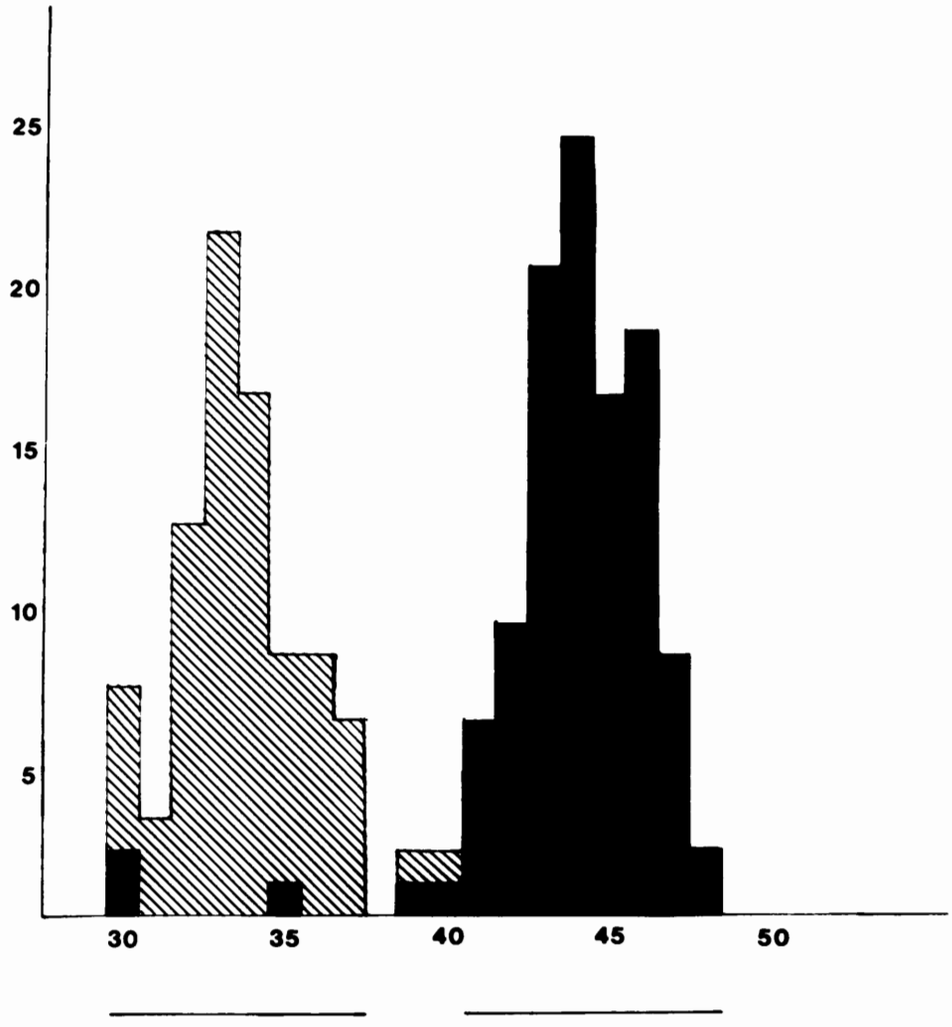

Figure 2. Frequency distribution of lateral scale row counts from the anal fin origin to the base of the caudal fin of *Gobionellus oceanicus* complex specimens. Bars represent 95% confidence intervals. Black = Gulf of Mexico, lined = Caribbean Sea and South Atlantic.

A two-tailed t-test using $t_{.05} = 1.96$ showed that the sample did not differ significantly from a normal distribution ($t_s = 0.197$; Sokal and Rohlf, 1969).

To further assess variation across the *Gobionellus oceanicus* complex, principal components analyses were conducted for 61 males and 60 females independently, using 14 morphometric and 2 meristic characters (Tables 4, 5). For both males and females, best separation of population samples was obtained with the second and third components. Figure 4 shows the separation of Gulf of Mexico males from Caribbean and South American males. Specimens from North Carolina and Florida occurred within and between the two clusters. The most important contributors to both of the components by far were total lateral scale rows and predorsal scale rows (Table 4). Both variables had a high positive loading on the second component. On the third component, lateral scale number had a low negative coefficient and predorsal scale row number had a high positive coefficient. Two paratypes of *Gobionellus gracillimus* fell within the cluster of Gulf of Mexico specimens. Similar results were obtained with the females (Fig. 5). Loadings on components two and three were very similar to that obtained with males, except that caudal fin length also contributed somewhat to the second component (Table 5).

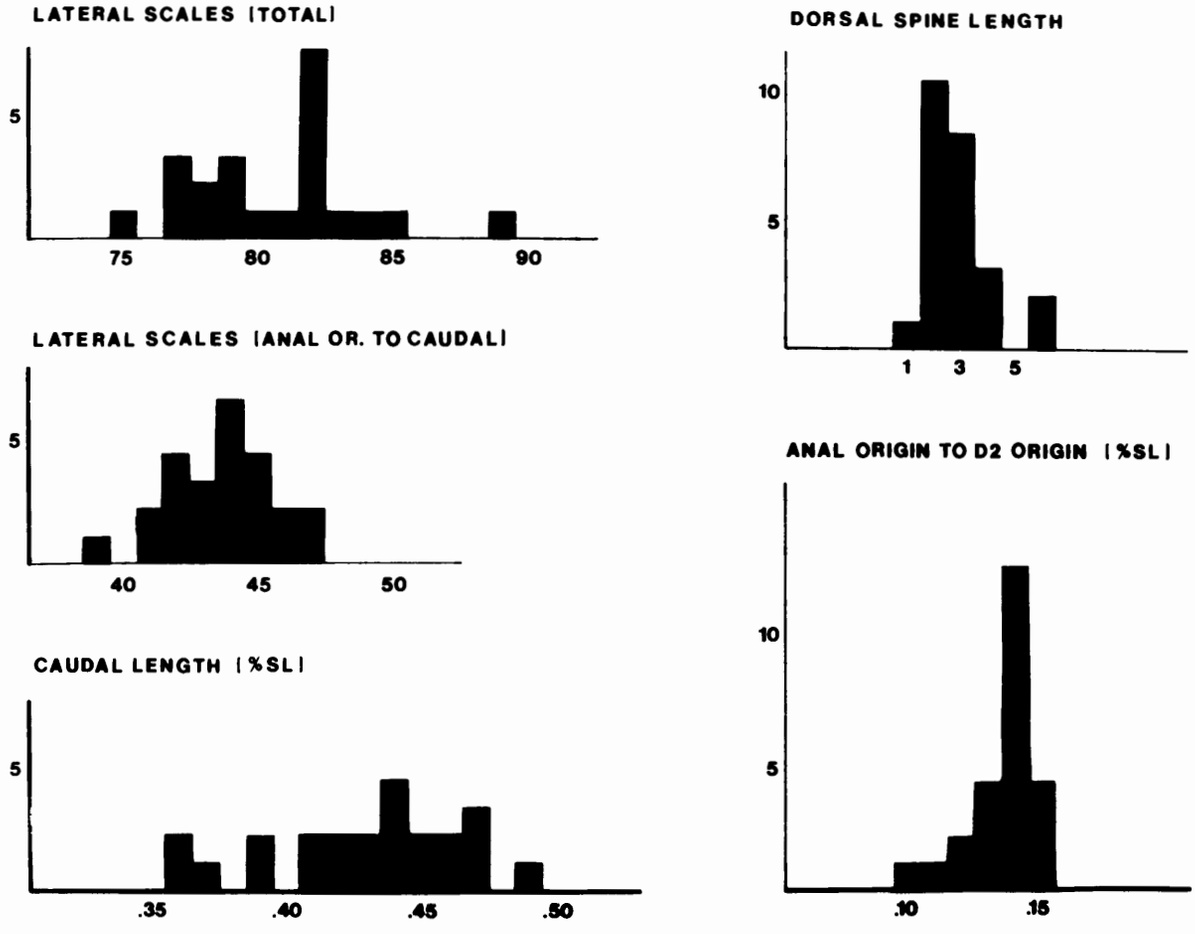

Figure 3. Frequency distribution of measurements and counts of characters diagnostic of *Gobionellus gracillimus* for males 120 mm SL or larger.

Meristic characters were omitted from the analyses to permit a focus on morphometric variation. Roughly 90% of the variance in mensural data for males and females (analyzed separately) was accounted for by the first principal component (Tables 6, 7). The first component in both analyses reflected differences in size; all the variables were strongly correlated with standard length. Some subtle variation was found, but not between northern and southern populations as distinguished by scale counts. Separation of males identified as *G. gracillimus* from other specimens was accomplished (Fig. 6) with principal components one and two. The second component had strongest negative loadings for distance from the eye to D1 origin, interorbital width, anal fin terminus to D2 terminus, and anal origin to D2 origin (Table 6). Strong positive loadings were obtained for pectoral fin length, pelvic fin length and caudal fin length. Specimens from northeastern South American waters were grouped mainly on the left end of the scale. They were characterized by longer napes, deeper bodies and larger interorbital distances than specimens with higher scores along this axis. Paratypes of *G. gracillimus* fell at the opposite extreme and had longer fins. Plots of scores of principal components one and three distinguished female *G. gracillimus* paratypes (Fig. 7). The first component reflected individual size, but the third component had a very high positive coefficient for orbit size and moderately low negative loadings for two body depth characters (Table 7). The females identified as *G. gracillimus* were therefore primarily separated on the basis of orbit size.

Table 4. Principal component coefficients, eigenvalues and cumulative percentages of variance for *Gobionellus oceanicus* complex males (Meristic and morphometric variables were used)

	PRIN 1	PRIN 2	PRIN 3
Standard length	0.275466	−0.005472	0.036689
Total lateral scales	−0.000568	0.705329	−0.601982
Predorsal scales	0.004104	0.674556	0.699797
Head width	0.257491	0.052099	−0.224785
Orbit length	0.260395	0.011783	0.068601
Eye to D1 origin	0.270144	−0.007962	0.127426
Snout length	0.270339	0.038313	−0.110577
Jaw length	0.275274	−0.015547	0.026374
Head length	0.276794	0.007307	−0.031872
Interorbital width	0.258342	−0.054352	0.179269
Caudal peduncle length	0.273573	0.070810	−0.018407
Anal fin-D2 (terminus)	0.268880	−0.112925	0.095243
Anal fin-D2 (origin)	0.268608	−0.089614	0.010301
Pectoral length	0.264869	−0.028480	−0.099951
Pelvic length	0.255300	0.113798	−0.095657
Caudal length	0.264914	0.016239	0.018763
Eigenvalue	12.80944	1.50434	0.62712
Cumulative	0.80059	0.89461	0.93381

Allozymic Analysis.—Individual electromorphs were interpreted as allelic products and allelic frequencies were calculated for variable loci. Variation at 21 presumptive gene loci was assayed in 31 specimens representing four population samples of the *G. oceanicus* complex. Fifteen of the 21 loci assayed, M-Aat-A, S-Aat-A, Ak-A, Ak-B, Ck-A, Gpi-A, S-Icdh-A, Lap, Ldh-A, Ldh-C, M-Mdh-A, S-Mdh-A, S-Mdh-B, Me, and Sod-A, were fixed for common alleles across all samples. A total of 15 alleles were resolved at the six variable loci (Table 8). With the exception of the Gpi-B and M-Icdh-A loci, variation among population samples at the polymorphic loci was restricted to occurrences of one or two rare alleles.

Table 5. Principal component coefficients, eigenvalues and cumulative percentages of variance for *Gobionellus oceanicus* complex female (Meristic and morphometric variables were used)

	PRIN 1	PRIN 2	PRIN 3
Standard length	0.276738	0.035956	−0.054871
Total lateral scales	0.112637	0.567405	0.788409
Predorsal scales	0.051163	0.746954	−0.556848
Head width	0.267462	−0.021889	0.015697
Orbit length	0.255432	−0.072750	−0.005814
Eye to D1 origin	0.273152	0.048575	−0.068765
Snout length	0.271437	0.017945	0.005952
Jaw length	0.276367	−0.018870	−0.026449
Head length	0.277256	0.004914	−0.010656
Interorbital width	0.265761	0.031946	−0.119083
Caudal peduncle length	0.269900	0.044167	−0.038423
Anal fin-D2 (terminus)	0.273159	−0.067797	−0.112574
Anal fin-D2 (origin)	0.271893	−0.037449	−0.046925
Pectoral length	0.264971	−0.091966	0.048446
Pelvic length	0.267030	−0.044822	0.149690
Caudal length	0.190418	−0.300911	0.064636
Eigenvalue	12.80755	1.28225	0.67005
Cumulative	0.80047	0.88061	0.92249

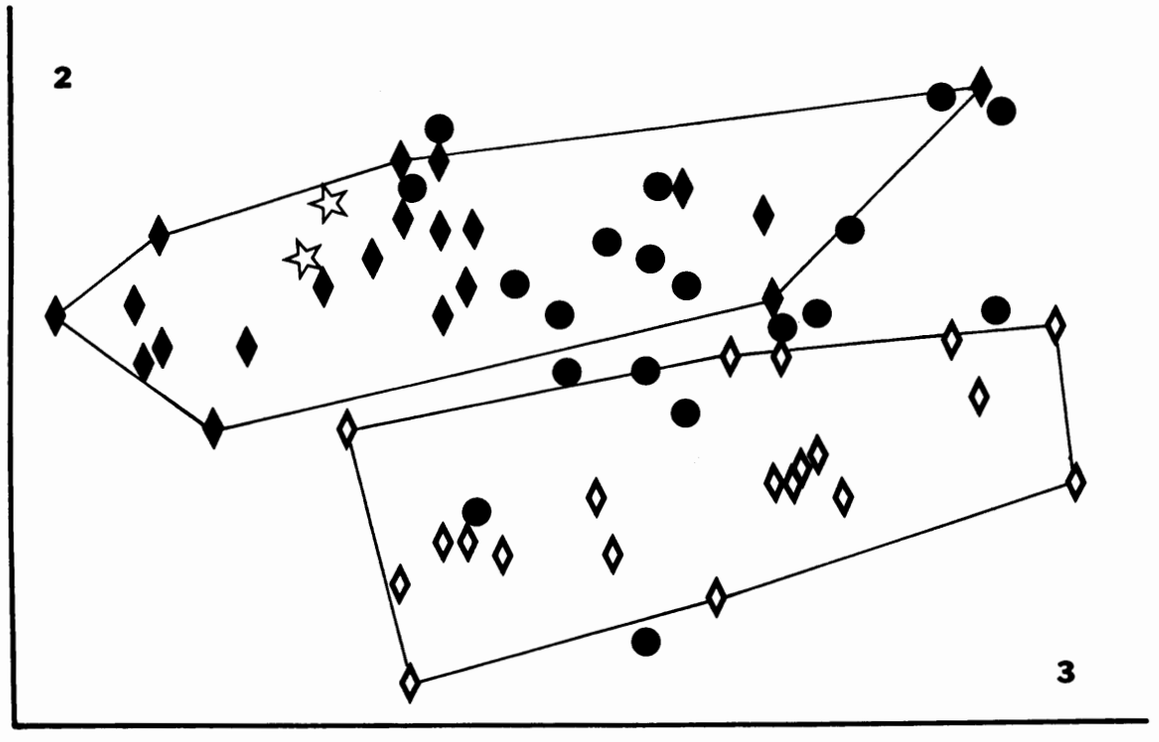

Figure 4. Principal components analysis of males of the *Gobionellus oceanicus* complex using meristic and morphometric variables. Components 2 and 3 are plotted. Stars = *Gobionellus gracillimus* types, open diamonds = Caribbean and South Atlantic specimens, solid diamonds = Gulf of Mexico specimens, dots = North Atlantic (east coast of U.S.) specimens.

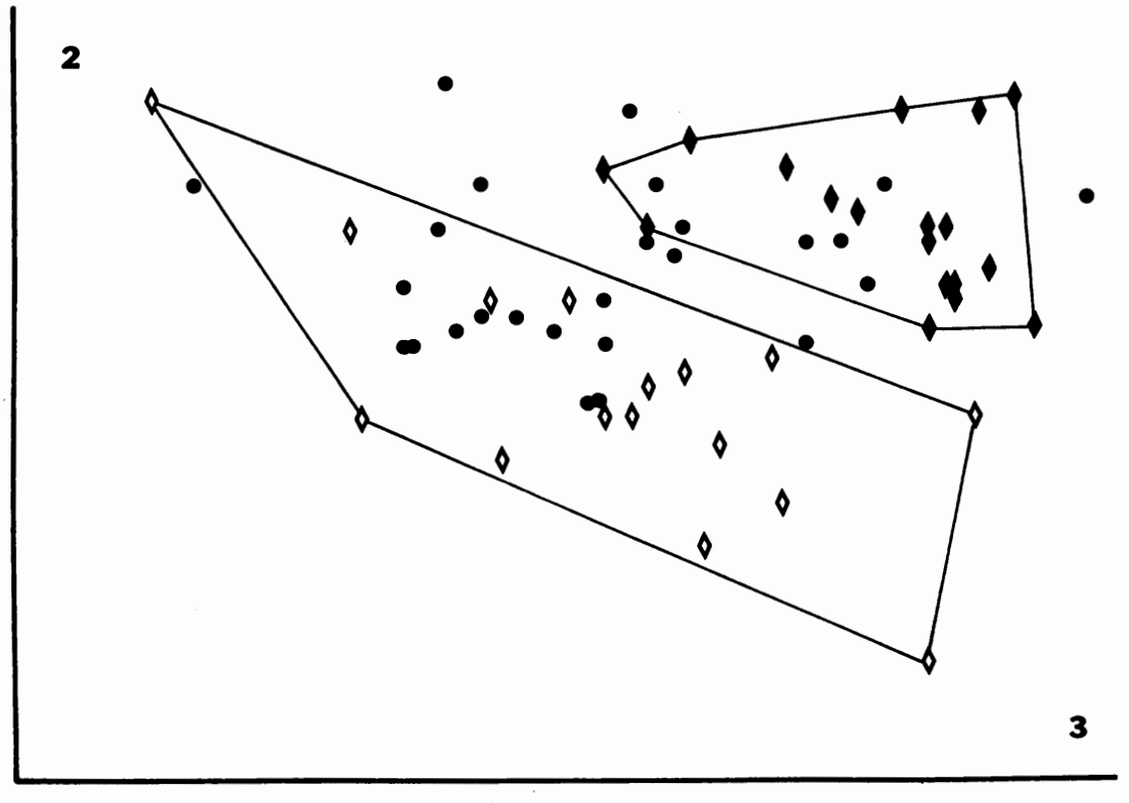

Figure 5. Principal components analysis of *Gobionellus oceanicus* complex females using meristic and morphometric variables. Components 2 and 3 are plotted. See Figure 4 for key to symbols.

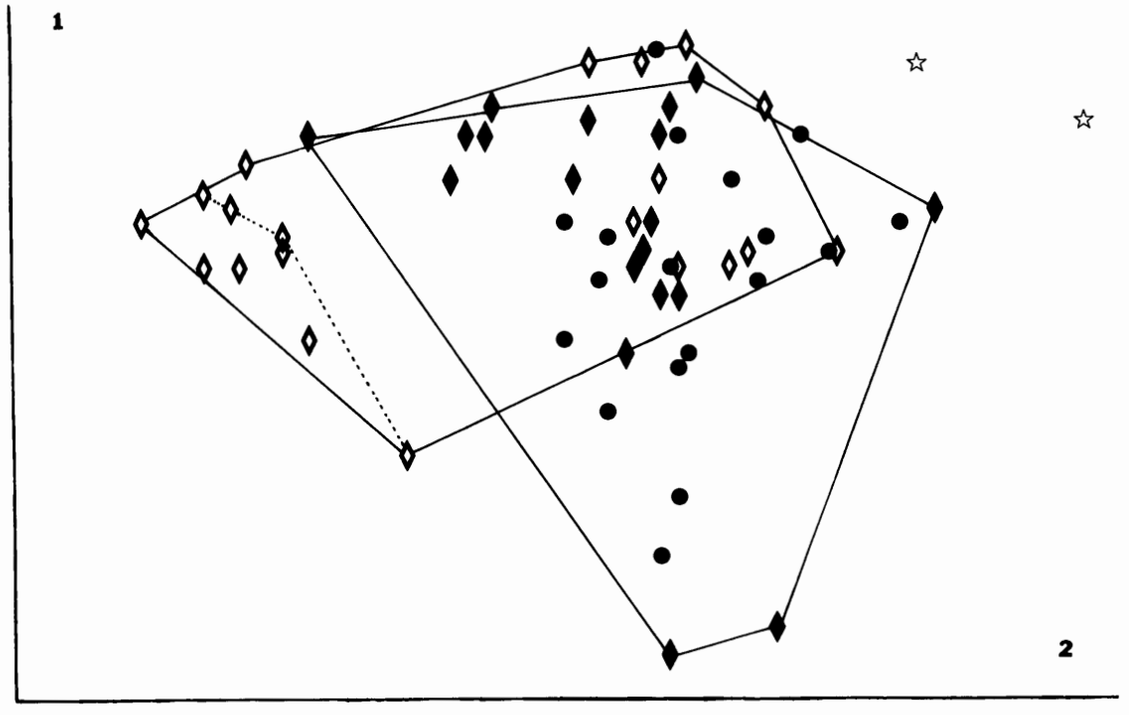

Figure 6. Principal components analysis of *Gobionellus oceanicus* complex males using morphometric variables only. Components 1 and 2 are plotted. See Figure 4 for key to symbols. Dotted line encloses specimens from northeastern South America.

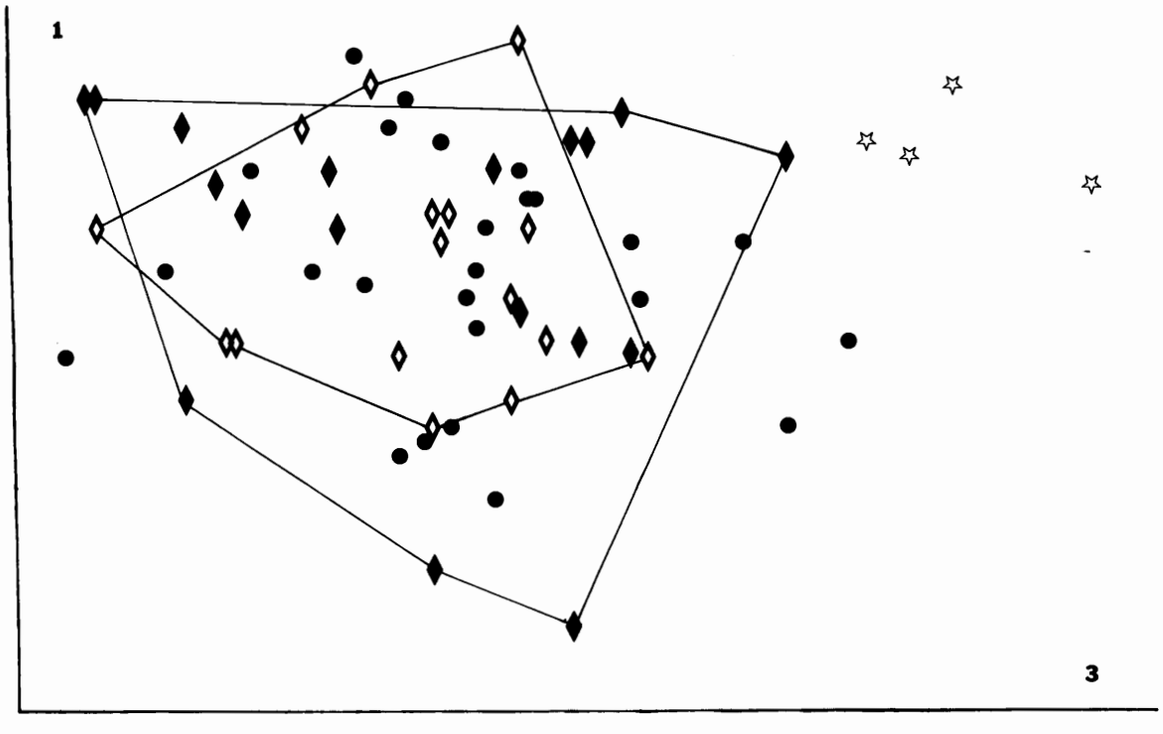

Figure 7. Principal components analysis of *Gobionellus oceanicus* complex females using morphometric variables only. See Figure 4 for key to symbols.

Table 6. Principal component coefficients, eigenvalues and cumulative percentages for *Gobionellus oceanicus* complex males from analyses using only morphometric variables

	PRIN 1	PRIN 2	PRIN 3
Standard length	0.275275	−0.185875	−0.139282
Head width	0.258047	0.201542	0.648925
Orbit length	0.260143	0.162803	−0.456409
Eye to D1 origin	0.269377	−0.330694	−0.186016
Snout length	0.270380	0.170502	0.258195
Jaw length	0.275633	0.074869	−0.189781
Head length	0.277153	−0.024693	−0.028308
Interorbital width	0.258413	−0.301266	0.218252
Caudal peduncle length	0.273627	−0.034189	−0.101032
Anal fin-D2 (terminus)	0.268834	−0.414711	0.023556
Anal fin-D2 (origin)	0.268900	−0.314766	0.215619
Pectoral length	0.263950	0.300394	−0.013406
Pelvic length	0.255802	0.491370	0.093798
Caudal length	0.264901	0.242915	−0.315020
Eigenvalue	12.77879	0.33017	0.24061
Cumulative	0.91277	0.93635	0.95354

The Gpi-B^a allele occurred with greatest frequency in the Indian River, Florida sample. Conversely, the Gpi-B^b allele was predominant in the Rio Tonala and Rio Grande samples. Rio Tonala and Rio Grande samples shared the M-Icdh-A^a allele in low frequency, while Louisiana and Florida samples were fixed for the M-Icdh-A^b allele.

Examination of the association of the Gpi-B^a and Gpi-B^b alleles with total lateral scale row number across all samples (Table 9) showed that specimens with 74 scale rows or fewer were homozygous for Gpi-B^a. All of these specimens were from Indian River, Florida. Three of the specimens from Indian River and one from the Rio Grande had higher lateral scale row counts, yet were also homozygous for Gpi-B^a. Genotype proportions in the Indian River and the Rio Grande samples were in agreement with predictions based on Hardy-Weinberg expectations (χ^2 = 0.10 and 0.29, respectively, with 2 df).

Table 7. Principal component coefficients, eigenvalues and cumulative percentages for *Gobionellus oceanicus* complex females using only morphometric variables

	PRIN 1	PRIN 2	PRIN 3
Standard length	0.278901	−0.101096	−0.061300
Head width	0.270323	−0.085168	−0.180714
Orbit length	0.255087	0.057185	0.764595
Eye to D1 origin	0.273342	−0.128048	−0.165167
Snout length	0.273753	−0.060057	−0.097675
Jaw length	0.278751	−0.002320	0.117756
Head length	0.279331	−0.038024	−0.010468
Interorbital width	0.268304	−0.051477	0.177817
Caudal peduncle length	0.272298	−0.159882	0.007450
Anal fin-D2 (terminus)	0.274673	−0.048847	−0.297285
Anal fin-D2 (origin)	0.270795	−0.105499	−0.374991
Pectoral length	0.268612	0.018720	0.083587
Pelvic length	0.268819	0.014179	0.197348
Caudal length	0.198399	0.956829	−0.146895
Eigenvalue	12.59247	0.54298	0.24591
Cumulative	0.89946	0.93825	0.95581

Table 8. Allele frequencies at six variable loci in four samples of the *G. oceanicus* complex (Sample size is given in parentheses beneath each sample locality)

Locus	Rio Tonala Mexico (3)	Rio Grande Texas (11)	Bayou Choupique Louisiana (1)	Indian River Florida (16)
Gpi-B				
a	0.167	0.364	0.500	0.844
b	0.833	0.636	0.500	0.125
c				0.031
M-Icdh-A				
a	0.167	0.045		
b	0.833	0.955	1.000	1.000
Ldh-B				
a	1.000	1.000	1.000	0.938
b				0.031
c				0.031
Pgdh-A				
a				0.063
b	1.000	1.000	1.000	0.938
G-3-pdh-A				
a		0.091		
b	1.000	0.909	1.000	1.000
Pgm-A				
a		0.045		
b	1.000	0.955	1.000	1.000

Discussion

Notable variation was found in the *Gobionellus oceanicus* complex in lateral scale row number, fin length, orbit size, distribution of alleles at the Gpi-A locus, body depth, and several other body measurements. Only two different forms of the *Gobionellus oceanicus* complex were distinguished by lateral scale row number. The distribution of scale-row counts corroborates Ginsburg's (1932) earlier recognition of northern (*G. hastatus*) and southern (*G. oceanicus*) forms. Principal component analyses including meristic data also gave evidence of northern and southern groups. However, while both univariate and multivariate analyses incorporating the scale counts effectively distinguished the northern and southern forms, those analyses also showed specimens of intermediate condition occurring along the eastern coast of the United States where ranges of the two forms overlap. The distribution of scale row number does not appear to be correlated simply with latitude. Specimens of *G. hastatus* from the Rio Tonala, Mexico are from a more southerly locale than most *G. oceanicus* specimens examined from the Greater Antilles. *G. hastatus* specimens from Tampico were obtained at about the same latitude as *G. oceanicus* specimens from Havana. Thus, the difference in scale row number between the two forms seems to have a genetic component. This is also implied by the intermediate counts found along the eastern coast of the United States. Graphical representation of principal component scores for specimens obtained from multivariate analyses of morphometric characters alone did not separate forms identifiable by scale counts.

Genetic divergence among Gulf of Mexico and Indian River population samples at 21 gene loci was minor. No fixed differences were observed among population

Table 9. The association of Gpi-B genotypes with total lateral scale row number (F = Florida, L = Louisiana, M = Mexico, T = Texas)

Lateral scale rows	Genotype				
	AA	AB	BB	BC	CC
64	F	—	—	—	—
66	F	—	—	—	—
67	2F	—	—	—	—
70	2F	—	—	—	—
71	2F	—	—	—	—
73	F	—	—	—	—
74	F	—	—	—	—
77	—	—	T	—	—
79	2 (F, T)	T	M	—	—
80	—	—	M	—	—
81	F	3 (F, M, T)	—	—	—
83	—	2 (F, T)	T	—	—
84	—	—	T	F	—
86	—	2 (F, L)	—	—	—

samples and, in fact, genic variation among samples, beyond the occurrence of unique, rare alleles, was limited to two loci. Genetic distances among populations, using both Nei's (1972) and Rogers' (1972) formulas (Table 10), fell within the range generally reported among conspecific populations of a variety of marine and estuarine species (Johnson, 1975; Vawter et. al., 1980; Winans, 1980; Grant and Utter, 1984; Grant, 1986; Present, 1987). Specimens from Indian River identifiable by scale counts as *G. oceanicus* did not show fixed allelic differences from those specimens with scale counts typical of *G. hastatus*. Genotype frequencies for the Gpi-B locus in the Indian River sample were consistent with Hardy-Weinberg expectations. A deficiency of heterozygotes would have indicated hybridization between two species as opposed to introgression between subspecies or a breeding population not characterized by conspicuous genetic differentiation. However, Indian River specimens identifiable from scale counts as *G. oceanicus* were consistently homozygous for the Gpi-B^a allele (Table 9). Those from the same sample assignable to *G. hastatus* did not show a strict association with any of the three alleles resolved at this locus.

Based on existing current patterns, gene flow between northern and southern populations of a panmictic marine species in the midwestern Atlantic would be expected to follow a south to north direction. As noted, scale counts from southeastern Florida supported extensive intergradation between northern and southern populations that elsewhere differ sharply in scale counts. The appearance in Gulf collections of a few "outliers" and a few specimens with lateral scale counts falling

Table 10. Values of Nei's (1972), above the diagonal, and Roger's (1972), below the diagonal, genetic distances among populations of the *Gobionellus oceanicus* species complex

Population	1	2	3	4
1. Bayou Choupique, LA	—	0.007	0.007	0.001
2. Indian R., FL	0.023	—	0.025	0.013
3. Rio Grande, TX	0.024	0.047	—	0.003
4. Rio Tonala, MX	0.015	0.038	0.022	—

between 95% confidence intervals constructed for the *G. oceanicus* and *G. hastatus* morphs supported limited introgression in the Gulf of Mexico. The pattern of allelic distributions in the Indian River sample between members identifiable as northern vs. southern forms (Table 9) suggested active recruitment of the *Gobionellus oceanicus* morphotype from the south. The occurrence of the Gpi-B^a allele in the homozygous condition in the southern form in the Indian River and the higher frequency of the Gpi-B^a allele in specimens of the northern form from the Indian River (64%) than in samples of the latter form from the Gulf of Mexico are both concordant with the hypothesis of south to north introgression based on existing current patterns. Due to the small sample sizes available for this study, results from the allozymic analysis should be regarded as preliminary, but supportive of conclusions derived from the morphological analyses.

The pattern of variation of the morphological and allozymic characters examined did not support the northern and southern species hypothesis. In fact, only the lateral scale row counts and the correlated differences in Gpi-B allele frequency distributions seen in the sample from Indian River indicated any differentiation of northern and southern populations. Variability of mensural features was primarily size-related. Some features did allow the discrimination of *G. gracillimus* paratypes in the multivariate analyses. These features were not coincident with lateral scale counts as proposed by Ginsburg (1953). Two of the features were body depth measurements and may have reflected condition of the fish. Ginsburg (1953) suggested that *G. gracillimus* were best distinguished at sizes over 120 mm SL. The paratypes used in the analyses were large specimens (SL $\geqq$ 120 mm). An examination of the characters used by Ginsburg (1953) to distinguish *G. gracillimus* from *G. hastatus* gave no support for the recognition of *G. gracillimus*. The suggestion that *G. hastatus* and *G. gracillimus* represent ecological subspecies or races (Ginsburg, 1953) was not considered in this study. A test of that hypothesis would have required a much different analytical approach. It would also have required the distinction of *G. gracillimus* and *G. hastatus,* a task that does not appear to be possible. It is our belief, based on morphological analyses of 195 specimens and allozymic analysis of 31 specimens, that the *G. gracillimus* paratypes do not represent a distinct species, but merely represent an extreme of the variation that may be found within a single polytypic species.

We recognize the three nominal species of the *Gobionellus oceanicus* complex as conspecific. The name *Gobionellus oceanicus* has priority with *Gobionellus hastatus* and *G. gracillimus* becoming junior synonyms. Our recognition of a single polymorphic species is supported by: 1) the lack of reliable morphological characters for distinguishing *G. gracillimus,* 2) the breakdown of the single morphological character diagnostic of *G. hastatus* and *G. oceanicus* where their ranges overlap, 3) the absence of conspicuous genetic divergence, i.e., fixed allelic differences, among samples from the Gulf of Mexico and southeastern Florida, 4) the absence of conspicuous genetic differences, i.e., fixed allelic differences, among specimens within the Florida sample identifiable morphologically as *G. hastatus* and *G. oceanicus,* and 5) the allozymic evidence of introgression between *G. hastatus* and *G. oceanicus*.

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