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(Centrarchidae): Meristics, Morphometrics,
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THE UNIVERSITY OF ALABAMA
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Variation of the Spotted Sunfish, *Lepomis punctatus* Complex (Centrarchidae): Meristics, Morphometrics, Pigmentation and Species Limits

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ABSTRACT: Warren, Melvin L., Jr., 1992. Variation of the spotted sunfish, *Lepomis punctatus* complex (Centrarchidae): meristics, morphometrics, pigmentation and species limits. Bulletin Alabama Museum of Natural History, Number 12:1-47, 23 tables, 27 figures. Two subspecies of the spotted sunfish, *Lepomis punctatus*, have been recognized by some authors: the nominate, eastern form and *L. p. miniatus*, a western form. No published information defines the taxa involved, their geographical limits, or their zone of contact. I reject application of the polytypic biological species concept to these taxa and diagnose two phylogenetic species on the basis of the presence (*L. miniatus*) or absence (*L. punctatus*) of red-orange coloration on the sides of breeding males. Univariate and principal component analyses of 10 meristic, 6 pigmentation, and to a lesser extent, 42 morphometric characters support the existence of two well-differentiated phylogenetic species. *Lepomis punctatus* also differs from *L. miniatus* in having smaller scales, numerous discrete black spots on the sides of the body, and longer, thinner gill rakers. In addition, the two species are essentially monomorphic for different alleles at the glucose phosphate isomerase A locus. Concordant variation among the data indicates a well-defined contact zone in the Florida panhandle from Perdido Bay east to the Apalachicola Bay drainage. *Lepomis punctatus* occurs on the Atlantic Slope from the Cape Fear River, North Carolina, southward and throughout peninsular Florida, and *L. miniatus* occurs on the Gulf Slope from Mobile Basin west to south Texas and north in the Mississippi River Valley to the Illinois River of Illinois in the north, Red River of southeastern Oklahoma in the west, and the lower Ohio River of Kentucky and Indiana in the east. Populations in Lookout Creek (Tennessee River drainage), Georgia, and Coosa River (Mobile Basin), Georgia, were not assignable to species and probably represent past introgression between the two species or are semi-isolated, independently derived populations. *Lepomis punctatus* and *L. miniatus* are hypothesized to be products of geographic isolation caused by one or more Mio-Pliocene high-level sea stands, which split an ancestral species into a west Gulf Slope-Mississippi Valley-Mobile Basin vicariant and a peninsular Florida-Atlantic Slope vicariant. Establishment of secondary contact in the Florida panhandle occurred during one or more major sea-level regressions.

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Introduction

The spotted sunfish, *Lepomis punctatus* (Valenciennes, 1831), is one of 11 species (family Centrarchidae) currently assigned to the genus. The geographic range includes the

Atlantic Slope from the Cape Fear River southward, west on the Gulf Slope to southern Texas, and north in the Mississippi River Valley to the Illinois River (Fig. 1). In an

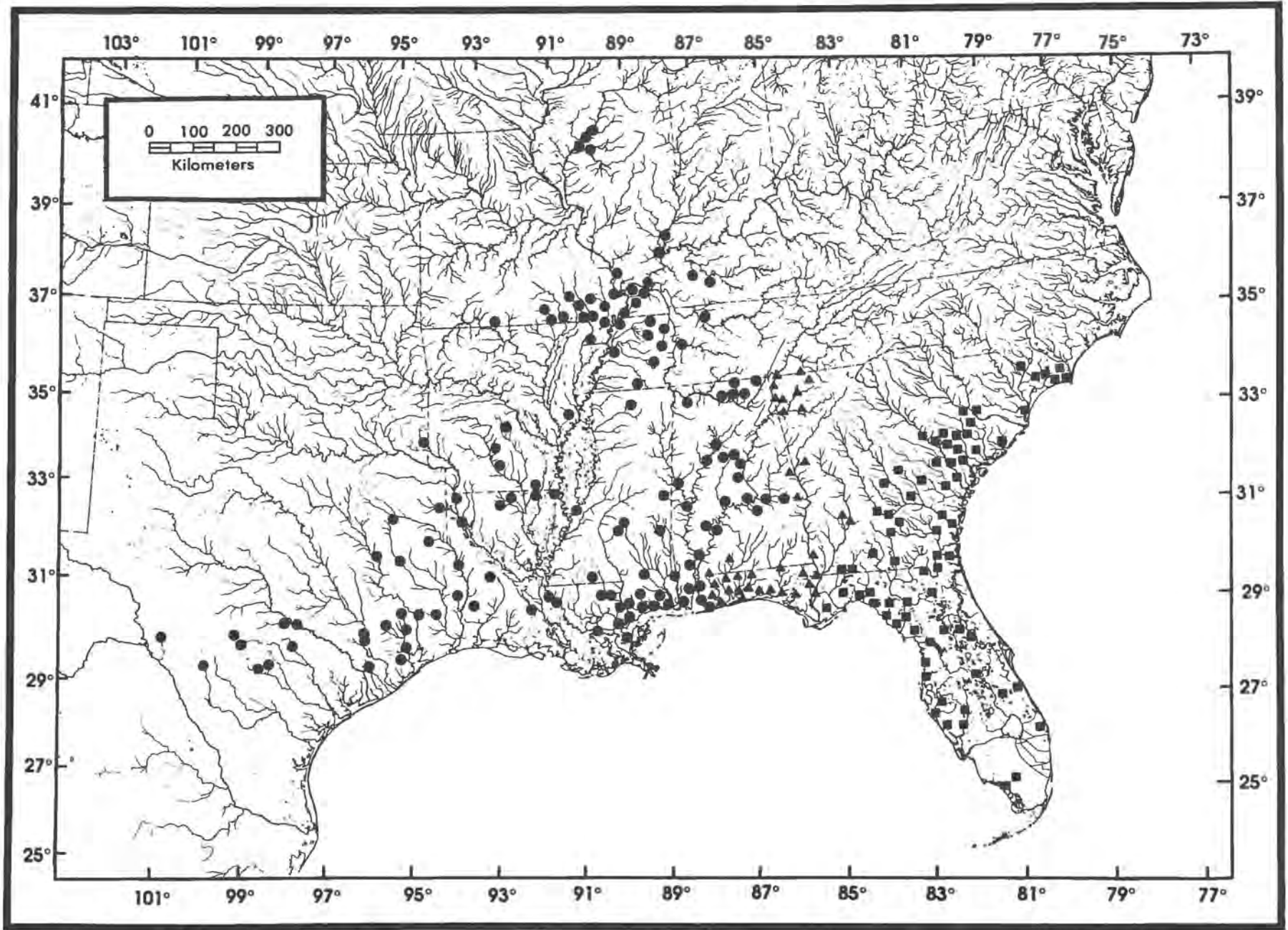


Figure 1. Distribution of the *Lepomis punctatus* complex as represented by material examined. Proximate localities are plotted as individual symbols. Solid circles represent *L. miniatus*; squares, *L. punctatus*; and triangles, contact zone populations (*L. miniatus* x *L. punctatus*).

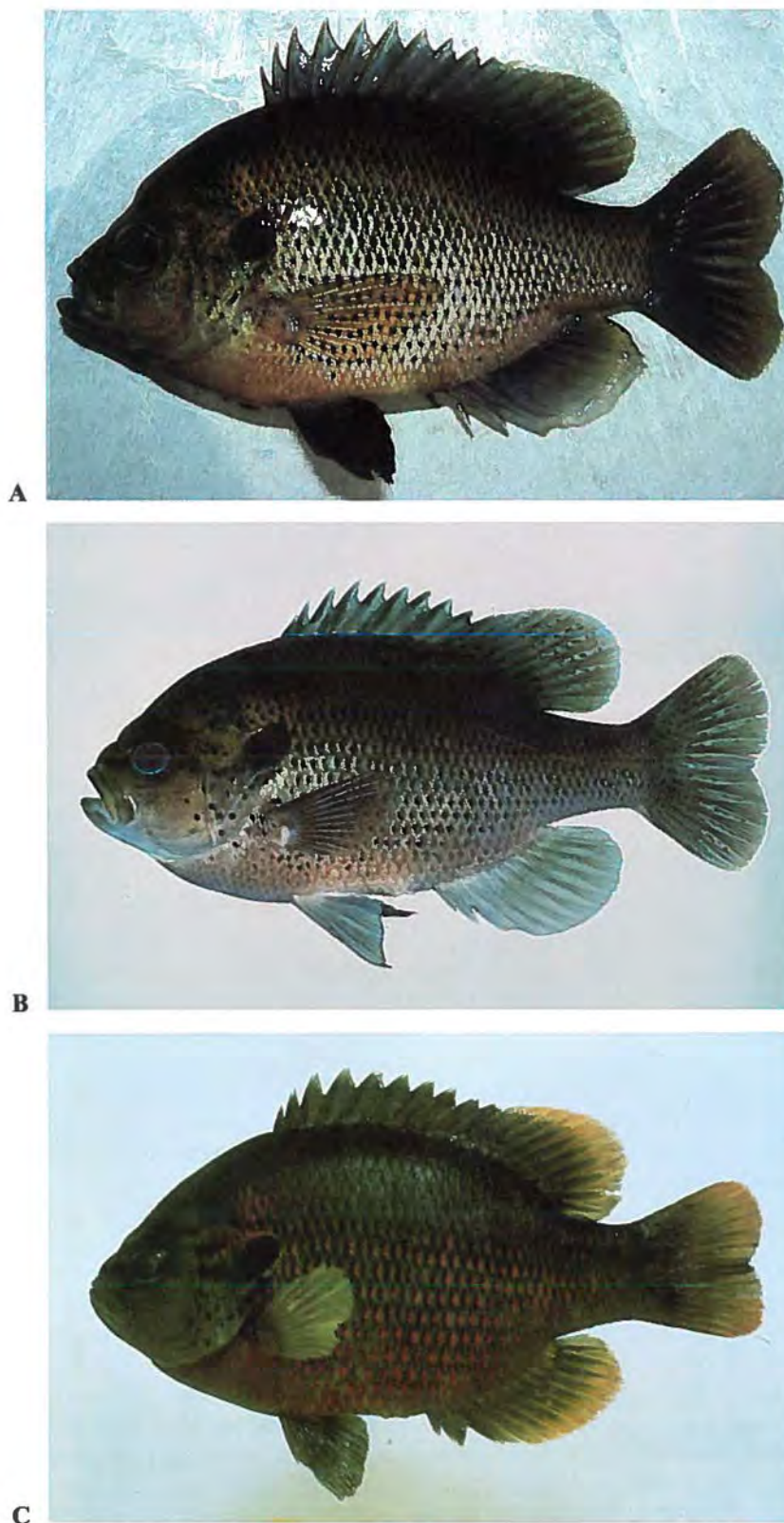


Fig. 2. Lateral views of *Lepomis punctatus*, *L. miniatus* x *L. punctatus*, and *L. miniatus*. A) *Lepomis punctatus*, breeding male, ca. 140 mm total length, Lake Osborne, Palm Beach Co., Florida, 17 January 1992 (photo by Noel M. Burkhead); B) *Lepomis miniatus* x *L. miniatus*, body length unknown, Turkey Gobbler Creek (Yellow River drainage) Okaloosa Co., Florida, 22 May 1990 (photo by Noel M. Burkhead); C) *L. miniatus*, breeding male, 114 mm SL, Lake Portchartrain, Orleans Parrish, Louisiana, 3 April 1982 (photo by L. M. Page).

unpublished revision of the Centrarchidae, Bailey (1938) recognized *L. p. punctatus*, an eastern form (Fig. 2); *L. p. miniatus*, a western form (Fig. 2); and an undescribed subspecies (based on two specimens) from the upper Coosa River. From the time of Bailey's (1938) work until recently, only cursory descriptions of, or more often allusions to, differentiated taxa within *L. punctatus* were forthcoming (Hubbs and Allen, 1943; Bailey et al., 1954; Carr and Goin, 1955; Swift et al., 1977). Bailey et al. (1954) briefly discussed the nominal eastern and western forms, noting that they graded insensibly in color pattern and scale size from one to the other in drainages of western Florida, southwestern Georgia, and southeastern Alabama. As judged from field observations of pigmentation patterns, Swift et al. (1977) proscribed a much narrower zone of contact between the two subspecies in extreme western Florida and the Mobile Bay region. Bailey et al. (1954) stated that a thorough analysis was desirable to define the taxa involved, their geographical limits, and their zone of contact. In a recent study of mitochondrial DNA (mtDNA) variation in fishes of the southeastern United States, Birmingham and Avise (1986) recognized two phylogeographic clades of *L. punctatus*: an eastern clade from the Atlantic Slope and peninsular Florida; and a western clade from the Apalachicola River west along the Gulf Slope to the Calcasieu River, Louisiana.

The shortcomings of recognizing subspecies from both theoretical and practical perspectives have been elaborated by recent authors (Wiley, 1981; Cracraft, 1983, 1987, 1989; Donoghue, 1985; McKittrick and Zink, 1988; Frost and Hillis, 1990). Much of the decision to recognize subspecies depends on subjective interpretation of what comprises "differing taxonomically" and a sufficient "degree of difference" or indirect measures of the degree of reproductive isolation and assessments of the relative width of the contact zone (Mayr, 1969). Because of confusion associated with the evolutionary status of polytypic versus monotypic species and perception of an overemphasis on reproductive isolation, some authors have suggested abandonment of the subspecies category and the biological species concept (BSC) (Cracraft, 1983, 1987, 1989; Donoghue, 1985; McKittrick and Zink, 1988; Echelle, 1990; Frost and Hillis, 1990). Given the difficulty of measuring reproductive disjunction and its controversial role in speciation, Cracraft (1983, 1987, 1989) cogently argues that a more objective and process-free species concept, the phylogenetic species concept (PSC), might be founded on the general theory that evolution occurs and produces differentiated taxa. The PSC is appealing both from the standpoint of objectivity in defining comparable evolutionary units (i.e., diagnosability in the context of propinquity by descent) and the analogous extension of phylogenetic methods to alpha taxonomy (Rosen, 1978, 1979; Donoghue, 1985; de Queiroz and Donoghue, 1988).

McKittrick and Zink (1988) suggest that critical analysis of taxa presently recognized as subspecies is a logical starting point in the search for phylogenetic species. I used univariate

and multivariate analyses of meristic, pigmentation, and morphometric characters and qualitative evaluation of color patterns of breeding males of the species currently known as *L. punctatus* to: 1) test the hypothesis that the taxa recognized by Bailey (1938) and Bailey et al. (1954) are phylogenetic species; 2) delineate the extent of contact zones, if any, among taxa; and 3) provide diagnoses and descriptions of any taxa recognized. For brevity, I refer to all populations under consideration here as the *L. punctatus* complex, but ultimately assign specific epithets to populations or groups of populations in the section entitled Species Descriptions.

Methods

NOMENCLATURE.—Bailey and Robins (1988) pointed out that the genus-group name *Lepomis* Rafinesque, 1819 has been consistently treated as masculine but as interpreted by them is classically feminine, necessitating the emendation of several species names in the genus (e.g., *L. punctatus* becomes *L. punctata*). Etnier and Warren (1990) concluded that *Lepomis* properly can be interpreted as masculine under the International Code of Zoological Nomenclature (ICZN, 1985). Pending a ruling by the Commission, I consider the genus-group name *Lepomis* as masculine under Article 80 of the Code (ICZN, 1985).

MORPHOLOGICAL METHODS.—Ten scale and fin-ray counts were made and six spot indices scored on 1219 specimens (Table 1). Morphometric data analyzed included 40 variables (Table 2) taken from 348 specimens selected from the pool of specimens used in the meristic analyses to insure adequate coverage of geographic and allometric variation. Counts and measurements (dial calipers, nearest 0.05 mm) followed Hubbs and Lagler (1964) unless defined otherwise. Standard length (SL) is used throughout. Institutional abbreviations are from Leviton et al. (1985), except as noted in Acknowledgments. Scale rows below the lateral line were counted from the first row contacting the urogenital opening upward and forward to the row below the lateral-line scale. Breast scale rows were counted following Cashner and Suttkus (1977).

Indices were devised to quantify the degree of spotting on the head and body (Table 1). In part, following Swift et al. (1977), a spot on the body was defined as a discrete, black, punctation at the anterior edge of the exposed scale field. Often spots were vertically elongate or quadrate and sometimes extended slightly under the overlapping edge of the next anterior scale. The longitudinal areas between the spots on overlapping scale rows and the posterior portion of the exposed scale field were distinctly lighter than the anterior basal spot. Dark pigmentation not originating at the anterior scale base or originating at the anterior base but becoming gradually diffuse on the posterior, dorsal, and ventral exposed scale field was not scored as a spot. Spots on the cheek and opercle were not exclusive to anterior scale edges; hence, any discernible pigment forming a more-or-less discrete punctation in these areas was considered a spot.

Table 1. Scale and fin-ray counts and spot indices (abbreviations in parentheses) used to quantify meristic and pigmentation variation in the *Lepomis punctatus* complex.

| Count or Index |
|---|
| Lateral-line scales |
| Scale rows above lateral line |
| Scale rows below lateral line |
| Transverse scale rows (= rows above and below + 1) |
| Scale rows above caudal peduncle |
| Scale rows below caudal peduncle |
| Caudal peduncle scale rows (= rows above and below + 2) |
| Left cheek scale rows |
| Right cheek scale rows |
| Breast scale rows |
| Left pectoral-fin rays |
| Right pectoral-fin rays |
| Spots above lateral line (SPALL) |
| Spots below lateral line (SPBLL) |
| Caudal peduncle spots above lateral line (CPSPA) |
| Caudal peduncle spots below lateral line (CPSPB) |
| Body spots (BDSP) (= SPALL + SPBLL + CPSPA + CPSPB) |
| Opercle spots (OPSP) |
| Cheek spots (CKSP) |
| Head Spots (HDSP) (= OPSP + CKSP) |

For spot indices above and below the lateral line (SPALL and SPBLL, respectively) and on the caudal peduncle (CPSPA and CPSPB, respectively), a spot was scored if it occurred on a scale in the corresponding scale count and/or on the scale to either side. The cheek spot index (CKSP) includes the total number of spots on the right cheek and preopercle (left, if damaged on the right) and the opercle spot index (OPSP) those on the right opercle and subopercle (left, if damaged on the right).

Coloration of breeding males was recorded from live material, color transparencies of freshly preserved individuals, literature accounts, or descriptions provided by colleagues. Diagnostic or distinguishing colors were compared and classified following Jacobson (1948).

Truss-geometric protocol (Humphries et al., 1981; Strauss and Bookstein, 1982; Bookstein et al., 1985) was used in part to archive body form and included 29 measurements distributed among four sagittal truss cells and one ventral cell with appended posterior and anterior triangles (Table 2; Fig. 3). Eleven additional measurements were included in the morphometric analysis (Table 2). The same measurement protocol also was applied to 20 males and 20 females from a single population (UF 32728, Peace River drainage); sex was determined by visual inspection of the gonads. Soft dorsal-fin length (D2LN) was taken as the greatest distance from the posterior base of the last dorsal-fin spine to the posterior edge of the soft dorsal fin. Anal-fin length (ALN) was the greatest distance from the anterior base of the first anal spine to the posterior edge of the fin. Lip width (LIPW) was taken as the greatest fleshy, vertical distance at the anterior tip of the upper lip.

The first gill arch was removed from 437 specimens (Table 3), and length and greatest fleshy width of the longest gill raker on the ventral arm of the arch were measured with an ocular micrometer and recorded to the nearest eyepiece unit. Gill raker data were not necessarily taken from the same specimens used to evaluate other morphometric variables and are treated separately.

Table 2. Distance measures used in evaluating morphometric variability in the *Lepomis punctatus* complex. A = anal fin; C = caudal fin; D1 = spinous dorsal fin; D2 = soft dorsal fin; H = horizontal; L = left; LN = length; P1 = pectoral fin; P2 = pelvic fin; R = right; SP = spine; V = vertical or oblique; W = width.

| Measurement | Abbreviation |
|--|--------------|
| Standard length | SL |
| P1 length | P1LN |
| P2 length | P2LN |
| D2 length | D2LN |
| A length | ALN |
| Length of first D1 spine | D1SP1 |
| Length of sixth D1 spine | D1SP6 |
| Length of last D1 spine | D1SP10 |
| Head length | HDLN |
| Orbit length | ORBIT |
| Lip width | LIPW |
| Ventral Cell and Appended Triangles | |
| Right upper jaw length | I-R11 |
| Right maxilla tip to dorsal P1 insertion | R11-R12 |
| Right P1 insertion to ventral base C | R12-9 |
| Left upper jaw length | I-L11 |
| Left maxilla tip to dorsal P1 insertion | L11-L12 |
| Left P1 insertion to ventral base C | L12-9 |
| Width left to right dorsal P1 insertions | L12-R12 |
| Width left to right posterior maxilla tips | L11-R11 |
| Sagittal Truss Cells | |
| Lip to interorbital pore | H1-2 |
| Interorbital pore to D1 origin | H2-4 |
| D1 origin to base last spine | H4-6 |
| Last D1 spine base to posterior base D2 | H6-8 |
| Posterior base D2 to dorsal base C | H8-10 |
| Lip to lateral P2 insertion | H1-3 |
| Lateral P2 insertion to A origin | H3-5 |
| A origin to posterior base A | H5-7 |
| Posterior base A to ventral base C | H7-9 |
| Lip to D1 origin | V1-4 |
| Lateral P2 insertion to interorbital pore | V3-2 |
| Lateral P2 insertion to D1 origin | V3-4 |
| Lateral P2 insertion to base last D1 spine | V3-6 |
| A origin to D1 origin | V5-4 |
| A origin to base last D1 spine | V5-6 |
| A origin to posterior base D2 | V5-8 |
| Posterior base A to base last D1 spine | V7-6 |
| Posterior base A to posterior base D2 | V7-8 |
| Posterior base A to dorsal base C | V7-10 |
| Ventral base C to posterior base D2 | V9-8 |
| Ventral to dorsal base C | V9-10 |

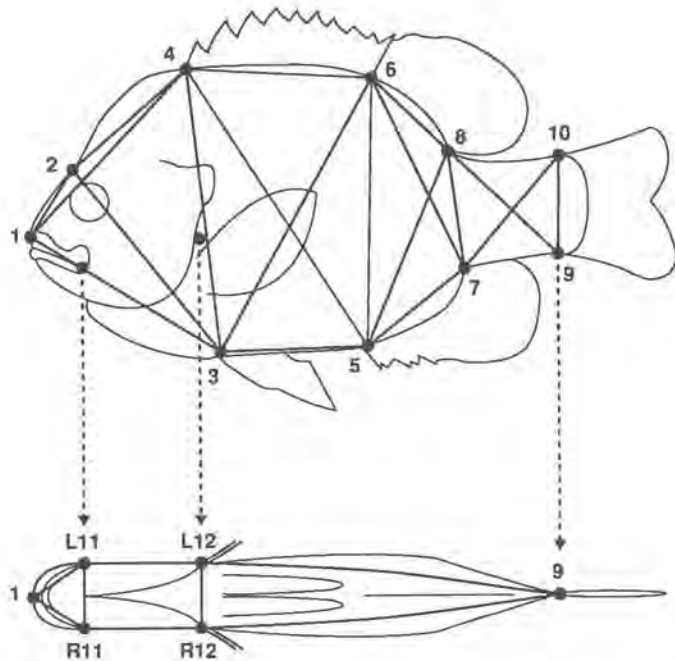


Figure 3. Diagrammatic representation of truss-network distance measures applied to the *Lepomis punctatus* complex. Numbers refer to homologous landmarks listed below.

Landmark

1. Tip of upper lip (premaxillae)
2. Interorbital pore
3. Pelvic-fin insertion
4. Origin spinous (1st) dorsal
5. Origin anal fin
6. Posterior base last dorsal spine
7. Posterior base anal fin
8. Posterior base soft (2nd) dorsal fin
9. Ventral base caudal fin
10. Dorsal base caudal fin
- R11. Right posterior maxilla tip
- R12. Right dorsal insertion pectoral fin
- L11. Left posterior maxilla tip
- L12. Left dorsal insertion pectoral fin

ANALYTICAL METHODS.—Meristic and morphometric data were analyzed separately following Chernoff (1982) and Chernoff et al. (1982). Univariate and multivariate analyses were conducted on the Southern Illinois University at Carbondale mainframe computer using programs available in SAS 5.18 (SAS Institute, Inc., 1985). Principal components were factored from the correlation matrix of meristic characters and the covariance matrix of log-transformed morphometric characters following recommendations of Bookstein et al. (1985).

Sample sizes were <5 from several drainages and many intradrainage localities. To reduce error associated with small sample sizes, I successively combined samples from

intradrainage or proximate interdrainage localities into 70 populations (i.e., composite locality samples) and these populations into 39 combined drainage samples (referred to as combined drainages [=CD 1-39]; see Table 3) when examination of meristic frequency tables and results of analysis of variance failed to reveal meaningful geographic variation. One-way analyses of variance (ANOVA) were performed among 70 populations on 12 meristic variables and on principal component scores of 1219 individuals for 10 meristic variables. To reduce subjectivity in forming combined drainages, separate one-way ANOVAs of the first principal component scores (produced in the aforementioned analysis) were conducted among populations of each combined drainage comprised of two or more of the 70 populations. The level of significance for all ANOVAs was $P < 0.01$.

The analyses of the spot indices were conducted separately from those of other data and focused on variation among the 39 combined drainages identified for the meristic data (Table 3). Many individuals among some combined drainages had scores of zero on several or all of the indices, producing skewed distributions and heterogeneous variances. Inspection of scatterplots revealed a positive, curvilinear relationship between the spot indices and SL in many populations. To linearize the relationship between SL and the indices and reduce heteroscedasticity, the spot indices and SL were transformed using the $\log_{10}(x + 1)$ and $\log_{10}(x)$ transforms, respectively (Sokal and Rohlf, 1981). To provide simple univariate comparisons among combined drainages, size-adjusted spot indices were calculated as follows:

$$\log_{10}(\text{Index} + 1) \times [\log_{10}(\text{SL})]^{-1} \times 1000,$$

where "Index" refers to spot indices listed in Table 1.

Multivariate analysis of the spot indices was accomplished by principal components analysis (PCA) of the correlation matrix of the residuals (Thorpe 1976, 1983a) produced by the following regression:

$$\log_{10}(\text{Index} + 1) = b_0 + b_1 \log_{10}(\text{SL}) + e$$

where: b_0 and b_1 are constants; and e is the residual.

Multivariate analysis of the morphometric data was accomplished using sheared PCA (Humphries et al. 1981, Bookstein et al. 1985) to eliminate overall size effects. To identify sexual dimorphism and test for the possible confounding among size, shape, and sex in subsequent analyses (Bookstein et al., 1985), males and females from one population were subjected to sheared PCA. A sheared PCA also was conducted on 348 individuals using combined drainage (Table 3) as a grouping variable ($n = 27$). Variation in gill raker shape was summarized by calculating the average ratio plus or minus two standard errors of length to width for each combined drainage.

Given the large number of individuals in the analyses and the degree of overlap in individual scores among some combined drainages, it is not practical to interpret multi-

Table 3. Combined drainages and included populations with sample sizes used to analyze meristic, spot, and morphometric variation in the *Lepomis punctatus* complex. Combined drainages represented in the morphometric analysis are indicated by **. N_1 = sample size for meristic and spot index data; N_2 = sample size for morphometric data; N_3 = sample size for gill raker data.

| No. Combined Drainage (= CD) - N_1 (N_2 , N_3) | Populations |
|---|---|
| 1. Illinois River* - 30 (10, 12) | Illinois R. drainage |
| 2. Ohio River* - 40 (16, 11) | Green R.; Wabash R. and Ohio R. minor drainages |
| 3. Lookout Creek* - 15 (4, 4) | Lookout Cr., GA (upper Tennessee R. drainage) |
| 4. Tennessee River* - 31 (16, 10) | Crow Cr. to Big Spring, AL; Duck R. to Big Sandy R., TN |
| 5. Middle Mississippi Rivereastern minor drainages - 27 (0, 12) | Wolf Lake, IL to Hatchie R., TN |
| 6. St. Francis River and White River* - 44 (13, 14) | Castor R. to St. Francis R.; White R. |
| 7. Yazoo River - 10 (0, 3) | Yazoo River |
| 8. Red River and lower Mississippi River Embayment* - 51 (14, 9) | Red R. and Ouachita R.; Atchafalaya Basin, Bayou La Fourche, and lower Mississippi River minor drainages |
| 9. Lake Pontchartrain* - 31 (13, 18) | Lake Pontchartrain and Lake Borgne minor drainages |
| 10. Sabine Lake and Calcasieu River* - 22 (16, 9) | Calcasieu R., Sabine R., and Neches R. |
| 11. Galveston Bay* - 18 (15, 4) | San Jacinto R.; Trinity R. and Galveston Bay minor drainages |
| 12. Brazos River to Colorado River - 32 (0, 3) | Brazos R. and San Bernard R.; Colorado R. |
| 13. San Antonio Bay to Rio Grande* - 31 (16, 6) | Guadalupe R.; San Antonio R. and Nueces R.; Devils R. |
| 14. Pearl River - 13 (0, 2) | Pearl R. drainage |
| 15. Bay St. Louis to Biloxi Bay - 38 (0, 11) | Bay St. Louis; Biloxi Bay |
| 16. Pascagoula River and Escatawpa River - 13 (0, 4) | Pascagoula R. and Escatawpa R. |
| 17. Coosa River* - 38 (10, 20) | Coosa R. drainage |
| 18. Tallapoosa River - 17 (0, 5) | Tallapoosa R. drainage |
| 19. Alabama River* - 32 (10, 14) | Coosa-Tallapoosa confluence to Cahaba R.; Rockwest Ck. and Dunns Ck., Wilcox Co., AL |
| 20. Tombigbee River - 22 (0, 12) | Tombigbee R. drainage |
| 21. Mobile Bay tributaries* - 15 (9, 5) | Mobile Bay minor tributaries |
| 22. Perdido Bay and minor coastal tributaries* - 41 (11, 15) | Perdido Bay; coastal tributaries from Mobile Bay to Perdido Bay |
| 23. Pensacola Bay* - 81 (12, 36) | Escambia R.; Blackwater R. and Pond Cr.; Yellow R.; E. Bay R. |
| 24. Choctawhatchee Bay and minor coastal tributaries* - 59 (11, 28) | Choctawhatchee Bay drainage and Santa Rosa Sound drainages |
| 25. St. Andrews Bay* - 13 (10, 9) | St. Andrews Bay drainage |
| 26. Chattahoochee River - 17 (0, 7) | drainage north of confluence with Flint R. |
| 27. Flint River - 10 (0, 4) | Flint R. drainage |
| 28. Chipola River and Apalachicola River* - 14 (10**, 6) | drainage south of confluence with Flint River |
| 29. New River to California Creek* - 63 (8, 39) | New R. and Ochlockonee R.; St. Marks (Wakulla R.); Aucilla R.; Econfinia R.; Fenholloway R.; Steinhatchee R. and California Cr. |
| 30. Suwannee River* - 30 (10, 11) | Suwannee R. drainage |
| 31. Waccasassa River to Pithlachascotee River - 19 (0, 2) | Waccasassa R. and Withlacoochee R.; Weeki Wachee Swamp and Pithlachascotee R. |
| 32. Tampa Bay - 17 (0, 8) | Tampa Bay drainage |
| 33. Peace River and Myakka River* - 28 (40, 6) | Peace R.; Myakka R. |
| 34. Everglades and south Florida drainages* - 53 (11, 17) | Kissimmee R.; lower Everglades; Loxahatchie R.; Sebastian Cr. |
| 35. St. Johns River and St. Marys River* - 40 (10, 14) | St. Johns R.; St. Marys R. |
| 36. Satilla River - 16 (0, 3) | Satilla R. |
| 37. Altamaha River* - 29 (13, 14) | Altamaha R. |
| 38. Ogeechee River to Edisto River* - 75 (11, 12) | Ogeechee R.; Savannah R.; Coosawhatchie R. and St. Helena Sound (Ashpoo and Combahee rivers); Edisto R. |
| 39. Cooper River to Cape Fear River* - 44 (29***, 18) | Cooper R. and Santee R.; Peedee R., Waccamaw R., and Royal Oak Swamp; Cape Fear R. |

** includes 2 specimens from the Flint River

*** 20 and 9 specimens from Peedee (CD 39a) and Cape Fear (CD 39b) rivers, respectively

variate ordinations that include all individuals (Thorpe, 1983a). To facilitate interpretation, character means (or for spot indices, mean residuals) for combined drainages were subjected to PCA. Although the use of the mean of each character eliminates variation of individuals within combined drainages, it does allow trends and patterns in the data to be summarized (Thorpe, 1983a; Matthews, 1987).

Before the data set is reduced to character means, it is desirable to know if some individuals from at least some localities can be distinguished in principal component space; if they cannot, random results might be expected in an ordination based on group means (Chernoff, 1982; Matthews, 1987). Following the approach of Chernoff (1982) and Matthews (1987), I randomly selected two sets

of five localities each with the stipulations that within a set no two localities come from the same drainage and that the number of individuals from a selected locality was at least five. This procedure was followed independently for meristic, spot index, and morphometric data. The resulting matrices from individuals within each set of five populations and for each data set was factored by PCA (sheared PCA for morphometric data); the principal component scores of individuals were plotted on the first two principal axes and examined for localities that were distinguishable. In each set of randomly chosen localities for each of meristic, spot index, and morphometric data (Appendix A, Figs. A1-A6), the ordination of individuals by locality demonstrated that

individuals at some localities among the combined drainages are distinguishable and that use of mean values in PCA will not produce random or misleading results.

Results

For brevity, variation of meristic, spot index, and morphometric data in the *L. punctatus* complex is summarized by geographic region. The geographic regions and included combined drainages (Table 3) are: the Mississippi River Valley (CD 1-9); west Gulf Slope (CD 10-13); middle Gulf Slope (CD 14-16); Mobile Basin (CD 17-21); Florida panhandle (CD 22-28); peninsular Florida (CD 29-34); and Atlantic Slope (CD 35-39).

Table 4. Frequency distributions of lateral-line scales in *Lepomis miniatus* (CD 1-2, 4-16, 18-21), *L. punctatus* (CD 29-39), and populations in presumed contact zones (CD 3, 17, 22-28).

| Combined Drainage (CD) | Lateral-line Scales | | | | | | | | | | | | | | | | n | \bar{x} | SD |
|---|---------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|--|----|-----------|------|
| | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | | | | |
| 1. Illinois R. | | 1 | 1 | 3 | 5 | 9 | 7 | 2 | 2 | | | | | | | | 30 | 37.97 | 1.61 |
| 2. Ohio R. | | 1 | 5 | 7 | 12 | 10 | 4 | 1 | | | | | | | | | 40 | 37.03 | 1.35 |
| 3. Lookout Cr. | | | | | | | 3 | 9 | 1 | 1 | 1 | | | | | | 15 | 40.20 | 1.08 |
| 4. Tennessee R. | 1 | 2 | 6 | 8 | 9 | 5 | | | | | | | | | | | 31 | 36.19 | 1.30 |
| 5. Middle Miss. R. minor drainages | | | 1 | 6 | 9 | 6 | 5 | | | | | | | | | | 27 | 37.30 | 1.14 |
| 6. St. Francis R. and White R. | 1 | 1 | 3 | 12 | 11 | 9 | 3 | 2 | 2 | | | | | | | | 44 | 37.09 | 1.67 |
| 7. Yazoo R. | | | | 6 | 2 | 2 | | | | | | | | | | | 10 | 36.60 | 0.84 |
| 8. Red R. and lower Miss. R. embayment | | 3 | 2 | 8 | 10 | 15 | 7 | 3 | 3 | | | | | | | | 51 | 37.57 | 1.70 |
| 9. L. Pontchartrain | | | 2 | 4 | 7 | 8 | 6 | 4 | | | | | | | | | 31 | 37.77 | 1.43 |
| 10. Sabine L. and Calcasieu R. | | | 2 | 1 | 5 | 3 | 4 | 7 | | | | | | | | | 22 | 38.23 | 1.66 |
| 11. Galveston Bay | | | 1 | 0 | 5 | 5 | 6 | 1 | | | | | | | | | 18 | 38.00 | 1.19 |
| 12. Brazos R. to Colorado R. | 1 | 4 | 5 | 12 | 4 | 4 | 1 | 1 | | | | | | | | | 32 | 37.09 | 1.55 |
| 13. San Antonio R. to Rio Grande | | 3 | 4 | 2 | 8 | 12 | 1 | 1 | | | | | | | | | 31 | 37.94 | 1.53 |
| 14. Pearl R. | | | 1 | 6 | 2 | 2 | 2 | | | | | | | | | | 13 | 37.85 | 1.28 |
| 15. Bay St. Louis to Biloxi Bay | | 3 | 7 | 12 | 8 | 2 | 5 | 1 | | | | | | | | | 38 | 38.47 | 1.54 |
| 16. Pascagoula R. and Escatawpa R. | | | 2 | 2 | 2 | 3 | 4 | | | | | | | | | | 13 | 39.38 | 1.50 |
| 17. Coosa R. | 2 | 2 | 4 | 9 | 8 | 6 | 5 | 1 | 1 | | | | | | | | 38 | 37.79 | 1.83 |
| 18. Tallapoosa R. | | 2 | 2 | 1 | 4 | 4 | 1 | 3 | | | | | | | | | 17 | 38.24 | 1.95 |
| 19. Alabama R. | | | 5 | 7 | 12 | 5 | 1 | 2 | | | | | | | | | 32 | 37.88 | 1.31 |
| 20. Tombigbee R. | | 1 | 4 | 3 | 5 | 2 | 4 | 2 | 1 | | | | | | | | 22 | 38.27 | 1.93 |
| 21. Mobile Bay tribs. | | | | 2 | 3 | 4 | 2 | 2 | 2 | | | | | | | | 15 | 39.33 | 1.63 |
| 22. Perdido Bay and minor coastal tribs. | | | | | 3 | 6 | 9 | 10 | 7 | 4 | 2 | | | | | | 41 | 40.78 | 1.57 |
| 23. Pensacola Bay | | | 1 | 0 | 10 | 14 | 16 | 15 | 13 | 10 | 2 | | | | | | 81 | 40.51 | 1.73 |
| 24. Choctawhatchee Bay and minor coastal tribs. | | | | | 4 | 8 | 8 | 22 | 6 | 8 | 1 | 2 | | | | | 59 | 40.95 | 1.63 |
| 25. St. Andrews Bay | | | | | | 2 | 5 | 1 | 4 | 1 | 0 | 0 | 1 | | | | 13 | 42.77 | 1.30 |
| 26. Chattahoochee R. | | 2 | 1 | 2 | 5 | 2 | 2 | 2 | 1 | | | | | | | | 17 | 39.35 | 2.03 |
| 27. Flint R. | | | 1 | 0 | 2 | 1 | 4 | 1 | 0 | 0 | 1 | | | | | | 10 | 40.60 | 2.12 |
| 28. Chipola R. and Apalachicola R. | | | | | 1 | 2 | 3 | 4 | 1 | 0 | 3 | | | | | | 14 | 42.00 | 1.92 |
| 29. New R. to California Cr. | | | | | 4 | 0 | 8 | 8 | 17 | 16 | 8 | 1 | 1 | | | | 63 | 41.98 | 1.69 |
| 30. Suwannee R. | | | | | 3 | 6 | 2 | 6 | 6 | 5 | 2 | | | | | | 30 | 41.97 | 1.83 |
| 31. Waccasassa R. to Pithlachascotee R. | | | | | 5 | 1 | 5 | 4 | 3 | 1 | | | | | | | 19 | 40.11 | 1.59 |
| 32. Tampa Bay | | | | | | | 4 | 7 | 3 | 1 | 1 | 0 | 1 | | | | 17 | 42.53 | 1.59 |
| 33. Peace R. and Myakka R. | | | | | 1 | 3 | 5 | 9 | 6 | 2 | 2 | | | | | | 28 | 41.07 | 1.46 |
| 34. Everglades and south Florida drainages | | | | 2 | 4 | 14 | 13 | 11 | 5 | 4 | | | | | | | 53 | 40.09 | 1.48 |
| 35. St. Johns R. and St. Marys R. | | | | | 4 | 7 | 6 | 3 | 11 | 6 | 3 | | | | | | 40 | 41.00 | 1.84 |
| 36. Satilla R. | | | | | 1 | 4 | 1 | 4 | 4 | 1 | 1 | | | | | | 16 | 40.81 | 1.68 |
| 37. Altamaha R. | | | | | 1 | 4 | 6 | 5 | 6 | 4 | 1 | 2 | | | | | 29 | 41.28 | 1.81 |
| 38. Ogeechee R. to Edisto R. | | | | | 7 | 10 | 22 | 21 | 10 | 3 | 1 | 1 | | | | | 75 | 40.47 | 1.43 |
| 39. Cooper R. to Cape Fear R. | | | | | 4 | 5 | 11 | 13 | 4 | 3 | 3 | 1 | | | | | 44 | 40.77 | 1.70 |

Table 5. Frequency distributions of transverse scale rows in *Lepomis miniatus* (CD 1-2, 4-16, 18-21), *L. punctatus* (CD 29-39), and populations in presumed contact zones (CD 3, 17, 22-28)

| Combined Drainage (CD) | Transverse Scale Rows | | | | | | | | | | n | \bar{x} | SD |
|---|-----------------------|----|----|----|----|----|----|----|----|---|----|-----------|------|
| | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | | | | |
| 1. Illinois R. | | | 2 | 8 | 9 | 9 | 2 | | | | 30 | 21.03 | 1.07 |
| 2. Ohio R. | | | 7 | 21 | 11 | 1 | | | | | 40 | 20.15 | 0.74 |
| 3. Lookout Cr. | | | | 5 | 7 | 1 | 2 | | | | 15 | 21.00 | 1.00 |
| 4. Tennessee R. | 1 | 3 | 18 | 6 | 3 | | | | | | 31 | 19.23 | 0.88 |
| 5. Middle Miss. R. minor drainages | | | 1 | 15 | 11 | | | | | | 27 | 20.37 | 0.56 |
| 6. St. Francis R. and White R. | | 2 | 9 | 17 | 12 | 4 | | | | | 44 | 20.16 | 1.01 |
| 7. Yazoo R. | | 1 | 3 | 2 | 3 | 1 | | | | | 10 | 20.00 | 1.25 |
| 8. Red R. and lower Miss. R. embayment | | | 6 | 21 | 22 | 2 | | | | | 51 | 20.39 | 0.75 |
| 9. L. Pontchartrain | | | 2 | 13 | 11 | 5 | | | | | 31 | 20.61 | 0.84 |
| 10. Sabine L. and Calcasieu R. | | | 3 | 13 | 5 | 1 | | | | | 22 | 20.18 | 0.73 |
| 11. Galveston Bay | | | 2 | 9 | 6 | 1 | | | | | 18 | 20.33 | 0.77 |
| 12. Brazos R. to Colorado R. | | | 3 | 5 | 15 | 9 | | | | | 32 | 20.94 | 0.91 |
| 13. San Antonio R. to Rio Grande | | | | 9 | 11 | 8 | 3 | | | | 31 | 21.16 | 0.97 |
| 14. Pearl R. | 1 | | 4 | 7 | 1 | | | | | | 13 | 19.62 | 0.77 |
| 15. Bay St. Louis to Biloxi Bay | | | 12 | 17 | 9 | | | | | | 38 | 19.92 | 0.75 |
| 16. Pascagoula R. and Escatawpa R. | | | 2 | 7 | 4 | | | | | | 13 | 20.15 | 0.69 |
| 17. Coosa R. | 1 | | 13 | 16 | 7 | 1 | | | | | 38 | 19.84 | 0.86 |
| 18. Tallapoosa R. | | | 5 | 7 | 5 | | | | | | 17 | 20.00 | 0.79 |
| 19. Alabama R. | | 3 | 6 | 14 | 9 | | | | | | 32 | 19.91 | 0.93 |
| 20. Tombigbee R. | | | 7 | 11 | 4 | | | | | | 22 | 19.86 | 0.71 |
| 21. Mobile Bay tribs. | | | 2 | 6 | 4 | 3 | | | | | 15 | 20.53 | 0.99 |
| 22. Perdido Bay and minor coastal tribs. | | | 4 | 14 | 16 | 5 | 2 | | | | 41 | 20.68 | 0.99 |
| 23. Pensacola Bay | | | 5 | 29 | 29 | 13 | 5 | | | | 81 | 20.80 | 0.99 |
| 24. Choctawhatchee Bay and minor coastal tribs. | | | 4 | 15 | 20 | 20 | | | | | 59 | 20.95 | 0.94 |
| 25. St. Andrews Bay | | | | 1 | 1 | 6 | 4 | 1 | | | 13 | 22.23 | 1.01 |
| 26. Chattahoochee R. | | | 2 | 6 | 6 | 3 | | | | | 17 | 20.59 | 0.94 |
| 27. Flint R. | | | | 1 | 4 | 5 | | | | | 10 | 21.40 | 0.70 |
| 28. Chipola R. and Apalachicola R. | | | 1 | 2 | 9 | 2 | | | | | 14 | 21.79 | 0.97 |
| 29. New R. to California Cr. | | | | 1 | 9 | 18 | 27 | 7 | 1 | | 63 | 22.52 | 0.98 |
| 30. Suwannee R. | | | | 1 | 2 | 7 | 17 | 3 | | | 30 | 22.63 | 0.89 |
| 31. Waccasassa R. to Pithlachascotee R. | | | | | 1 | 4 | 11 | 3 | | | 19 | 22.84 | 0.76 |
| 32. Tampa Bay | | | | | | | 3 | 4 | 7 | 3 | 17 | 23.58 | 1.00 |
| 33. Peace R. and Myakka R. | | | | | 1 | 7 | 13 | 3 | 4 | | 28 | 23.07 | 1.05 |
| 34. Everglades and south Florida drainages | | | | | 6 | 18 | 22 | 6 | 1 | | 53 | 22.58 | 0.91 |
| 35. St. Johns R. and St. Marys R. | | | | | 6 | 10 | 13 | 9 | 2 | | 40 | 22.78 | 1.12 |
| 36. Satilla R. | | 1 | 0 | 5 | 6 | 3 | 1 | | | | 16 | 21.83 | 1.17 |
| 37. Altamaha R. | | | | | 4 | 16 | 5 | 4 | | | 29 | 22.31 | 0.89 |
| 38. Ogeechee R. to Edisto R. | | | 1 | 8 | 33 | 21 | 11 | 1 | | | 75 | 21.48 | 0.96 |
| 39. Cooper R. to Cape Fear R. | | | | 2 | 4 | 17 | 15 | 6 | | | 44 | 22.43 | 1.00 |

MERISTICS.—One-way ANOVA of each of 12 meristic characters and scores on the first principal component from 10 meristic characters of 1219 individuals indicated significant differences ($P < 0.001$) among 70 populations of the *L. punctatus* complex. There were no significant differences in scores on the first principal component of 10 meristic characters (ANOVA; $P > 0.02$) among populations within each combined drainage tested. Significant differences (ANOVA; $P < 0.001$) were present among combined drainages in scores on the first principal component from 10 meristic characters.

Variation in selected individual scale and fin-ray counts of samples from 39 combined drainages are summarized as

frequency distributions in Tables 4-7. Means, ranges, and standard deviations of selected scale counts are summarized in Figs. 4-8. Right and left cheek scale rows and right and left pectoral-fin ray counts are summarized as frequency distributions in Appendix A (Tables A1-A2).

Principal components analysis for 10 meristic characters indicates principal components one (PC-I) and two (PC-II) account for 64% (50.6% and 13.4%, respectively) of the total variance among 1219 individuals (Table 8). Loadings show PC-I is associated with scale counts and PC-II with pectoral-fin ray counts. Individuals with low scale counts have low scores on PC-I and those with high scale counts have high scores on PC-I. Similarly, individuals with low numbers of

pectoral-fin rays have low scores on PC-II and those with high numbers of pectoral-fin rays high scores on PC-II.

Using meristic character means, principal component scores were calculated for each of the 39 combined drainages (Table 9, Fig. 9). PC-I accounts for 80.5% and PC-II for 10.9% of the total variance in mean meristic values. Loadings on PC-I indicate it is primarily a scale count component; combined drainages with high mean scale counts have high scores on PC-I. PC-II is associated with pectoral-fin ray counts, but the left mean pectoral-fin ray count loaded higher on PC-I than on PC-II, and the loadings on the right mean pectoral-fin ray count are similar on both PC-I and PC-II. Ordination of the scores of 39 combined drainages delimited

by geographic region (Fig. 9) shows the Mississippi River Valley (CD 1-9), west Gulf Slope (CD 10-13), middle Gulf Slope (CD 14-16), and Mobile Basin (CD 17-21) completely separate on PC-I from peninsular Florida (CD 29-34) and the Atlantic Slope (CD 35-39). The Florida panhandle (CD 22-28) broadly overlaps the Atlantic Slope (CD 35-39) and to a lesser extent the Mississippi River Valley (CD 1-9; notably Lookout Creek, CD 3) but is completely separate from peninsular Florida, Mobile Basin, and the west and middle Gulf Slope. Mobile Basin and the middle Gulf Slope are separated on PC-II from the Mississippi River Valley and west Gulf Slope. The polarity of scores on PC-I (Fig. 10) is negative (i.e., low mean scale numbers) for all combined

Table 6. Frequency distributions of total caudal peduncle scale rows in *Lepomis miniatus* (CD 1-2, 4-16, 18-21), *L. punctatus* (CD 29-39), and populations in presumed contact zones (CD 3, 17, 22-28)

| Combined Drainage (CD) | Caudal Peduncle Scale Rows | | | | | | | | | | n | \bar{x} | SD | |
|---|----------------------------|----|----|----|----|----|----|----|----|----|---|-----------|-------|------|
| | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | | | | |
| 1. Illinois R. | | | | | 13 | 7 | 10 | | | | | 30 | 19.90 | 0.88 |
| 2. Ohio R. | | | | 2 | 25 | 9 | 4 | | | | | 40 | 19.38 | 0.74 |
| 3. Lookout Cr. | | | | | | 3 | 11 | 1 | | | | 15 | 20.87 | 0.52 |
| 4. Tennessee R. | | | 5 | 12 | 9 | 5 | | | | | | 31 | 18.45 | 0.96 |
| 5. Middle Miss. R. minor drainages | | | 1 | 1 | 10 | 12 | 3 | | | | | 27 | 19.56 | 0.89 |
| 6. St. Francis R. and White R. | | | 1 | 8 | 21 | 11 | 3 | | | | | 44 | 19.16 | 0.89 |
| 7. Yazoo R. | 1 | 0 | 0 | 0 | 6 | 3 | | | | | | 10 | 18.90 | 1.45 |
| 8. Red R. and lower Miss. R. embayment | | | 2 | 5 | 29 | 12 | 2 | 1 | | | | 51 | 19.20 | 0.89 |
| 9. L. Pontchartrain | | | | 3 | 12 | 9 | 6 | 1 | | | | 31 | 19.68 | 1.01 |
| 10. Sabine L. and Calcasieu R. | | | | | 15 | 4 | 3 | | | | | 22 | 19.45 | 0.74 |
| 11. Galveston Bay | | | | 1 | 10 | 4 | 3 | | | | | 18 | 19.50 | 0.86 |
| 12. Brazos R. to Colorado R. | | | | 1 | 7 | 8 | 14 | 2 | | | | 32 | 20.28 | 0.99 |
| 13. San Antonio R. to Rio Grande | | | | | 5 | 11 | 15 | | | | | 31 | 20.32 | 0.75 |
| 14. Pearl R. | | 2 | 7 | 4 | | | | | | | | 13 | 18.15 | 0.69 |
| 15. Bay St. Louis to Biloxi Bay | | 1 | 3 | 24 | 6 | 4 | | | | | | 38 | 19.24 | 0.85 |
| 16. Pascagoula R. and Escatawpa R. | | 2 | 1 | 9 | 1 | | | | | | | 13 | 18.69 | 0.85 |
| 17. Coosa R. | | | | 2 | 19 | 11 | 5 | 1 | | | | 38 | 19.58 | 0.89 |
| 18. Tallapoosa R. | | | | 3 | 8 | 6 | | | | | | 17 | 19.18 | 0.73 |
| 19. Alabama R. | | | 1 | 6 | 20 | 4 | 1 | | | | | 32 | 18.94 | 0.76 |
| 20. Tombigbee R. | | | 1 | 2 | 10 | 6 | 3 | | | | | 22 | 19.36 | 1.00 |
| 21. Mobile Bay tribs. | | | | 1 | 6 | 3 | 5 | | | | | 15 | 19.80 | 1.01 |
| 22. Perdido Bay and minor coastal tribs. | | | | | 10 | 8 | 19 | 3 | 1 | | | 41 | 20.44 | 1.03 |
| 23. Pensacola Bay | | | | | 10 | 18 | 39 | 11 | 3 | | | 81 | 20.74 | 0.97 |
| 24. Choctawhatchee Bay and minor coastal tribs. | | | | | 5 | 12 | 35 | 7 | | | | 59 | 20.75 | 0.78 |
| 25. St. Andrews Bay | | | | | | | 9 | 3 | 1 | | | 13 | 21.38 | 0.65 |
| 26. Chattahoochee R. | | | | | 1 | 9 | 6 | 0 | 1 | | | 17 | 20.47 | 0.87 |
| 27. Flint R. | | | | | | 1 | 7 | 1 | 1 | | | 10 | 21.20 | 0.79 |
| 28. Chipola R. and Apalachicola R. | | | | | 1 | 3 | 5 | 3 | 2 | | | 14 | 21.14 | 1.17 |
| 29. New R. to California Cr. | | | | | | 3 | 37 | 12 | 11 | | | 63 | 21.49 | 0.84 |
| 30. Suwannee R. | | | | | | 4 | 17 | 4 | 5 | | | 30 | 21.33 | 0.92 |
| 31. Waccasassa R. to Pithlachascotee R. | | | | | 2 | 3 | 10 | 3 | 1 | | | 19 | 20.89 | 0.99 |
| 32. Tampa Bay | | | | | | | 8 | 7 | 2 | | | 17 | 21.65 | 0.70 |
| 33. Peace R. and Myakka R. | | | | | 1 | 2 | 16 | 7 | 2 | | | 28 | 21.25 | 0.84 |
| 34. Everglades and south Florida drainages | | | | | 4 | 7 | 34 | 8 | | | | 53 | 20.87 | 0.76 |
| 35. St. Johns R. and St. Marys R. | | | | | 2 | 6 | 25 | 3 | 3 | 1 | | 40 | 21.05 | 0.99 |
| 36. Satilla R. | | | | | 2 | 1 | 7 | 4 | 2 | | | 16 | 21.19 | 1.17 |
| 37. Altamaha R. | | | | | | 2 | 11 | 9 | 6 | 1 | | 29 | 21.75 | 0.99 |
| 38. Ogeechee R. to Edisto R. | | | | | 14 | 18 | 33 | 6 | 4 | | | 75 | 20.57 | 1.06 |
| 39. Cooper R. to Cape Fear R. | | | | | 5 | 12 | 21 | 6 | | | | 44 | 20.64 | 0.87 |

Table 7. Frequency distributions of breast scale rows in *Lepomis miniatus* (CD 1-2, 4-16, 18-21), *L. punctatus* (CD 29-39), and populations in presumed contact zones (CD 3, 17, 22-28).

| Combined Drainage (CD) | Breast Scale Rows | | | | | | | | | | n | \bar{x} | SD |
|---|-------------------|----|----|----|----|----|----|----|----|----|----|-----------|------|
| | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | | | |
| 1. Illinois R. | | | 4 | 2 | 19 | 4 | 1 | | | | 30 | 14.87 | 0.94 |
| 2. Ohio R. | 1 | 2 | 24 | 8 | 5 | | | | | | 40 | 13.35 | 0.86 |
| 3. Lookout Cr. | | | | 3 | 7 | 5 | | | | | 15 | 15.13 | 0.74 |
| 4. Tennessee R. | | 2 | 15 | 11 | 2 | 1 | | | | | 31 | 13.52 | 0.85 |
| 5. Middle Miss. R. minor drainages | | 3 | 12 | 6 | 6 | | | | | | 27 | 13.56 | 0.97 |
| 6. St. Francis R. and White R. | | 5 | 20 | 8 | 10 | 1 | | | | | 44 | 13.59 | 1.04 |
| 7. Yazoo R. | 1 | 1 | 7 | 1 | | | | | | | 10 | 12.80 | 0.79 |
| 8. Red R. and lower Miss. R. embayment | | 3 | 27 | 7 | 14 | | | | | | 51 | 13.63 | 0.96 |
| 9. L. Pontchartrain | | 1 | 5 | 14 | 11 | | | | | | 31 | 14.13 | 0.81 |
| 10. Sabine L. and Calcasieu R. | | 1 | 13 | 4 | 4 | | | | | | 22 | 13.50 | 0.86 |
| 11. Galveston Bay | | | 8 | 6 | 4 | | | | | | 18 | 13.78 | 0.81 |
| 12. Brazos R. to Colorado R. | | | 6 | 8 | 16 | 1 | 1 | | | | 32 | 14.47 | 0.95 |
| 13. San Antonio R. to Rio Grande | | | 4 | 4 | 14 | 5 | 3 | 1 | | | 31 | 15.06 | 1.24 |
| 14. Pearl R. | | 2 | 9 | 2 | | | | | | | 13 | 13.00 | 0.58 |
| 15. Bay St. Louis to Biloxi Bay | | 4 | 16 | 9 | 8 | 1 | | | | | 38 | 13.63 | 1.02 |
| 16. Pascagoula R. and Escatawpa R. | | 2 | 7 | 3 | 1 | | | | | | 13 | 13.31 | 1.03 |
| 17. Coosa R. | | | 20 | 7 | 8 | 2 | 1 | | | | 38 | 13.87 | 1.09 |
| 18. Tallapoosa R. | | 1 | 13 | 3 | | | | | | | 17 | 13.12 | 0.49 |
| 19. Alabama R. | 2 | 0 | 17 | 8 | 5 | | | | | | 32 | 13.44 | 0.98 |
| 20. Tombigbee R. | | 3 | 6 | 3 | 10 | | | | | | 22 | 13.91 | 1.15 |
| 21. Mobile Bay tribs. | | 1 | 5 | 3 | 6 | | | | | | 15 | 13.93 | 1.03 |
| 22. Perdido Bay and minor coastal tribs. | | | 2 | 10 | 22 | 6 | 1 | | | | 41 | 14.85 | 0.82 |
| 23. Pensacola Bay | | | 5 | 16 | 43 | 13 | 3 | 0 | 1 | | 81 | 14.96 | 0.98 |
| 24. Choctawhatchee Bay and minor coastal tribs. | | 3 | 28 | 13 | 13 | 1 | 1 | | | | 59 | 13.73 | 1.03 |
| 25. St. Andrews Bay | | | | | 3 | 1 | 8 | 1 | | | 13 | 16.54 | 0.97 |
| 26. Chattahoochee R. | | | 3 | 2 | 10 | 2 | | | | | 17 | 14.65 | 0.93 |
| 27. Flint R. | | | | 3 | 3 | 3 | 0 | 1 | | | 10 | 15.30 | 1.25 |
| 28. Chipola R. and Apalachicola R. | | | | | 3 | 5 | 5 | 1 | | | 14 | 16.29 | 0.91 |
| 29. New R. to California Cr. | | | | 2 | 10 | 18 | 27 | 5 | 1 | | 63 | 16.41 | 1.01 |
| 30. Suwannee R. | | | | | 7 | 9 | 12 | 1 | 1 | | 30 | 16.33 | 0.99 |
| 31. Waccasassa R. to Pithlachascotee R. | | | | | 5 | 4 | 5 | 2 | 2 | 1 | 19 | 16.74 | 1.52 |
| 32. Tampa Bay | | | | | | 4 | 9 | 3 | 1 | | 17 | 17.06 | 0.83 |
| 33. Peace R. and Myakka R. | | | | | 3 | 6 | 14 | 3 | 0 | 2 | 28 | 16.89 | 1.20 |
| 34. Everglades and south Florida drainages | | | | 1 | 10 | 11 | 25 | 4 | 2 | | 53 | 16.51 | 1.07 |
| 35. St. Johns R. and St. Marys R. | | | | | 6 | 12 | 21 | 1 | | | 40 | 16.43 | 0.78 |
| 36. Satilla R. | | | | 2 | 8 | 5 | 1 | | | | 16 | 15.31 | 0.79 |
| 37. Altamaha R. | | | | | 7 | 8 | 10 | 3 | 1 | | 29 | 16.41 | 1.09 |
| 38. Ogeechee R. to Edisto R. | | | | 1 | 36 | 18 | 17 | 1 | | | 75 | 15.69 | 0.92 |
| 39. Cooper R. to Cape Fear R. | | | | 1 | 18 | 11 | 12 | 1 | 1 | | 44 | 15.93 | 1.04 |

drainages in the Mississippi River Valley (with the exception of Lookout Creek, CD 3), west Gulf Slope, middle Gulf Slope, and Mobile Basin. Within these regions, Lookout Creek (CD 3) has the only positive score, the magnitude of which is comparable to those shown for the Florida panhandle (e.g., Pensacola Bay, CD 23). The Tennessee River (CD 4) has the lowest score (-142) in the Mississippi River Valley; the remainder of the region (excluding Lookout Creek) has scores ranging from -132 in the Yazoo River (CD 7) to -23 in the Illinois River (CD 1). Within the west Gulf Slope, Sabine Lake-Calcasieu River (CD 10) and Galveston Bay (CD 11) have lower PC-I scores than the Brazos River-Colorado River (CD 12) and San Antonio River-Rio Grande

(CD 13) (-85 and -93 vs. -34 and -29, respectively). The Pearl River (CD 14) on the middle Gulf Slope has the lowest score observed in any region (-152). Within Mobile Basin, Mobile Bay (CD 21) has the highest PC-I score (-25); other scores ranged from -66 in the Tallapoosa River (CD 18) to -96 in the Alabama River (CD 19). A shift to positive values (i.e., high mean scale numbers) occurs east of Mobile Basin in the Florida panhandle (CD 22-28, except Chattahoochee River, CD 26), and positive scores are shown throughout peninsular Florida and the Atlantic Slope (CD 29-39). In the Florida panhandle the Chattahoochee River (CD 26) has the lowest and only negative score on PC-I (-21) and St. Andrews Bay (CD 29) the highest score (128). Combined

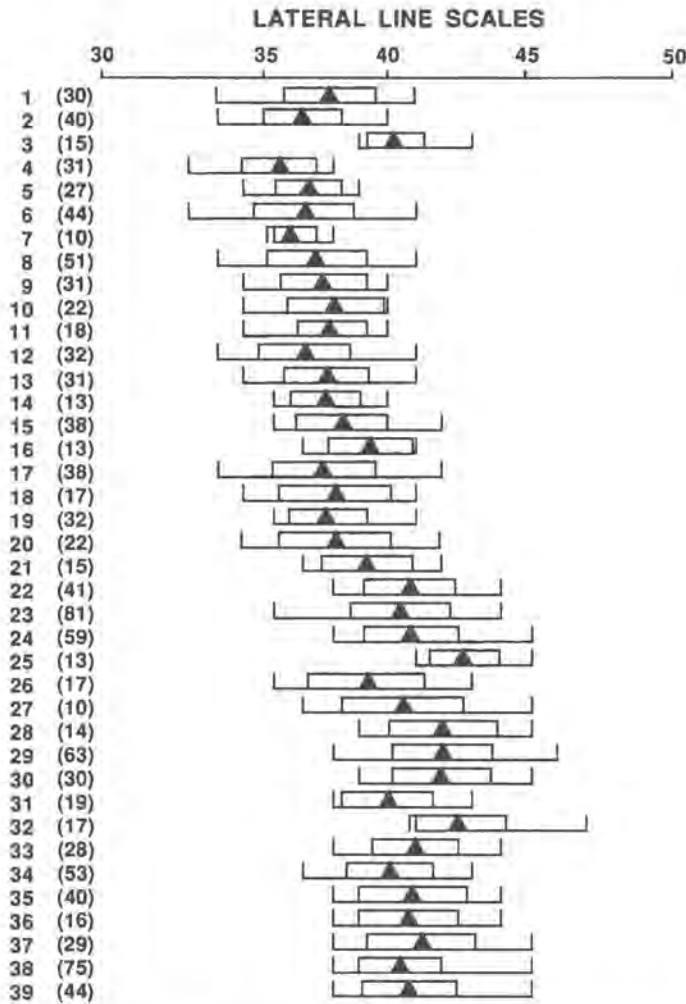


Figure 4. Means, ranges, and standard deviations of lateral-line scale counts of 1219 individuals of the *Lepomis punctatus* complex in 39 combined drainages. Mean counts are indicated by solid triangles, ranges by open boxes, and one standard deviation above and below the mean by enclosed boxes. Numbers to the far left are keyed to the combined drainages given in Table 3; parenthetical numbers indicate sample sizes.

drainages of the western Florida panhandle (i.e., Perdido Bay, Pensacola Bay, Choctawhatchee Bay, CD 22-24) all have lower positive scores (8 to 19) on PC-I relative to the scores (91 and 128) shown for the eastern Florida panhandle (i.e., St. Andrews Bay and the Chipola River-Apalachicola River, CD 25 and 28). Within the Apalachicola Bay system (CD 26-28) an increase in PC-I scores is shown among the Chattahoochee River, Flint River, and Chipola River-Apalachicola River (-21, 36, 91, respectively). Tampa Bay (CD 32) and Peace River-Myakka River (CD 33) have the highest scores on PC-I (207, 168, respectively) of any region, but all scores in peninsular Florida are relatively high with the lowest score (108) in the Everglades-south Florida drainages (CD 34). The St. Johns River-St. Marys River (CD 35)

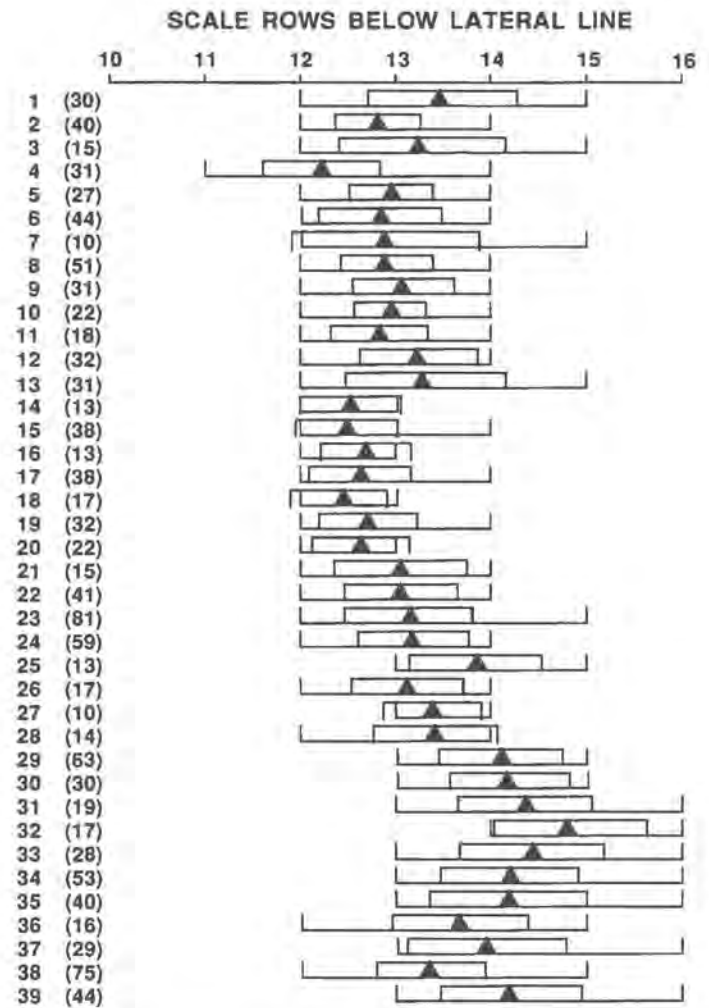


Figure 5. Means, ranges, and standard deviations of counts of scale rows below the lateral line of 1219 individuals of the *Lepomis punctatus* complex in 39 combined drainages. Mean counts are indicated by solid triangles, ranges by open boxes, and one standard deviation above and below the mean by enclosed boxes. Numbers to the far left are keyed to the combined drainages given in Table 3; parenthetical numbers indicate sample sizes.

and Altamaha River (CD 37) on the Atlantic Slope region have high positive scores comparable to values observed for peninsular Florida, but the remaining combined drainages of the region (Satilla River, Ogeechee River-Edisto River, Cooper River-Cape Fear River, CD 36, 38, and 39, respectively) have scores intermediate between those of the Florida panhandle and peninsular Florida regions. Scores within the Atlantic Slope and including Everglades-south Florida drainages (CD 34) also have a north-south alternation of high and low values.

An overview of the variation in meristic characters in the *L. punctatus* complex indicates that overlap in counts among the 39 combined drainages is considerable, but several concordant geographic patterns among scale counts are

apparent and supported by univariate and multivariate analyses. Modes (and usually means) (Tables 4-7; Figs. 4-8) and PC-I scores (Figs. 9-10) are lower in the Mississippi River Valley (CD 1-9), middle Gulf Slope (CD 14-17), west Gulf Slope (CD 10-13), and Mobile Basin (CD 17-21) than corresponding modes (and usually means) and scores in peninsular Florida and on the Atlantic Slope (CD 29-39). Concomitantly, the former regions (CD 1-21) generally have lower minimum and maximum counts than the latter (CD 29-39). In comparison, modes (and usually means) and PC-I scores are intermediate in value, fluctuate erratically, or increase gradually from west to east in the Florida panhandle. The range of counts in this area usually encompasses that shown for most combined drainages to the west and east

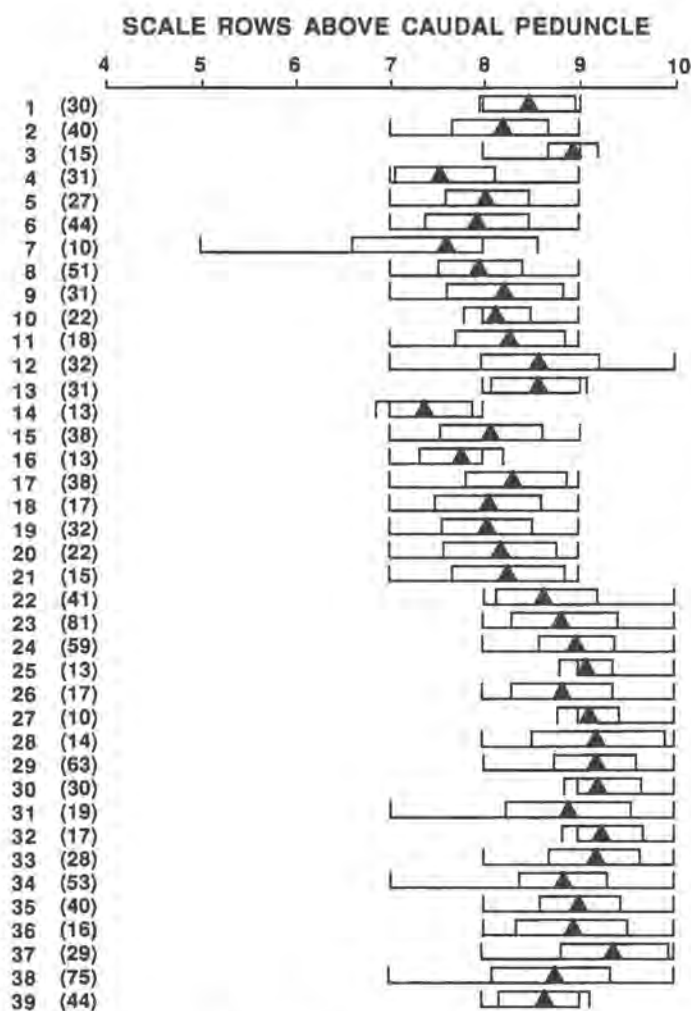


Figure 6. Means, ranges, and standard deviations of counts of scale rows above the caudal peduncle of 1219 individuals of the *Lepomis punctatus* complex in 39 combined drainages. Mean counts are indicated by solid triangles, ranges by open boxes, and one standard deviation above and below the mean by enclosed boxes. Numbers to the far left are keyed to the combined drainages given in Table 3; parenthetical numbers indicate sample sizes.

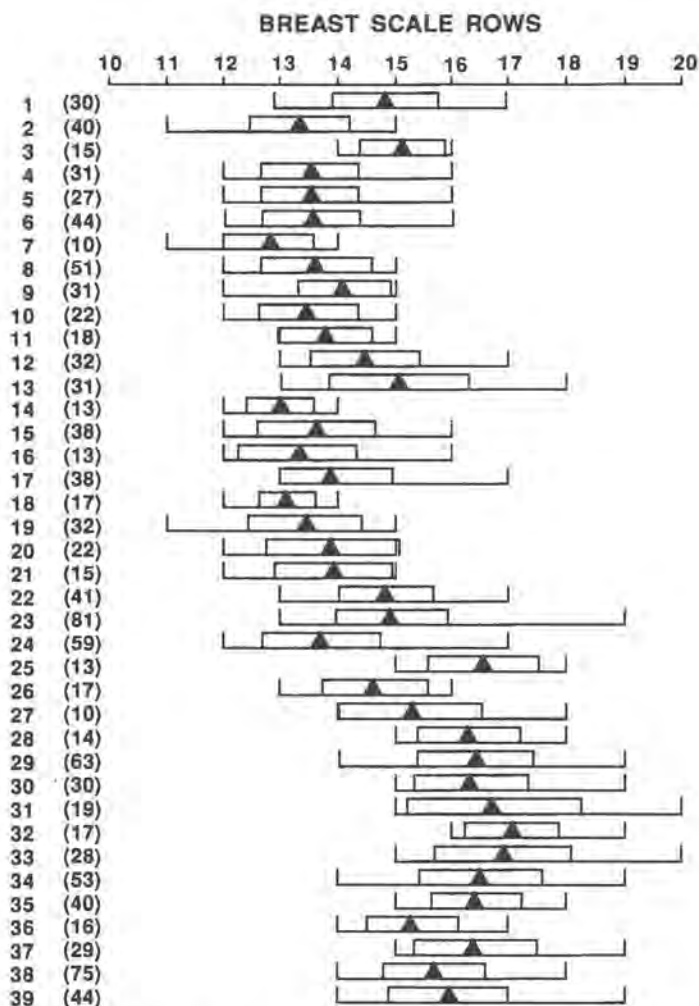


Figure 7. Means, ranges, and standard deviations of counts of breast scale rows of 1219 individuals of the *Lepomis punctatus* complex in 39 combined drainages. Mean counts are indicated by solid triangles, ranges by open boxes, and one standard deviation above and below the mean by enclosed boxes. Numbers to the far left are keyed to the combined drainages given in Table 3; parenthetical numbers indicate sample sizes.

(CD 1-21 and 29-39, respectively), or maximum and minimum values shift irregularly across the region. Within the Mississippi River Valley, Lookout Creek (CD 3) and the Illinois River (CD 1) generally have the highest means and modes and often have the highest maximum values in the region; the two also have the highest PC-I scores in the region. Several counts show a gradual increase in modes and means from east to west along the west Gulf Slope; PC-I scores reflect the increase (i.e., CD 10-11 vs CD 12 vs CD 13). Within the Apalachicola Bay system several modes and means and PC-I scores show a regular pattern of low values in the Chattahoochee River (CD 26), intermediate values in the Flint River (CD 27), and high values in the Chipola River-Apalachicola River (CD 28). The highest mean, modal,

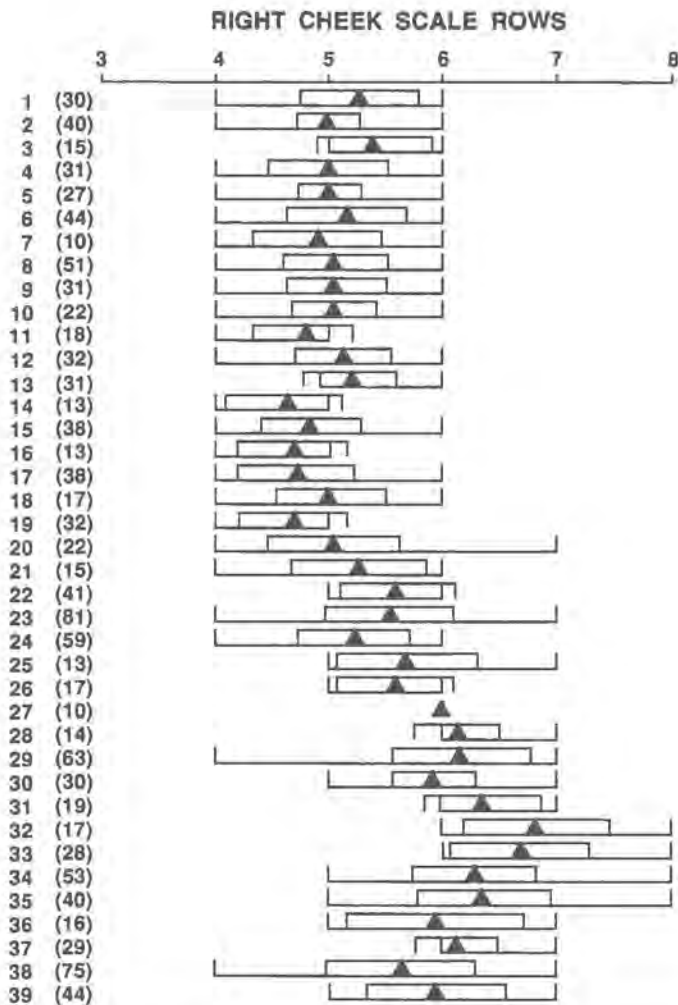


Figure 8. Means, ranges, and standard deviations of counts of right cheek scale rows of 1219 individuals of the *Lepomis punctatus* complex in 39 combined drainages. Mean counts are indicated by solid triangles, ranges by open boxes, and one standard deviation above and below the mean by enclosed boxes. Numbers to the far left are keyed to the combined drainages given in Table 3; parenthetical numbers indicate sample sizes.

maximum, and minimum values (and PC-I scores) among the 39 combined drainages consistently occur in Tampa Bay (CD 32) and Peace River-Myakka River (CD 33) in peninsular Florida with decreasing means, modes, and scores in combined drainages to the north, south, and east. Variation along the Atlantic Slope is shown primarily in alternating high and low means and PC-I scores. The St. Johns River-St. Marys River and the Altamaha River (CD 35 and 37, respectively) have consistently higher means than the intervening Satilla River and the Ogeechee River-Edisto River (CD 36 and 38, respectively). Means in the Cooper River-Cape Fear River are inconsistent with values both higher and lower than the Ogeechee River-Edisto River combined drainage to the south.

Table 8. Principal component loadings for 10 meristic variables on 1219 individuals of the *Lepomis punctatus* complex.

| Variable | Principal Component | |
|----------------------------------|---------------------|--------|
| | I | II |
| Lateral-line scales | 0.719 | 0.041 |
| Scale rows above lateral line | 0.727 | -0.112 |
| Scale rows below lateral line | 0.787 | -0.119 |
| Scale rows above caudal peduncle | 0.740 | -0.134 |
| Scale rows below caudal peduncle | 0.733 | -0.208 |
| Left cheek scale rows | 0.763 | -0.119 |
| Right cheek scale rows | 0.782 | -0.140 |
| Breast scale rows | 0.812 | -0.171 |
| Left pectoral-fin rays | 0.492 | 0.759 |
| Right pectoral-fin rays | 0.467 | 0.780 |
| % Total Variance | 50.6 | 13.4 |

Table 9. Principal component loadings for 10 meristic character means of the *Lepomis punctatus* complex in 39 combined drainages.

| Variable | Principal Component | |
|----------------------------------|---------------------|--------|
| | I | II |
| Lateral-line scales | 0.901 | 0.095 |
| Scale rows above lateral line | 0.973 | -0.040 |
| Scale rows below lateral line | 0.935 | -0.125 |
| Scale rows above caudal peduncle | 0.907 | -0.181 |
| Scale rows below caudal peduncle | 0.924 | -0.221 |
| Left cheek scale rows | 0.934 | -0.185 |
| Right cheek scale rows | 0.945 | -0.211 |
| Breast scale rows | 0.961 | -0.150 |
| Left pectoral-fin rays | 0.758 | 0.627 |
| Right pectoral-fin rays | 0.687 | 0.698 |
| % Total Variance | 80.5 | 10.9 |

SPOT INDICES.—The means of the size-adjusted spot indices for 39 combined drainages (Table 10) are geographically incongruent between indices scored from the body (SPALL, SPBLL, CPSPB, CPSPA) and indices scored on the head (CKSP, OPSP). The means of size-adjusted BDSP and HDSP (Table 10; Figs. 11-12) and the percentage of individuals examined in each drainage with scores of zero for BDSP or HDSP (Figs. 13-14) summarize the patterns expressed by size-adjusted means of individual indices comprising BDSP and HDSP. The BDSP means (Table 10; Fig. 11) and percentage of individuals with scores of zero on BDSP (Fig. 13) reveal two distinct groups: one with few or no body spots in the Mississippi River Valley, middle and west Gulf Slopes, and Mobile Basin (CD 1-21) and a second with numerous body spots on most individuals in the Florida panhandle, peninsular Florida, and the Atlantic Slope (CD 22-39). An abrupt shift from low to high mean BDSP (and conversely, high to low percentage of individuals with scores

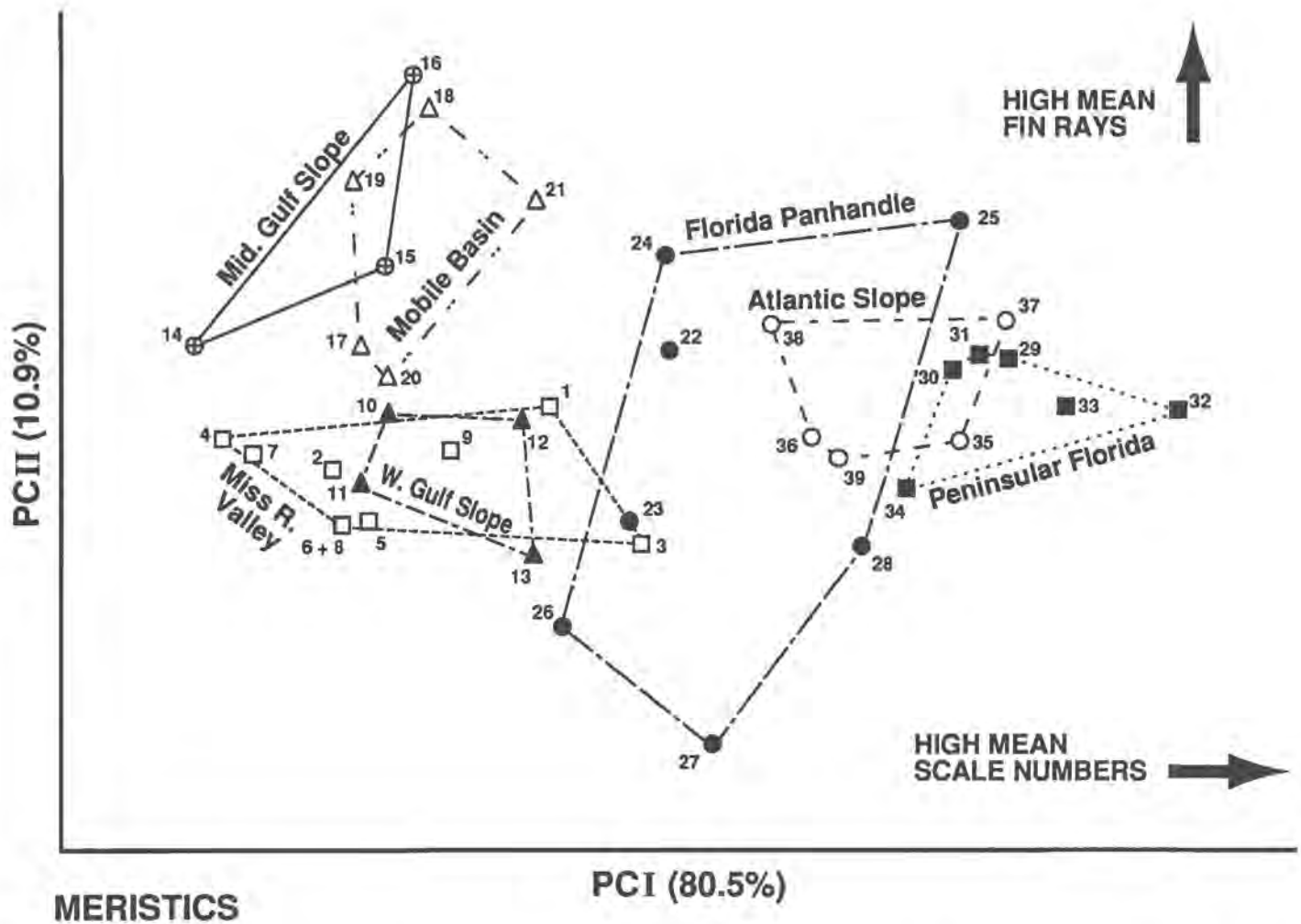


Figure 9. Meristic PCA axes I and II derived from mean meristic characters from each of 39 combined drainages (numbered as in Table 3), with polygons bounding combined drainages of seven geographic regions.

of zero on BDSP) occurs between Mobile Bay (CD 21) and Pensacola Bay (CD 23); Perdido Bay (CD 22) has intermediate values. Within the group with few body spots (CD 1-21), Lookout Creek (CD 3) and the Coosa River (CD 17) have the highest means and lowest percentage of individuals with scores of zero on BDSP, results influenced by the high proportion of SPALL and SPBL in each of these combined drainages (Table 10). Bay St. Louis-Biloxi Bay (CD 15) also has a relatively high mean for BDSP and a low percentage of individuals with scores of zero on BDSP, a result of high proportions of CPSPA and CPSPB (Table 10). Within the strongly spotted group (CD 22-39), Perdido Bay (CD 22) and the Flint River (CD 27) have relatively low means for BDSP and high percentages of individuals with scores of zero for BDSP.

Variation in the means of size-adjusted HDSP (Table 10; Fig. 12) and percentage of individuals with scores of zero for HDSP (Fig. 14) reveal three primary groups among 39 combined drainages; the groups are defined by low, intermediate, or high means for size-adjusted HDSP and

conversely, high, intermediate, or low percentages of individuals with scores of zero for HDSP. The lowest mean HDSP and highest percentage of individuals with scores of zero for HDSP include the Mississippi River Valley, west Gulf Slope, and the Pearl River (CD 1-14). The Illinois River (CD 1) is an exception with a relatively high mean, and most individuals show positive scores for HDSP. Intermediate means and percentages of individuals with scores of zero for HDSP are shown for most of the middle Gulf Slope (except Pearl River, CD 14), Mobile Basin, and Perdido Bay (CD 15-22); the lowest means and highest percentage of individuals with scores of zero for HDSP within this group are seen in the Alabama River (CD 19) and Perdido Bay (CD 22). The highest means and lowest percentages of individuals with scores of zero for HDSP occur in the Florida panhandle (except Perdido Bay, CD 22), peninsular Florida, and Atlantic Slope (CD 23-39). Within this group, the Flint River (CD 27) and Chipola River-Apalachicola River (CD 28) have the lowest means and highest percentages of individuals with scores of zero for HDSP.

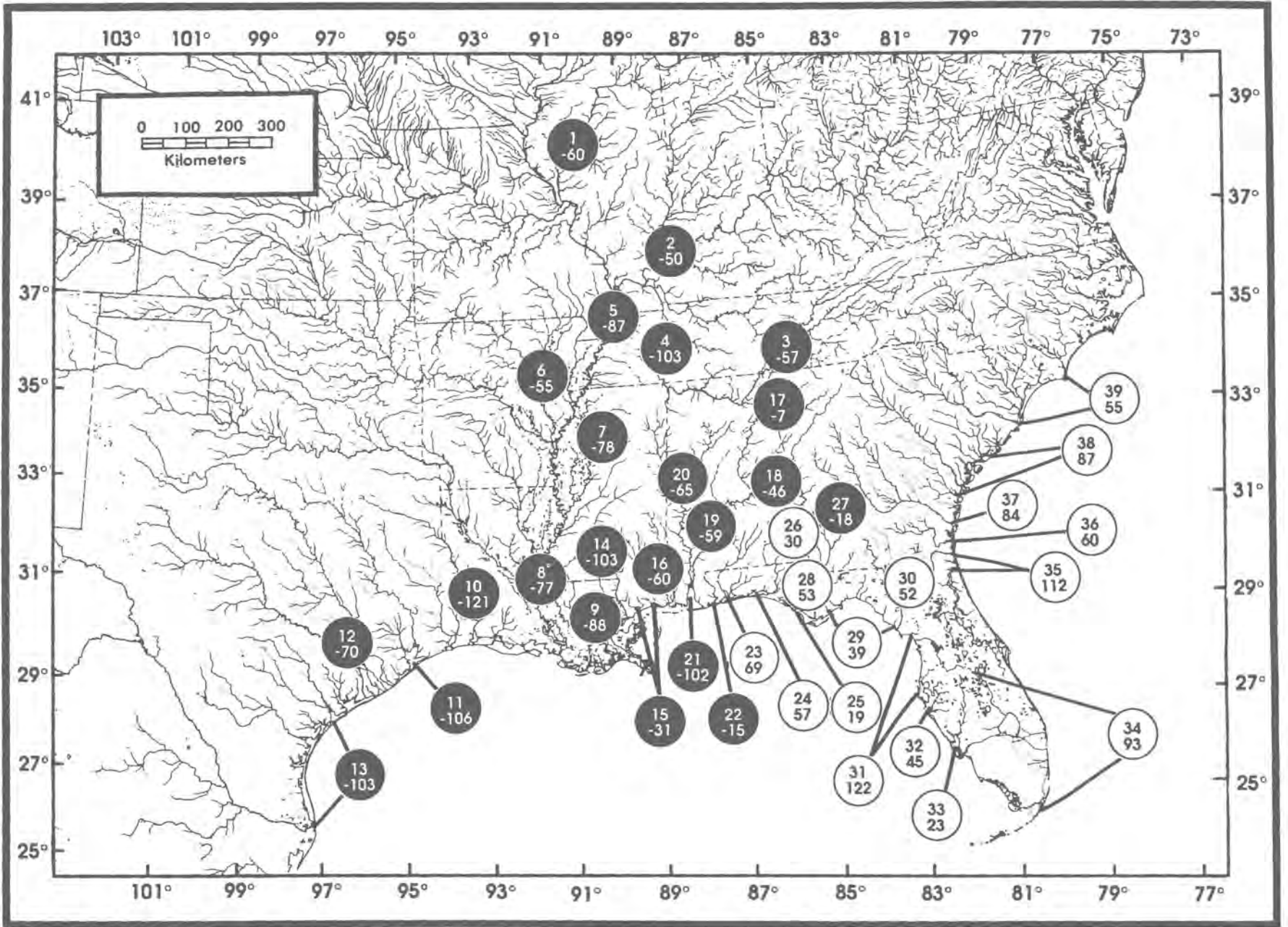


Figure 10. Geographic distribution, magnitude, and polarity of scores on meristic PCA axis I for the *Lepomis punctatus* complex in 39 combined drainages. The upper number in each circle indicates the combined drainage (as numbered in Table 3); the lower number is the score for that combined drainage on PCA axis I. Solid circles indicate negative scores, open circles positive scores.

Table 10. Sample sizes, means, and standard errors for size-adjusted spot indices for *Lepomis miniatus* (CD 1-2, 4-16, 18-21), *L. punctatus* (CD 29-39), and populations in presumed contact zones (CD 3, 17, 22-28) in 39 combined drainages. Means are calculated from the log number of spots plus one in thousandths of the log standard length ([log 'spot index' + 1] X [log SL⁻¹] x 1000). One standard error of the mean is given beneath each respective mean.

| Combined Drainage (CD) | n | Spot Index | | | | | | | |
|---|----|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | | SPALL | SPBLL | CPSPA | CPSPB | OPSP | CKSP | BDSP | HDSP |
| 1. Illinois R. | 30 | 31 14.9 | 77 28.8 | 14 9.9 | 13 9.4 | 30 36.5 | 25 36.0 | 101 33.1 | 404 38.9 |
| 2. Ohio R. | 40 | 0 0 | 20 14.3 | 4 3.9 | 9 9.1 | 140 33.2 | 129 28.8 | 27 16.7 | 19 41.3 |
| 3. Lookout Cr. | 15 | 94 37.5 | 199 47.9 | 0 0 | 35 23.8 | 173 51.8 | 80 31.1 | 252 57.1 | 202 56.9 |
| 4. Tennessee R. | 31 | 16 11.2 | 27 16.0 | 0 0 | 27 14.9 | 100 31.0 | 109 31.6 | 61 23.5 | 160 40.2 |
| 5. Middle Miss. R. minor drainages | 27 | 0 0 | 0 0 | 0 0 | 0 0 | 150 36.9 | 199 38.3 | 0 0 | 272 45.7 |
| 6. St. Francis and White River | 44 | 14 10.0 | 4 4.4 | 0 0 | 6 6.5 | 103 25.3 | 109 24.4 | 25 12.4 | 160 32.5 |
| 7. Yazoo R. | 10 | 0 0 | 0 0 | 36 35.9 | 36 35.9 | 107 54.6 | 57 30.3 | 50 50.4 | 124 63.3 |
| 8. Red R. and lower Miss. R. embayment | 51 | 22 11.0 | 8 7.8 | 12 8.5 | 8 5.8 | 105 23.7 | 45 14.8 | 40 16.3 | 126 26.5 |
| 9. L. Pontchartrain | 31 | 93 24.8 | 65 25.5 | 9 8.7 | 0 0 | 155 32.0 | 192 29.7 | 130 34.2 | 276 35.2 |
| 10. Sabine L. and Calcasieu R. | 22 | 0 0 | 0 0 | 0 0 | 0 0 | 64 29.6 | 54 22.5 | 0 0 | 87 37 |
| 11. Galveston Bay | 18 | 0 0 | 0 0 | 0 0 | 0 0 | 38 26.5 | 18 17.7 | 0 0 | 43 30.9 |
| 12. Brazos R. to Colorado R. | 32 | 12 11.6 | 10 10.0 | 0 0 | 8 8.2 | 105 30.8 | 111 30.1 | 23 16.8 | 160 40.8 |
| 13. San Antonio R. to Rio Grande | 31 | 0 0 | 0 0 | 9 8.8 | 0 0 | 74 23.7 | 61 26.9 | 9 8.7 | 101 33.8 |
| 14. Pearl R. | 13 | 20 19.7 | 0 0 | 0 0 | 0 0 | 19 19.0 | 25 16.8 | 20 19.7 | 37 26.3 |
| 15. Bay St. Louis to Biloxi Bay | 38 | 95 24.2 | 44 17.7 | 71 20.9 | 75 23.2 | 324 31.0 | 241 31.7 | 199 35.1 | 402 36.9 |
| 16. Pascagoula R. and Escatawpa R. | 13 | 35 25.5 | 19 18.8 | 0 0 | 0 0 | 285 70.4 | 231 58.0 | 42 31.9 | 365 78.0 |
| 17. Coosa R. | 38 | 149 26.4 | 151 28.6 | 40 16.0 | 75 23.2 | 347 35.8 | 231 35.1 | 261 39.7 | 406 42.9 |
| 18. Tallapoosa R. | 17 | 103 31.9 | 9 9.4 | 0 0 | 0 0 | 269 46.9 | 261 44.5 | 106 33.3 | 367 60.9 |
| 19. Alabama R. | 32 | 21 11.7 | 0 0 | 5 4.6 | 0 0 | 195 41.4 | 174 37.0 | 25 12.4 | 257 48.6 |
| 20. Tombigbee R. | 22 | 30 20.9 | 11 11.1 | 55 24.0 | 53 24.8 | 302 45.7 | 232 44.0 | 106 38.9 | 382 53.0 |
| 21. Mobile Bay tribs. | 15 | 41 28.2 | 16 16.4 | 25 24.9 | 16 16.4 | 311 53.7 | 213 49.5 | 74 41.4 | 370 64.4 |
| 22. Perdido Bay and minor coastal tribs. | 41 | 122 25.3 | 226 34.3 | 101 22.7 | 72 20.5 | 24 33.2 | 133 27.8 | 323 41.5 | 281 39.2 |
| 23. Pensacola Bay | 81 | 242 18.8 | 406 19.2 | 188 20.1 | 225 21.5 | 402 25.2 | 294 21.4 | 536 25.9 | 477 28.1 |
| 24. Choctawhatchee Bay and minor coastal tribs. | 59 | 253 21.1 | 366 21.8 | 163 22.8 | 203 26.0 | 487 21.2 | 341 22.6 | 531 23.1 | 564 24.8 |
| 25. St. Andrews Bay | 13 | 249 57.2 | 445 25.1 | 62 34.5 | 139 45.2 | 347 51.1 | 195 49.0 | 541 38.9 | 408 57.1 |
| 26. Chattahoochee R. | 17 | 188 42.4 | 228 42.4 | 147 51.1 | 202 45.2 | 476 54.6 | 235 67.6 | 429 50.2 | 521 62.8 |
| 27. Flint R. | 10 | 178 63.6 | 101 57.1 | 114 49.5 | 82 42.7 | 229 81.4 | 174 66.8 | 273 91.7 | 274 96.1 |
| 28. Chipola R. and Apalachicola R. | 14 | 282 50.1 | 333 60.5 | 226 48.9 | 240 47.5 | 378 79.8 | 330 71.9 | 525 67.6 | 449 94.9 |
| 29. New R. to California Cr. | 63 | 244 22.7 | 318 27.8 | 108 20.6 | 113 22.1 | 408 23.5 | 324 22.5 | 446 32.9 | 503 27.1 |
| 30. Suwannee R. | 30 | 225 34.3 | 314 39.4 | 187 36.3 | 214 36.7 | 365 43.7 | 274 41.8 | 478 47.5 | 441 50.2 |
| 31. Wacassassa R. to Pithlachascotee R. | 19 | 280 45.1 | 396 46.0 | 271 47.2 | 288 45.3 | 656 48.6 | 546 52.1 | 546 63.4 | 758 46.8 |

Table 10. cont.

| Combined Drainage (CD) | n | Spot Index | | | | | | | |
|--|----|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | | SPALL | SPBLL | CPSPA | CPSPB | OPSP | CKSP | BDSP | HDSP |
| 32. Tampa Bay | 17 | 91 34.3 | 311 41.1 | 97 40.1 | 245 49.8 | 494 28.2 | 361 32.6 | 451 49.1 | 586 28.8 |
| 33. Peace R. and Myakka R. | 28 | 157 29.3 | 279 36.2 | 167 32.6 | 174 35.0 | 401 47.1 | 205 41.5 | 396 51.8 | 439 52.7 |
| 34. Everglades and south Florida drainages | 53 | 248 24.0 | 393 24.4 | 217 26.1 | 260 23.4 | 473 24.7 | 342 25.9 | 563 28.3 | 559 26.4 |
| 35. St. Johns R. and St. Marys R. | 40 | 317 25.0 | 451 27.6 | 272 30.2 | 295 27.3 | 474 38.2 | 389 34.2 | 615 36.0 | 568 41.1 |
| 36. Satilla R. | 16 | 230 48.4 | 315 57.2 | 109 44.3 | 195 45.2 | 407 43.0 | 272 44.9 | 441 78.0 | 485 48.3 |
| 37. Altamaha R. | 29 | 375 21.3 | 428 31.4 | 246 29.9 | 271 31.0 | 392 28.5 | 271 36.2 | 630 29.2 | 467 35.4 |
| 38. Ogeechee R. to Edisto R. | 75 | 211 20.1 | 353 23.4 | 201 20.7 | 234 21.2 | 401 25.8 | 324 22.9 | 503 30.0 | 499 28.1 |
| 39. Cooper R. to Cape Fear R. | 44 | 212 25.1 | 328 27.4 | 199 23.4 | 215 23.8 | 410 32.4 | 335 28.8 | 487 34.8 | 521 30.3 |

Principal component scores for 1219 individuals on spot residuals were calculated for PC-I and PC-II and the individual scores averaged for each of the combined drainages (Fig. 15). The first two principal components account for 79.8% of the total variance (Table 11; Fig. 15). The loadings on PC-I indicate it is a general spotting component. The highest loadings occur on spot residuals from spot indices scored from the body. Consequently, combined drainages with high spot residuals are farther to the right (Fig. 15). The highest loadings on PC-II are associated with spot residuals from indices scored on the head (CKSP and OPSP). The bi-polarity of the loadings (head vs body spot indices) indicates combined drainages with high mean scores on PC-II have relatively high numbers of head spots compared to numbers of body spots. The 39 combined drainages (referenced by the geographic regions defined previously) can be divided into two primary groups based on polarity of scores on PC-I (Figs. 15-16): 1) the Mississippi River Valley, middle Gulf Slope, west Gulf Slope, and Mobile Basin (CD 1-21), which all have negative scores on PC-I, and 2) the Florida panhandle, peninsular Florida, and Atlantic Slope (CD 22-39), which with few exceptions have positive scores on PC-I. Within the first group (CD 1-21), the Coosa River (CD 17) has the highest score (-7; Fig. 16) and the Sabine River-Calcasieu River (CD 10) the lowest (-121). A shift from negative to positive scores (i.e., few to many spots) occurs from Perdido Bay (CD 22) to Pensacola Bay (CD 23) (-15 vs 69, respectively) in the Florida panhandle. The only other negative score (-18) in the second group (CD 22-39) is shown for the Flint River (CD 27). The highest scores on PC-I occur in peninsular Florida. Within the first group (CD 1-21), variation on PC-II (contrast in numbers of head vs body spots) separates the west Gulf Slope from Mobile Basin, but the Mississippi River Valley and middle Gulf Slope show overlap with these geographic regions (Fig. 16). The second

group of combined drainages show broad overlap on PC-II; Waccasassa River-Pithlachascotee River (CD 31) and Tampa Bay (CD 32) have the highest scores and the Altamaha River (CD 37) the lowest.

An overview of variation in spotting of the *L. punctatus* complex indicates concordant geographic patterns among combined drainages and geographic regions that are supported by univariate and multivariate analyses. The Mississippi River Valley, west Gulf Slope, middle Gulf Slope, and Mobile Basin (CD 1-21) show little or no spotting in contrast to strong spotting shown for the Florida panhandle, peninsular Florida, and Atlantic Slope (CD 22-39).

Scores of combined drainages on PC-I from the meristic data and on PC-I from the spot residuals are significantly correlated ($r = 0.81$; $P < 0.001$). Combined drainages of the Mississippi River Valley, west Gulf Slope, middle Gulf Slope, and Mobile Basin (CD 1-21) have low scores on both axes (i.e., low numbers of scales and spots; Fig. 17) in contrast to high scores shown for peninsular Florida and the Atlantic Slope (CD 29-39). The combined drainages of the Florida panhandle (especially, CD 22-24 and 26-27) have intermediate values.

BREEDING COLORATION.—Geographic variation in male breeding coloration generally is consistent with that observed for the body spot indices, as well as the meristic data, and consisted primarily of the presence or absence of red-orange on the body and opercles (Fig. 2). The red-orange color pattern is reasonably well illustrated in Forbes and Richardson (1920), Douglas (1974), and Robison and Buchanan (1988) and, except as noted, was present on breeding males in the Mississippi River Valley, west Gulf Slope, middle Gulf Slope, Mobile Basin, and Perdido Bay drainages (CD 1-22). The intensity and hue of the color varied slightly among specimens observed but most closely

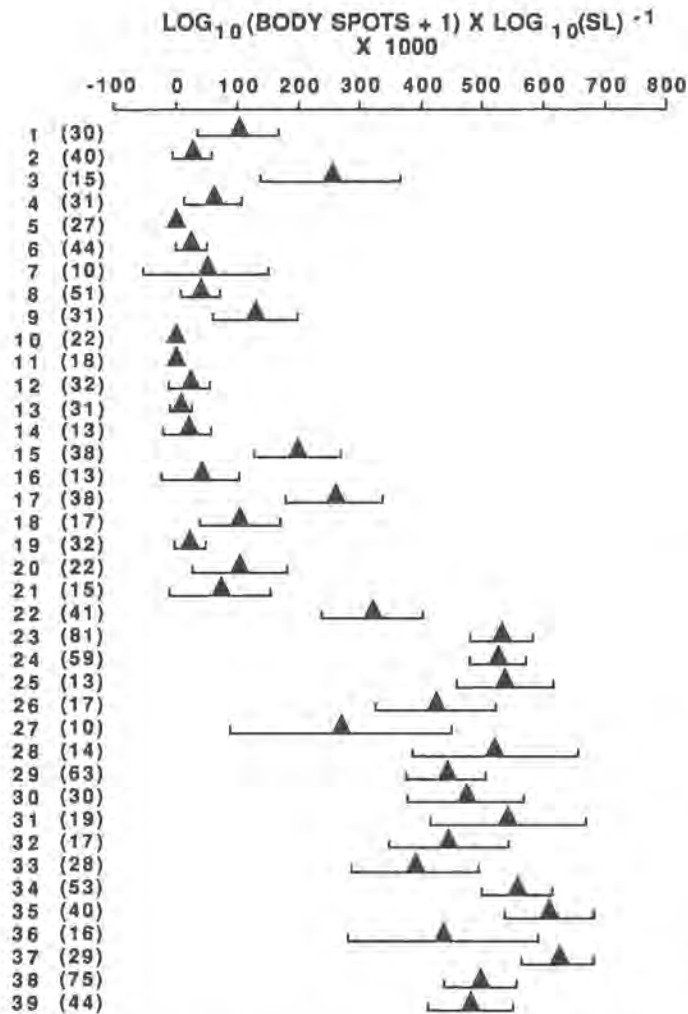


Figure 11. Means and standard errors of size-adjusted body spots of the *Lepomis punctatus* complex in 39 combined drainages. Means are indicated by solid triangles and two standard errors above and below the mean by horizontal lines. Numbers to the far left are keyed to the combined drainages given in Table 3; parenthetical numbers indicate sample sizes.

resembles 5pa, 5na, 6pa, or 6na in Jacobson (1948). The scales on the breast (isthmus to pelvic fins) and belly (pelvic fins to anal fin origin) vary from solid red-orange to red-orange on the posterior half to three-fourths of the exposed scale with a light cream or white area at the anterior scale base. The scale centers on the sides of the body (belly to one or two rows below the lateral line) are red-orange like the breast and belly, but the dorsal and ventral margins and often the anterior base of the scales are darkly and usually uniformly pigmented. The red-orange on each scale forms a roughly triangular area (pale in preservative) with an anteriorly directed, truncated apex. The overall effect is that of a horizontal chain of red-orange triangular spots alternating with horizontal bands of dark pigment. Smith-Vaniz (1968) illustrates the resultant pattern in a preserved speci-

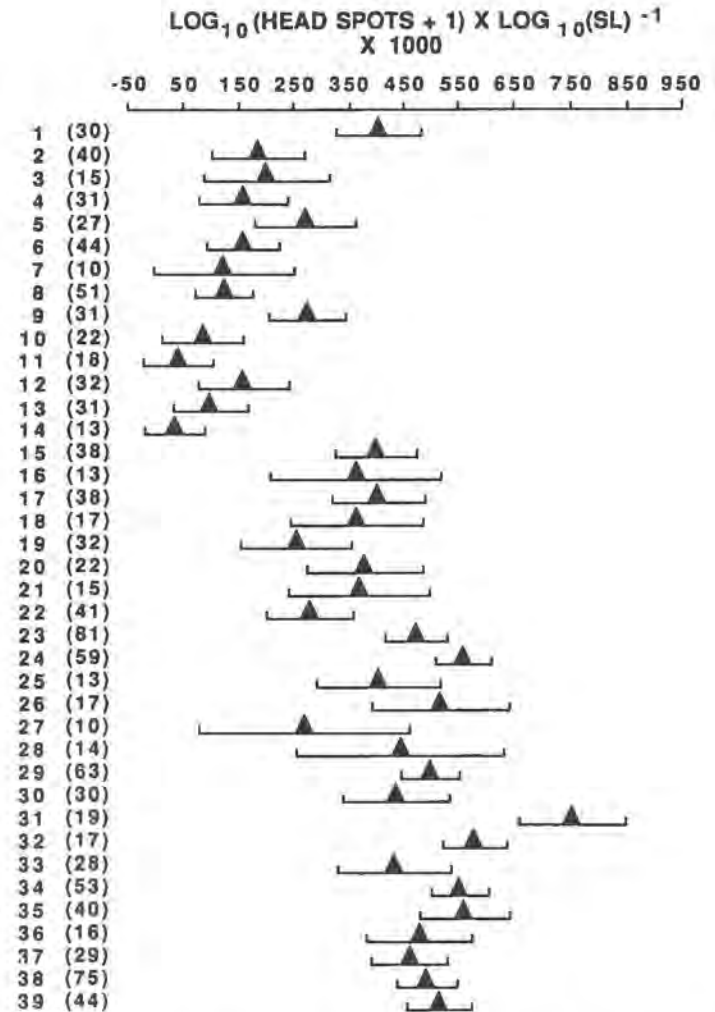


Figure 12. Means and standard errors of size-adjusted head spots of 1219 individuals of the *Lepomis punctatus* complex in 39 combined drainages. Means are indicated by solid triangles and two standard errors above and below the mean by horizontal lines. Numbers to the far left are keyed to the combined drainages given in Table 3; parenthetical numbers indicate sample sizes.

men. The red-orange rows are most intense at the level of the pectoral fin and gradually decrease in intensity dorsally and posteriorly towards the lateral line and caudal peduncle, respectively. Within these geographic regions, breeding males also show red-orange on the dorsal margin of the opercular tab that continues anteriorly and slightly ventrally to form a blotch of red-orange below the mid-dorsal margin of the opercle. An intense red-orange, quadrate-shaped area about 3 scale rows wide and 4 scale rows high is present above and slightly anterior to the tab. This area appears pale in preservative and resembles an abraded patch of scales. Specimens from Lookout Creek, collected in early August, had no red-orange coloration, but I am uncertain if they were post-spawning individuals or do not develop colors similar to other males in the Mississippi River Valley. Only one fresh

breeding male from the Coosa River drainage was examined, and although color was present on the breast, belly, and sides as noted above, the color was orange-yellow and most closely resembled color 3pa or 3na in Jacobson (1948). A color transparency of an individual collected in February (provided by D. A. Etnier) had a red-orange breast and belly but no red-orange on the sides. I am uncertain if these individuals are representative of typical breeding colors in Coosa River males.

With the exception of Perdido Bay, breeding males examined within the Florida panhandle, peninsular Florida, and Atlantic Slope drainages do not have horizontal rows of red-orange spots on the sides of the body (Fig. 2). Scales on the sides of the body generally have a bluish- to reddish-purple cast on an olivaceous background and resemble nonbreeding individuals to the west. The scale centers may be uniformly pigmented or paler than the scale margins. The latter condition is prevalent on the first five scale rows below the lateral line. The anterior scale base usually has a distinct, dark punctation, as described in Methods and Swift et al. (1977). Breeding coloration of the breast and belly is variable within these regions, but red-orange was not seen on any

specimens east of Perdido Bay. Typically, specimens were butterscotch yellow on the breast and anterior portion of the belly, colors most closely resembling 3pa, 3na, 3la, or 3nc in Jacobson (1948). Males freshly caught in May from the Aucilla, Steinhatchee, and Suwannee rivers had pinkish-orange and light yellow-orange (6ia and 4ia in Jacobson, 1948, respectively) breasts that faded posteriorly and dorsally on the belly to purplish. A color transparency (provided by F. C. Rohde) of an aquarium-held specimen from North Carolina has a few scale-rows on the breast and belly with a wash of yellow-orange (close to 4pa in Jacobson, 1948). Darkly pigmented breeding males often had a poorly defined pale area (most noticeable after preservation) above the opercular tab similar in color to the breast. The dorsal and ventral margins of the opercular tab were usually white or slightly tinged with yellow, but a large specimen from the Steinhatchee River had a pinkish-orange dorsal margin which continued anteriorly as a wash of pinkish-orange on the opercle. Although my personal observations of fresh breeding males were limited on the Atlantic Slope, colleagues working in those drainages indicate breeding males lack red-orange on the breast, belly, and sides. Bailey et al. (1954) also noted

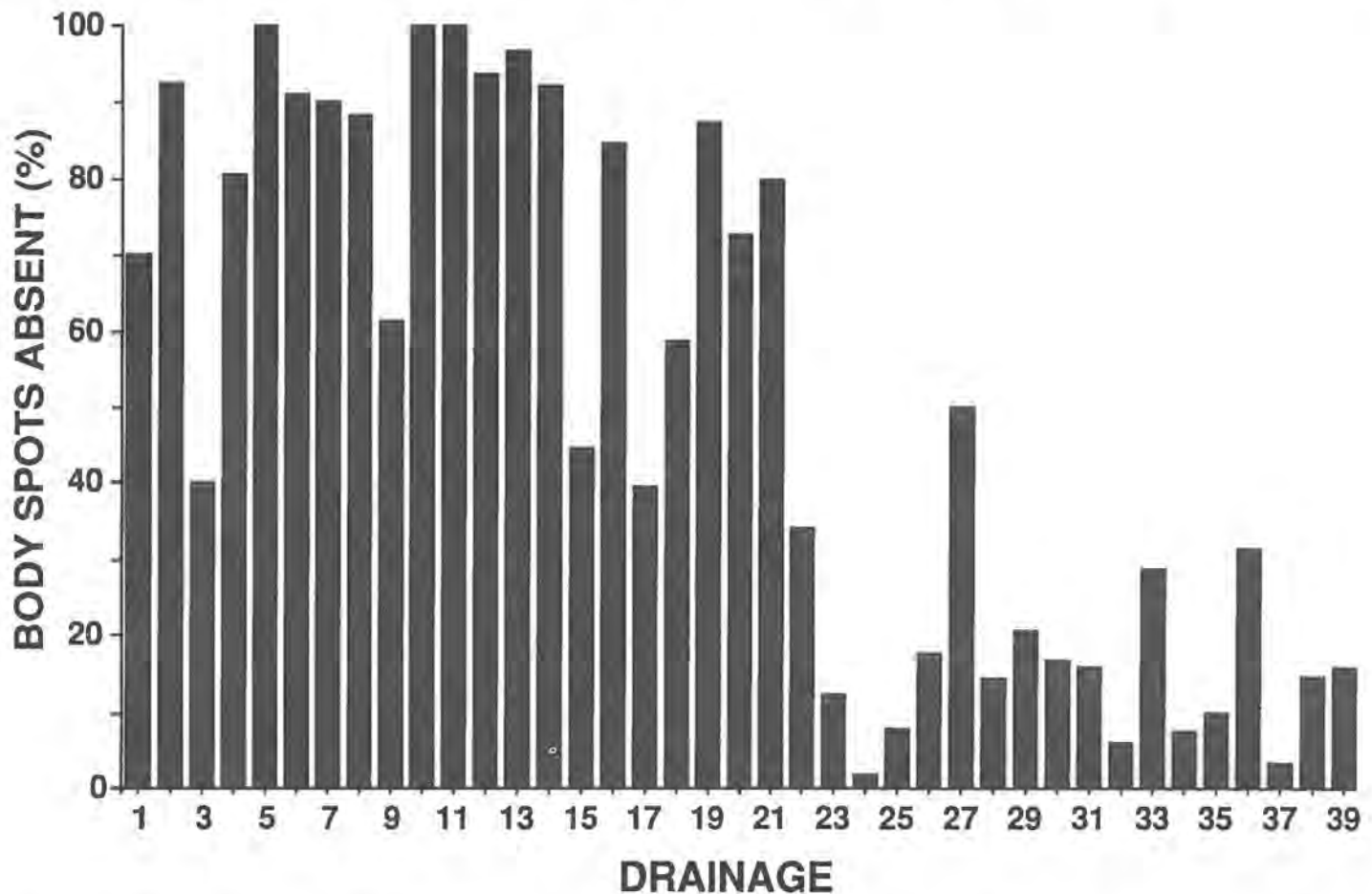


Figure 13. Percentage of individuals of the *Lepomis punctatus* complex examined in each of 39 combined drainages with body spots absent. Drainages on the abscissa are numbered as in Table 3.

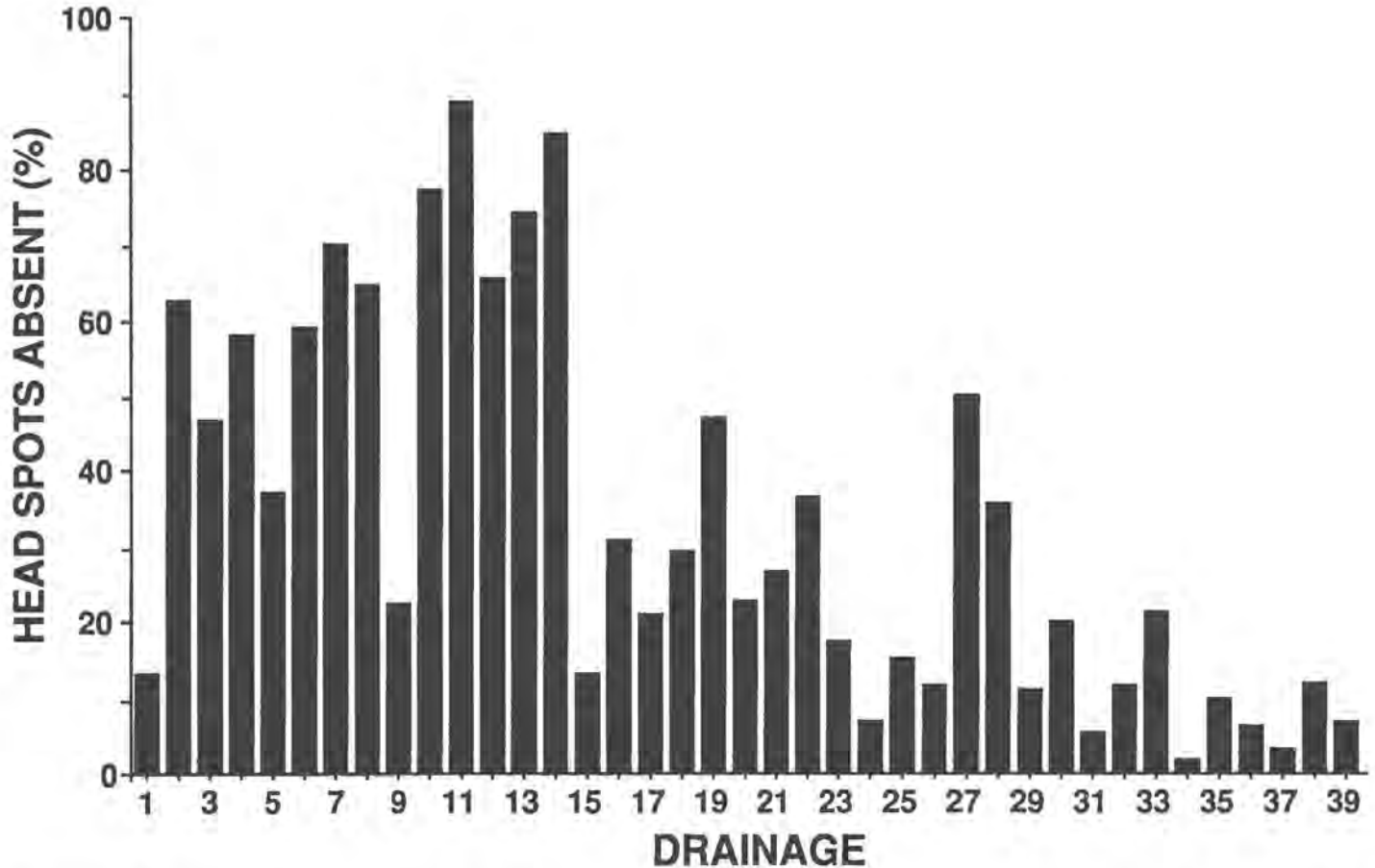


Figure 14. Percentage of individuals of the *Lepomis punctatus* complex examined in each of 39 combined drainages with head spots absent. Drainages on the abscissa are numbered as in Table 3.

Table 11. Principal component loadings for spot residuals on 1219 individuals of the *Lepomis punctatus* complex. Abbreviations for spot indices are given in Table 1.

| Spot Index | Principal Component | |
|------------------|---------------------|--------|
| | I | II |
| SPALL | 0.810 | -0.182 |
| SPBLL | 0.835 | -0.195 |
| CPSPA | 0.819 | -0.312 |
| CPSPB | 0.839 | -0.324 |
| OPSP | 0.794 | 0.505 |
| CKSP | 0.743 | 0.587 |
| % Total Variance | 65.2 | 14.6 |

the absence of horizontal rows of red spots on the sides of specimens in peninsular Florida and the Atlantic Slope drainages.

MORPHOMETRICS.—Sheared PCA of 20 males and 20 females revealed no differences between the sexes in the variables measured (Fig. 18). A sheared PCA was conducted on 348 individuals in 27 combined drainages (Table 3) to compute a within-group size component (Size) and two shape components (sheared PC-II and sheared PC-III) (Table 12).

The loadings on sheared PC-II contrast DISP1, DISP6, DISP10, ORBIT, LIPW, and H7-9 with L12-R12, L11-R11, and several posterior body depth measures (e.g., V5-6, V7-8, V7-6). A high mean or individual score on sheared PC-II indicates a relatively high spinous dorsal fin, large orbit, and thick lip in conjunction with a relatively thin and posteriorly elongate body. The loadings on sheared PC-III contrast DISP1, V5-6, and V5-8 with LIPW, H8-10, ORBIT, and to a lesser extent 1-R11 and 1-L11. Mean scores on sheared PC-II plotted against PC-III of each combined drainage (Fig. 19) show the Mississippi River Valley (CD 1, 2, 4, 6, 8, and 9, except Lookout Creek, CD 3), Mobile Basin (CD 17, 19, and 21), west Gulf Slope (CD 10, 11, 13), and Florida panhandle (CD 23, 24, 25, and 28) completely separated; the Atlantic Slope (CD 35, 37, 38, 39a, 39b), peninsular Florida (CD 29, 30, 33, and 34), and west Gulf Slope show overlap. Lookout Creek (CD 3) has a score (88) on sheared PC-II (Figs. 19-20) comparable to those of the Florida panhandle and peninsular Florida and the only positive score within the Mississippi River Valley and Mobile Basin. The remainder of the sheared PC-II scores (Figs. 19-20) in these regions range from extremely negative (-132, St. Francis River-White River, CD 6) to near zero (-4, Mobile Bay,

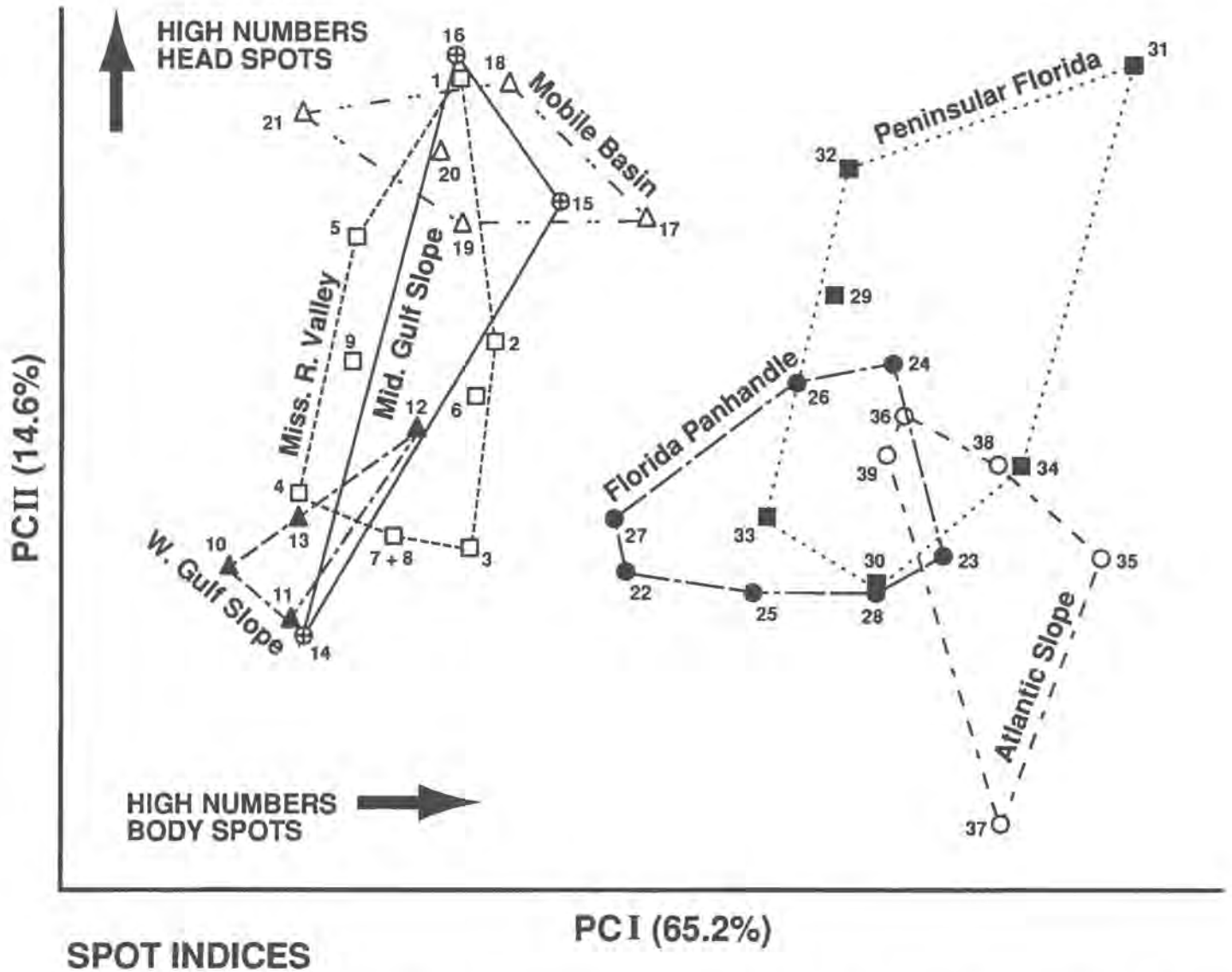


Figure 15. Average scores on PCA axes I and II for spot residuals of individuals of the *Lepomis punctatus* complex from each of 39 combined drainages (numbered as in Table 3), with polygons bounding combined drainages in seven geographic regions.

CD 21). East to west increases in sheared PC-II scores (from negative to positive values) are shown along the west Gulf Slope (CD 10, 11, 13); a similar south to north trend is shown along the Atlantic Slope (CD 35, 37, 38, 39a, 39b). A shift in scores from negative to positive is shown from Mobile Bay (CD 21) to Perdido Bay (CD 22). Most other PC-II scores in the Florida panhandle (CD 23, 24, and 28) have low positive values (except St. Andrews Bay, CD 25, with a relatively high score) in contrast to negative scores to the west (Mobile Basin and Mississippi River Valley) and high positive scores throughout most of peninsular Florida (except Kissimmee River, CD 34).

Means and ranges (as thousandths of SL) of morphometric variables with high loadings on shape components (sheared PC-II and PC-III) indicate considerable overlap

among geographic regions (Table 13). In some regions, such as the west Gulf Slope and Atlantic Slope, trends in means are not consistent with those observed in adjacent regions. Even so, several patterns shown among the means afford general support for the major trends indicated by those variables with the highest loadings on the sheared PCA (Table 12; Figs. 19-20). Mean proportional values contrast the short dorsal-fin spines (DISP1, DISP6, DISP10) in the Mississippi River Valley, west Gulf Slope, and Mobile Basin with long spines in peninsular Florida and to some extent the Atlantic Slope and Lookout Creek. The Mississippi River Valley, Mobile Basin, and Atlantic Slope have low means for ORBIT and caudal peduncle lengths (H7-9, H8-10) and high values for body width (L12-R12) and posterior body depths (V5-6, V5-8) (versus high mean ORBIT and caudal peduncle

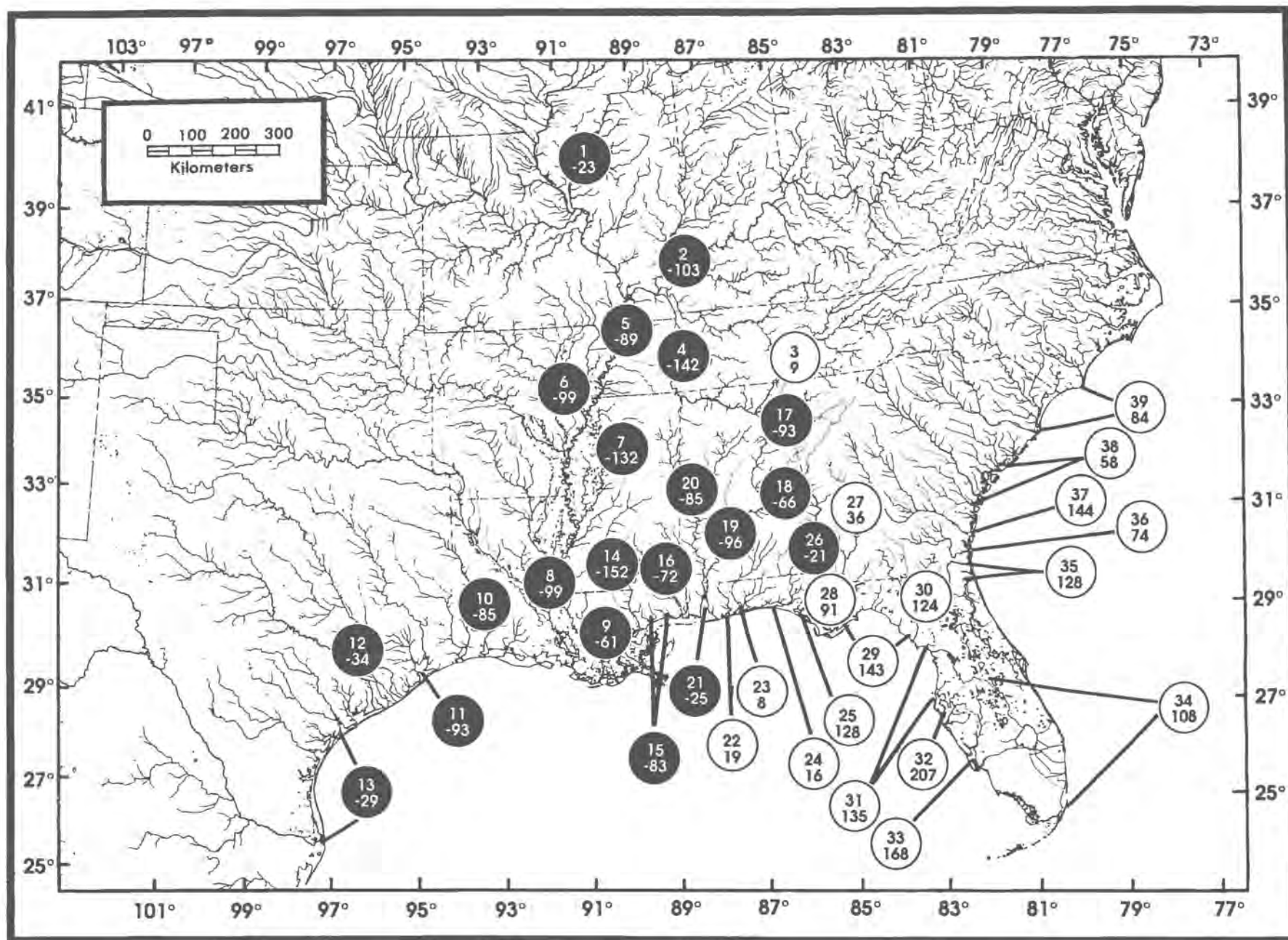


Figure 16. Geographic distribution, magnitude, and polarity of scores on spot residual PCA axis I for the *Lepomis punctatus* complex in 39 combined drainages. The upper number in each circle indicates the combined drainage (as numbered in Table 3); the lower number is the score for that combined drainage on PCA axis I. Solid circles indicate negative scores, open circles positive scores.

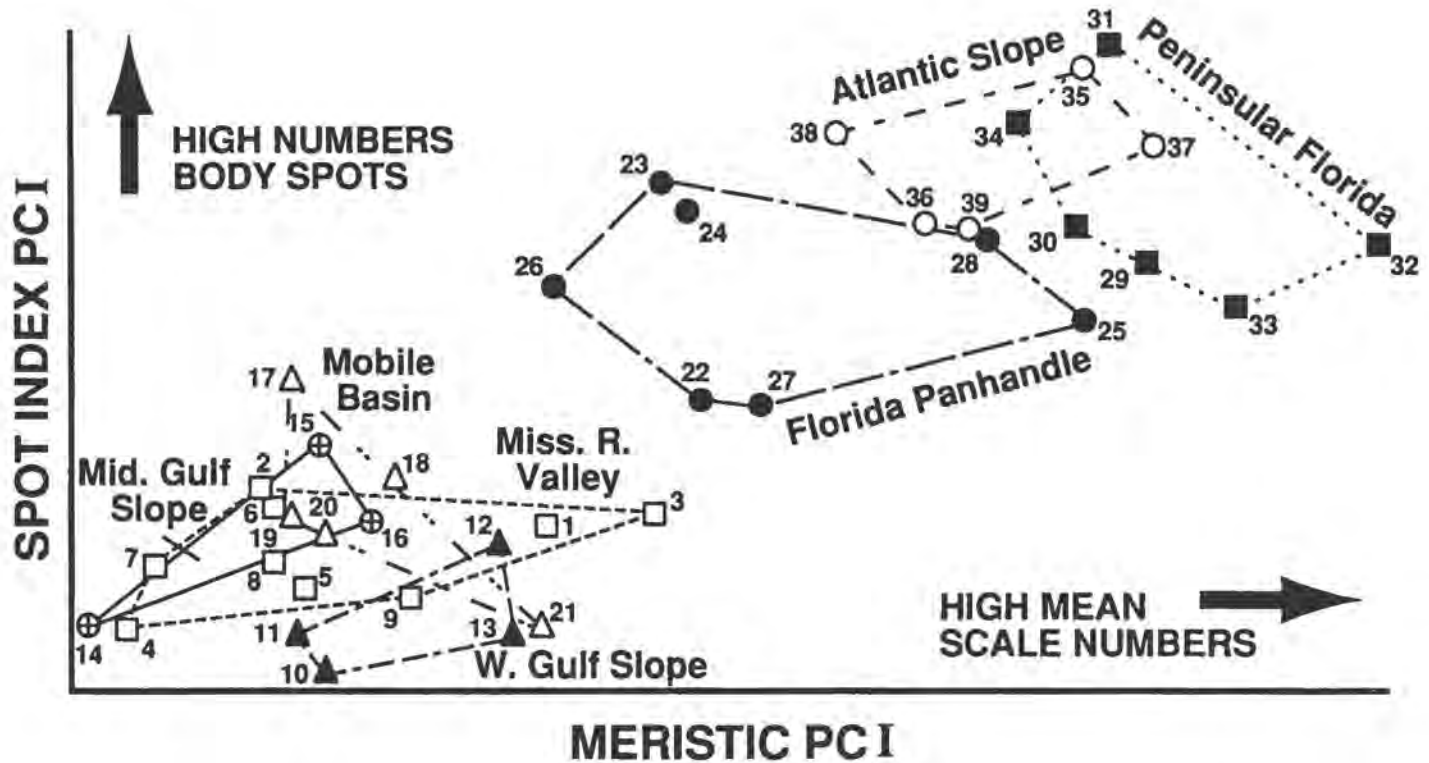


Figure 17. Scores on meristic PCA axis I and spot index PCA axis I for the *Lepomis punctatus* complex from each of 39 combined drainages (numbered as in Table 3), with polygons bounding combined drainages in seven geographic regions.

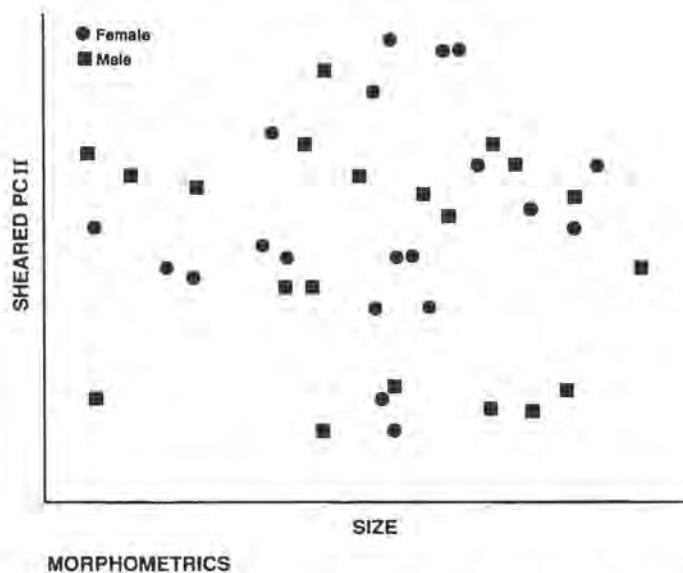


Figure 18. Sheared PCA axes I (Size) and II of 20 individuals each of males and females from a single population of the *Lepomis punctatus* complex.

length, and low mean posterior body depths and width in the Florida panhandle, peninsular Florida, and to some degree Lookout Creek). The west Gulf Slope has high mean ORBIT, low mean caudal peduncle lengths, low mean body width, and low mean posterior body depths and (with the

Mississippi River valley) has the shortest mean jaw lengths (1-L11, 1-R11). Mobile Basin has high means for LIPW and body width (L12-R12); the Mississippi River Valley low mean LIPW and relatively high mean body width; and Lookout Creek, Florida panhandle, and peninsular Florida high mean LIPW and low mean body width.

Although the range of values shows overlap, means of the ratio of the length to width of the longest gill raker by geographic region (Table 14) and for each combined drainage (Fig. 21) are lowest (<3.40) for the Mississippi River Valley (CD 1-9), middle Gulf Slope (CD 14-16), Mobile Basin (CD 17-21), and (with the exception of Galveston Bay, CD 11) the west Gulf Slope (CD 10-13). Lookout Creek (CD 3) has the highest mean ratio (3.36) in the Mississippi River Valley and middle Gulf Slope and the Illinois River (CD 1) the lowest (2.61; Fig. 21). On the west Gulf Slope (CD 10-13), Galveston Bay (CD 11) has the highest mean ratio (3.66) and San Antonio River-Rio Grande (CD 13) the lowest (2.55). Mean ratios in Mobile Basin range from 2.64 in the Tallapoosa River (CD 18) to 3.05 in Mobile Bay (CD 21). In the Florida panhandle, most combined drainages have means >3.40 , except Pensacola Bay (CD 23) and Choctawhatchee Bay (CD 24) with means of 3.04 and 3.06, respectively. Among combined drainages of peninsular Florida (CD 29-34) and the Atlantic Slope (CD 35-39), mean ratios are consistently >3.70 and range from 3.72 in the Suwannee River (CD 30) to 4.89 in the Satilla River (CD 36).

Table 12. Sheared principal component loadings for 40 morphometric variables on 348 specimens of the *Lepomis punctatus* complex in 27 combined drainages. Abbreviations are given in Table 2.

| Measurement | Size | Sheared PC-II | Sheared PC-III |
|-------------|-------|---------------|----------------|
| SL | 0.148 | 0.009 | -0.017 |
| P1LN | 0.146 | 0.107 | -0.041 |
| P2LN | 0.152 | 0.040 | -0.012 |
| D2LN | 0.162 | -0.023 | -0.064 |
| ALN | 0.158 | -0.009 | 0.035 |
| DISP1 | 0.132 | 0.609 | 0.553 |
| DISP6 | 0.108 | 0.342 | 0.075 |
| DISP10 | 0.122 | 0.305 | -0.028 |
| HDLN | 0.152 | -0.015 | -0.057 |
| ORBIT | 0.110 | 0.228 | -0.181 |
| LIPW | 0.174 | 0.195 | -0.573 |
| I-R11 | 0.180 | 0.018 | -0.167 |
| R11-12 | 0.130 | 0.033 | 0.016 |
| R12-9 | 0.155 | -0.019 | -0.008 |
| I-L11 | 0.176 | 0.028 | -0.162 |
| L11-L12 | 0.130 | 0.083 | 0.002 |
| L12-9 | 0.154 | -0.014 | -0.008 |
| L12-R12 | 0.188 | -0.228 | 0.051 |
| L11-R11 | 0.210 | -0.185 | -0.141 |
| H1-2 | 0.138 | 0.085 | -0.150 |
| H2-4 | 0.153 | 0.020 | 0.011 |
| H4-6 | 0.170 | -0.072 | 0.134 |
| H6-8 | 0.169 | -0.125 | 0.047 |
| H8-10 | 0.144 | 0.134 | -0.198 |
| H1-3 | 0.146 | 0.023 | 0.032 |
| H3-5 | 0.168 | -0.090 | -0.015 |
| H5-7 | 0.165 | -0.085 | 0.091 |
| H7-9 | 0.140 | 0.175 | -0.122 |
| V1-4 | 0.148 | 0.035 | -0.026 |
| V3-2 | 0.158 | 0.001 | 0.044 |
| V3-4 | 0.171 | -0.098 | 0.113 |
| V3-6 | 0.170 | -0.119 | 0.103 |
| V5-4 | 0.173 | -0.109 | 0.134 |
| V5-6 | 0.177 | -0.163 | 0.178 |
| V5-8 | 0.169 | -0.127 | 0.171 |
| V7-6 | 0.176 | -0.130 | 0.112 |
| V7-8 | 0.173 | -0.138 | 0.091 |
| V7-10 | 0.152 | 0.002 | -0.025 |
| V9-8 | 0.150 | -0.001 | -0.040 |
| V9-10 | 0.176 | -0.101 | 0.069 |

Discussion

GEOGRAPHIC PATTERNS AND DIFFERENTIATION.—Patterns in geographic variation in the *L. punctatus* complex are congruent among most of the quasi-independent data sets analyzed. Major trends in geographic variation as expressed in multivariate scores and univariate means, modes, ranges, and frequency distributions can be summarized as follows: 1) character differentiation or categorical variation (*sensu* Thorpe, 1985) between western populations (Mississippi River Valley, middle Gulf Slope, west Gulf Slope, and Mobile Basin) and eastern populations

(peninsular Florida and the Atlantic Slope) vs relative character homogeneity within eastern and western populations; 2) coincidence of categorical variation “steps” (i.e., the bluff between a flat character valley that abuts a flat character plateau), discontinuous or discordant variation, character intermediacy, and character mosaics within the Florida panhandle drainages (Perdido Bay to the Apalachicola Basin); and 3) discontinuous and discordant variation in semi-isolated populations within major drainages which otherwise show relative homogeneity of characters among populations, especially the Lookout Creek populations in the Mississippi River Valley and to a lesser extent the Coosa River population in Mobile Basin.

The categorical variation between eastern and western populations indicates that two well-differentiated epiphenotypes (*sensu* Wiley, 1981) are subsumed under the name *L. punctatus*, supporting in part the initial findings of Bailey (1938). Differentiation is evident in and complementary among multivariate scores for the meristic and spot index data (Figs. 9-10 and 15-17); several univariate meristic characters (e.g., scale rows above the caudal peduncle, breast scale rows, cheek scale rows; Figs. 6-8 and Tables 7); color of breeding males (presence or absence of red-orange pigment); spot indices scored from the body (e.g., SPBLL) (Figs. 11 and 13, Table 10); and ratio of length to width of the longest gill raker (Fig. 21, Table 14). The morphometric data coincide only in part with the patterns among other characters and separate some eastern from western populations, but broad overlap occurs among geographically distant regions (Table 13, Fig. 15-16). Given the differentiation between the epiphenotypes, it is not surprising that the distributions of mtDNA genotypes (Birmingham and Avise, 1986) and allozyme frequencies (Warren and Grady, in prep.) also reflect independent evolutionary histories for eastern and western populations.

CONTACT OR “HYBRID” ZONES.—There is no clear consensus on the definition of a hybrid zone (Littlejohn and Watson, 1985; Harrison and Rand, 1989), and its usage is irretrievably confused in the literature (Barton and Hewitt, 1985). The confusion stems in part from its use in describing interbreeding between putative species or subspecies and populations, narrow vs wide contact zones, clines involving few and many characters, and only clines maintained by a balance between dispersal and selection against hybrids. Many definitions are dependent upon an a priori taxonomic ranking of the populations under study or the presumed outcome of interactions between populations (Woodruff, 1973). Mayr (1963) equated hybrid belt with a zone of secondary intergradation; however, Endler (1977) demonstrated it is impossible to distinguish primary from secondary contact without historical evidence (Barton and Hewitt, 1985) or phylogenetic hypotheses indicating that interbreeding is between non-sister taxa (Rosen, 1978, 1979; Wiley, 1981). Endler (1977) defined a hybrid zone as a narrow belt in which individuals display greatly increased variability in fitness and

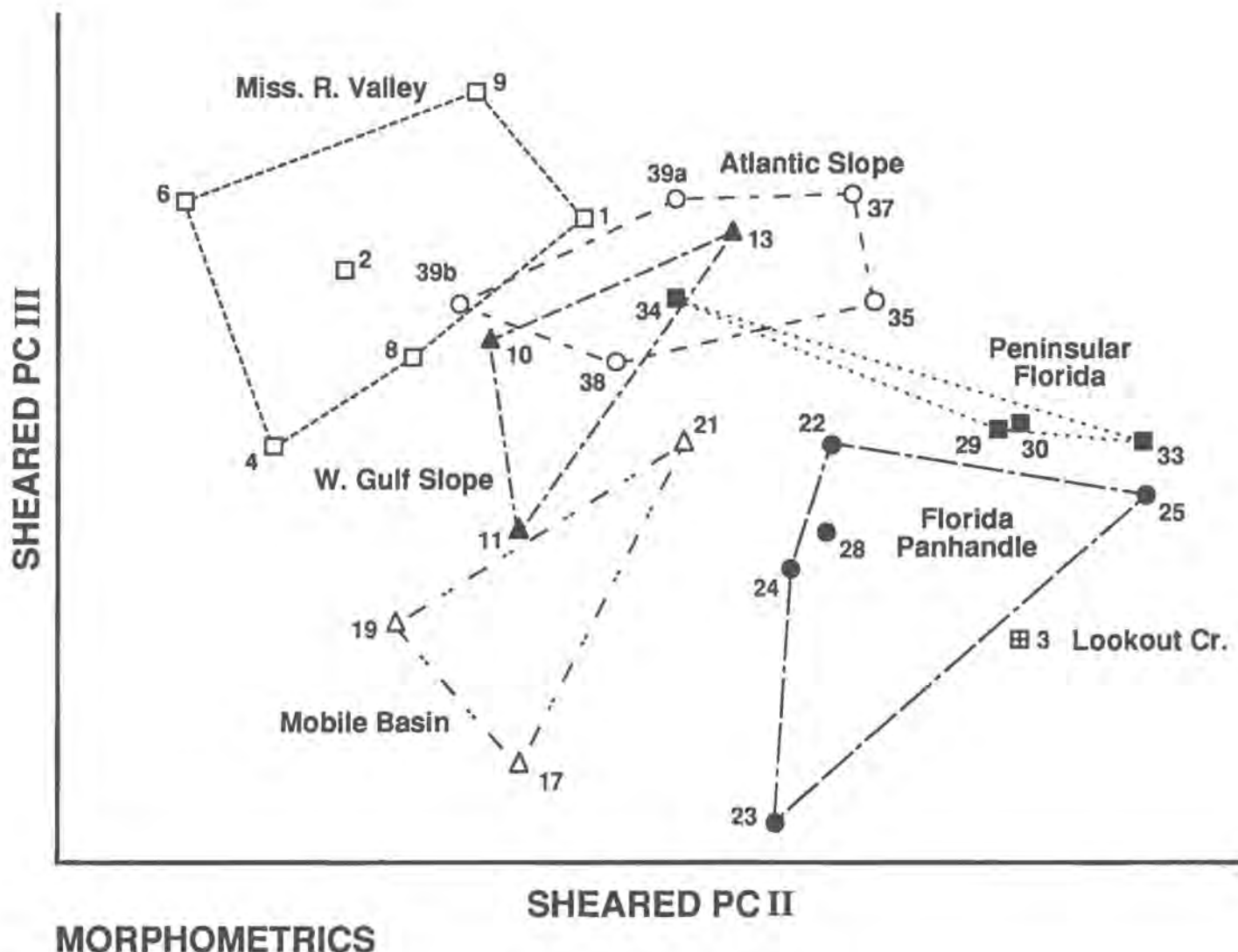


Figure 19. Average scores on sheared PCA axes II and III for individuals of the *Lepomis punctatus* complex from each of 27 combined drainages (numbered as in Table 3), with polygons bounding combined drainages in six geographic regions.

morphology, compared to that expected from random mixing, that separates distinct groups of relatively uniform sets of populations. Barton and Hewitt (1985) use hybrid zone simply to refer to a cline defined as "a gradient or set of gradients in morphology or gene frequency, at one or more loci." Thorpe (1985) suggested that "stepped clines" (i.e., a smooth unidirectional change of character score in space interrupted by a step) should be distinguished from categorical variation (i.e., a flat character valley abutting a flat character plateau).

Wiley (1981) subsumes zones of hybridization and intergradation into the "contact zone." The same populations may show both hybridization and intergradation depending on the characters analyzed (Wiley, 1981; Butlin, 1989): oligogenic and single-locus characters produce zones of overlap with hybridization (i.e., zones containing both parental types plus hybrid individuals), and multigenic and quantitative characters produce zones of intergradation or

"true" hybrid zones (i.e., zones where no parental forms are found, except at the edges of the zone). Butlin (1989) contends that true zones of overlap with hybridization probably only occur where hybrids are completely sterile.

Much of the character variation of populations of the Florida panhandle consists of the coincidence of multiple character "steps." Such "stepped" variation is often associated with the presence of genetic barriers (Barton and Hewitt, 1985). Multivariate (PC-I) scores from meristic, spot index, and morphometric data show abrupt, coincidental "stepped" variation in the Florida panhandle, with the steps occurring in Perdido Bay or Pensacola Bay (Figs. 10, 16, and 20). In addition, the red-orange rows of spots on the sides of breeding males, typical of the western epiphenotype, are absent east of Perdido Bay, and are replaced by the black-spotted pattern, typical of the eastern epiphenotype (Fig. 2).

Although interpretation of individual characters can be misleading in terms of general patterns of differentiation

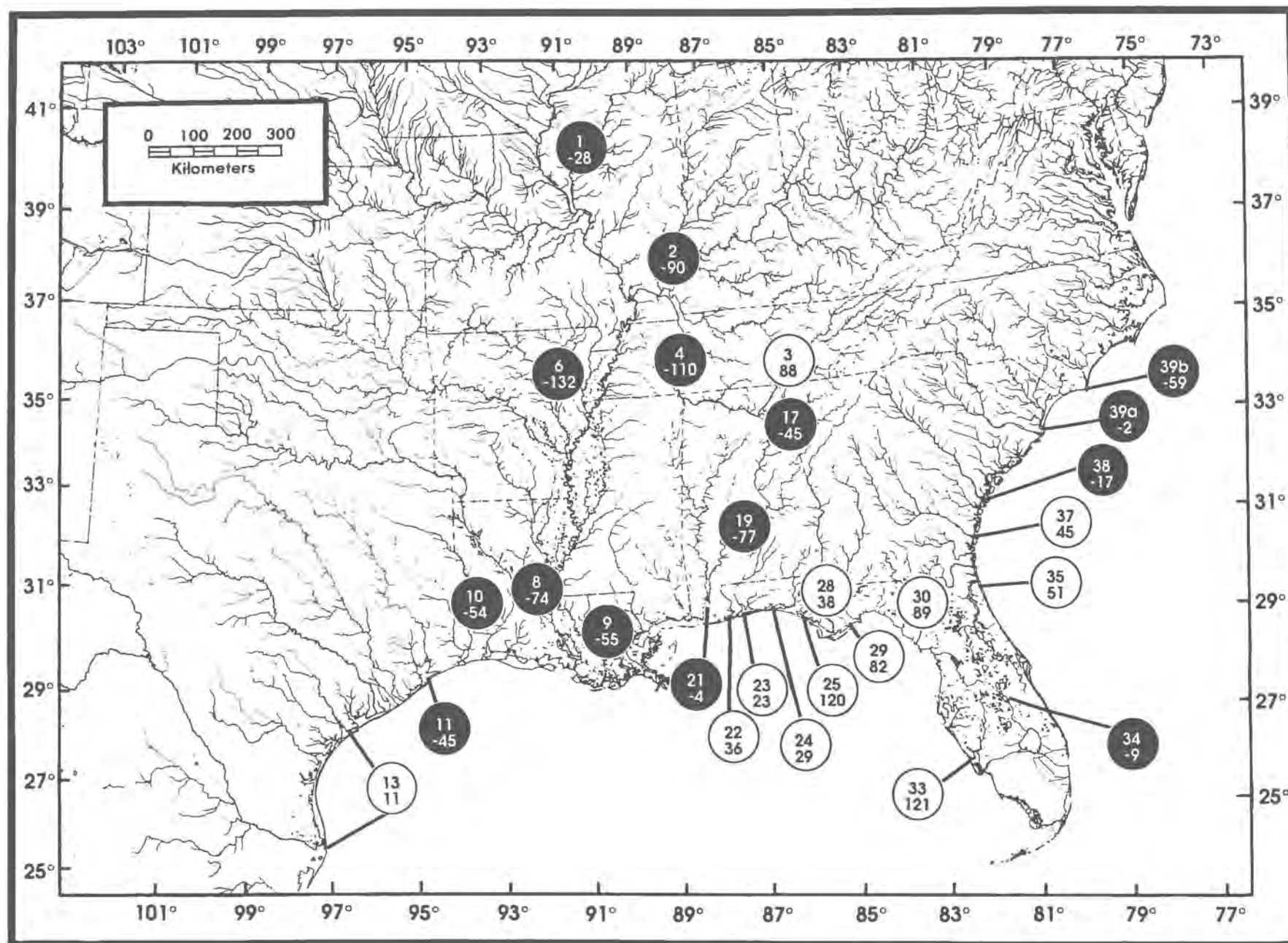


Figure 20. Geographic distribution, magnitude, and polarity of scores on sheared PCA axis II for the *Lepomis punctatus* complex in 27 combined drainages. The upper number in each circle indicates the combined drainage (as numbered in Table 3); the lower number is the score for that combined drainage on PCA axis II. Solid circles indicate negative scores, open circles positive scores.

Table 13. Means and ranges (in parentheses) of morphometric data for the *Lepomis punctatus* complex by geographic region, including standard length (SL) in millimeters and proportional measurements in thousandths of SL. Proportional measurements include only those variables with high absolute loadings on shape components (sheared PC-II and PC-III). Abbreviations for variables are given in Table 2. * = lowest mean(s); ** = highest mean(s).

| Drainage/Region | SL (mm) | DISP1 | DISP6 | DISP10 | ORBIT |
|-----------------------------------|------------------------|------------------|--------------------|--------------------|-------------------|
| Mississippi R. Valley (n = 82) | 76.7 (39.7-120.3) | *66 (43-92) | *160 (114-214) | *144 (103-175) | *95 (73-116) |
| Lookout Creek (n = 4) | 84.0 (66.9-104.5) | 73 (59-92) | 168 (146-187) | 160 (153-168) | **104 (96-114) |
| West Gulf Slope (n = 47) | *73.6 (40.5-123.7) | 69 (42-85) | 166 (129-201) | 150 (124-179) | 101 (87-130) |
| Mobile Basin (n = 29) | 78.2 (42.7-129.0) | *66 (45-83) | 161 (118-186) | 149 (110-175) | 99 (78-122) |
| Florida Panhandle (n = 54) | **89.4 (51.0-136.9) | 69 (53-87) | 164 (125-213) | 155 (116-186) | 102 (80-125) |
| Peninsular Florida (n = 69) | 85.9 (42.8-153.2) | **79 (59-103) | **177 (118-212) | **158 (124-187) | 102 (75-126) |
| Atlantic Slope (n = 63) | 81.1 (42.1-118.6) | 78 (46-111) | 168 (133-213) | 153 (117-189) | 98 (83-123) |

| Drainage/Region | LIPW | L12-R12 | L11-R11 | H7-9 | H8-10 |
|-----------------------|-----------------|--------------------|------------------|--------------------|--------------------|
| Mississippi R. Valley | *18 (13-24) | 156 (113-200) | 87 (65-130) | 171 (140-208) | 168 (140-275) |
| Lookout Creek | **22 (19-26) | 147 (144-151) | *82 (69-95) | 177 (165-186) | 172 (160-187) |
| West Gulf Slope | *18 (9-24) | 146 (111-183) | 85 (62-107) | 171 (144-198) | 172 (145-226) |
| Mobile Basin | **22 (18-26) | 160** (109-201) | **95 (67-132) | 173 (137-202) | 175 (143-197) |
| Florida Panhandle | 21 (16-27) | 146 (115-175) | 89 (63-127) | **183 (150-272) | **182 (155-262) |
| Peninsular Florida | 21 (15-26) | *144 (114-176) | 86 (65-150) | 182 (150-247) | 179 (154-215) |
| Atlantic Slope | 20 (14-25) | 153 (117-185) | 89 (67-112) | *169 (146-196) | *166 (134-188) |

| Drainage/Region | V5-6 | V5-8 | I-R11 | I-L11 |
|-----------------------|--------------------|--------------------|--------------------|-------------------|
| Mississippi R. Valley | 443 (372-549) | 373 (221-460) | 109 (89-136) | *107 (89-131) |
| Lookout Creek | *392 (385-408) | *346 (343-354) | **121 (116-125) | 114 (108-118) |
| West Gulf Slope | 407 (321-550) | 353 (180-395) | *107 (83-133) | *107 (83-132) |
| Mobile Basin | 422 (373-485) | 362 (320-407) | 115 (94-140) | 114 (94-137) |
| Florida Panhandle | 411 (361-455) | 353 (302-422) | 120 (94-149) | **118 (96-141) |
| Peninsular Florida | 413 (338-515) | 356 (296-407) | 111 (97-133) | 110 (87-125) |
| Atlantic Slope | **444 (366-532) | **377 (331-457) | 116 (95-167) | 113 (97-134) |

Table 14. Sample size (n), mean (x), standard error (SE), and range for ratios of the length to width of the longest gill raker for 437 individuals of the *Lepomis punctatus* complex in seven geographic regions.

| Region | n | Gill Raker Length/Width | | |
|-----------------------|-----|-------------------------|-------|-----------|
| | | \bar{x} | SE | Range |
| Mississippi R. Valley | 93 | 2.92 | 0.048 | 1.69-4.00 |
| West Gulf Slope | 22 | 3.09 | 0.143 | 1.35-4.20 |
| Middle Gulf Slope | 17 | 3.20 | 0.129 | 2.00-4.00 |
| Mobile Basin | 56 | 2.89 | 0.060 | 1.57-3.89 |
| Florida Panhandle | 105 | 3.29 | 0.066 | 1.28-5.00 |
| Peninsular Florida | 83 | 3.90 | 0.059 | 2.00-5.43 |
| Atlantic Slope | 61 | 3.94 | 0.073 | 2.75-5.67 |

(Thorpe, 1985), most univariate characters within the Florida panhandle show only slight deviation from multivariate patterns. For example, mean scale rows above the caudal peduncle (Fig. 6) form a relatively smooth, incremental gradient that extends from Perdido Bay to St. Andrews Bay; Pensacola Bay and Choctawhatchee Bay are at the approximate center of the cline. Other univariate characters within the Florida panhandle, such as scale rows below the lateral line (Fig. 5), are simply intermediate, rather than incremental, between those of the parental epiphenotypes, and usually show two unidirectional steps, one at Perdido Bay and another immediately east of the Apalachicola Basin. Discontinuity or character discordance, rather than incremental change or intermediacy, is another variational pattern among and within populations of the Florida panhandle. For example, erratic fluctuation across the panhandle drainages is shown for mean ratio of length to width of the longest gill raker (Fig. 21), mean breast scale rows (Fig. 7), and mean right cheek scale rows (Fig. 8). Within population discordance is shown in Pensacola Bay and Choctawhatchee Bay which have relatively low PC-I scores for mean numbers of scales (i.e., most like the western epiphenotype), but high scores for body spots (i.e., most like the eastern epiphenotype) (Fig. 17). These populations possess a mosaic of characters with presumptive origins in the parental epiphenotypes (e.g., Choctawhatchee Bay: low numbers of breast scale rows and right cheek scale rows relative to scale rows above the caudal peduncle and body spots). The discordant west-east pattern of modal shifts of right vs left cheek scale rows (Appendix A, Table A1) within the Florida panhandle is likely another manifestation of the segregation and recombination of the eastern and western parental genotypes within this region. Such variation may involve increased fluctuating asymmetry which is associated with developmental instability in hybrid populations in other centrarchids (Graham and Felley, 1985). The population in St. Andrews Bay consistently shows high multivariate scores or univariate means for the meristic, morphometric, and gill raker ratio data, suggesting a strong historical influence of the eastern epiphenotype that may be associated with the relative isolation of this small drainage from others (Swift et al., 1986).

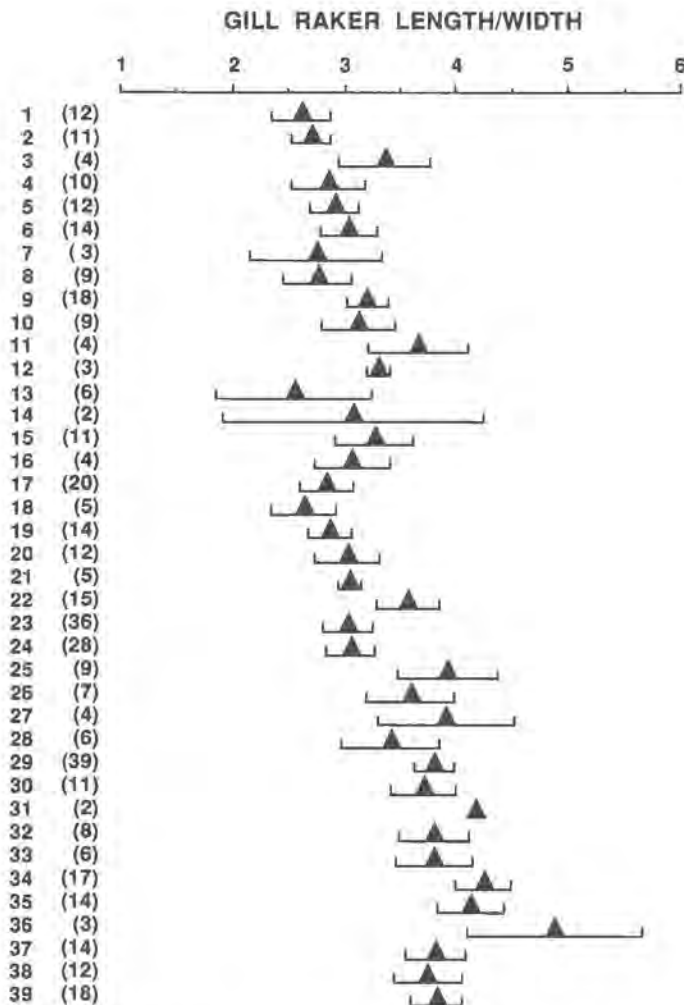


Figure 21. Means and standard errors of the ratio of length to width of the longest gill raker of the *Lepomis punctatus* complex in 39 combined drainages. Means are indicated by solid triangles and two standard errors above and below the mean by horizontal lines. Numbers to the far left are keyed to the combined drainages given in Table 3; parenthetical numbers indicate sample sizes.

The character variation observed within the Florida panhandle populations relative to the homogeneity displayed among those of each parental epiphenotype indicates a well-defined contact zone exists in the region. Given the "hybrid zone" produced by some characters and the "zone of intergradation" produced by others, I follow Wiley (1981) and simply refer to the region involved as a contact zone. Perdido Bay consistently delimits the western extent of the contact zone as manifested in "steps" for univariate and multivariate data, initiation of character intermediacy, and the eastern termination of the typical breeding color of western males. The eastern edge of the contact zone is judged to lie in the Apalachicola Basin (Chattahoochee, Flint, and Apalachicola rivers). The Apalachicola Basin is associated with the termination of intermediate values or clines for

meristic characters (e.g., scale rows below the lateral line or right cheek scale rows, respectively) and PC-I scores for the meristic and spot index data show discordance suggestive of influence of the western epiphenotype in the Chattahoochee River and Flint River populations (Figs. 10 and 16).

CONTACT ZONE DYNAMICS.—Birmingham and Avise (1986) found an east-west break in mtDNA genotypes of the *L. punctatus* complex with the Apalachicola River forming the easternmost limits of a phylogeographic clade extending west to the Calcasieu River, evidence which also supports recognition of the Apalachicola Basin as the eastern limit of the contact zone. Interestingly their results indicate the contact zone populations (i.e., east to Apalachicola Basin) have western mtDNA genotypes, but my data show considerable intermediacy in morphology in the contact zone, and populations east of Pensacola Bay are essentially monomorphic for GpiA^e, an allele diagnostic for the eastern epiphenotype (Warren and Grady, in prep.). In a "hybrid swarm" population between subspecies of *Lepomis macrochirus*, Avise et al. (1984a) found that mtDNA and allozyme genotypes of the subspecies were associated approximately at random. Marker allozyme frequencies and mtDNA genotypes were concordant within "pure" populations of both subspecies. It is possible that Birmingham and Avise (1986) simply missed the eastern mtDNA genotype in the contact zone, because of limited geographic coverage and small samples. Alternatively, the matriarchal transmission genetics of mtDNA versus that of characters mediated by the nuclear genome may be responsible for the observed discordance. Within contact zones, nonconcordant or directional (Ferris et al., 1983; Powell, 1983; Lamb and Avise, 1986) and concordant (Szymura et al., 1985; Birmingham and Avise, 1986) variation has been observed between mtDNA genotypes and allozyme markers. The mtDNA pattern in the contact zone described here is directional relative to color pattern of breeding males, but complements the observed influence of the western epiphenotype in meristic and spot index characters in the Apalachicola Basin (e.g., Flint and Chattahoochee rivers). The mtDNA pattern may be related to historical demographic influences (Avise et al., 1984a,b), but other factors such as mating behavior or differential dispersal rates of the sexes (Szymura et al., 1985; Lamb and Avise, 1986; Avise, 1989) may be implicated. Without detailed mapping, the microgeographic dynamics of mtDNA and other characters within the zone can not be resolved. It is apparent however that matriarchal lineages of the western mtDNA genotype are present as far east as the Apalachicola Basin, but the western patriarchal breeding color pattern stops much farther to the west in Perdido Bay.

In the apparent absence of an environmental transition or geographic barrier within the contact zone and the relative homogeneity displayed within each parental epiphenotype over a wide range of environmental conditions, the maintenance of the contact zone is not likely a result of adaptive differentiation along an environmental gradient or across

abrupt spatial changes in environment (Endler, 1977). This of course does not exclude these as factors in the formation of the zone. Likewise, a model invoking heterozygote or recombinant advantage in the particular environment of the contact zone (Moore, 1977) is not compelling. Admittedly, environmental gradients can be found in most areas of the zone (e.g., upstream to downstream increase in salinity in lower reaches of coastal drainages). The gradients, however, are likely gradual and widespread relative to the variation observed. In addition, both eastern and western epiphenotypes and contact zone populations share a common and similar environment in the vicinity of the contact zone along the Gulf Coast. Other possibilities accounting for the maintenance of the contact zone include selective equality of the epiphenotypes and their recombinants (i.e., neutral introgression) or selection against intermediate genotypes (Barton and Hewitt, 1985; Hewitt, 1989). In the case of neutrality, initially steep character gradients decline as a function of generation time since first contact and dispersal rate (Endler, 1977). Conversely, a contact zone involving heterozygote and recombinant disadvantage may be stable for long periods due to the balance between dispersal of the opposing parental epiphenotypes into the zone and selection against intermediate genotypes ("tension zones," Key, 1981); may form steep character gradients; and may act as a genetic barrier to gene flow at other loci (Barton and Hewitt, 1983, 1985; Hewitt, 1989). Avise and Smith (1974) concluded that alleles across several loci (and mtDNA genotypes, Avise et al., 1984a) in a contact zone between epiphenotypes of *Lepomis macrochirus* were behaving as neutral markers of intergradation but noted evidence of the possible influence of selection. In the present case, unambiguous determination of factors operating to maintain the contact zone is not possible with the data at hand, but the structure of the zone suggests several modes and intensities of selection may be operating depending on the particular character under consideration. For example, the abrupt shift in the breeding color of males is a "stepped" pattern often associated with a genetic barrier (Barton and Hewitt, 1983, 1985). If other less abrupt character gradients are considered, introgression may be interpreted as neutral (e.g., some meristic characters) or even directional (e.g., mtDNA genotype). Perhaps the most important aspects of the contact zone in terms of my objectives are: 1) it involves several character sets and is geographically well-defined; 2) it indicates incomplete reproductive isolation between the epiphenotypes; and 3) it implies separate evolutionary histories for the two epiphenotypes.

DISCORDANT POPULATIONS.—The population in Lookout Creek, a small southern tributary to the Tennessee River in northeastern Georgia, shows discontinuous and discordant variation with other populations in the Tennessee River drainage and entire Mississippi River Valley. Likewise, populations in the upper Coosa River, a tributary of the Alabama River in northeastern Georgia, show discordance relative to the remainder of Mobile Basin. Both the Coosa

River and Lookout Creek populations have high frequencies of GpiA⁵, an allele absent from other Mississippi River Valley samples and essentially absent in Mobile Basin samples, but diagnostic for the eastern epiphenotype (Warren and Grady, in prep.). Multivariate scores and univariate means for meristic and morphometric data also consistently show the Lookout Creek population as a decided Mississippi River Valley outlier. In meristic and morphometric multivariate space, Lookout Creek is closest to populations in Pensacola Bay (Fig. 9) and the Florida panhandle (Fig. 19), respectively. The Coosa River population shows morphological discordance of spot indices with multivariate scores (Fig. 15) and univariate means (Fig. 12) similar to those of populations in Perdido Bay and the Flint River.

Two alternative hypotheses may account for the morphological (and genetic) variation observed in the Lookout Creek population. First, the population may have originated from a recent, and likely inadvertent, introduction by man into the drainage of stock from the Florida panhandle or perhaps peninsular Florida. *Lepomis auritus*, which has been widely introduced in the Tennessee River drainage (D. A. Etnier, pers. comm.), is common in Lookout Creek (pers. obs.). It is feasible that progenitors of the Lookout Creek population were accidentally mixed in hatchery ponds with *L. auritus* or other gamefish prior to stocking. If a native population representative of the western epiphenotype was present in Lookout Creek prior to the introduction, the genotypic frequencies at the GpiA locus (Warren and Grady, in prep.) and morphological data suggest that introgression favored the introduced stock. Second, the Lookout Creek population may represent a relict of an ancestral epiphenotype. Lookout Creek enters the Tennessee River just east of Walden's Gorge, near Chattanooga, Tennessee. The Tennessee River courses westward through the deep gorge to breach the southern extension of the Cumberland Plateau. The history of the formation of the gorge is equivocal (see summaries in Starnes and Etnier, 1986; Mayden, 1987, 1988), but a Tertiary connection of the upper Tennessee River to rivers of Mobile Basin has been hypothesized (and is supported by faunal patterns and systematic data [Mayden, 1988; Mayden and Kuhajda, 1989]), with subsequent capture of the upper Tennessee by the lower Tennessee at Walden's Gorge. Thus, the upper Tennessee River (and hence Lookout Creek) may have had communication with Gulf Coastal rivers prior to capture. Given the lowland affinities associated with the *L. punctatus* complex, the upland physiography of the gorge and associated plateau possibly served to isolate or semi-isolate the Lookout Creek populations from the western epiphenotype in the middle and lower Tennessee Rivers.

Similar hypotheses may account for the variation shown by the Coosa River population. The population most closely resembles the western epiphenotype meristically with intermediacy restricted to spotting pattern and frequency of GpiA⁵ (Warren and Grady, in prep.). Birmingham and Avise (1986) reported only western mtDNA genotypes from the Coosa River. If a native population was in place and alien

stock was introduced, whether naturally or by man, subsequent introgression favored the western epiphenotype. For example, relatively recent stream capture between headwaters along the divide of the Coosa and Tennessee rivers has probably occurred (Starnes and Etnier, 1986) and may have introduced the "Lookout Creek" genome into the otherwise western epiphenotypic populations in the Coosa River. Bryant et al. (1979) implicated a stream capture, first noted by Campbell (1896) and later invoked by Ramsey (1965), between the Etowah River (Coosa River drainage) and Chestatee River (upper Chattahoochee Rivers) as a probable explanation for the presence of *Notropis lutipinnis*, *Ericymba buccata*, and *Ameiurus brunneus*, in the Coosa River system. It is plausible that Gulf Coast populations of spotted sunfish also may have entered the Coosa River as a result of this capture. The presence of a federal fish hatchery near Cohutta, Georgia, in the Coosa River drainage raises the possibility that it could be the source of introduced stock. As speculated for Lookout Creek, the Coosa population also may represent a relictual epiphenotype which has introgressed with downstream populations of the western epiphenotype in the Alabama River.

ZOOGEOGRAPHY.—Contact zones are the focus of many evolutionary studies because concepts of speciation and population evolution are dependent on the proposed origin of zones (Thorpe, 1984; Barton and Hewitt, 1985). Although the nature of a contact zone does not enable one to discern between primary and secondary contact (Endler, 1977), it is desirable nevertheless to generate hypotheses concerning the zoogeography of interacting populations and the origin of contact zones (Endler, 1982; Thorpe, 1984; Avise et al., 1987).

I believe the best explanation of the present distribution and differentiation of the eastern and western epiphenotypes in relation to the contact zone involves a model of secondary contact following isolation across a zoogeographic barrier(s) (Thorpe, 1982, 1983b, 1984; Barton and Hewitt, 1985; Avise et al., 1987; Hewitt, 1989). Several lines of evidence are supportive of secondary contact: 1) geological history of the contact zone and peripheral regions (reviewed by Swift et al., 1986 and Gilbert, 1987); 2) molecular clock estimates of mtDNA genotype divergence between the epiphenotypes (Bermingham and Avise, 1986); 3) correlation of geographic placement of mtDNA genetic discontinuities with other southeastern fishes (Bermingham and Avise, 1986); 4) distributional limits of fish (Swift et al., 1977, 1986; Gilbert, 1987) and pelecypods (Butler, 1989) in the region; and 5) vicariance patterns of clades of fishes and aquatic reptiles distributed in or near the contact zone (Wiley and Mayden, 1985).

Swift et al. (1986) reviewed the zoogeography of the freshwater fishes of the Gulf Slope of the southeastern United States and concluded that lowland vicariant patterns in the ichthyofauna could be accounted for by eustatic cycles superimposed on physiographic features and drainage trends.

Two major high-level sea stands have been identified (reviewed by Swift et al., 1986 and Gilbert, 1987): a Miocene high-level stand which reached 80-100 m above present sea level and lasted about 6 million years (MY); and a Pliocene stand which reached 50-80 m above present sea level and lasted about 1 or 2 MY. Three Pleistocene high stands followed which reached 10-20 m above present level and lasted about 30 to 100 x 10³ years. Each of the high stands was followed by sea-level depressions that in the case of the Plio-Pleistocene were relatively sudden and brief in duration. The high Miocene and Pliocene stands eliminated or greatly reduced small coastal drainages of the contact zone, including those in the area from Perdido Bay to St. Andrews Bay, and resulted in insularization of the Florida peninsula (Gilbert, 1987). Larger drainages with upland headwaters (e.g., Alabama, Chattahoochee-Apalachicola, and Altamaha rivers or their precursors) were well isolated and may have provided refugia for ancestral populations. An insular refugium may have existed on the Ocala uplift in north-central peninsular Florida.

On the assumption that the rate of sequence divergence in mammals (Brown et al., 1979) was applicable to fishes, Bermingham and Avise (1986) provisionally suggested a divergence time of 2.5 to 4.0 million years ago (MYA) between eastern and western mtDNA genotypes, a date coinciding with the Pliocene high-level sea stand noted previously. As judged from present distributions and degree of differentiation of taxa in the Florida peninsula, Gilbert (1987) also regarded the Pliocene and attendant insularization as a probable scenario for the isolation and derivation of several differentiated populations of fishes in peninsular Florida (e.g., *Opsopoeodus emiliae*, *Micropterus salmoides*, and *Lepomis macrochirus*). Regardless of the absolute divergence time between eastern and western epiphenotypes, the geological history of the contact zone and peripheral regions indicates that at least two major episodes of range fragmentation and long-term isolation of ancestral *L. punctatus* populations may have occurred in the Mio-Pliocene. The relatively brief and minor high sea-level stands in the Pleistocene probably acted primarily to constrain dispersal, but additional range fragmentation may have occurred.

Zoogeographic discontinuities as evidenced in geographic placement of mtDNA phylogenetic breaks among populations of *Lepomis gulosus*, *L. microlophus*, and *Amia calva* are highly concordant with those observed for the eastern and western epiphenotypes, and in the case of the *Lepomis* populations, estimated time of divergence agrees with a Pliocene vicariance (Bermingham and Avise, 1986; Avise et al., 1987). The shifts in mtDNA genotype for both *L. microlophus* and *A. calva* are centered in the Apalachicola River; *L. gulosus* shows a shift further west in Perdido Bay and the Alabama River. The mtDNA genetic discontinuities within each species were interpreted as the result of "long-term, extrinsic (i.e., zoogeographic) barriers to gene flow" (Avise et al., 1987). Swift et al. (1986) phenetically clustered drainages of the southeastern United States based on

presence and absence of fish species and identified two major clusters, one to the west of (and including) the Apalachicola River and another to the east of the Apalachicola River. Given the stable position of the Apalachicola River in the latter half of the Cenozoic, Gilbert (1987) suggested long-term physiographic independence of the Apalachicola from eastern drainages may be involved in the faunal dichotomy. Butler (1989) also documented a distinct east-west distributional break associated with the Apalachicola River among unionids, many of which are endemic to drainages either to the east or west of the Apalachicola but are not distributed in both.

Wiley and Mayden (1985) depicted numerous examples of distributions of clades of fishes, turtles, and snakes along the central Gulf Slope that may be exemplars of large-scale vicariance events and vicariance speciation (Wiley, 1981). There are three particularly striking features among their examples that relate to the data of my study: 1) numerous clades have taxa that are endemic or nearly so to the drainages extending from Perdido Bay to Apalachicola Bay (i.e., the contact zone described herein) with sister taxa or close relatives occurring to the west of Perdido Bay (including Mobile Basin) and/or east of the Apalachicola Basin (e.g., *Etheostoma beanii* species group; *Etheostoma chlorosomum* and *E. davisoni*; *Hybopsis winchelli* and *H. cf. winchelli*); 2) sister taxa have areas of sympatry limited to the drainages from about Mobile Bay to Apalachicola Bay (e.g., *Pteronotropis hypselopterus* species group); and 3) several taxa distributed primarily in peninsular Florida and the Atlantic Slope show range terminations and replacement with western taxa or form contact zones with western taxa along the eastern divide of Mobile Basin (i.e., the western edge of the contact zone described herein) (e.g., *Fundulus confluentus* vs *F. pulvereus*; *Nerodia taxispilota* vs *N. rhombifera*; *Farancia a. abacura* vs *F. a. reinwardti*; *Agkistrodon p. leucostoma* vs *A. p. conanti*; *Sternotherus m. minor* vs *S. m. peltifer*). Independent of considerations of geological history and degree of differentiation among taxa, these distributions emphasize that coastal drainages from Mobile Bay to Apalachicola Bay have been theatres of vicariance and have variously served as refugia, zoogeographic barriers, and contact zones for a large number of taxa. Presently, the lack of phylogenetic hypotheses for the genus *Lepomis* and many of the species cited above precludes a strict vicariance analysis, but it is apparent that general correlative vicariance patterns among several groups are present, providing the minimal requirement for reconstruction of the history of speciation (Cracraft, 1982).

These factors and the present distribution of the eastern and western epiphenotypes suggest the following zoogeographic scenario: 1) an ancestral population was split by one or more Mio-Pliocene high-level sea stands into a west Gulf Slope-Mississippi Valley-Mobile Basin vicariant and a Florida peninsular-Atlantic Slope vicariant; 2) one or more major sea-level regressions allowed range expansion of both vicariants into the Florida panhandle and probable estab-

lishment of secondary contact; and 3) Pleistocene eustatic cycles alternately restrained and enhanced dispersal into and within the contact zone, shaping the structure of the present-day contact zone.

Taxonomic Considerations

RANKING ALTERNATIVES.—Species are real entities, whether or not we recognize them, and the naming of a species represents a hypothesis that the named unit corresponds to an actual entity in nature (Brothers, 1985). Depending on the application of particular species definitions, at least two alternatives are relevant to the taxonomic ranking of the eastern and western epiphenotypes currently subsumed under the binomen *Lepomis punctatus*: 1) recognize one polytypic biological species consisting of two subspecies (*L. p. punctatus* and *L. p. miniatus*) or 2) recognize two separate species (*L. punctatus* and *L. miniatus*). Under the biological species concept (BSC) (Mayr, 1969, 1982a), *L. punctatus* would be considered polytypic given that the stricture of reproductive disjunction is violated in the contact zone and the extent of hybridization between populations is a critical determinant of taxonomic status (Mayr, 1969; Cracraft, 1987). The evolutionary species concept (ESC) (Simpson, 1961; as modified by Wiley, 1978, 1981) provides no practical guidance concerning contact zones, but a case could be made to recognize two species. Hybridization per se is no reason to reject the eastern and western epiphenotypes as evolutionary species since they are maintaining separate identities in spite of gene flow (Wiley, 1981). Likewise, application of the phylogenetic species concept (PSC) (Cracraft, 1983, 1987, 1989) would result in recognition of two species (i.e., evolutionary units) since each epiphenotype is "an irreducible cluster of organisms, within which there is a parental pattern of ancestry and descent" and "is diagnosably distinct from other such clusters" (Cracraft, 1987).

BIOLOGICAL SPECIES CONCEPT.—The BSC has been criticized by many recent authors, both on practical and theoretical grounds (e.g., Sokal and Crovello, 1970; Wiley, 1978, 1981; Mishler and Donoghue, 1982; Cracraft, 1983, 1987, 1989; Donoghue, 1985; Paterson, 1985; Rosenberg, 1985; Raven, 1986; McKittrick and Zink, 1988; Templeton, 1989). One of the primary criticisms of the BSC is the confounding of pattern and process in speciation (Wiley, 1981; Cracraft, 1982, 1983; Donoghue, 1985; Raven, 1986). Put quite simply, it is undesirable to restrict the discovery of patterns of diversity to particular explanations of diversity (Raven, 1986). Thus, a species concept should be as independent as possible from particular processes of speciation or our recovery of pattern may be biased toward a particular process (Cracraft, 1983, 1987; Chandler and Gromko, 1989). The existence of a contact zone between differentiated taxa is a case in which the biological species concept (BSC) is difficult to apply (Cracraft, 1983, 1987, 1989) and may lead to taxonomic actions that result in illogical taxa (Rosen, 1978, 1979). For example, the BSC fails to recover patterns of

taxonomic differentiation (i.e., evolutionary units), like that displayed by the eastern and western epiphenotypes, because the emphasis of the BSC is on the process of reproductive disjunction (whether of a primary or secondary nature [Chandler and Gromko, 1989]) not the discovery of taxonomic differentiation (Cracraft, 1987, 1989). The BSC effectively excludes recognition and comparability of a large class of evolutionary taxa, namely that consisting of those populations that are diagnostically distinct but not completely reproductively isolated from other such populations (Cracraft, 1983, 1989). From a practical standpoint, the ranking criterion of reproductive isolation can rarely be applied to populations directly (Mayr, 1969), but as in the present study, it must be inferred from a grouping criterion derived from other characters (e.g., morphology or biochemistry) (Donoghue, 1985; McKittrick and Zink, 1988); hence, the inference of reproductive isolation is inherently subjective. Appeals to "degrees" or "levels" of reproductive isolation as tests of speciation (e.g., Matthews et al., 1982; Dowling and Moore, 1984; Dowling et al., 1989) and debates over ranking as subspecies vs semispecies vs species (e.g., Black and Howell, 1979; Wooten et al., 1988) are symptomatic of the struggle of systematic ichthyologists (and others) attempting to apply the BSC on one hand and tacitly acknowledge on the other that reproductive disjunction is neither necessary nor sufficient for speciation. In the practice of alpha-level taxonomy, some ichthyologists have abandoned the BSC as inapplicable (e.g., Etnier and Starnes, 1986), relaxed the reproductive isolation criterion (e.g., Etnier and Bailey, 1989), or rejected ranking of taxa based on degree of differentiation (e.g., Buth and Mayden, 1981). Others explicitly acknowledge that rigid application of the BSC "to the point that it transcends all other criteria of relationships is unwarranted" (Matthews et al., 1982). Without rigid application of the reproductive disjunction standard, the recognition of explicitly biological species is not independent of a taxonomist's bias concerning the degree of reproductive isolation necessary for species recognition. As pointed out by several authors (Wiley, 1981; Donoghue, 1985; McKittrick and Zink, 1988; Endler, 1989), there is no necessary correspondence between breeding and phenotypic or genotypic differentiation, therefore interbreeding can not logically be used as evidence of conspecificity (Rosen, 1978, 1979; Donoghue, 1985).

POLYTYPIC BIOLOGICAL SPECIES.—One might argue that recognition of two subspecies within *L. punctatus* would acknowledge the pattern of taxonomic differentiation (i.e., two evolutionary units) and simultaneously signify incomplete reproductive isolation. The subspecies category, however, portends evolutionary unit to some authors (e.g., Barrowclough, 1982; O'Neill, 1982) and convenience category to others (e.g., Mayr, 1982b). In fact, the concept of the polytypic biological species is a taxonomic construct, not an evolutionary one (Cracraft, 1983, 1987, 1989), the greatest perceived benefit of which is considered simplification of

classification (Mayr, 1969). In ichthyology as in other systematic disciplines, there is no consensus on the ontology or definition of subspecies. Rosen (1979) rejects subspecies as a methodological concept and argues that within the framework of phylogenetic systematics, the subspecies is unobservable and undefinable. Matthews et al. (1982) suggest the subspecies category is of heuristic value in recognition of patterns of variation in fish species. They ostensibly use the category subspecies as a temporary ranking pending further systematic evaluation, a tactic also taken by others (e.g., Burr, 1979). Schaeffer and Cavender (1986), citing Mayr's (1969) subspecies definition, suggest that subspecies have taxonomic utility but should be recognized only if objective, non-arbitrary, qualitative discontinuities exist among populations. Their view of the ontological status of subspecies is unclear, but they do emphasize that no necessary evolutionary connotation is intended in the category. Other ichthyologists name subspecies to facilitate communication, help support conservation efforts of rare species, and because there is "too much overlap" with other populations to justify full species status (Miller and Fuiman, 1987). Thus, the "subspecies" as an evolutionary lineage of *L. punctatus* will be confounded with subspecies as a taxonomic convenience (Wiley, 1981).

Notwithstanding this confusion, if subspecies are recognized as evolutionary units, then what are polytypic species? Logically, both a particular subspecies and the polytypic species of which it is a member can not be evolutionary units (Cracraft, 1989). Further, a polytypic species like *L. punctatus* would contain more than one evolutionary unit, whereas monotypic species within *Lepomis* and other taxa would contain only one unit. Obviously, the denigration of evolutionary units, as exemplified in recognition of polytypic species, can result in inappropriate groups for studies in comparative biology, evolutionary history, and inter- and intracladal diversity (Rosen, 1978, 1979; Wiley, 1981; McKittrick and Zink, 1988; Cracraft, 1989). I agree with Cracraft (1989) who concluded that under the polytypic biological species concept there is no consistent, objectively defined unit of evolution and the concept does not provide a sound ontological basis for the study of the pattern or process of speciation.

EVOLUTIONARY AND PHYLOGENETIC SPECIES.—The ESC and PSC are definitions of species used primarily in phylogenetic systematics. It is instructive to note there is no consensus regarding the nature of species-as-taxa or the importance of species among phylogenetic systematists, but neither is there a consensus on either question within the rest of the biological community (Wiley and Mayden, 1985). The ESC has been criticized as non-operational (Rosen, 1978, 1979; Templeton, 1989). Rosen (1979) considered the "evolutionary species" as a decorative version of Regan's (1926) definition that a species is what a good taxonomist says it is. Brothers (1985) suggests non-operationalism is a desirable feature of the ESC because it means changes in the concept

are not necessary if new criteria for species are found (i.e., the lack of operationalism avoids constraining the discovery of pattern by the inclusion of particular results of speciation). Although lack of operationalism certainly is not unique to the ESC (e.g., see Sokal and Crovello, 1970) and may be a desirable attribute of a theoretical species concept, it also is desirable to have an operational species definition that is a good approximation to the theoretical concept (Cracraft, 1987; Endler, 1989) and that has practical implications for taxonomic grouping and ranking (Donoghue, 1985; McKittrick and Zink, 1988). Within the framework of a parental pattern of ancestry and descent, the PSC emphasizes a general result of evolution (i.e., differentiated taxa), rather than a particular process, and thus is unbiased from any preconceptions of those processes (aside from the process of differentiation) (Cracraft, 1983, 1987). Wiley (1981) emphasizes the need to first document historical patterns of genealogical descent and then attempt to determine processes that may be responsible for the observed patterns. When interpreted in the context of ancestor-descendant populations, the use of diagnostic characters in the PSC is a practical and reasonable measure of species identity and indicates independent evolutionary tendencies and historical fate, all prescriptions of the ESC (Wiley, 1978, 1981). I believe, as Endler (1989) tacitly suggests, that the PSC as formulated by Cracraft (1983, 1987) might serve as an operational extension of the ESC as presented and discussed by Wiley (1978, 1981). I am not sure that these authors and other proponents (Echelle, 1990; Frost and Hillis, 1990) of the respective concepts would share my assessment, but for the remainder of this discussion I shall limit my comments to the PSC under the assumption that it is a reasonable operational surrogate of the ESC.

If one accepts that strictly genealogical classification is a desirable goal in systematics, then substantial benefit accrues in following the PSC. Under the PSC, systematists do not need to resort to inherently subjective rules of thumb, such as the relative width of a contact zone or comparisons of average genetic distances among congeners, to group or rank taxa on the basis of inferred reproductive isolation. The grouping and ranking criteria under the PSC are explicit; taxa are recognized in terms of their hypothesized status as diagnosable evolutionary units. Since subspecies are not evolutionary units and have no ontological status under the PSC, the taxon species, being by definition an evolutionary unit, is rendered comparable in speciation analysis, biogeographic analysis, assessment of intra- and intercladal diversity patterns, or estimation of evolution rates among taxa (Cracraft, 1983).

It likely is apparent from the foregoing discussion that I believe the eastern and western epiphenotypes, currently considered as the biological species *L. punctatus*, each comprise an evolutionary unit and should be recognized as phylogenetic species. I have presented evidence of differentiation between the two which bespeaks of separate evolutionary histories (i.e., lineage independence and cohesion).

The fact that the two interbreed is certainly an important issue, but should be distinct from the delineation of species limits (Cracraft, 1983, 1989; Zink and Remsen, 1986; McKittrick and Zink, 1988; Zink, 1988). Further, I do not accept the prediction of genetic cohesion (e.g., coalescence) that often is assumed if contact zones exist between differentiated populations (McKittrick and Zink, 1988). There is ample evidence that populations on either side of a contact zone may evolve independently (Endler, 1977, 1989; Barton and Hewitt, 1985, 1989; Hewitt, 1989). I recommend that *L. punctatus* and *L. miniatus* be recognized as species and offer the following formal redescrptions in that context.

Species Descriptions

Lepomis punctatus (Valenciennes)

Blackspotted Sunfish

Figure 2

Bryttus punctatus Valenciennes in Cuvier and Valenciennes 1831:462-463 (original description, [Charleston, South Carolina, *vide* Jordan 1880:224 and C. R. Gilbert, in litt.]).

Bryttus reticulatus Valenciennes in Cuvier and Valenciennes 1831:463-464 (*vide* Jordan 1880:224 and C. R. Gilbert, in litt.).

Lepomis apiatus Cope 1877 [1878?]:66 (issued 18 January 1878 *vide* Bailey, 1938) and in Jordan 1877:25.

Lepomis stercorarius Gill MS. in Jordan 1877:26 (*nomen nudum*).

TYPES.—Two presumed syntypes (MNHN A.2891 and MNHN 1701) are extant in the Museum National D'Histoire Naturelle (C. R. Gilbert, in litt.). A third specimen (MNHN 2835, 192 mm SL, Charleston, South Carolina, Holbrook collector) exceeds the maximum length (149 mm) reported in the original description (Cuvier and Valenciennes, 1831:462-463) and is not considered a type (M. L. Bauchot in litt. to C. R. Gilbert). There is no mention in the original description (Cuvier and Valenciennes, 1831:462-463) of the provenance or collectors of any of the types. The label locality given for MNHN 1701 is Philadelphia (Lesueur collector), an obvious error. Jordan (1880:224) examined "the types of this species" and gave the locality and collector as Charleston and Holbrook, respectively. I hereby designate MNHN A.2891 (118 mm SL, Charleston, South Carolina, Holbrook collector) as lectotype.

DIAGNOSIS.—A species of *Lepomis* distinguished from all congeners, except *L. miniatus*, by the following: iridescent turquoise-colored crescent (colors 171a or 171a in Jacobson, 1948) outlining the ventral curvature of the otherwise dark or red iris (colors fading quickly in preservative); and uniformly narrow silvery, creamy, pinkish, or white margins on the dorsal, caudal, and anal fins (margins fading in preservative).

Distinguished from *L. miniatus* by the following: absence

in breeding males of red-orange, horizontal rows of spots on the sides; absence in breeding males of red-orange pigment on breast, belly, dorsal margin of opercular tab, and blotches above and anterior to opercular tab (these may be diffuse yellow, pinkish-orange, or yellow-orange [colors 3ia, 3la, 3nc; 6ia; and 4ia, respectively, in Jacobson, 1948]); presence of discrete, dark spots on the anterior exposed scale bases of the body, often one spot per scale, forming irregular horizontal rows on the sides and dorsum, especially prevalent on the lower sides at the level of the pectoral fins.

ADDITIONAL DIAGNOSTIC CHARACTERS.—Other distinguishing characters include: black opercular tab, not produced, stiff to bony margin, narrowly bordered above and below by pale (in preservative), posterior border pale or wanting; absence on cheek and opercle of pale wavy lines or dark bars, these often speckled with small, discrete, dark spots; pectoral fin short not extending beyond front of eye when bent forward towards eye; gill rakers on first arch moderate to long (longest usually >3.3 times longer than wide); mouth moderate, upper jaw extending to or just beyond front of eye; absence of posterior dark blotch in soft dorsal fin; and lateral line complete.

Lepomis punctatus is further distinguished from other congeners including *L. miniatus* by a combination of the following characters (data preceded by "usually" indicate 90% of counts fall within the indicated interval): both left and right cheek scales 4-8 (usually 5-7); sum of left and right cheek scales 8-16 (usually 10-14); breast scales 14-20 (usually 15-18); scales above lateral line 6-9 (usually 7-8) and below lateral line 12-16 (usually 13-15); transverse scales 19-25 (usually 21-24); caudal-peduncle scales 7-10 (usually 8-10) above lateral line, 9-12 (usually 9-11) below lateral line, 19-24 (usually 20-23) total; sum of right cheek, breast, caudal-peduncle and transverse scales below lateral line 41-53 (usually 43-50); lateral line scales 37-47 (usually 38-44); and index of spots 0-12 (usually 3-12) below lateral line, 0-7 (usually 3-7) above lateral line in specimens >80 mm SL.

DESCRIPTION.—Scale counts appear in Tables 15-21. A frequency distribution expressed as (16) 17-20 (21) indicates that 90% of the counts or proportions are between 17 and 20, with the extremes 16 and 21. A breeding male is depicted in Figure 2.

A small to moderate-sized *Lepomis*, the largest specimen examined 153 mm SL; the Florida state record is 163 mm SL (R. S. Butler, pers. comm.). Dorsal fin IX-XI, (9) 10-11 (12), modally X, 11. Anal fin III, 9-11, modally III, 10. Both right and left pectoral fin rays (12) 13-14 (15), modally 14. Lateral-line scales (37) 38-44 (47), modally 41 (Table 15). Scales above lateral line (6) 7-8 (9), modally 7 and scales below lateral line (12) 13-15 (16), modally 14. Transverse scales (19) 21-24 (25), modally 23 (Table 16). Caudal-peduncle scales (7) 8-10 (10), modally 9 above lateral line and (9) 9-11 (12), modally 10 below lateral line. Total caudal-peduncle scales (19) 20-23 (24), modally 21 (Table 17). Both left and right cheek scales (4) 5-7 (8), modally 6 (Tables 19 and 20). Gill rakers moderate to long, ratio of length to width of longest raker (2.00) 3.20-4.85 (5.67), $\bar{x} + 2\text{SE} = 3.92 + 0.091$, over 90% of individuals examined >3.30 (n=144). Black, opercular tab not produced; stiff to bony margin; outlined above and below with narrow white margins (may be diffuse yellow-orange to pinkish-orange in breeding males), and posteriorly with an extremely narrow, white margin, often wanting. Three (in preservative) pale blotches usually present in adults (most noticeable in males): the most prominent directly above dorsal margin of opercular tab; a second anterior to black tab below mid-dorsal margin of opercle and continuous with the dorsal margin of the tab; and a third, often poorly developed or absent, posterior dorsal to the eye. Cheeks, opercles, sides, and dorsum usually speckled with discrete, black spots; spots on sides often in irregular horizontal rows; spots on dorsum often larger than those on sides, cheeks, and opercles. Speckling, mottling, or discrete spots usually present on scaly base of caudal fin (and sometimes basal membranes) and continuing, especially in individuals <80 mm SL, as dark, but often diffuse, marks on scales from the caudal peduncle (especially ventral half) to anal fin origin. Soft dorsal fin base may have one to many short vertical streaks beside each ray, less often in soft anal fin. In adult males soft dorsal, soft anal, and caudal fins with distal one-half to one-third reddish-brown, narrowly edged in paler, the proximal portions dusky to black; spinous dorsal and spinous anal fins dusky; pectoral fins clear to reddish-brown; and pelvic fins dusky to black in breeding males.

DISTRIBUTION.—*Lepomis punctatus* occurs, primarily

Table 15. Frequency distributions of lateral-line scales in *Lepomis punctatus*, *L. miniatus*, and populations in presumed contact zones.

| Species/Populations | Lateral-line Scales | | | | | | | | | | | | | | n | \bar{x} | |
|--|---------------------|----|----|----|-----|-----|----|----|----|----|----|----|----|----|---|-----------|-------|
| | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | | | 47 |
| <i>Lepomis punctatus</i> | | | | | 2 | 31 | 51 | 83 | 84 | 79 | 49 | 25 | 8 | 1 | 1 | 414 | 41.02 |
| Lookout Creek (CD 3) | | | | | | | 3 | 9 | 1 | 1 | 1 | | | | | 15 | 40.20 |
| Perdido Bay to Apalachicola Basin (CD 22-28) | | | | 3 | 2 | 19 | 36 | 38 | 58 | 38 | 25 | 9 | 7 | | | 235 | 40.80 |
| Coosa River (CD 17) | | 2 | 2 | 4 | 9 | 8 | 6 | 5 | 1 | 1 | | | | | | 38 | 37.79 |
| <i>Lepomis miniatus</i> | 2 | 9 | 33 | 79 | 117 | 124 | 85 | 37 | 27 | 4 | | | | | | 517 | 37.68 |

Table 16. Frequency distributions of transverse scale rows in *Lepomis punctatus*, *L. miniatus*, and populations in presumed contact zones.

| Species/Populations | Transverse Scale Rows | | | | | | | | | n | \bar{x} |
|--|-----------------------|----|----|-----|-----|-----|-----|----|----|-----|-----------|
| | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | | |
| <i>Lepomis punctatus</i> | | | 2 | 12 | 71 | 127 | 141 | 50 | 11 | 414 | 22.42 |
| Lookout Creek (CD 3) | | | | 5 | 7 | 1 | 2 | | | 15 | 21.00 |
| Perdido Bay to Apalachicola Basin (CD 22-28) | | | 16 | 66 | 78 | 61 | 13 | 1 | | 235 | 20.97 |
| Coosa River (CD 17) | | 1 | 13 | 16 | 7 | 1 | | | | 38 | 19.84 |
| <i>Lepomis miniatus</i> | 1 | 10 | 94 | 208 | 155 | 44 | 5 | | | 517 | 20.27 |

Table 17. Frequency distributions of total caudal peduncle scale rows in *Lepomis punctatus*, *L. miniatus*, and populations in presumed contact zones.

| Species/Populations | Caudal Peduncle Scale Rows | | | | | | | | | n | \bar{x} | |
|--|----------------------------|----|----|----|-----|-----|-----|----|----|---|-----------|-------|
| | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | | | 24 |
| <i>Lepomis punctatus</i> | | | | | 30 | 58 | 219 | 69 | 36 | 2 | 414 | 21.07 |
| Lookout Creek (CD 3) | | | | | | 3 | 11 | 1 | | | 15 | 20.87 |
| Perdido Bay to Apalachicola Basin (CD 22-28) | | | | | 27 | 51 | 120 | 28 | 9 | | 235 | 20.75 |
| Coosa River (CD 7) | | | | 2 | 19 | 11 | 5 | 1 | | | 38 | 19.58 |
| <i>Lepomis miniatus</i> | 1 | 0 | 16 | 56 | 243 | 121 | 76 | 4 | | | 517 | 19.37 |

Table 18. Frequency distributions of breast scale rows in *Lepomis punctatus*, *L. miniatus*, and populations in presumed contact zones.

| Species/Populations | Breast Scales Rows | | | | | | | | | n | \bar{x} | |
|--|--------------------|----|-----|-----|-----|-----|-----|----|----|---|-----------|-------|
| | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | | | 20 |
| <i>Lepomis punctatus</i> | | | | 9 | 110 | 106 | 153 | 24 | 9 | 3 | 414 | 16.27 |
| Lookout Creek (CD 3) | | | | 3 | 7 | 5 | | | | | 15 | 15.13 |
| Perdido Bay to Apalachicola Basin (CD 22-28) | | 3 | 38 | 44 | 97 | 31 | 18 | 3 | 1 | | 235 | 14.79 |
| Coosa River (CD 17) | | | 20 | 7 | 8 | 2 | 1 | | | | 38 | 13.87 |
| <i>Lepomis miniatus</i> | 4 | 31 | 218 | 110 | 134 | 14 | 5 | 1 | | | 517 | 13.79 |

Table 19. Frequency distributions of left and right cheek scale rows in *Lepomis punctatus*, *L. miniatus*, and populations in presumed contact zones.

| Species/Populations | Scale Rows | | | | | | | | | | | | n | \bar{x} |
|--|------------|-----|-----|----|---|-----------|-------------|-----|-----|----|---|-----|------|-----------|
| | Left Cheek | | | | | | Right Cheek | | | | | | | |
| | 4 | 5 | 6 | 7 | 8 | \bar{x} | 4 | 5 | 6 | 7 | 8 | | | |
| <i>Lepomis punctatus</i> | 3 | 62 | 261 | 84 | 4 | 6.06 | 5 | 45 | 262 | 96 | 6 | 414 | 6.13 | |
| Lookout Creek (CD 3) | | 10 | 5 | | | 5.33 | | 9 | 6 | | | 15 | 5.40 | |
| Perdido Bay to Apalachicola Basin (CD 22-28) | 6 | 128 | 93 | 8 | | 5.44 | 4 | 104 | 123 | 4 | | 235 | 5.54 | |
| Coosa River (CD 17) | 13 | 24 | 1 | | | 4.68 | 12 | 25 | 1 | | | 38 | 4.71 | |
| <i>Lepomis miniatus</i> | 58 | 404 | 54 | 1 | | 5.00 | 57 | 400 | 59 | 1 | | 517 | 5.01 | |

Table 20. Frequency distributions of the sum of left and right cheek scale rows in *Lepomis punctatus*, *L. miniatus*, and populations in presumed contact zones.

| Species/Populations | Sum Left and Right Cheek Scale Rows | | | | | | | | | n | \bar{x} |
|--|-------------------------------------|----|-----|----|-----|----|----|----|----|-----|-----------|
| | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | | |
| <i>Lepomis punctatus</i> | 2 | 3 | 29 | 48 | 210 | 54 | 61 | 4 | 3 | 414 | 12.19 |
| Lookout Creek (CD 3) | | | 7 | 5 | 3 | | | | | 15 | 10.73 |
| Perdido Bay to Apalachicola Basin (CD 22-28) | 2 | 5 | 86 | 57 | 76 | 6 | 3 | | | 235 | 10.98 |
| Coosa River (CD 17) | 10 | 5 | 21 | 2 | | | | | | 38 | 9.39 |
| <i>Lepomis miniatus</i> | 29 | 57 | 348 | 51 | 30 | 2 | | | | 517 | 10.01 |

Table 21. Frequency distributions of the sum of right cheek scale rows, breast scale rows, and caudal peduncle and transverse scale rows below the lateral line in *Lepomis punctatus*, *L. miniatus*, and populations in presumed contact zone.

| Species/Populations | Sum of Right Cheek Scales, Breast Scales, and Caudal Peduncle and Transverse Scales Below Lateral Line | | | | | | | | | | | | | | | | | | | n | \bar{x} |
|--|--|----|----|----|----|-----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|-----------|
| | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | | |
| <i>Lepomis punctatus</i> | | | | | | | 5 | 8 | 25 | 36 | 58 | 59 | 98 | 54 | 34 | 20 | 8 | 8 | 1 | 414 | 46.53 |
| Lookout Creek (CD 3) | | | | | | | | 4 | 4 | 3 | 1 | 2 | 1 | | | | | | | 15 | 43.73 |
| Perdido Bay to Apalachicola Basin (CD 22-28) | | | | 3 | 4 | 14 | 21 | 37 | 53 | 33 | 27 | 25 | 10 | 5 | 2 | 1 | | | | 235 | 43.40 |
| Coosa River (CD 17) | | | | 7 | 8 | 7 | 1 | 8 | 6 | 1 | | | | | | | | | | 38 | 40.45 |
| <i>Lepomis miniatus</i> | 1 | 3 | 9 | 28 | 76 | 124 | 93 | 68 | 65 | 29 | 13 | 4 | 3 | 1 | | | | | | 517 | 40.93 |

on the Coastal Plain, from the Cape Fear River, North Carolina, south in Atlantic Slope drainages to the Everglades and north and west in East Gulf Slope drainages to the Ochlockonee River of southwestern Georgia and the eastern panhandle of Florida (Fig. 1). The species forms a contact zone with *L. miniatus* from the Apalachicola Basin west to Perdido Bay (see Discussion). Rohde et al. (1979) listed the Neuse River as the northeastern termination of the range of *L. punctatus* (repeated by Lee, 1980; Stauffer et al., 1982; and Hocutt et al., 1986). I examined the specimens on which the Neuse River record is based (E. F. Menhinick, pers. comm.) and considered them *Lepomis* hybrids.

Lepomis miniatus Jordan
Redspotted Sunfish
Figure 2

Lepiopotomus miniatus Jordan, 1877:26 (original description, Tangipahoa River, Louisiana).

Lepomis garmani Forbes, 1884:68 (*nomen nudum*); Forbes 1885:135 (original description, Little Fox River at Phillipstown, and Wabash River and Drew Pond at Carmi [Illinois]).

TYPES.—Jordan (1877:26) originally described *L. miniatus* from the Tangipahoa River, Louisiana, based on five specimens (USNM 16918); however, the label with USNM 16198

gives the locality as Tangipahoa River, Mississippi (received from Fred Mather). One specimen (81.8 mm SL) was removed from the syntype series and recataloged as USNM 106504 (label locality: Tangipahoa River, Louisiana) on 26 February 1938. I have examined the five specimens of the syntypic series (including USNM 106504); as first revisor I hereby designate USNM 106504 (81.8 mm SL) as lectotype and restrict the type locality to the Tangipahoa River, Louisiana, as originally indicated by Jordan (1877). I re-identified two of the smaller specimens in USNM 16918 as *Lepomis megalotis* and *Lepomis gulosus*. The two other syntypes represent *L. miniatus* (68.2 and 87.2 mm SL).

DIAGNOSIS.—A member of the genus *Lepomis* distinguished from all congeners, except *L. punctatus*, by the following: iridescent turquoise-colored crescent (colors 171a or 171a in Jacobson, 1948) outlining the ventral curvature of the otherwise dark or red iris (colors fading quickly in preservative); and uniformly narrow silvery, creamy, pinkish, or white margins on the dorsal, caudal, and anal fins (fading in preservative).

Distinguished from *L. punctatus* by the following: presence in breeding males of red-orange, horizontal rows of spots (colors 5pa, 5na, 6pa, or 6na in Jacobson, 1948) from one to two scale rows below the lateral line to the belly, the red-orange pigment covers the scale centers, and the rows resemble a chain of rough triangles with anteriorly directed,

truncated apices; presence in breeding males of red-orange pigment covering the breast, belly, dorsal margin of the opercular tab, and three quadrate to circular blotches located below the mid-dorsal margin of the opercle and anterior to the black opercular spot, above the opercular tab, and just above and behind the eye, the latter usually diffuse; and absence of discrete, dark spots on the anterior exposed scale bases of the body; if present, spots on the body are diffuse or only slightly darker than dorsal and ventral scale margins and do not form horizontal rows.

ADDITIONAL DIAGNOSTIC CHARACTERS.—Other distinguishing characters include: black opercular tab, not produced, stiff to bony margin, narrowly bordered above and below by pale (in preservative), posterior border pale or wanting; absence on cheek and opercle of pale wavy lines or dark bars, these usually plain with short, dark streaks or diffuse spots on the preopercle and subopercle; two or three dusky lines often present posterior to eye; pectoral fin short not extending beyond front of eye when bent forward towards eye; gill rakers on first arch moderate (longest usually 2.5-3.5 times longer than wide); mouth moderate, upper jaw extending to or just beyond front of eye; absence of posterior, dark blotch in soft dorsal fin; and lateral line complete.

Lepomis miniatus is further distinguished from other congeners including *L. punctatus* by a combination of the following characters (data preceded by "usually" indicate 90% of the counts fall within the indicated interval): both left and right cheek scales 4-7 (usually 4-6); sum of left and right cheek scales 8-13 (usually 8-12); breast scales 11-18 (usually 12-15); scales above lateral line 4-8 (usually 6-7) and below lateral line 11-15 (usually 12-14); transverse scales 17-23 (usually 19-22); caudal-peduncle scales 5-10 (usually 7-9) above lateral line, 8-11 (usually 9-10) below lateral line, 15-22 (usually 18-21) total; sum of right cheek, breast, and transverse and caudal-peduncle scales below lateral line 35-48 (usually 38-44); lateral line scales 33-42 (usually 35-41); index of spots 0-6 (usually 0) below lateral line, 0-3 (usually 0) above lateral line in specimens >80 mm SL.

DESCRIPTION.—Scale counts appear in Tables 15-21. A frequency distribution expressed as (16) 17-20 (21) indicates that 90% of the counts or proportions are between 17 and 20, with the extremes 16 and 21. Breeding males are illustrated in Figure 2 and by a color transparency in Douglas (1974:423, Plate XIII) and Robison and Buchanan (1988:377) and by half-tone in Smith-Vaniz (1968:188, Fig. 134). A superb water-color illustration of a nonbreeding or post-spawning male appears in Forbes and Richardson (1920, facing p. 253).

A small to moderate-sized *Lepomis*, the largest specimen examined 129 mm SL. Dorsal fin IX-X1,(9) 10-11 (12), modally X,11. Anal fin III,9-11, modally III,10. Both right and left pectoral fin rays (12) 13-14 (15), modally 13. Lateral-line scales (33) 35-41 (42), modally 38 (Table 15). Scales above lateral line (4) 6-7 (8), modally 6 and scales below lateral line (11) 12-14 (15), modally 13. Transverse scales (17) 19-22 (23),

modally 20 (Table 16). Caudal-peduncle scales (5) 7-9 (10), modally 8 above lateral line and (8) 9-10 (11), modally 9 below lateral line. Total caudal-peduncle scales (15) 18-21 (22), modally 19 (Table 17). Both left and right cheek scales (4) 4-6 (7), modally 5 (Tables 19 and 20). Gill rakers moderate to long, ratio of length to width of longest raker (1.35) 2.10-3.80 (4.20), $\bar{x} + 2SE = 2.96 + 0.077$, over 90% of individuals examined <3.5 (n=164). Black, opercular tab not produced; stiff to bony margin; outlined above and below with narrow white margins (breeding males with dorsal margin suffused with red-orange pigment), and posteriorly with an extremely narrow, white margin, often wanting. Three (in preservative) pale blotches usually present in adults (most noticeable in males); the most prominent directly above dorsal margin of opercular tab; a second anterior to black tab below mid-dorsal margin of opercle and continuous with the dorsal margin of the tab; and a third, usually less distinct, posteriodorsal to the eye. Spots on head, if present, variable but usually most prominent on the preopercle and subopercle, often diffuse or coalescing to form dark streaks. Two to three diffuse bars often radiate posterior to the eye. Speckling, mottling, or diffuse spots often present on scaly base of caudal fin (usually in individuals <80 mm SL) and continuing as dark, but diffuse, marks on scales from the caudal peduncle (especially ventral half) to anal fin origin. Soft dorsal fin base, and less often soft anal fin base, may have one or more spots or short vertical streaks beside each ray. Breeding males with soft dorsal, soft anal, and caudal fins with distal one-half to one-third diffuse red-orange to reddish-brown, narrowly edged in paler, the proximal portions dusky to black; spinous dorsal and spinous anal fins dusky; pectoral fins clear to orange or red-orange; and pelvics dusky to black.

DISTRIBUTION.—*Lepomis miniatus* occurs from the Illinois River, Illinois, south in the Mississippi River Valley (including recent records from the Cumberland River [Warren et al., 1991]) to the Gulf Slope (Fig. 1). On the Gulf Slope the species occurs or did occur from the Nueces River and possibly the Rio Grande, Texas (see below), east to and inclusive of Mobile Basin, Alabama. From Perdido River east to the Apalachicola Basin *L. miniatus* forms a contact zone with *L. punctatus* (see Discussion). Populations in the upper Coosa River of Mobile Basin and in Lookout Creek of the Tennessee River drainage are intermediate in several characters and provisionally are considered hybrids between *L. punctatus* and *L. miniatus* (see Discussion).

Warren (1990) recently reported the first positive records of *L. miniatus* (as *L. punctatus*) from the Devils River (Rio Grande drainage), Texas (TNHC 5702) and discussed the provenance of these and unsubstantiated records of the species from the drainage (Robinson, 1959; records repeated by Lee, 1980, in part; Contreras and Escalante, 1984; and Courtenay and Kohler, 1986). The source of the species in Devils River is equivocal and may be the result of accidental introduction of the species in the river during routine

stockings of gamefish. Alternatively, the species may be native to the lower Rio Grande and simply restricted in distribution within the system.

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Material Examined

Specimens of *Lepomis miniatus*, *L. punctatus*, and contact zone populations (*L. miniatus* x *L. punctatus*) used for analysis of morphological variation. Parenthetical numbers following drainage names reference combined drainages (Table 3) and those after catalog numbers refer to sample sizes used in meristic and spot index, morphometric, and gill raker analyses, respectively. Complete locality data is presented in Warren (1989).

Alabama.

Lepomis miniatus. Alabama River Drainage (19): SIUC 12059 (6, 0, 4), SIUC 12079 (2, 0, 0), SIUC 14438 (2, 0, 0), UAIC 815.06 (1, 1, 1), UAIC 2113.02 (6, 5, 4), UAIC 2409.03 (2, 0, 1). Cahaba River Drainage (19): UAIC 4680.12 (6, 1, 2), UAIC 4704.02 (2, 0, 2), UMMZ 168647 (5, 3, 0). Escatawpa River Drainage (16): UAIC 3765.09 (1, 0, 1), UAIC 4038.03 (1, 0, 1). Gulf of Mexico Minor Coastal Tributaries (22): UAIC 149.06 (2, 2, 2), UMMZ 123937 (7, 3, 2), UMMZ 124043 (3, 0, 0). Mobile Bay Minor Tributaries (21): SIUC 6156 (1, 0, 0), SIUC 15133 (2, 2, 0), UAIC 845.01 (1, 1, 1), UAIC 2433.06 (1, 1, 1), UAIC 4066.04 (3, 3, 2), UMMZ 86805 (5, 0, 0), UMMZ 163582 (2, 2, 1). Tallapoosa River Drainage (18): AU 21950 (11, 0, 1), UAIC 1238.13 (3, 0, 2), UAIC 1471.08 (3, 0, 2). Tennessee River Drainage (4): AU 17923 (1, 0, 0), SIUC 12406 (4, 3, 1), SIUC 15106 (1, 0, 0), UMMZ 103515 (1, 0, 0), UMMZ 114710 (1, 0, 0), UMMZ 115274 (1, 0, 0), UMMZ 115731 (1, 0, 0), UMMZ 122618 (11, 5, 2), UMMZ 122668 (1, 0, 0), UMMZ 201011 (1, 0, 0), UT 90.546 (3, 3, 3). Tombigbee River Drainage (20): AU 19529 (9, 0, 1), UAIC 495.09 (2, 0, 2), UAIC 1840.03 (1, 0, 1), UAIC 3303.06 (1, 0, 1), UAIC 4226.09 (1, 0, 1), UAIC 4408.14 (2, 0, 2), UAIC 5795.08 (1, 0, 1), UAIC 4235.06 (2, 0, 2), UK 14508 (1, 0, 1), UMMZ 97805 (1, 0, 0).

Lepomis miniatus x *L. punctatus*. Chattahoochee River Drainage (26): AU 12578 (6, 0, 3), UAIC 2643.05 (8, 2, 3). Choctawhatchee River Drainage (24): UAIC 1596.12 (4, 2, 4). Coosa River Drainage (17): TCWC 4021.10 (4, 1, 2), UMMZ 175821 (1, 0, 0). Escambia River Drainage (23): UT 90.65 (3, 0, 2). Perdido Bay Drainage (22): AU 14767 (3, 0, 0), AU 16862 (6, 0, 2), SIUC 12744 (3, 0, 0), SIUC 15209 (2, 0, 2), UAIC 3124.08 (1, 1, 1), UF-FSU 5962 (6, 4, 3).

Arkansas.

Lepomis miniatus. Red River Drainage (3): SIUC 2450 (1, 0, 0), SIUC 3707 (2, 2, 1), SIUC 6192 (1, 1, 1), UT 90.122 (1, 1, 1), UT 90.514 (7, 1, 3). White River Drainage (6): UF-FSU 14529 (9, 3, 2).

Florida.

Lepomis punctatus. Atlantic Ocean Minor Drainages (34): UT 90.725

(6, 0, 3). Aucilla River Drainage (29): UF/FSU 23801 (8, 0, 6), UF/FSU 24498 (2, 0, 0), UT 90.589 (5, 0, 3). Econfina River Drainage (29): UAIC 1001.13 (1, 0, 1), UF/FSU 23772 (4, 0, 2). Fenholloway River Drainage (29): UAIC 993.13 (1, 0, 1), UF/FSU 24356 (4, 0, 4), UF/FSU 24412 (4, 0, 1), UMMZ 158169 (1, 0, 0). Gulf of Mexico Minor Drainages (29): UF/FSU 13861 (3, 0, 3), UF/FSU 21927 (1, 0, 0). Lake Okeechobee (Kissimmee River)-Caloosahatchie River-Lower Everglades Drainage (34): INHS 74754 (2, 0, 2), UF/FSU 10581 (10, 0, 2), UF 34563 (10, 0, 5), UF/FSU 22779 (25, 11, 5). Myakka River Drainage (33): UF 34980 (10, 0, 3). Ochlockonee River Drainage (29): UF/FSU 3597 (7, 7, 6). Peace River Drainage (33): UF 32728 (10, 40, 0), UT 90.353 (8, 0, 3). Pithlachascootee River Drainage (31): UF/FSU 1899 (2, 0, 1). St. Johns River Drainage (35): INHS 74737 (3, 0, 3), KU 17172 (15, 0, 5), SIUC 6393 (1, 0, 1), UF/FSU 2499 (10, 10, 0). St. Marks River Drainage (29): KU 17408 (2, 0, 1), SIUC 12746 (6, 0, 5), UF/FSU 3449 (2, 0, 2). St. Marys River Drainage (35): UF 1935 (3, 0, 0), UF 28956 (2, 0, 1), UF/FSU 6430 (3, 0, 3). Steinhatchee River Drainage (29): UF/FSU 24202 (2, 0, 0), UF/FSU 24807 (8, 0, 5). Suwannee River Drainage (30): UF 34043 (3, 3, 1), UF/FSU 8202 (8, 0, 0), UF/FSU 8750 (7, 7, 7), UL 1001 (4, 0, 0), SIUC 9836 (3, 0, 3), SIUC 15223 (1, 0, 0). Tampa Bay Drainage (32): UAIC 2109.02 (2, 0, 2), UAIC 2110.15 (10, 0, 3), UF 35102 (5, 0, 3). Waccasassa River Drainage (31): UF/FSU 13180 (4, 0, 1). Weekiwachee Swamp Drainage (31): UMMZ 158868 (10, 0, 0). Withlacoochee River Drainage (31): UMMZ 176251 (2, 0, 0), UMMZ 176266 (1, 0, 0).

Lepomis miniatus x L. punctatus. Apalachicola River Drainage (28): KU 17436 (2, 0, 0), UAIC 1000.12 (1, 0, 1), UMMZ 110995 (1, 1, 0), UMMZ 154207 (2, 1, 1), UMMZ 158196 (1, 1, 1), UMMZ 158207 (2, 1, 1), UMMZ 163484 (7, 3, 3). Choctawhatchee Bay Drainage (23): SIUC 12105 (8, 5, 7), SIUC 12204 (6, 1, 3), UAIC 2900.08 (10, 0, 3), UAIC 2902.01 (2, 1, 1), UAIC 3070.06 (3, 0, 0), UAIC 3073.12 (4, 0, 2), UAIC 3076.02 (1, 2, 2), UAIC 3659.02 (1, 0, 1), UAIC 3748.04 (5, 0, 0), UAIC 4901.14 (6, 0, 2), UAIC 5236.07 (2, 0, 1), UAIC 5243.05 (4, 0, 1), UAIC 5376.05 (2, 0, 1). Pensacola Bay Drainage (23): SIUC 12121 (8, 0, 0), UAIC 2804.13 (7, 3, 3), UAIC 2820.06 (2, 2, 2), UAIC 3567.16 (10, 0, 5), UAIC 3576.05 (7, 0, 5), UAIC 6769.12 (4, 0, 1), UF/FSU 5076 (15, 0, 2), UF/FSU 8485 (10, 7, 6), UF/FSU 13528 (6, 0, 4), UF/FSU 13541 (10, 0, 6). Perdido Bay Drainage (22): UF/FSU 2968 (7, 0, 2), UF/FSU 4766 (1, 1, 1). Santa Rosa Sound Drainage (24): UAIC 3657.10 (1, 0, 1). St. Andrews Bay Drainage (25): UF/FSU 2832 (13, 10, 9).

Georgia.

Lepomis punctatus. Altamaha River Drainage (36): AU 9060 (1, 0, 0), AU 11345 (3, 1, 2), AU 18413 (5, 1, 4), UF/FSU 11525 (1, 0, 0), UG 157 (1, 0, 0), UG 482 (2, 0, 1), UG 1465 (5, 3, 2), UG 1467 (10, 8, 5), UMMZ 158080 (1, 0, 0). Ochlockonee River Drainage (29): UF/FSU 2894 (1, 1, 1), UG 1342 (1, 0, 0). Ogeechee River Drainage (36): AU 13973 (1, 0, 1), KU 5017 (1, 0, 1), UG 150E (2, 0, 0), UG 152 (2, 0, 0), UG 551 (1, 0, 1), UMMZ 155216 (1, 0, 0). Satilla River Drainage (36): AU 5017 (5, 0, 3), UG 791 (9, 0, 0), UG 1474 (1, 0, 0), UG 1574 (1, 0, 0). Savannah River Drainage (37): AU 24217 (1, 1, 1), AU 24392 (1, 0, 0), AU 24479 (1, 0, 0), AU 24544 (1, 1, 0), NLU 43801 (0, 1, 0), UG 243 (1, 0, 0). St. Marys River Drainage (35): UG 1144 (1, 0, 0), UG 1438 (1, 0, 1), UMMZ 88544 (1, 0, 0). Suwannee River Drainage (30): UG 185 (2, 0, 0), UF 458 (1, 0, 0), UG 557 (1, 0, 0).

Lepomis miniatus x L. punctatus. Chattahoochee River Drainage (26): KU 17804 (2, 0, 1), UAIC 1134.13 (1, 0, 0). Coosa River Drainage (17): AU 8408 (1, 1, 1), AU 8820 (2, 0, 1), AU 9282 (4, 0, 3), AU 10548 (2, 0, 1), UAIC 2913.02 (1, 0, 0), UMMZ 168824 (5, 4, 1), UT 90.272 (4, 2, 2), UT 90.748 (2, 0, 2), UT 90.760 (1, 0, 1). Flint River Drainage (27): AU 7322 (5, 0, 2), UF 9803 (4, 1, 2), UT 90.34 (1, 1, 0). Lookout Creek (Tennessee River) Drainage (3): SIUC 12084 (1, 0, 1), UG 689A (7, 1, 3), UG 689 (5, 3, 0), UT 90.504 (2, 0, 0).

Illinois.

Lepomis miniatus. Illinois River Drainage (1): INHS 14526 (4, 1, 2), INHS 14835 (3, 3, 3), INHS 15070 (8, 3, 4), INHS 15072 (2, 0, 2), INHS 85598 (3, 0, 1), INHS 85600 (4, 0, 0), INHS uncat. (4, 2, 0), SIUC 15364 (1, 1, 0). Middle Mississippi River Minor Drainages (5): INHS 18142 (1, 0, 1),

SIUC 15860 (1, 0, 0). Ohio River Minor Drainages (2): SIUC 14434 (1, 0, 0), SIUC 15234 (3, 0, 0), SIUC 15309 (1, 0, 0), SIUC 15321 (1, 0, 0). Wabash River Drainage (2): INHS 9594 (1, 1, 1), INHS 26601 (1, 0, 1), SIUC 14435 (2, 0, 0), SIUC 15309 (1, 0, 0).

Kentucky.

Lepomis miniatus. Green River Drainage (2): SIUC 7378 (1, 1, 0), SIUC 7597 (1, 1, 0), SIUC 10305 (5, 1181744, 3), SIUC 10944 (9, 4, 3), SIUC 11017 (1, 1, 0), SIUC 13220 (2, 1, 0). Ohio River Minor Drainages (2): INHS 78654 (1, 1, 1), SIUC 7919 (6, 0, 0), SIUC 7936 (5, 5, 3). Middle Mississippi River Minor Drainages (5): SIUC 504 (3, 0, 2), SIUC 836 (1, 0, 0), SIUC 9585 (3, 0, 0), SIUC 17667 (5, 0, 3), SIUC 17668 (2, 0, 1), UT 90.673 (1, 0, 0).

Louisiana.

Lepomis miniatus. Atchafalaya Basin Drainage (8): NLU 1896 (2, 0, 0), NLU 2771 (8, 0, 0). Bayou La Fourche Drainage (8): UMMZ 203103 (1, 0, 0). Calcasieu River Drainage (10): NLU 38741 (2, 0, 0), UMMZ 170598 (1, 0, 0). Gulf of Mexico Minor Drainages (31): INHS 87049 (4, 0, 4), UMMZ 156915 (2, 0, 0). Lake Pontchartrain Drainage (31): INHS 87028 (10, 8, 4), KU 20249 (3, 1, 3), SIUC 12762 (6, 4, 6), UMMZ 170678 (2, 0, 0). Mississippi River Minor Drainages (8): UMMZ 156930 (1, 0, 0). Pearl River Drainage (14): AU 14063 (1, 0, 0), NLU 11370 (2, 0, 0), NLU 49903 (1, 0, 0), NLU 60110 (2, 0, 0), SIUC 2925 (1, 0, 1), SIUC 5413 (1, 0, 0). Red River Drainage (8): SIUC 13575 (10, 3, 2), SIUC 15334 (2, 0, 0), UMMZ 161276 (1, 0, 0), UMMZ 161301 (1, 1, 0), UMMZ 184115 (2, 0, 0), UMMZ 184173 (2, 1, 0), UMMZ 211883 (2, 1, 0). Sabine Lake Drainage (10): NLU 1725 (1, 1, 0), NLU 1866 (0, 1, 0).

Mississippi.

Lepomis miniatus. Bay St. Louis Drainage (15): UMMZ 155416 (1, 0, 0), UMMZ 163648 (11, 0, 3), UMMZ 163706 (1, 0, 0). Biloxi Bay Drainage (15): UAIC 1729.09 (1, 0, 0), UMMZ 140095 (2, 0, 0), UMMZ 140099 (11, 0, 4), UMMZ 155438 (1, 0, 0). Escatawpa River Drainage (16): UAIC 4028.19 (3), UF 28090 (2, 0, 0), UF/FSU 13372 (3, 0, 1), UMMZ 155454 (1, 0, 0). Gulf of Mexico Minor Drainages (15): TCWC 317.11 (10, 0, 3). Pascagoula River Drainage (16): UMMZ 163730 (1, 0, 0), UT 90.525 (1, 0, 1). Pearl River Drainage (14): KU 15134 (1, 0, 1), KU 16885 (1, 0, 0), NLU 20058 (1, 0, 0), NLU 20188 (2, 0, 0). Tangipahoa River Drainage (9): INHS 80009 (4, 0, 1). Tombigbee River Drainage (20): UAIC 4398.15 (1, 0, 1). Yazoo River Drainage (7): UT 90.536 (9, 0, 3), UMMZ 146056 (1, 0, 0).

Missouri.

Lepomis miniatus. St. Francis River Drainage (6): KU 9222 (1, 0, 1), KU 9231 (1, 0, 1), KU 9367 (1, 0, 0), KU 9384 (1, 0, 0), KU 9397 (1, 0, 0), KU 9418 (1, 0, 1), KU 9580 (7, 0, 3). White River Drainage (6): KU 11016 (1, 1, 1), KU 10942 (1, 1, 1), KU 11295 (2, 2, 1), SIUC 17669 (1, 1, 0), UMMZ 117436 (1, 0, 0), UMMZ 117526 (2, 0, 0), UMMZ 188607 (14, 5, 3).

North Carolina.

Lepomis punctatus. Atlantic Ocean Minor Drainages (38): SIUC 11325 (2, 0, 1). Cape Fear Drainage (38): NCSM 872 (6, 6, 3), NCSM 1018 (1, 1, 0), NCSM 1861 (1, 1, 0), NCSM 2401 (3, 0, 1), NCSM 5461 (1, 1, 0). Peedee River Drainage (38): NCSM 1282 (1, 0, 0), NCSM 2084 (5, 0, 4), NCSM 6728-6729 (10, 1, 2), NCSM 10827 (4, 0, 4), NCSM 14179 (0, 9, 0), NCSM 14216 (0, 10, 0).

Oklahoma.

Lepomis miniatus. Red River Drainage (8): UMMZ 110875 (3, 1, 0), UMMZ 73083 (4, 0, 0).

South Carolina.

Lepomis punctatus. Ashpoo River Drainage (37): CF 3009 (1, 0, 0), CF 3022 (1, 0, 1). Combahee River Drainage (37): CF 3006 (1, 0, 0), CF 3011 (1, 0, 1), CF 3013-3014 (2, 0, 0), CF 3015 (1), CF 3023 (1, 0, 0), CF 3024

(1, 0, 0), CF 3025 (1, 0, 0), CF 3026 (1, 0, 1), CF 3027 (1, 0, 1), CU 11277 (2, 0, 0). Cooper River Drainage (38): UMMZ 87259 (2, 0, 2). Coosawhatchie River Drainage (37): CF 3002 (1, 0, 0), CF 3007 (1, 0, 0), SIUC 11320 (2, 0, 0). Edisto River Drainage (37): CF 3015-3021 (7, 0, 2), CU 15167 (1, 0, 0). Peedee River Drainage (38): GMBL uncat. (1, 0, 0). Santee River Drainage (38): CF 501 (1, 0, 0), CF 659 (1, 0, 0), CF 660 (1, 0, 0), CF 663 (1, 0, 0), CF 665-667 (3, 0, 1), CU 26247 (4, 0, 0). Savannah River Drainage (37): CF 9410 (5, 0, 0), CU 15252 (0, 1, 0), UF 42708 (1, 1, 0), UG 242 (4, 3, 0), UG 365 (1, 1, 0), UG 1286 (7, 0, 2), UG 1325A (1, 0, 0), UG 1328 (6, 0, 0), UG 1397 (1, 0, 0), UG 1496 (1, 0, 0), UMMZ 135555 (2, 2, 1).

Tennessee.

Lepomis miniatus. Middle Mississippi River Minor Drainages (5): UMMZ 124496 (1, 0, 0), UT 90.57 (2, 0, 1), UT 90.66 (2, 0, 1), UT 90.194 (1, 0, 0), UT 90.568 (3, 0, 2), UT 90.751 (1, 0, 1). Tennessee River Drainage (4): UMMZ 181774 (3, 3, 3), UT 90.90 (2, 2, 1).

Lepomis miniatus x *L. punctatus*. Conasauga River Drainage (17): SIUC 12170 (3, 0, 3), SIUC 12179 (2, 1, 2), UF 26469 (3, 0, 0), UT 90.93 (1, 0, 1), UT 90.747 (2, 0, 2).

Texas.

Lepomis miniatus. Brazos River Drainage (12): UF/FSU 643 (10, 0, 3). Colorado River Drainage (12): TNHC 1082 (10, 0, 0), TNHC 3141 (6, 0, 0), TNHC 5388 (1, 0, 0), TNHC 10534 (3, 0, 0). Galveston Bay Drainage (11): TCWC 210.14 (1, 1, 1), TCWC 626.3 (2, 1, 2), TNHC 645 (2, 0, 0), TNHC 1210 (3, 3, 0), TNHC 1350 (1, 1, 0), TNHC 2795 (1, 1, 0), TNHC 2810 (1, 0, 0), TNHC 5452 (2, 2, 0), TNHC 6042 (3, 3, 0), UMMZ 142902 (1, 1, 1), UMMZ 162891 (1, 1, 0). Guadalupe River Drainage (13): INHS 74257 (3, 2, 2), TCWC 1457.2 (1, 1, 1), TCWC 2073.2 (6, 0, 1), TNHC 2085 (1, 1, 0), TNHC 2982 (5, 4, 0), UT 90.231 (5, 5, 2). Nueces River Drainage (13): TCWC 1491.1 (1, 0, 0). Rio Grande Drainage (13): TNHC 5702 (3, 3, 0). Sabine Lake Drainage (10): SIUC 16053 (0, 5, 0), SIUC 16058 (0, 3, 0), TCWC 561.2 (3, 0, 0), TCWC 790.3 (4, 2, 3), TCWC 854.5 (1, 0, 1), TCWC 1262.7 (2, 1, 0), TCWC 1323.2 (1, 0, 1), TCWC 1490.1 (1, 0, 1), UMMZ 127333 (1, 0, 0), UT 90.254 (5, 3, 3). San Antonio River Drainage (13): TNHC 5328 (2, 0, 0), TNHC 8952 (2, 0, 0). San Bernard River Drainage (12): UMMZ 170326 (2, 0, 0). Red River Drainage (8): TCWC 3189.13 (1, 0, 1), TCWC 3190.16 (2, 0, 0).

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APPENDIX A

Table A1. Frequency distributions of left and right cheek scale rows in *Lepomis miniatus* (CD 1-2, 4-16, 18-21), *L. punctatus* (CD 29-39), and populations in presumed contact zones (CD 3, 17, 22-28).

| Drainage | Scale Rows | | | | | | | | | | | | | | | |
|---|------------|----|----|----|---|----|-----------|------|-------------|----|----|----|---|-----------|------|------|
| | Left Cheek | | | | | n* | \bar{x} | SD | Right Cheek | | | | | \bar{x} | SD | |
| 4 | 5 | 6 | 7 | 8 | 4 | | | | 5 | 6 | 7 | 8 | | | | |
| 1. Illinois R. | | 20 | 9 | 1 | | 30 | 5.37 | 0.56 | 1 | 20 | 9 | | | | 5.27 | 0.52 |
| 2. Ohio R. | 4 | 36 | | | | 40 | 4.90 | 0.30 | 3 | 36 | 1 | | | | 4.95 | 0.32 |
| 3. Lookout Cr. | | 10 | 5 | | | 15 | 5.33 | 0.49 | | 9 | 6 | | | | 5.40 | 0.51 |
| 4. Tennessee R. | 2 | 23 | 6 | | | 31 | 5.13 | 0.50 | 4 | 23 | 4 | | | | 5.00 | 0.52 |
| 5. Middle Miss. R. minor drainages | | 25 | 2 | | | 27 | 5.07 | 0.27 | 1 | 25 | 1 | | | | 5.00 | 0.28 |
| 6. St. Francis R. and White R. | 2 | 33 | 9 | | | 44 | 5.16 | 0.48 | 3 | 31 | 10 | | | | 5.16 | 0.53 |
| 7. Yazoo R. | 3 | 7 | | | | 10 | 4.70 | 0.48 | 2 | 7 | 1 | | | | 4.90 | 0.57 |
| 8. Red R. and lower Miss. R. embayment | 7 | 40 | 4 | | | 51 | 4.94 | 0.47 | 4 | 40 | 7 | | | | 5.06 | 0.47 |
| 9. L. Pontchartrain | 4 | 19 | 8 | | | 31 | 5.13 | 0.62 | 2 | 25 | 4 | | | | 5.06 | 0.44 |
| 10. Sabine L. and Calcasieu R. | 2 | 19 | 1 | | | 22 | 4.95 | 0.38 | 1 | 19 | 2 | | | | 5.05 | 0.38 |
| 11. Galveston Bay | 2 | 16 | | | | 18 | 4.89 | 0.32 | 4 | 14 | | | | | 4.78 | 0.43 |
| 12. Brazos R. to Colorado R. | 1 | 27 | 4 | | | 32 | 5.09 | 0.39 | 1 | 26 | 5 | | | | 5.13 | 0.42 |
| 13. San Antonio R. to Rio Grande | 1 | 27 | 3 | | | 31 | 5.06 | 0.36 | | 25 | 6 | | | | 5.19 | 0.40 |
| 14. Pearl R. | 5 | 8 | | | | 13 | 4.62 | 0.51 | 5 | 8 | | | | | 4.62 | 0.51 |
| 15. Bay St. Louis to Biloxi Bay | 4 | 28 | 2 | | | 38 | 4.84 | 0.49 | 7 | 30 | 1 | | | | 4.84 | 0.44 |
| 16. Pascagoula R. and Escatawpa R. | 1 | 12 | | | | 13 | 4.92 | 0.28 | 4 | 9 | | | | | 4.69 | 0.48 |
| 17. Coosa R. | 13 | 24 | 1 | | | 38 | 4.68 | 0.53 | 12 | 25 | 1 | | | | 4.71 | 0.52 |
| 18. Tallapoosa R. | 4 | 11 | 3 | | | 17 | 5.00 | 0.61 | 2 | 13 | 2 | | | | 5.00 | 0.50 |
| 19. Alabama R. | 8 | 24 | | | | 32 | 4.75 | 0.44 | 10 | 22 | | | | | 4.69 | 0.47 |
| 20. Tombigbee R. | 4 | 15 | 3 | | | 22 | 4.95 | 0.58 | 2 | 18 | 1 | 1 | | | 5.05 | 0.58 |
| 21. Mobile Bay tribs. | 1 | 14 | | | | 15 | 4.93 | 0.26 | 1 | 9 | 5 | | | | 5.27 | 0.59 |
| 22. Perdido Bay and minor coastal tribs. | | 21 | 19 | 1 | | 41 | 5.51 | 0.55 | | 16 | 25 | | | | 5.61 | 0.49 |
| 23. Pensacola Bay | 3 | 42 | 35 | 1 | | 81 | 5.42 | 0.59 | 2 | 34 | 44 | 1 | | | 5.54 | 0.57 |
| 24. Choctawhatchee Bay and minor coastal tribs. | 3 | 45 | 10 | 1 | | 59 | 5.15 | 0.52 | 2 | 42 | 15 | | | | 5.22 | 0.49 |
| 25. St. Andrews Bay | | 8 | 3 | 2 | | 13 | 5.54 | 0.78 | | 5 | 7 | 1 | | | 5.69 | 0.63 |
| 26. Chattahoochee R. | | 8 | 8 | 1 | | 17 | 5.59 | 0.62 | | 7 | 10 | | | | 5.59 | 0.51 |
| 27. Flint R. | | 2 | 8 | | | 10 | 5.80 | 0.42 | | | 10 | | | | 6.00 | 0.00 |
| 28. Chipola R. and Apalachicola R. | | 2 | 10 | 2 | | 14 | 6.00 | 0.55 | | | 12 | 2 | | | 6.14 | 0.36 |
| 29. New R. to California Cr. | | 8 | 38 | 17 | | 63 | 6.14 | 0.62 | 1 | 4 | 41 | 17 | | | 6.17 | 0.61 |
| 30. Suwannee R. | | 6 | 23 | 1 | | 30 | 5.83 | 0.46 | | 3 | 26 | 1 | | | 5.93 | 0.37 |
| 31. Waccasassa R. to Pithlachascotee R. | | 1 | 12 | 6 | | 19 | 6.26 | 0.56 | | | 12 | 7 | | | 6.37 | 0.50 |
| 32. Tampa Bay | | | 6 | 9 | 2 | 17 | 6.76 | 0.66 | | | 5 | 10 | 2 | | 6.82 | 0.64 |
| 33. Peace R. and Myakka R. | | 1 | 10 | 15 | 2 | 28 | 6.64 | 0.68 | | | 11 | 15 | 2 | | 6.68 | 0.61 |
| 34. Everglades and south Florida drainages | | 1 | 39 | 13 | | 53 | 6.23 | 0.47 | | 1 | 37 | 14 | 1 | | 6.28 | 0.53 |
| 35. St. Johns R. and St. Marys R. | | 5 | 23 | 12 | | 40 | 6.18 | 0.64 | | 1 | 24 | 14 | 1 | | 6.38 | 0.59 |
| 36. Satilla R. | | 6 | 10 | | | 16 | 5.62 | 0.50 | | 5 | 7 | 4 | | | 5.94 | 0.77 |
| 37. Altamaha R. | | 2 | 23 | 4 | | 29 | 6.06 | 0.46 | | | 25 | 4 | | | 6.14 | 0.35 |
| 38. Ogeechee R. to Edisto R. | 3 | 24 | 45 | 3 | | 75 | 5.64 | 0.63 | 4 | 22 | 46 | 3 | | | 5.64 | 0.65 |
| 39. Cooper R. to Cape Fear R. | | 8 | 32 | 4 | | 45 | 5.91 | 0.52 | | 9 | 28 | 7 | | | 5.96 | 0.61 |

* Sample sizes apply to both counts.

Table A2. Frequency distributions of left and right pectoral-fin rays in *Lepomis miniatus* (CD 1-2, 4-16, 18-21), *L. punctatus* (CD 29-39), and populations in presumed contact zones (CD 3, 17, 22-28).

| Drainage | Left Pectoral Rays | | | | | | | Right Pectoral Rays | | | | | | | |
|---|--------------------|----|----|----|----|----|-----------|---------------------|----|----|----|----|----|-----------|------|
| | 11 | 12 | 13 | 14 | 15 | n* | \bar{x} | SD | 11 | 12 | 13 | 14 | 15 | \bar{x} | SD |
| 1. Illinois R. | | | 17 | 13 | | 30 | 13.43 | 0.50 | | 1 | 13 | 16 | | 13.50 | 0.57 |
| 2. Ohio R. | | 1 | 33 | 6 | | 40 | 13.13 | 0.40 | | 1 | 28 | 11 | | 13.25 | 0.49 |
| 3. Lookout Cr. | | 1 | 10 | 3 | 1 | 15 | 13.27 | 0.70 | | | 11 | 3 | 1 | 13.33 | 0.62 |
| 4. Tennessee R. | | 2 | 26 | 3 | | 31 | 13.03 | 0.41 | | | 22 | 9 | | 13.29 | 0.46 |
| 5. Middle Miss. R. minor drainages | | 1 | 22 | 4 | | 27 | 13.11 | 0.42 | | 1 | 21 | 5 | | 13.15 | 0.46 |
| 6. St. Francis R. and White R. | | 2 | 34 | 8 | | 44 | 13.14 | 0.46 | | 2 | 35 | 7 | | 13.11 | 0.44 |
| 7. Yazoo R. | | | 9 | 1 | | 10 | 13.10 | 0.32 | | | 8 | 2 | | 13.20 | 0.42 |
| 8. Red R. and lower Miss. R. embayment | | 4 | 42 | 5 | | 51 | 13.02 | 0.42 | | 1 | 42 | 8 | | 13.14 | 0.40 |
| 9. L. Pontchartrain | | 1 | 20 | 10 | | 31 | 13.29 | 0.53 | | 2 | 17 | 12 | | 13.32 | 0.60 |
| 10. Sabine L. and Calcasieu R. | | | 19 | 3 | | 22 | 13.14 | 0.35 | | | 13 | 9 | | 13.41 | 0.50 |
| 11. Galveston Bay | | | 15 | 3 | | 19 | 13.16 | 0.37 | | 1 | 14 | 3 | | 13.11 | 0.46 |
| 12. Brazos R. to Colorado R. | | | 20 | 12 | | 32 | 13.38 | 0.49 | | 1 | 14 | 17 | | 13.50 | 0.57 |
| 13. San Antonio R. to Rio Grande | | 1 | 22 | 8 | | 31 | 13.23 | 0.50 | | 2 | 21 | 8 | | 13.19 | 0.54 |
| 14. Pearl R. | | 2 | 8 | 3 | | 13 | 13.08 | 0.64 | | | 9 | 4 | | 13.31 | 0.48 |
| 15. Bay St. Louis to Biloxi Bay | | 1 | 20 | 16 | 1 | 38 | 13.45 | 0.60 | | | 18 | 19 | 1 | 13.55 | 0.55 |
| 16. Pascagoula R. and Escatawpa R. | | | 5 | 5 | 3 | 13 | 13.85 | 0.80 | | | 4 | 8 | 1 | 13.77 | 0.60 |
| 17. Coosa R. | | 2 | 19 | 17 | | 38 | 13.39 | 0.59 | | 2 | 19 | 17 | | 13.39 | 0.59 |
| 18. Tallapoosa R. | | | 6 | 10 | 1 | 17 | 13.71 | 0.59 | | | 3 | 13 | 1 | 13.88 | 0.49 |
| 19. Alabama R. | | 1 | 11 | 20 | | 32 | 13.59 | 0.56 | | 1 | 11 | 18 | 2 | 13.66 | 0.65 |
| 20. Tombigbee R. | | 1 | 14 | 7 | | 22 | 13.27 | 0.55 | | 1 | 12 | 8 | 1 | 13.41 | 0.67 |
| 21. Mobile Bay tribs. | | | 2 | 13 | | 15 | 13.87 | 0.35 | | | 5 | 10 | | 13.67 | 0.49 |
| 22. Perdido Bay and minor coastal tribs. | | | 18 | 22 | 1 | 41 | 13.59 | 0.55 | | | 15 | 25 | 1 | 13.66 | 0.53 |
| 23. Pensacola Bay | | 3 | 54 | 24 | | 81 | 13.26 | 0.52 | | 2 | 47 | 31 | 1 | 13.38 | 0.56 |
| 24. Choctawhatchee Bay and minor coastal tribs. | | 1 | 15 | 42 | 1 | 59 | 13.73 | 0.52 | | 1 | 11 | 46 | 1 | 13.80 | 0.48 |
| 25. St. Andrews Bay | | | | 12 | 1 | 13 | 14.08 | 0.28 | | | | 13 | | 14.00 | 0.00 |
| 26. Chattahoochee R. | | | 15 | 2 | | 17 | 13.12 | 0.33 | | | 1 | 13 | 3 | 13.12 | 0.49 |
| 27. Flint R. | | 1 | 6 | 3 | | 10 | 13.20 | 0.63 | | 1 | 0 | 8 | 1 | 12.90 | 0.74 |
| 28. Chipola R. and Apalachicola R. | | | 7 | 7 | | 14 | 13.50 | 0.52 | | | 8 | 6 | | 13.43 | 0.51 |
| 29. New R. to California Cr. | | | 14 | 43 | 6 | 63 | 13.87 | 0.55 | | | 14 | 41 | 8 | 13.90 | 0.59 |
| 30. Suwannee R. | | | 7 | 23 | | 30 | 13.77 | 0.43 | | | 7 | 21 | 2 | 13.83 | 0.53 |
| 31. Waccasassa R. to Pithlachascotee R. | | | 5 | 13 | 1 | 19 | 13.79 | 0.54 | | | 3 | 12 | 4 | 14.05 | 0.62 |
| 32. Tampa Bay | | | 2 | 12 | 2 | 17 | 14.00 | 0.50 | | | 1 | 14 | 1 | 13.94 | 0.43 |
| 33. Peace R. and Myakka R. | | 1 | 3 | 23 | 1 | 28 | 13.86 | 0.53 | | 1 | 2 | 22 | 3 | 13.96 | 0.58 |
| 34. Everglades and south Florida drainages | | | 20 | 33 | | 53 | 13.62 | 0.49 | | 1 | 17 | 35 | | 13.64 | 0.52 |
| 35. St. Johns R. and St. Marys R. | | | 16 | 21 | 3 | 40 | 13.68 | 0.62 | | | 13 | 22 | 5 | 13.80 | 0.65 |
| 36. Satilla R. | | 1 | 5 | 10 | | 16 | 13.56 | 0.62 | | | 5 | 11 | | 13.69 | 0.48 |
| 37. Altamaha R. | | | 7 | 15 | 7 | 29 | 14.00 | 0.71 | | | 5 | 20 | 4 | 13.97 | 0.57 |
| 38. Ogeechee R. to Edisto R. | | | 24 | 48 | 3 | 75 | 13.72 | 0.53 | | | 18 | 53 | 4 | 13.81 | 0.51 |
| 39. Cooper R. to Cape Fear R. | | | 18 | 26 | | 44 | 13.59 | 0.50 | | | 16 | 28 | | 13.64 | 0.49 |

* Sample sizes apply to both counts.

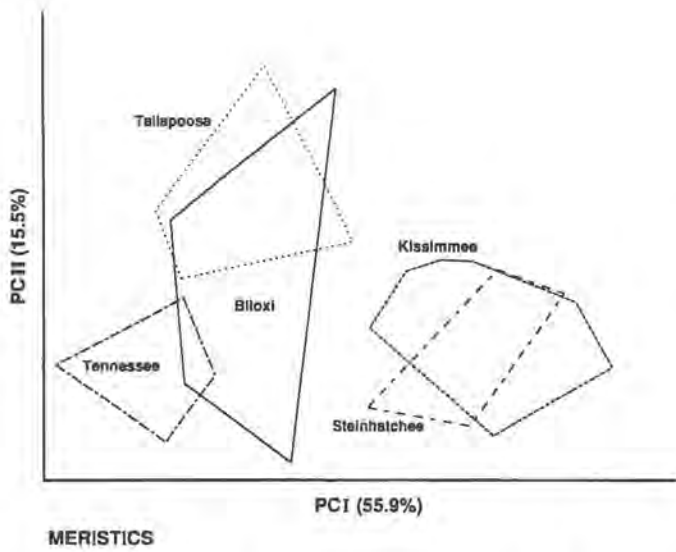


Figure A1. Meristic PCA axes I and II, with polygons bounding individuals of the *Lepomis punctatus* complex from the first set of five randomly selected localities.

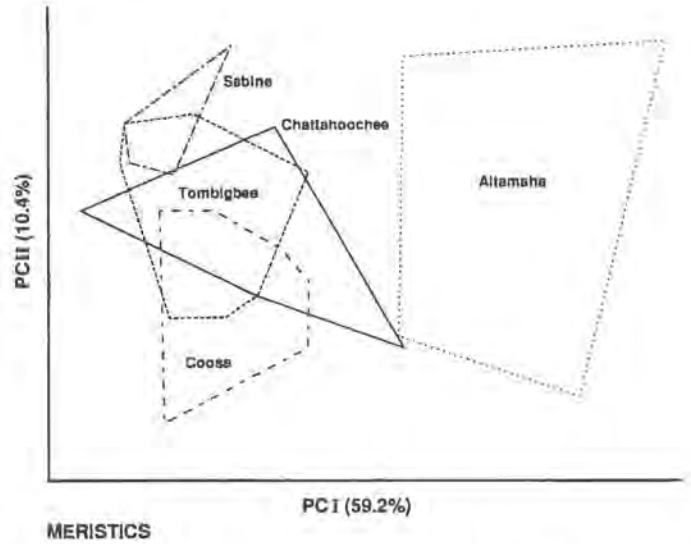


Figure A2. Meristic PCA axes I and II, with polygons bounding individuals of the *Lepomis punctatus* complex from the second set of five randomly selected localities.

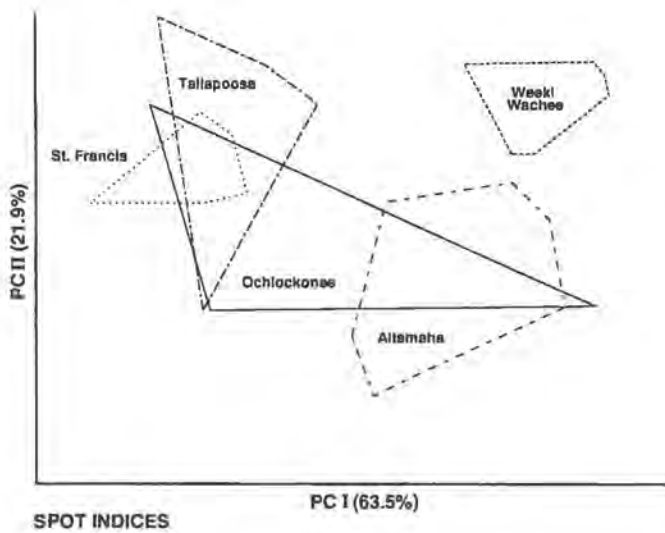


Figure A3. Spot residual PCA axes I and II, with polygons bounding individuals of the *Lepomis punctatus* complex from the first set of five randomly selected localities.

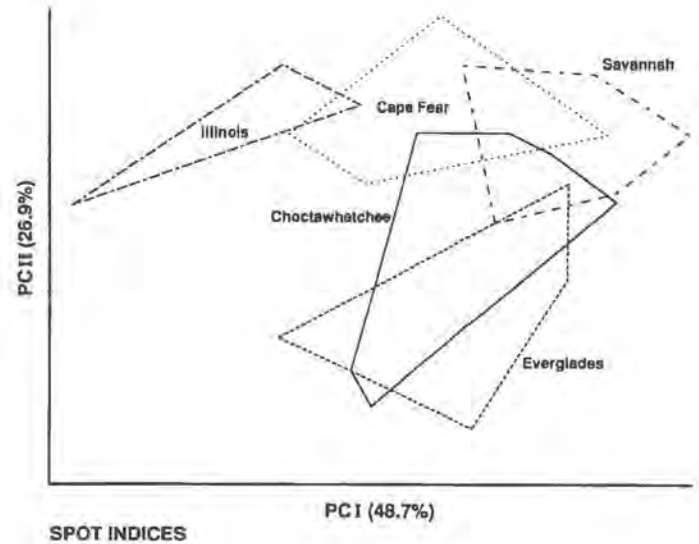


Figure A4. Spot residual PCA axes I and II, with polygons bounding individuals of the *Lepomis punctatus* complex from the second set of five randomly selected localities.

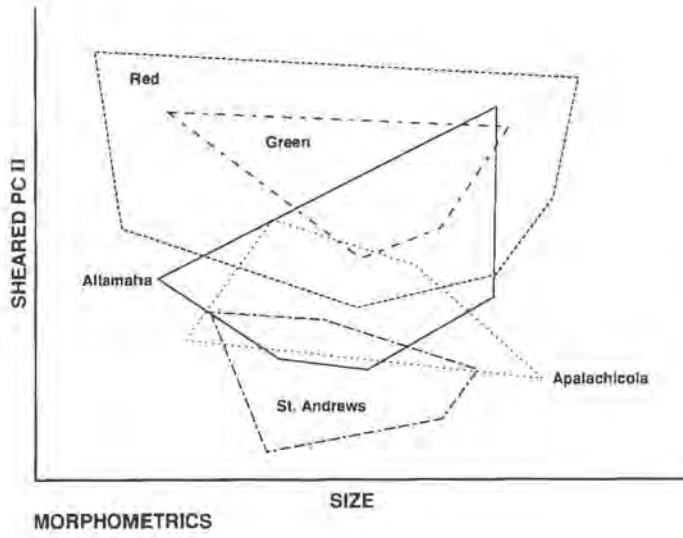


Figure A5. Sheared PCA axes I (Size) and II, with polygons bounding individuals of the *Lepomis punctatus* complex from the first set of five randomly selected localities.

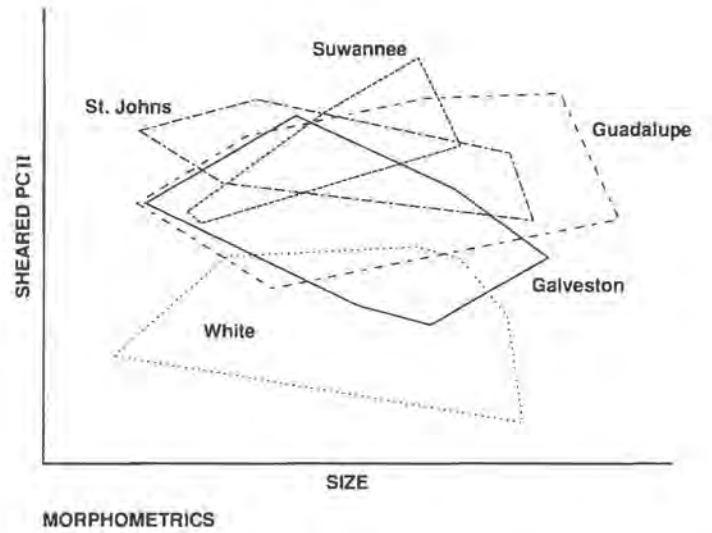


Figure A6. Sheared PCA axes I (Size) and II, with polygons bounding individuals of the *Lepomis punctatus* complex from the second set of five randomly selected localities.

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