

## Morphological diversity of the *Cynoscion* group (Perciformes: Sciaenidae) in the Gulf of Guayaquil region, Ecuador: A comparative approach

Windsor E. Aguirre<sup>a,b</sup> & Virginia R. Shervette<sup>c</sup>

<sup>a</sup>Gulf Coast Research Laboratory, Department of Biological Sciences, University of Southern Mississippi, 703 East Beach Drive, Ocean Springs, MS 39566-7000, U.S.A

<sup>b</sup>Present address: Department of Ecology and Evolution, State University of New York at Stony Brook, 650 Life Sciences Building, Stony Brook, NY 11794, U.S.A (e-mail: waguirre@life.bio.sunysb.edu)

<sup>c</sup>Department of Wildlife and Fisheries, Texas A&M University, College Station, TX 77843-225, U.S.A

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### Synopsis

We assess morphological diversity of species of the *Cynoscion* group in the Gulf of Guayaquil (GOG) using traditional morphometric methods. Five species from the GOG assemblage (*C. albus*, *C. analis*, *C. phoxocephalus*, *C. squamipinnis*, and *Isopisthus remifer*) are compared to four species from a relatively well-studied assemblage in the western Atlantic (*C. arenarius*, *C. nebulosus*, *C. nothus*, and *C. regalis*). The two regional species assemblages broadly overlap in morphology, but sympatric species segregate relatively well within each assemblage. The GOG species segregate primarily along the major axis of shape variation in the study, which is associated with variation in the anal, second dorsal, and caudal fins. The western Atlantic species segregate primarily along the second major axis of shape variation, which is most strongly associated with variation in gill raker length, and less strongly with pectoral fin length, eye diameter, and length of the third dorsal spine. Patterns of morphological divergence among the western Atlantic species support the hypothesis that morphological divergence is associated with ecological divergence. Comparisons across assemblages indicate that morphological divergence among species in the GOG is substantial. Consequently, *Cynoscion* species in the GOG may be highly divergent in ecological habits, which would have important management implications, but further ecological research is needed. This study provides a first glimpse into the major patterns of morphological diversification in the *Cynoscion* group.

### Introduction

The Gulf of Guayaquil (GOG) in Ecuador is the largest estuary on the Pacific coast of South America (Pesantes Vigano 1998, Yoong & Reinoso 1999). Unfortunately, it is also among the most severely threatened (Bryant et al.<sup>1</sup>, Pesantes

Vigano 1998). Guayaquil, the largest and economically most important city in Ecuador, sits in the heart of the Gulf (Figure 1). With over two million inhabitants, the city's demands for estuarine resources are intense, and exploitation of coastal resources is often poorly regulated due to lack of resources for management. For example, although the development of shrimp aquaculture in the GOG in the 1980s and early 1990s brought a large influx of revenue (Parks & Bonifaz 1994), it also resulted in the loss of approximately 20–50% of the mangrove forest for creation of shrimp

<sup>1</sup> Bryant D., E. Rodenburg, T. Cox & D. Nielsen. 1995. Coastlines at Risk: an Index of Potential Development-Related Threats to Coastal Ecosystems. WRI Indicator Brief, World Resources Institute, Washington, D.C.

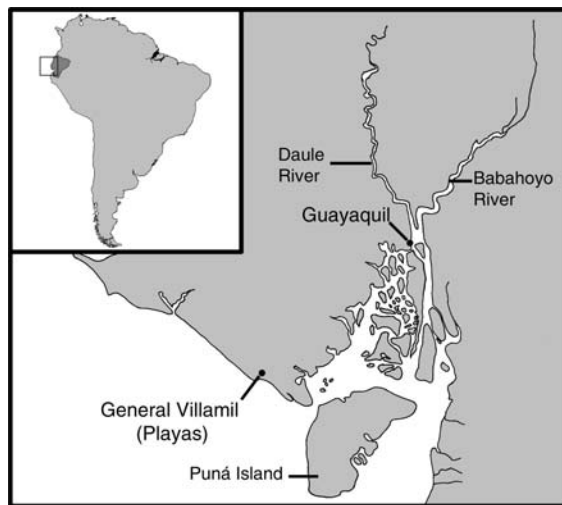


Figure 1. Gulf of Guayaquil region, Ecuador, with the collection ports (Guayaquil and General Villamil) indicated.

ponds (CLIRSEN<sup>2</sup>). The effects of the increasing demands for coastal resources and degradation of coastal habitats on the fish community of the GOG remains unknown.

The Sciaenidae, commonly known as drums or croakers, are a dominant component of the GOG's fish community, both in terms of biomass and number of species. They are also of great economic importance, especially to local populations along the coast and the fishermen that supply them (Herrera & Peralta 1999, Marín de López et al. 1999, Herrera et al. 2001). Among the Sciaenidae, members of the *Cynoscion* group (*sensu* Chao 1978), tend to be particularly important. Species of this group are major predators of fish and crustaceans, and some may be keystone species (e.g., Guest & Gunter 1958). They are also among the most sought after species in the GOG because of the high quality of their flesh (Herrera & Peralta 1999, Marín de López et al. 1999, Herrera et al. 2001). Seven species of this group have been reported for coastal waters of Ecuador (Béarez 1996, 2001) and at least five species occur in the GOG region (unpublished data). Four of these species are in the genus *Cynoscion*, and the fifth is in the genus *Isopisthus*. Genera in the

<sup>2</sup> Centro de Levantamientos Integrados de Recursos Naturales (CLIRSEN). 1992. Estudio Multitemporal de los Manglares, Camaroneras y Areas Salinas de la Costa Ecuatoriana, Actualizado a 1991. Quito, Ecuador.

*Cynoscion* group are closely related phylogenetically (Chao 1978, Sasaki 1989) and are probably not monophyletic as presently recognized (Aguirre 2000). Despite their ecological and economic importance, very little is known about how species in the *Cynoscion* group occurring in the GOG segregate ecologically. They are often treated as if they are ecologically equivalent and are frequently identified only to genus. Thus potential interspecific differences in susceptibility to habitat degradation or overexploitation are presently unknown.

In this paper, we explore morphological diversity of species in the *Cynoscion* group (genera *Cynoscion* and *Isopisthus*) occurring in the GOG using traditional morphometric methods. The GOG assemblage is compared to a much better known assemblage from the western Atlantic (WA) coast of the U.S.A. The species in the WA assemblage are known to differ in the ecological roles they play (see below), providing a baseline roughly indicating the degree of morphological differentiation expected among a sympatric assemblage that segregates ecologically. By comparing the GOG assemblage to that in the WA, we assess the extent to which morphological differentiation among species in these assemblages is comparable, and hypothesize on the ecological significance. This study also identifies the variables that are most highly correlated with the directions of major morphological variation across assemblages, providing a first glimpse into patterns of morphological diversification in the *Cynoscion* group.

### The western Atlantic *Cynoscion* assemblage

We provide a brief summary of ecological relations among the four species occurring in the WA. *Cynoscion nebulosus* and *C. nothus* occur both in the Gulf of Mexico (GOM) and the Atlantic coast of the U.S.A., whereas *C. arenarius* and *C. regalis* are allopatric sister species (Weinstein & Yerger 1976, Paschall 1986) with *C. arenarius* occurring in the GOM and *C. regalis* occurring off the Atlantic coast of the U.S.A.<sup>3</sup>

<sup>3</sup> Cordes & Graves (2003) have recently presented evidence that *C. regalis* and *C. arenarius* hybridize in the southeastern U.S.A., but the extent of hybridization and potential range overlap is unknown.

*Cynoscion nebulosus*, the spotted seatrout, is a relatively large species that generally occurs in shallow inshore waters and areas rich in seagrass (Tabb 1961, Patillo et al. 1997, Hoese & Moore 1998). It is highly prized by recreational and commercial fishermen, and has been strongly impacted by fisheries pressures (Patillo et al. 1997, Chao 2002). *Cynoscion nothus*, the silver seatrout, is the smallest of the WA *Cynoscion*, typically measuring 200 mm standard length (SL) or less (Sutter & McIlwain 1987) and rarely exceeding 250 mm SL (Chao 2002). It generally is found farther off shore in deeper waters than the other WA *Cynoscion* (Byers 1981, Shipp 1986, Sutter & McIlwain 1987, Hoese & Moore 1998). *Cynoscion nebulosus* and *C. nothus* are almost completely allotopic, rarely being collected in the same habitats. In the GOM, *C. arenarius*, the sand seatrout, is generally intermediate to *C. nebulosus* and *C. nothus* in terms of its size, feeding habits, and the habitats in which it occurs (Ginsburg 1931, Guest & Gunter 1958, Sutter & McIlwain 1987, Shipp 1986, Ditty et al. 1991, Hoese & Moore 1998). *Cynoscion regalis*, the Atlantic weakfish, replaces *C. arenarius* along the Atlantic coast of the U.S.A. It is a commercially important species that reaches much larger sizes than *C. arenarius* (Table 1, Mercer 1989, Chao 2002).

## Materials and methods

We studied five species of the *Cynoscion* group from the GOG and four species from the WA (Table 1). The GOG species came from fish markets in Guayaquil and General Villamil (Playas), in Guayas Province, Ecuador (Figure 1). A sixth species from the *Cynoscion* group, *C. stolzmanni*, may occur in the GOG. Large adults are common farther north in Manabí Province (P. Béarez personal communication), and it has been listed for the GOG in fisheries surveys of the region. However, the senior author (WEA) did not collect this species during multiple surveys of fish markets from 1997 to 1999. *Cynoscion nortoni*, a species recently described from deep waters (100–200 m) off of Pto. Lopez, in the province of Manabí (Béarez 2001), was not collected either. Omission of *Cynoscion* potentially occurring in the GOG makes this study conservative in terms of absolute morphological diversity of the assemblage. We collected the three WA species occurring in the Gulf of Mexico off the coasts of Texas, Louisiana, Mississippi, and Florida, and *C. regalis* off the coasts of Georgia, South Carolina, and in Delaware Bay. Specimens were fixed in 10% formalin, stored in 70% ethanol, and deposited in the Gulf Coast Research Laboratory Ichthyological Collection in Ocean Springs, Mississippi, U.S.A. (Appendix 1). We took 20 linear measures, to the

Table 1. Species included in this study.

Species	SL <sup>L</sup>	Distribution	n	SL <sup>mn</sup>	SL <sup>rg</sup>	SL <sup>sd</sup>
<b>GOG</b>						
<i>C. albus</i>	to 700	GOG north to southern Mexico	15	214.5 ± 22.7	124–352	87.9
<i>C. analis</i>	300–450	GOG south to Chile	22	235.8 ± 4.1	200–273	19.3
<i>C. phoxocephalus</i>	to 600	Peru north to southern Mexico	20	245.3 ± 14.2	121–318	63.4
<i>C. squamipinnis</i>	400–640	Peru north to Gulf of California	51	244.5 ± 7.6	125–341	53.9
<i>I. remifer</i>	to 350	Peru north to Gulf of California	39	203.8 ± 3.4	170–248	21.1
<b>WA</b>						
<i>C. arenarius</i>	300–450	GOM	66	195.0 ± 3.0	119–251	24.1
<i>C. nebulosus</i>	400–700	GOM and Atlantic to New York	41	197.0 ± 9.1	57–306	58.1
<i>C. nothus</i>	250–400	GOM and Atlantic to Virginia	50	161.0 ± 2.3	96–188	15.9
<i>C. regalis</i>	500–900	Atlantic: Nova Scotia to Florida	28	192.9 ± 6.3	149–259	33.2

Abbreviations are as follows: GOG is Gulf of Guayaquil, GOM is Gulf of Mexico. WA is western Atlantic coast of U.S.A. including the GOM. SL<sup>L</sup> is the standard length reported in the literature (in mm), distribution is the geographic range, n is the number of specimens measured, and SL<sup>mn</sup>, SL<sup>rg</sup>, and SL<sup>sd</sup> are the mean (± standard error), range and standard deviation of the SL of specimens measured in this study. Sources: Chao (1995) for GOG, Chao (2002) for WA.

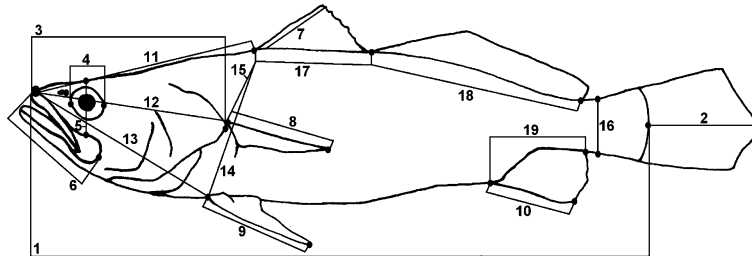


Figure 2. Linear measures taken with the exception of gill raker length (20), which is not shown. Measures are defined in Appendix 2.

nearest 0.1 mm with Mitutoyo digital calipers, on the left side of the body of preserved specimens (Figure 2, Appendix 2).

We carried out a principal component analysis (PCA) on the  $\log_{10}$  transformed linear measures to assess the degree of morphological divergence. This allowed us to create a 'morphospace' by plotting specimens on the first few major axes of morphological variation (PC axes). Principal component analysis is an ordination technique commonly used to reduce the dimensionality of multivariate data sets by searching for patterns of covariation among the original variables. It has been routinely applied to explore patterns of morphological variation in fishes (e.g., Bookstein et al. 1985). The PCA included all nine species, but scores for the WA and GOG assemblages are plotted separately to facilitate visualization and interpretation. A singular value decomposition on the log-transformed, centered data matrix ( $X$ ) was performed such that  $X = U \cdot D \cdot V^t$  (for details see Lattin et al. 2003). Using this approach, eigenvalues are the squares of the diagonal of the  $D$  matrix, factor scores (projections of specimens onto PC axes) are the product of the  $U$  and  $D$  matrices, and factor loadings (correlations between variables and principal components) are the correlation between the original centered data matrix and the scores matrix. This approach yields results that are identical to the more usual eigenvalue analysis. We used the factor loadings to identify the variables contributing most strongly to the morphological divergence among species, and used the scatter of species and euclidean distances among species means in the morphospace to evaluate the morphological divergence among species. A biplot depicting variables in the same space as the species means allowed visualization of the relationship among the variables. The variable

scores on the PC axes come directly from eigenvector coefficients (divided by two for scaling purposes).

## Results

Principal component I accounts for 86.7% of the variance in the data and we consider it a size component because all the variables measured have high positive loadings on it (the lowest loading is 0.804 for anal fin base length and the mean is 0.933) and it is highly correlated with SL ( $r = 0.993$ ). Principal components II, III, IV, and V account for 5.5, 2.4, 1.6, and 0.95% of the total variance respectively, corresponding to approximately 41.5, 18.3, 11.9, and 7.2% of the shape (non-size) variation. Principal components II and III together include 59.8% of the shape variation and form a space in which sympatric species segregate well (Figure 3). These axes are used to define the two major directions of shape variation in this analysis and the space they form is henceforth referred to as the morphospace. Principal components II and III summarize the overall shape divergence among species relatively well. The correlation between euclidean distances among species means for nearest neighbors in the space formed by PC's II and III (Figure 4a) and in the total shape space (PC's II–XX) is 0.754 ( $n = 8$  species pairs,  $p = 0.031$ ).

Four of the 20 variables measured contribute most heavily to the PC axes II and III, and three other variables have moderately large loadings on PC III (Table 2). The three variables with relatively high loadings on PC II are: 2. Caudal fin length ( $-0.315$ ), 18. Second dorsal fin base length ( $-0.442$ ), and 19. Anal fin base length (0.577). The

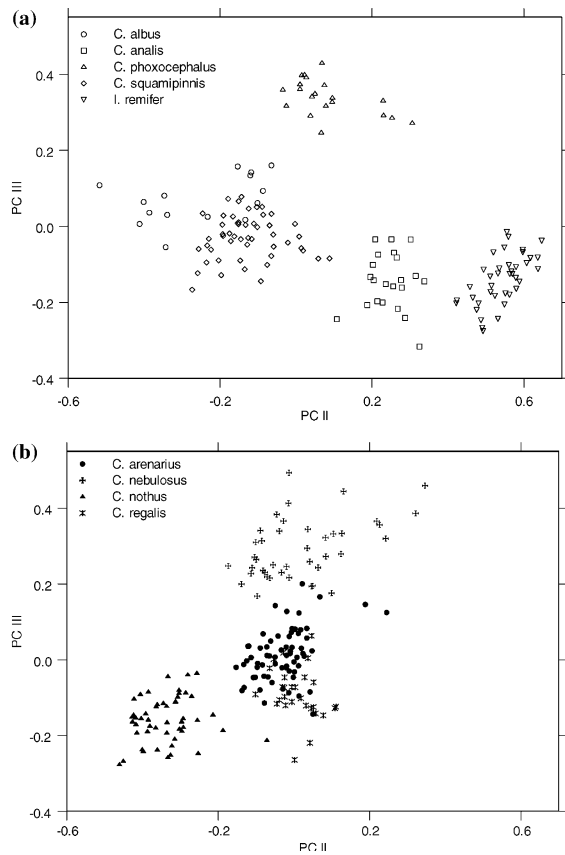


Figure 3. Principal component plot depicting the two major axes of morphological variation. A single analysis was carried out for both WA and GOG assemblages, but these are plotted separately to facilitate visualization and interpretation; (a) GOG assemblage, (b) WA assemblage.

last of these variables has the highest loading on a shape axis in the study. The strong influence of the anal fin base (variable 19) is obvious from the biplot in which it appears as a long vector running parallel to PC II (Figure 4b). The three variables with large loadings on PC II are strongly correlated as expected even when size is taken into account. We size-standardized the variables by taking the residuals of the regression of each variable on PC I. The size-standardized variables caudal fin length and second dorsal fin base are positively correlated ( $r=0.522$ ) and both are negatively correlated with the anal fin base ( $r=-0.485$  and  $-0.829$  respectively). The strength of the association between the second dorsal fin base and the anal fin base is particularly striking. Species with a long second dorsal fin have a short anal fin

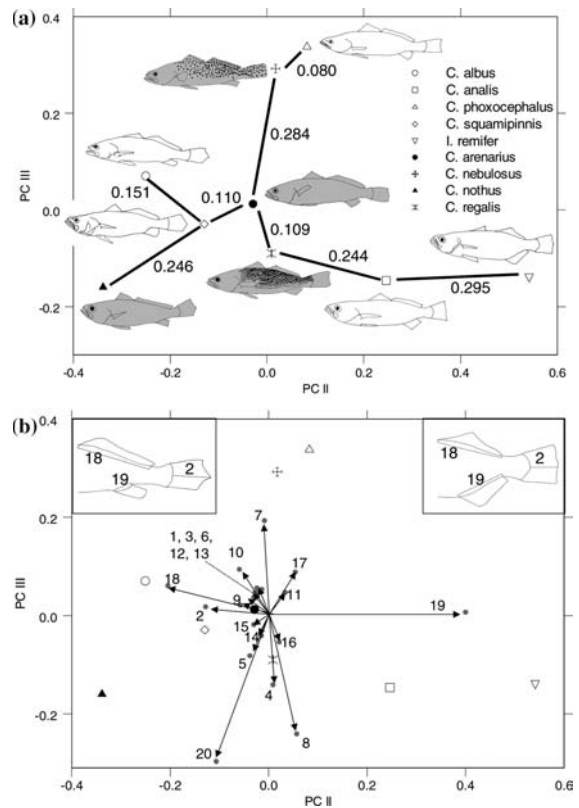


Figure 4. Principal component plot depicting species means and variables; (a) Species means in the PC morphospace, clear fish are from the GOG and filled (gray) fish are from the WA, lines (edges) unite most similar species and numbers indicate euclidean distances between species means in the morphospace, (b) biplot of species means and variables on PC's II and III. Species means are depicted with the same symbols as in Figure 4a and vectors are variables identified by numbers as indicated in Figure 2 and Appendix 2. Insets are extreme GOG phenotypes for variables with high loadings on PC II, left inset is based on a typical specimen of *C. albus* and right on a specimen of *I. remifer*.

and vice versa, and a long second dorsal and short anal fin base is associated with a long caudal fin (Figure 4b). For the species examined, these variables appear to be integrated forming distinct 'caudal' phenotypes. Gill raker length (GRL, variable 20) contributes most heavily to PC III with a factor loading of  $-0.445$ . Three other variables had moderately high loadings on PC III: 8. Pectoral fin length ( $-0.298$ ), 4. Eye diameter ( $-0.287$ ), and 7. Length of third dorsal spine ( $0.250$ ). Pairwise correlations among these variables are much weaker than among the variables

Table 2. Factor loadings (correlations between original variables and PC axes) for PC I–V. See Appendix 2 and Figure 2 for variable definitions.

Var.	PC I	PC II	PC III	PC IV	PC V
1	0.993	-0.029	0.074	-0.018	0.047
2	0.860	-0.315	0.030	0.360	0.009
3	0.988	-0.057	0.070	-0.054	-0.007
4	0.861	0.027	-0.287	-0.293	0.103
5	0.959	-0.091	-0.132	-0.109	0.036
6	0.987	-0.063	0.053	0.018	0.012
7	0.903	-0.016	0.250	-0.102	-0.322
8	0.915	0.107	-0.298	0.049	-0.136
9	0.972	-0.130	0.032	0.095	0.009
10	0.919	-0.133	0.141	0.284	0.027
11	0.988	0.069	0.064	0.012	0.033
12	0.986	-0.059	0.067	-0.028	0.008
13	0.979	-0.051	0.080	-0.094	0.041
14	0.977	-0.032	-0.059	-0.032	0.059
15	0.974	-0.064	-0.026	-0.103	0.065
16	0.970	0.046	-0.077	-0.081	0.064
17	0.957	0.104	0.112	-0.137	0.025
18	0.871	-0.442	0.087	-0.006	0.099
19	0.804	0.577	0.007	0.106	0.032
20	0.805	-0.239	-0.445	0.073	-0.113

with high loadings on PC II, and ranged from 0.245 to 0.315. Gill raker length, pectoral fin length, and eye diameter were positively correlated with one another and negatively correlated with the length of the third dorsal spine.

Species in the GOG and WA assemblages do not segregate by region (Figure 4a). With nine species examined there are eight edges uniting species means based on similarity in the morphospace. Of these, four join WA with GOG species and four join GOG with GOG and WA with WA species (two each). That is, half of the species are most similar to species in the same region and half to species in a different region. This suggests that morphological relationships among species from the two regions are relatively complex. The smallest euclidean distances in the morphospace were 0.080 between *C. nebulosus* (WA) and *C. phoxocephalus* (GOG), 0.109 between *C. arenarius* (WA) and *C. regalis* (WA), 0.110 between *C. arenarius* and *C. squamipinnis* (GOG) and 0.151 between *C. squamipinnis* and *C. albus* (GOG). Once again, these were split evenly between pairs with members from the same and different regions.

The GOG and WA species segregate primarily along different PC axes and the divergence among species within each assemblage was generally comparable. The GOG species segregate

largely on PC II, the primary axis of shape variation (Figure 3a). *Cynoscion albus* and *I. remifer* fall out at the extremes of PC II for the GOG assemblage. *Isopisthus remifer* differs considerably from typical *Cynoscion* along this axis by having a relatively short second dorsal fin, a relatively short caudal fin, and a greatly expanded anal fin. *Cynoscion analis* is intermediate between *I. remifer* and other *Cynoscion* along this axis. This is in accordance with previous descriptions of phenotypic similarity between *C. analis* and *I. remifer* (e.g., Hildebrand 1946, Schwarzhans 1993), and recent evidence from mtDNA sequence data indicating that they are closely related phylogenetically (Aguirre 2000). With the exception of *C. albus* and *C. squamipinnis*, there is generally little overlap among the GOG species. Several individuals of *C. albus* fall into the *C. squamipinnis* cluster although most *C. albus* have lower scores on PC axis II or larger scores on PC axis III. *Cynoscion phoxocephalus* appears relatively isolated in the morphospace, it is intermediate on PC II but segregates considerably on PC III. The WA species segregate primarily on PC III, although *C. nothus* segregates from the other species on PC II as well (Figure 3b). In *C. nothus*, the caudal fin and base of the second dorsal fin are longer, and the base of the anal fin is shorter

than in the other WA species. *Cynoscion nebulosus* and *C. nothus* segregate completely on PC III and largely on PC II, indicating that these species differ substantially in morphology. *Cynoscion arenarius* largely overlaps with its allopatric sister species *C. regalis*, indicating that there has been little divergence in shape between these two closely related species. The morphological similarity between these species, however, may be somewhat influenced by hybridization, as evidence of hybridization has recently been reported (Cordes and Graves 2003). *Cynoscion arenarius* and *C. regalis* fall in an intermediate position in the morphospace (Figure 4a) suggesting that their shape may be generalized for the clade.

## Discussion

Principal component analysis is a useful method for exploring patterns of variation in multivariate data sets, but it is not a method intended to find differences among groups *per se*, like discriminant analysis (e.g., Lattin et al. 2003). The segregation of species in the morphospace defined by PC's II and III thus indicates that there are substantial morphological differences among species within both assemblages. The observed segregation among sympatric species is in accordance with classical theory on the structuring of communities. Divergence among closely related species along phenotypic axes is expected to reduce interspecific competition (MacArthur & Levins 1967, Schoener 1974).

The primary objective of this study was to compare the degree of absolute morphological diversity among species of the poorly known GOG assemblage with that of the better-known WA assemblage. The results clearly indicate that morphological diversity among species of the GOG assemblage is large when compared to the WA assemblage. Relative to the WA assemblage, species in the GOG occupied a broad portion of the morphospace, generally segregated well, and diverged primarily along the major axis of shape variation (PC II) in the study. Two species in the GOG assemblage (*C. analis* and *I. remifer*) also occupy a novel portion of the morphospace.

Although we do not have data on the functional significance of the morphological differences doc-

umented, the correlations between the original variables and PC's II and III (i.e., the factor loadings), provide us with some potential indications.

The major axis of shape variation in this study (PC II) is strongly influenced by median fins. Very little is known about the functional significance of variation in median fin phenotypes, but they are generally thought to be associated with differences in maneuverability and propulsion (e.g., Lauder et al. 2002, Lauder and Drucker 2004). The magnitude of the variation in median fin phenotypes observed among these phylogenetically closely related species makes the *Cynoscion* group a good candidate for future studies of the functional and adaptive significance of median fin evolution. The anal fin, which was singled out by Lauder & Drucker (2004) as a fin whose specific function was virtually unknown, represents a particularly important source of variability in morphology among the members of the *Cynoscion* group. Not only does it differentiate *Isopisthus* from typical *Cynoscion*, but there is quite a bit of variation within the genus *Cynoscion* as well. This is a key trait commonly used to rapidly distinguish *C. nothus* from *C. arenarius* in the field during bottom fish surveys in the northern Gulf of Mexico because *C. nothus* has an obviously shorter anal fin base with less rays (Shipp 1986, Hoese & Moore 1998). *Cynoscion albus* also has a shorter anal fin base than most *Cynoscion* examined and as previously noted *C. analis* has a long anal fin base that is almost comparable to that of *Isopisthus*. Future work on the functional basis of differences in medial fins in general, and the anal fin in particular, may thus provide insight into one of the key ways in which the *Cynoscion* group has diversified.

Gill raker length is the variable with the highest loading on PC III. Gill rakers are extremely important for feeding acting as a sieve that retains small prey items in the digestive tract as water is expelled through the operculum after strikes, and GRL (and number) is a good indicator of the size of the prey taken (Nikolsky 1963, Bentzen & McPhail 1984). Species with longer and more numerous gill rakers typically feed on smaller prey items while species with fewer short gill rakers typically feed on larger prey items. Thus PC III is probably associated with feeding habits. The size of the eye may be associated with the ability to

detect prey and thus is also potentially attributable to divergence in feeding habits, but the relationship between the pectoral fin length and the third dorsal spine length with GRL is more obscure. Divergence of species along PC III may be associated with adaptations for feeding on prey of different sizes, perhaps based on availability in different habitats. If this is the case, *Cynoscion nebulosus* and *C. phoxocephalus* are adapted to feed on the largest items (they tend to have shorter gill rakers and relatively smaller eyes), and *C. nothus*, *C. analis*, *I. remifer*, and to some extent *C. regalis* are adapted to feed on smaller items (they have longer gill rakers and relatively larger eyes). It is worth noting that there is some tendency for larger species to appear adapted to feed on relatively larger prey (e.g., *C. nebulosus* and *C. phoxocephalus*) and smaller species to feed on relatively smaller prey (e.g., *C. nothus*, *C. analis*, and *I. remifer*), which could indicate the existence of common allometric growth trajectories for traits associated with feeding across the group.

Understanding how the GOG species actually segregate ecologically will have to wait for the appropriate ecological studies, and we hope that our work stimulates such research efforts. However, associations between morphology and ecology are often strong when evaluated (Webb 1984, Ehlinger & Wilson 1988, Wainwright 1988, Losos 1990, Douglas & Matthews 1992, Ricklefs & Miles 1994, but see Gould & Lewontin 1979), suggesting that some predictions are possible. Indeed, the pattern of morphological divergence among the better-studied WA *Cynoscion* assemblage in this study is in accordance with a general association between morphology and ecology. *Cynoscion nebulosus* and *C. nothus*, which are highly divergent ecologically, are distant from each other in the morphospace, and the sister species *C. arenarius* and *C. regalis*, which are generally considered ecologically intermediate, are in an intermediate position in the morphospace. Thus assuming that the divergence in morphology documented is associated with divergence in ecology, we expect that *I. remifer* will be the most divergent species ecologically in the GOG, and *C. analis* will be intermediate between it and typical *Cynoscion*. We also expect that *C. phoxocephalus* will be the more divergent of the typical GOG *Cynoscion*. In terms of cross-regional comparisons, *C. squamipinnis* is

similar in shape to *C. arenarius*, the WA species that was generally intermediate morphologically for the WA assemblage, suggesting that *C. squamipinnis* may be an ecologically intermediate species in the GOG. Surprisingly, the most similar species in the morphospace were the allopatric *C. phoxocephalus* (GOG) and *C. nebulosus* (WA). Although the phylogeny of the *Cynoscion* group has not been fully resolved yet, mtDNA sequence data clearly indicate that these two species are not closely related phylogenetically (Aguirre 2000), suggesting that their similarity represents convergence along these two shape axes.

In summary, we find evidence of extensive morphological divergence among species of the *Cynoscion* group in the GOG. Given the extent to which the GOG ecosystem has been impacted by anthropomorphic influences and the intense fisheries pressures exerted on the region, research aimed at achieving a detailed understanding of ecological relationships among the GOG species appears long overdue. Data collected from fisheries landings and stock assessment surveys should be reported individually for each species as continued ignorance of ecological differences among species in the GOG could have grave consequences for their persistence in the future.

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## References

- Aguirre, W.E. 2000. Phylogenetic vs. ecophenotypic influences on interspecific variability of sagittae in the genera *Cynoscion* and *Isopisthus* (Teleostei: Sciaenidae). M.Sc. Thesis, Department of Biological Sciences, University of Southern Mississippi, Hattiesburg, Mississippi. 144 pp.
- Béarez, P. 1996. Lista de los peces marinos del Ecuador continental. *Revista de Biología Tropical* 44: 731–741.
- Béarez, P. 2001. Description of a new weakfish, *Cynoscion nortoni*, from Ecuador with a note on the distribution of *Umbrabussingi* (Perciformes: Sciaenidae). *Revista de Biología Tropical* 49 (Suppl. 1): 59–65.
- Bentzen, P. & J.D. McPhail. 1984. Ecology and evolution of sympatric sticklebacks (*Gasterosteus*): specialization for alternative trophic niches in the Enos Lake species pair. *Canadian Journal of Zoology* 62: 2280–2286.
- Bookstein, F.L., B. Chernoff, R.L. Elder, J.M. Jr. Humphries, G.R. Smith & R.E. Strauss. 1985. Morphometrics in evolutionary biology. The Academy of Natural Sciences of Philadelphia, Special Publication 15. 277 pp.
- Byers, S.M. 1981. Trophic relationships of two sympatric sciaenid fishes, *Cynoscion arenarius* and *Cynoscion nothus*, in the north central Gulf of Mexico. M. Sc. Thesis, University of Southern Mississippi, Hattiesburg, MS. 70 pp.
- Chao, N.L. 1978. A basis for classifying western Atlantic Sciaenidae (Teleostei: Perciformes). NOAA Technical Report Circular 415. 64 pp.
- Chao, N.L. 1995. Sciaenidae. pp. 1427–1518. In: W. Fischer, F. Krupp, W. Schneider, W. Sommer, K.E. Carpenter & V.H. Niem, (eds), *Guía Fao para la Identificación de Especies para los Fines de la Pesca. Pacific-centro Oriental. Volumen III, Vertebrados – Parte II*, FAO, Roma.
- Chao, N.L. 2002. Sciaenidae. pp. 1583–1653. In: K.E. Carpenter, (eds), *The living marine resources of the western Central Atlantic. Volume 2: Bony fishes, part 2 (Opisthognathidae to Molidae), sea turtles and marine mammals*. FAO species identification guide for fishery purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5, FAO, Rome.
- Cordes, J.F. & J.E. Graves. 2003. Investigation of congeneric hybridization in and stock structure of weakfish (*Cynoscion regalis*) inferred from analyses of nuclear and mitochondrial loci. *Fisheries Bulletin* 101: 443–450.
- Ditty, J.G., M. Bourgeois, R. Kasprzak & M. Konikoff. 1991. Life history and ecology of sand seatrout *Cynoscion arenarius* Ginsburg, in the northern Gulf of Mexico: a review. *North-east Gulf Science* 12: 35–47.
- Douglas, M.E. & W.J. Matthews. 1992. Does Morphology Predict Ecology – Hypothesis-Testing within a Fresh-Water Stream Fish Assemblage. *Oikos* 65: 213–224.
- Ehlinger, T.J. & D.S. Wilson. 1988. Complex foraging polymorphism in bluegill sunfish. *Proceedings of the National Academy of Sciences* 85: 1878–1882.
- Ginsburg, I. 1931. On the difference in the habitat and the size of *Cynoscion arenarius* and *C. nothus*. *Copeia* 1931: 144.
- Gould, S.J. & R.C. Lewontin. 1979. The spandrels of San Marco and the Panglossian paradigm. *Proceedings of the Royal Society of London B* 205: 581–598.
- Guest, W.C. & G. Gunter. 1958. The sea trout or weakfishes (Genus *Cynoscion*) of the Gulf of Mexico. Gulf States Marine Fisheries Commission Technical Summary No. 1. 40 pp.
- Herrera, M. & M. Peralta. 1999. Aspectos biológicos – pesqueros de la corvina plateada. Instituto Nacional de Pesca, Guayaquil, Ecuador, *Boletín Científico y Técnico* 17: 1–25.
- Herrera, M., P. Solís-Coello, H. Vicuña, P. Macías, D. Coello, O. Moya, M. Luzuriaga & E. Elías. 2001. Estimación de la biomasa de los recursos demersales en la plataforma continental del Ecuador durante Julio de 1999. Instituto Nacional de Pesca, Guayaquil, Ecuador, *Boletín Científico y Técnico* 18: 1–112.
- Hildebrand, S.F. 1946. A descriptive catalog of the shore fishes of Peru. United States National Museum Bulletin 189. Smithsonian Institution, Washington D.C. 530 pp.
- Hoese, H.D. & R.H. Moore. 1998. Fishes of the Gulf of Mexico. Texas A & M University Press, College Station. 422 pp.
- Lattin, J.M., J.D. Carroll & P.E. Green. 2003. Analyzing multivariate data. Brooks/Cole, Thomson Learning, Inc., Pacific Grove, CA. 556 pp.
- Lauder, G.V. & E.G. Drucker. 2004. Morphology and experimental hydrodynamics of fish fin control surfaces. *IEEE Journal of Oceanic Engineering* 29: 556–571.
- Lauder, G.V., J.C. Nauen & E.G. Drucker. 2002. Experimental hydrodynamics and evolution: function of median fins in ray-finned fishes. *Integrative & Comparative Biology* 42: 1009–1017.
- Losos, J.B. 1990. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution* 44: 1189–1203.
- MacArthur, R.H. & R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101: 377–385.
- Marín de López, C., F. Ormaza González & L. Arriaga Ochoa. 1999. Estadísticas de los desembarques pesqueros en Ecuador 1985–1997. Instituto Nacional de Pesca, Guayaquil, Ecuador Edición Especial. 152 pp.
- Mercer, L.P. 1989. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico). Weakfish. Coastal Ecology Group Waterways Experimental Station, U.S. Fish and Wildlife Service, Biological Report 82 (11.109).
- Nikolsky, G.V. 1963. The ecology of fishes. Academic Press, London. 352 pp.
- Parks, P.J. & M. Bonifaz. 1994. Nonsustainable use of renewable resources: mangrove deforestation and mariculture in Ecuador. *Marine Resource Economics* 9: 1–18.
- Paschall, R.L., Jr. 1986. Biochemical systematics of the seatrouts of the western Atlantic, genus *Cynoscion*. M. Sc. Thesis, University of New Orleans, Louisiana. 99 pp.
- Patillo, M.E., T.E. Czaplá, D.M. Nelson & M.E. Monaco. 1997. Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Volume II: species life history summaries. ELMR Rep. No. 11, NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, Maryland. 377 pp.
- Pesantes Vigano, F. 1998. Comportamiento temporal y espacial de las características físicas, químicas y biológicas del Golfo de Guayaquil y sus afluentes Daule y Babahoyo entre 1994–1996. Instituto Nacional de Pesca, Edición Especial, Guayaquil, Ecuador. 420 pp.

- Ricklefs, R.E. & D.B. Miles. 1994. Ecological and evolutionary inferences from morphology: an ecological perspective. pp. 13–41. In: P.C. Wainwright & S.M. Reilly, (eds), Ecological morphology, integrative organismal biology, The University of Chicago Press, Chicago.
- Sasaki, K. 1989. Phylogeny of the family Sciaenidae, with notes on its zoogeography (Teleostei, Perciformes). *Memoirs of the Faculty of Fisheries, Hokkaido University* 36: 1–137.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science* 185: 27–39.
- Schwarzshans, W. 1993. A comparative morphological treatise of recent and fossil otoliths of the family Sciaenidae (Perciformes). *Piscium catalogus: Part Otolithi Piscium. Vol. I.* Verlag Dr. Friedrich Pfeil, Munchen. 245 pp.
- Shipp, R.L. 1986. Dr. Bob Shipp's guide to the fishes of the Gulf of Mexico. Marine Environmental Sciences Consortium of Alabama, Dauphin Island Sea Laboratory, Dauphin Island Alabama. 256 pp.
- Sutter, F.C. & T.D. McIlwain. 1987. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico). Sand seatrout and silver seatrout. Coastal Ecology Group Waterways Experimental Station, U.S. Fish and Wildlife Service, Biological Report 82 (11.72).
- Tabb, D.C. 1961. A contribution to the biology of the spotted seatrout, *Cynoscion nebulosus* (Cuvier) of east-central Florida. Institute of Marine Sciences of the University of Miami Technical Series No. 35, Miami. 24 pp.
- Wainwright, P.C. 1988. Morphology and Ecology: Functional basis of feeding constraints in Caribbean Labrid Fishes. *Ecology* 69: 635–645.
- Webb, P.W. 1984. Body form, locomotion and foraging in aquatic vertebrates. *American Zoologist* 24: 107–120.
- Weinstein, M.P. & R.W. Yerger. 1976. Protein taxonomy of the Gulf of Mexico and Atlantic Ocean seatrouts, genus *Cynoscion*. *Fisheries Bulletin* 74: 599–607.
- Yoong, F. & B. Reinoso. 1999. Biodiversidad del estuario interior del Golfo de Guayaquil, Instituto Nacional de Pesca, Guayaquil, Ecuador, *Boletín Científico y Técnico* 17: 1–32.

### Appendix 1. Materials examined

All specimens examined are deposited in the Gulf Coast Research Laboratory (GCRL) Museum located in Ocean Springs, Mississippi, USA. Catalog numbers are listed, followed by the number of specimens examined in parenthesis.

- Gulf of Guayaquil (GOG). *C. albus*: 31223 (8); 31240 (6); 31241 (1). *C. analis* 28139 (12); 28140 (4); 31250 (3); 31309 (3). *C. phoxocephalus*: 28141 (8); 31224 (4); 31244 (4); 31247 (3); 31251 (1). *C. squamipinnis*: 31225 (11); 31751 (40). *I. remifer*: 28137 (3); 31687 (5); 31688 (4); 31691 (27).
- Western Atlantic (WA). *C. arenarius*: 7164 (2); 29982 (2); 29983 (2); 29984 (1); 29985 (1); 29986 (4);

- 29987 (1); 29989 (1); 29990 (1); 29991 (2); 29992 (3); 29993 (2); 29994 (2); 29998 (1); 30005 (3); 30770 (20); 30772 (3); 30773 (11); 30776 (2); 31321 (1); 31323 (1). *C. nebulosus*: 924 (1); 1011 (2); 7266 (2); 7634 (1); 7735 (1); 7927 (1); 8155 (1); 29970 (2); 29971 (1); 29972 (6); 29973 (3); 29974 (4); 29975 (1); 29977 (1); 29978 (1); 29979 (1); 29981 (4); 30769 (2); 30774 (1); 30775 (4); 31316 (1). *C. nothus*: 30869 (2); 30870 (1); 30872 (5); 30873 (1); 30878 (6); 30879 (3); 30880 (11); 30881 (1); 30882 (6); 30883 (4); 30884 (10). *C. regalis*: 30820 (5); 30821 (6); 30823 (1); 30824 (1); 30825 (2); 30826 (2); 30827 (2); 30828 (6); 30829 (2); 30830 (1).

### Appendix 2. Definition of morphometric measurements taken

1. Standard Length (SL) – Tip of the snout to the end of the last caudal vertebra.
2. Caudal Fin Length – End of the last caudal vertebra to the posterior tip of the caudal fin.
3. Head Length – Tip of the snout to the posterior tip of the operculum.
4. Eye Diameter – Measured through the center of the eye parallel to the main axis of the body.
5. Head Depth – Measured perpendicular to the main axis of the body from the top of the head through the center of the eye to the dorsal edge of the upper lip.
6. Upper Jaw Length – Tip of the snout to the posterior tip of the maxilla.
7. Length of Third Dorsal Spine – Base to the distal tip of the third dorsal spine.
8. Pectoral Fin Length – Insertion of the pectoral fin to the distal tip of the second pectoral fin ray.
9. Pelvic Fin Length – Insertion of the pelvic fin to the distal tip of the first pelvic fin ray.
10. Anal Fin Length – Insertion of the anal fin to the distal tip of the first anal fin ray.
11. Snout to Dorsal Fin – Tip of the snout to the insertion of the first dorsal fin.
12. Snout to Pectoral Fin – Tip of the snout to the insertion of the pectoral fin.
13. Snout to Pelvic Fin – Tip of the snout to the insertion of the pelvic fin.
14. Body Depth – Insertion of the first dorsal fin to the insertion of the pelvic fin.
15. Dorsal Fin to Pectoral Fin – Insertion of the first dorsal fin to the insertion of the pectoral fin.
16. Depth of Caudal Peduncle – Measured perpendicular to the main axis of the fish through the narrowest portion of the caudal peduncle.
17. First Dorsal Fin Base Length – Insertion of the first to the last element on the first dorsal fin.
18. Second Dorsal Fin Base Length –

Insertion of the first to the last elements of the second dorsal fin. 19. Anal Fin Base Length – Insertion of the first to the last elements of the anal fin. 20. Gill

Raker Length (GRL) – Base to the distal tip of the gill raker at the junction of the upper and lower branches of the first gill arch.