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LUTJANUS AMBIGUUS (POEY), A NATURAL INTERGENERIC HYBRID OF *OCYURUS CHRYSURUS* (BLOCH) AND *LUTJANUS SYNAGRIS* (LINNAEUS)

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ABSTRACT

Poey (1860) described *Mesoprion* (=*Lutjanus*) *ambiguus*, a peculiar snapper that he thought might be a natural hybrid between *Ocyurus chrysurus* and *Lutjanus synagris*. Since its description, *L. ambiguus* has been declared a valid species by some authors, a hybrid by others. In this paper I present evidence for the hybrid origin of *L. ambiguus*. Fewer than thirty records for *L. ambiguus* exist in museums or in the literature, yet all collection data indicate it is a shallow-water coastal species inhabiting a heavily fished region. Its apparent rarity would be surprising for a valid species, but not so for a hybrid fish. *L. ambiguus* has been collected only at locations where the ranges of the supposed parental species overlap. Similarly an analysis of the spawning patterns and seasonality of shallow-water snappers demonstrates that *O. chrysurus* and *L. synagris* would be one of the most likely pairs to produce a natural hybrid. The meristic data, size and shape of the fins, and the life colors of *L. ambiguus* overlap or are intermediate between those of the proposed parental forms. The comparison of 18 meristic and morphometric characters from the presumed parental forms and the hybrid, using the Hubbs and Kuronuma (1941) Hybrid Index, yielded a mean index value of 42% for *L. ambiguus*, demonstrating the intermediacy of its morphology. Principal components analysis of the three groups also showed the intermediate placement of the specimens of *L. ambiguus*. The data strongly imply that *L. ambiguus* is a natural hybrid between two nominally distinct genera. Because *Ocyurus chrysurus* occasionally seems to hybridize with several species of *Lutjanus* in nature, the genera may be nearer in relationship than is indicated by the presently accepted classification.

Poey (1860) described a new lutjanid taxon as *Mesoprion* (=*Lutjanus*) *ambiguus* from one specimen taken near Havana, Cuba. The specific epithet was derived from Poey's observation that the holotype (probably USNM 13036) showed coloration and morphology that seemed a mix of the lane snapper (*Lutjanus synagris*) and the yellowtail (*Ocyurus chrysurus*). In his original description, and in a later redescription of the holotype and a second specimen (MCZ 9951), Poey (1875) stated his inclination to consider *L. ambiguus* a hybrid and a hermaphrodite. Jordan and Swain (1884) and Jordan and Evermann (1898) examined Poey's specimens, concluding that the blending of characters supported the hypothesis of a hybrid origin. The next account of *L. ambiguus*, other than in Jordan et al. (1930), was given by Breder (1948), in which he called it the Cuban snapper, a rare fish found only in Cuba and at Key West, Florida. Breder (1948) also mentioned the possibility of a hybrid origin. Briggs (1958) appeared to repeat Breder's Key West record—probably AMNH 4494 or 4793. Several additional specimens, unreported in the literature, were deposited in museum collections prior to 1960 (AMNH 18997, AMNH 19038, and AMNH 11175). The largest collection of *L. ambiguus*, 18 specimens, was made by canvassing fishing cooperatives along both coasts of Cuba during the summer of 1961 (Rodriguez-Pino, 1961). Luis R. Rivas (pers. comm.), familiar with the snapper fishery in Cuba at that time, believed that Rodriguez-Pino would have sorted through tens of thousands of snappers to find those 18 specimens. The number of specimens of *L. ambiguus* reported in the century following its description totalled 25.

Rodriguez-Pino (1961) concluded that *L. ambiguus* could be a valid species, but she could not disprove the possibility of it being a hybrid. Her histological study of the gonads showed that the specimens were not hermaphrodites. Starck in Starck and Schroeder (1971) apparently misinterpreted Rodriguez-Pino's (1961) conclusions because he cited her work as demonstrating that *L. ambiguus* was a valid species. Anderson (1967) compared meristic and morphometric characters of Poey's specimens to similarly sized specimens of *O. chrysurus* and *L. synagris,* concluding that *L. ambiguus* was intermediate in many characters and might be a hybrid.

Despite a number of references in the literature to *L. ambiguus,* Schwartz (1972, 1981) did not list this taxon in his world list of fish hybrids. In a catalogue of Cuban fishes, Duarte-Bello (1959) listed *L. ambiguus* as the Cuban snapper which ranged from Cuba to Key West; in a later supplement, Duarte-Bello and Buesa (1973) considered it a valid species, but mentioned parenthetically that it might be a hybrid of *O. chrysurus* and *L. synagris. Lutjanus ambiguus* did not appear in a recent listing of Cuban marine fishes (Guitart, 1977), nor in a paper on snappers of the Caribbean waters of Colombia (Acero and Garzon, 1985). Allen (1985) provided a synopsis of the diagnostic characters of *L. ambiguus* and remarked that it was formerly thought to be a hybrid, but he did not explain why, or by whom, it was no longer considered a hybrid. In a review of Allen (1985), Acero (1987) commented on the inclusion of *L. ambiguus* as a valid species without supporting data. Richards (1988), in a review of Polovina and Ralston (1987) in which Allen wrote a synopsis of the genus *Lutjanus,* stated it was unfortunate that Allen listed *L. ambiguus* as a valid species when it is "clearly an intergeneric hybrid of *Lutjanus synagris* and *Ocyurus chrysurus.*"

This review of the history of the taxon *L. ambiguus* demonstrates that its taxonomic status remains in confusion. In this paper I intend to provide support for the hybrid origin of *Lutjanus ambiguus* by the analysis of several data sets. I have examined all available specimens to take meristic and morphometric data which I compared to data from the supposed parental species. I mapped the distribution of collection localities for *L. ambiguus* against the ranges of the parental species. I also examined published accounts on the spawning seasonality and spawning sites for shallow-water western Atlantic snappers to demonstrate that the combination of *Ocyurus chrysurus* and *Lutjanus synagris* is among the most likely to produce a natural hybrid. Hubbs (1955) presented several general conditions that apply to hybrid fishes: the hybrid is usually intermediate in characters by which the parental forms differ; hybrids are very rare among marine fishes; and hybridization is a function of the environment in that it is more likely to occur when the parental species share similar spawning habitats and seasonality. I shall show that *L. ambiguus* is intermediate in most characters when compared to the probable parental forms, and that it has been collected only where those forms co-occur. I shall propose that the interbreeding of the genera *Ocyurus* and *Lutjanus* suggests a closer phylogenetic relationship than is currently indicated.

Materials and Methods

Meristic and morphometric data were taken following Hubbs and Lagler (1970), except that "maxillary length" is substituted for "upper jaw length." When applicable, measurements were made on the left side of the fish. Gillraker counts were taken from the first gill arch and include both developed rakers and rudiments on the upper and lower limbs of the arch. I chose specimens of the putative parents to match the size range of available *L. ambiguus* specimens to reduce allometric influence on character variation. Measurements were made using dial calipers and large dividers, and are expressed as thousandths of the standard length (SL). A dissecting microscope was used in counting fin rays, scales, and gill rakers. Measurements for all specimens of *L. ambiguus* are given in Appendix 1. I excerpted data for geographic ranges, spawning seasonality, and spawning habitat from literature references and museum records. The life color description of *L. ambiguus* is derived from an examination of a fresh specimen (UF 31652, Fig. 1). The calculation of the hybrid index (HI) comparing the measurements and counts of *L. ambiguus* to the parental forms followed the procedure of Hubbs and Kuronuma (1941). Mensural and count data were also examined using Principal Components Analysis (PCA) (SPSS-4.0 and SPSS-PC+, Norusis 1986) on the correlation matrix of the variables. The mean substitution procedure for missing variable values was used to insure inclusion of the maximum number of *L. ambiguus* in this analysis; specimen MCZ 9951 was excluded because of the large number of missing values (Appendix 1). Varimax (orthogonal) rotation made interpretation of the factors simpler. The scores for each specimen on the first two principal components were plotted in a scattergram that shows the relation among, and variation within, each known group in the direction of those components. On the scatterplot, presumed 95% confidence ellipses were computed and drawn around the three groups to indicate the distribution of the sample populations (SAS Version 6.06, 1989). This use of PCA does not attempt statistical inference from the data sets, nor should the ellipses be interpreted as strict bivariate 95% confidence intervals, because assumptions of normality were not satisfied (Neff and Smith 1979). PCA was used in this case to illustrate the relative placement of specimens of *L. ambiguus*.

Material Examined.—Acronyms for institutional collections follow Leviton et al. (1985), with two non-standard abbreviations: UMIM (University of Miami collections, now housed at UMML); EVER (Everglades National Park Museum). Fish sizes are reported in standard lengths. Specimens marked by an asterisk (*) were too small to include in the analyses:

Lutjanus ambiguus (10 specimens; Size range = 54 mm–266 mm): *Florida*—No locale given, AMNH 4793 (253 mm); Key West, AMNH 4494 (215 mm); Marquesas Keys, UMML 21923 (266 mm); Key Largo, UF 31652 (201 mm); *Cuba*—Havana region, MCZ 9951 (198 mm); USNM 13036 (192 mm); *Haiti*—Port-au-Prince, AMNH 18997* (54 mm); AMNH 19038* (69 mm); *Panama*—Caledonia Bay, AMNH 11175* (96 mm); *Venezuela*—Los Roques Archipelago, Isla Loco, AMNH 35999 (249 mm).

Lutjanus synagris (12 specimens; Size range = 196 mm–250 mm): *Florida*—Miami, UMML 33752 (2 specimens from lot; 222–243 mm); UMIM 6062 (2 specimens from lot; 220–238 mm); Key West, USNM 26584 (208 mm); *Bahamas*—Nassau, UF 3530 (197 mm); *Jamaica*—USNM 38521 (2 specimens from lot; 205–207 mm); W.N.W. of Kingston—UMML 6095 (2 specimens from lot; 198–250 mm); UMML uncatalogued (2 specimens from lot; 196–250 mm).

Ocyurus chrysurus (12 specimens; Size range = 187 mm–270 mm): *Florida*—Miami, UMIM 6063 (210 mm); UMML uncatalogued (212 mm); Florida Keys, UMML 19215 (270 mm); Key Largo, EVER (BISC47) (214 mm); Ellis Rock, UF 37436 (187 mm); Dry Tortugas, UF 31180 (191 mm); Lower Matecumbe Key, UMML 20487 (212 mm); *Mexico*—Campeche, UMIM 2414 (195 mm); *Cayman Islands*—Grand Cayman, UF 12969 (191 mm); *Colombia*—Providencia, UF 20582 (204 mm), UF 25602 (234 mm), UF 25888 (203 mm).

Results

Requests for records of *L. ambiguus* from museums produced only 10 specimens, three too small to be useful for these analyses. There were apparently no museum specimens or literature references for *L. ambiguus* from the Bahamas, Mexico, Jamaica, Puerto Rico, or Colombia. An additional 18 specimens were reported and examined by Rodriguez-Pino (1961) in Cuba, but she did not provide morphometric data. Therefore, I could not include her specimen data in my analyses. The coloration of a freshly killed *L. ambiguus* (UF 31652; Fig. 1) taken by angling on a shallow patch reef was intermediate between the presumed parents. Above the wide, yellow midlateral stripe was a second, narrower yellow stripe, above which were numerous yellow ovals on a blue-gray background. In preservative, those blotches faded to reveal a pattern of indistinct diagonal stripes above the midline and faint bars on the body. Below the midline, the base color was pinkish-orange, with six narrow yellow stripes along the length of the body. Anal, dorsal, and pelvic fins were yellow, pectoral fins clear, and the caudal fin orange. The midline stripe extended onto the head beneath the orbit, and the narrow stripes below the midline also extended into the head. The iris was orange-red, and there was no black blotch beneath the soft dorsal fin as in *L. synagris*. This color pattern closely agrees with that reported for *L. ambiguus* by Poey (1875) and Rodriguez-Pino (1961).

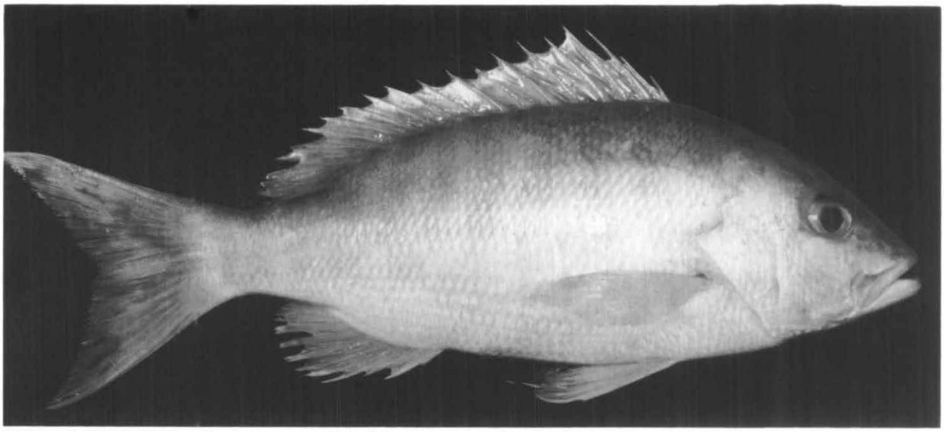

Figure 1. *Lutjanus ambiguus,* UF 31652, 20.1 cm SL, Key Largo, Florida. Right side of specimen was photographed because of damage to the left side of head.

The dentition, and the shape of the head and fins, appeared intermediate between the parental forms in all *L. ambiguus* examined. The canine teeth were small and weak, although slightly larger than in *Ocyurus.* The vomerine tooth patch in *L. ambiguus* is crescentric to chevron-shaped, with a medial posteriorly directly extension that is intermediate in length compared with the length of the tooth patches of the parental forms. The profile of the head in *L. ambiguus* sloped more steeply than in *Ocyurus,* but not to the degree seen in most *Lutjanus* spp. (Fig. 1). The shape of the dorsal and anal fins resembled *Ocyurus,* and although the caudal fin was less deeply forked than in *Ocyurus,* the caudal lobes were longer than in *L. synagris* (Fig. 1).

The meristic data from the seven specimens of *L. ambiguus* used in this study overlapped greatly with counts from 12 specimens each of *L. synagris* and *Ocyurus chrysurus* (Table 1). The gill-raker counts showed the best separation among the taxa, so were used in the PCA and Hybrid Index calculations with the morphometric values (Appendix 1). Fifteen morphometric and three meristic characters for the three taxa showed intermediacy for most characters in specimens of *L. ambiguus* (Table 2, Appendix 1). That intermediacy was demonstrated by calculating the hybrid index (Hubbs and Kuronuma, 1941) for *L. ambiguus,* an expression of the morphological distance of the arithmetic means of the hybrid's counts and measurements with relation to those of the two supposed parental species. Table 2 shows a mean hybrid index of 41.48 for *L. ambiguus,* in comparison with *L. synagris* and *O. chrysurus.* For individual characters, an index value of 50 indicates exact intermediacy for the hybrid, less than or more than 50 shows a closer affinity to the character states of Parent 1 or Parent 2, respec-

Table 1. Comparisons of meristic data for the three snapper taxa

	L. ambiguus	*L. synagris*	*O. chrysurus*
Dorsal-fin rays	X, 13	X, 12–13	X, 12–14
Anal-fin rays	III, 9	III, 8–9	III, 8–9
Pectoral-fin rays	15–16	15–16	15–16
Lateral-line scales	48–51	48–50	46–49
Gill rakers upper/lower	8–9/16–18	5–7/8–14	6–10/17–22

Table 2. Mean morphometric values expressed as thousandths of the standard length, and selected meristic data, used to calculate the hybrid index for *Lutjanus ambiguus*

	L. synagris (P1)	*L. ambiguus* (Hybrid)	*O. chrysurus* (P-2)	P1-P2	P1-hybrid	Hybrid index*
Standard length	219.50	224.86	210.25	—	—	—
Suborbital width	82.08	68.00	50.00	32.08	14.08	43.90
Maxillary length	150.00	137.43	121.42	28.58	12.57	43.98
Mandible length	186.67	175.33	157.33	29.33	11.34	38.65
Interorbital width	72.08	80.43	94.33	−22.25	−8.35	37.51
Body depth	348.33	344.83	335.25	13.08	3.50	26.78
Caudal peduncle depth	120.50	118.71	110.17	10.33	1.79	17.32
Pectoral-fin length	301.83	288.50	305.58	−3.75	13.33	—
Anal-fin length	254.08	236.83	234.92	19.17	17.25	90.00
Middle caudal-ray length	176.08	164.50	135.08	41.00	11.58	28.25
Upper caudal-ray length	264.75	293.67	396.09	−131.34	−28.92	22.02
Lower caudal-ray length	258.83	287.00	366.83	−108.00	−28.17	26.08
2nd anal-spine length	87.67	76.33	63.67	24.00	11.33	47.22
Pelvic-fin length	216.17	210.29	200.75	15.42	5.88	38.12
Head length	384.40	366.86	340.08	44.32	17.54	39.58
Snout length	143.90	129.57	116.33	27.57	14.33	51.98
Upper gill rakers	6.17	8.43	8.00	−1.83	−2.26	—
Lower gill rakers	11.17	15.71	20.25	−9.08	−4.54	50.02
Total gill rakers	17.33	24.14	28.25	−10.92	−6.81	62.35

* Mean Hybrid Index 41.48 ± SDI 17.04.

tively. Table 2 supports the qualitative impressions of fin size in the hybrid in that the upper and lower caudal lobes are longer than in *L. synagris,* but not nearly as long as in *Ocyurus.* The hybrid index values also showed a deeper caudal peduncle and body for the hybrid compared with *Ocyurus,* and a shorter depressed anal fin length than in *L. synagris.* The mean hybrid index value of 41.48 indicates a slight domination by *L. synagris* characters in the hybrids. In two characters, pectoral fin length and the number of rakers on the upper lobe on the first gill arch, the mean values for *L. ambiguus* fell outside the mean for either parent, so were not used in calculating the hybrid index value.

Table 3. Rotated factor pattern matrix derived from PCA analysis (* = factor loadings less than 0.5 in absolute value)

	Factor 1	Factor 2
Lower gill rakers	−0.94648	*
Interorbital width	−0.92118	*
Upper caudal-ray length	−0.91409	*
Lower caudal-ray length	−0.91235	*
Total gill rakers	−0.87796	*
Suborbital width	0.82152	*
Snout length	0.81356	*
Head length	0.77053	0.50626
Maxillary length	0.70886	0.63174
2nd anal-spine length	0.67046	0.59857
Mandible length	0.65745	0.62502
Pelvic-fin length	*	0.86958
Body depth	*	0.74136
Anal-fin length	*	0.73044
Mid caudal-ray length	0.57106	0.70192
Caudal peduncle depth	*	0.65722
Pectoral-fin length	*	0.62666
Upper gill rakers	*	0.60451

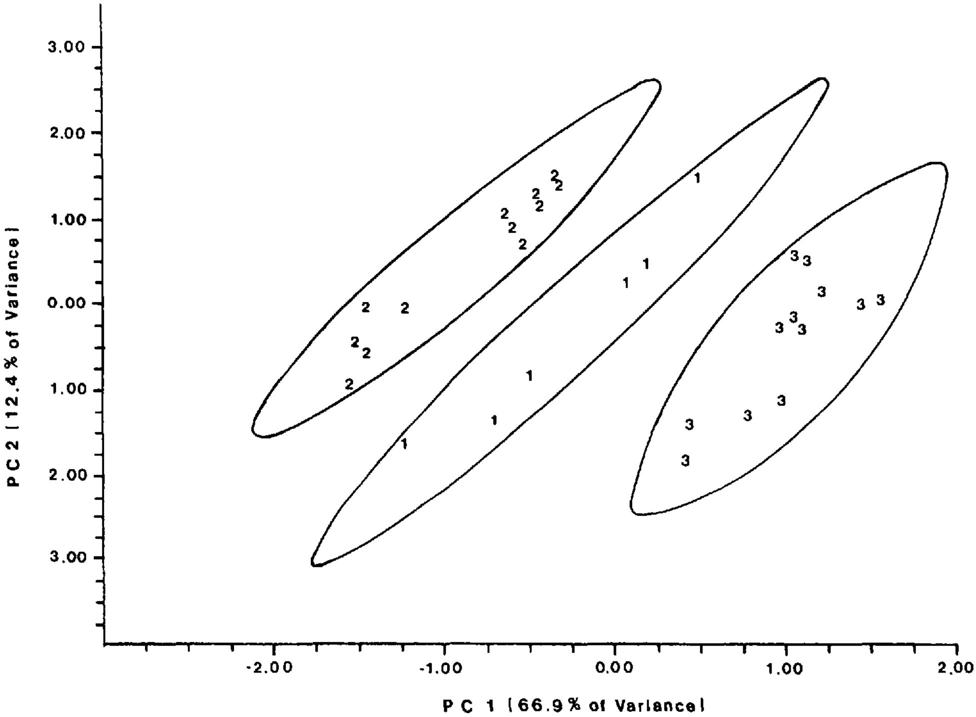

Figure 2. Positions of the specimens from the three groups in the projection on the first two principal components of the 18-character correlation matrix. The 95% confidence ellipses from each group were computed from the scores of each sample on the first two principal components. Numbers refer to taxonomic groups: 1 = *Lutjanus ambiguus*; 2 = *L. synagris*; 3 = *Ocyurus chrysurus*.

The mean coefficients of variation (C.V.) for the 18 characters of the three groups were similar: *L. ambiguus* = 6.77; *L. synagris* = 6.43; *O. chrysurus* = 6.40, indicating that, overall, the hybrid was only slightly more variable in characters than the parental forms. Although the coefficients of variation for most variables in the data sets were rather low, in each taxon one of the gill-raker counts was the most variable character.

Principal components analysis of the 18 variables produced two major factors with eigenvalues of 12.047 and 2.223, which together explained 79.3% of the variability in the data set; the remaining factors had eigenvalues less than 1.0. Factor one had high negative loadings for variables when character values for *L. synagris* were lower than in the other taxa (Table 3). The highest loadings on factor one were for caudal fin and cephalic measurements, and gill raker counts. Highest loadings on factor two were for various fin lengths, jaw measurements, and body and caudal peduncle depths (Table 3). The plot of the 95% confidence ellipses for the three groups shows complete separation from the two parental taxa of the six specimens assigned to *L. ambiguus* (Fig. 2).

Location data for *L. ambiguus* collected from museum records and the literature showed a distinctly West Indian/Caribbean distribution which extends into southern Florida (Fig. 3). Specimens have been reported only from waters where the ranges of the supposed parental species overlap (Allen, 1985), although not throughout their entire sympatric ranges. I was unable to find records from Mexico,

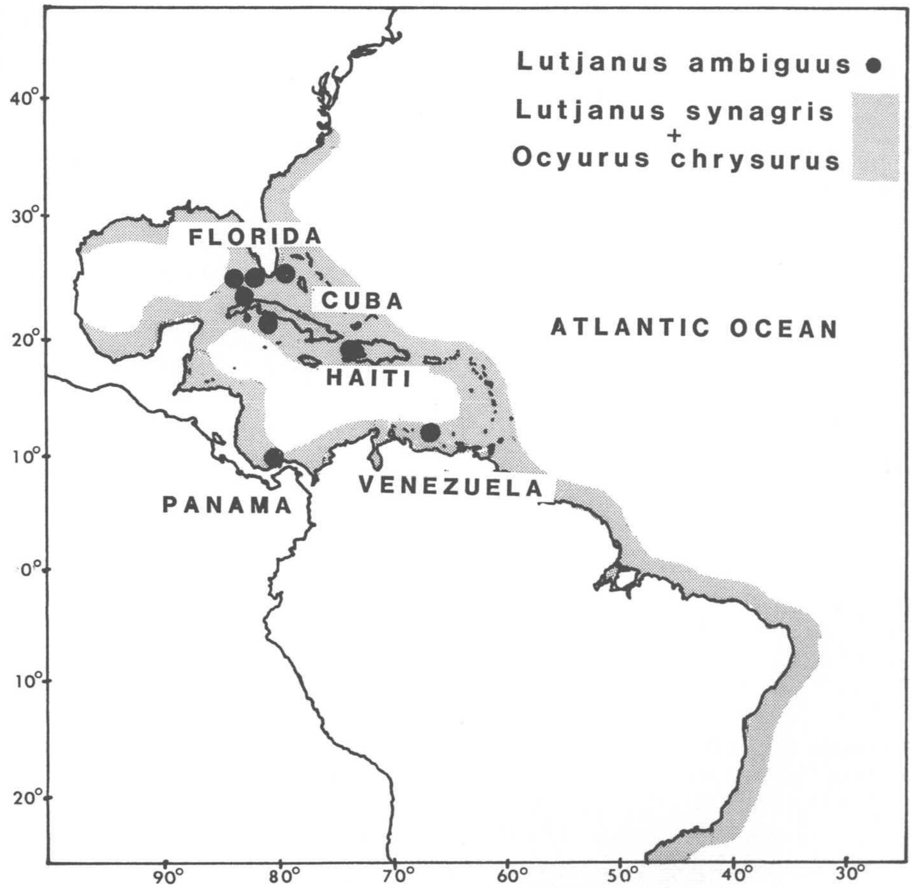

Figure 3. Distribution of *Lutjanus ambiguus* superimposed upon the ranges of the putative parental species, *Lutjanus synagris* and *Ocyurus chrysurus*.

Puerto Rico, the Bahamas, Jamaica, and for most of the Caribbean coast from Middle America to Colombia. Cuba has produced the majority (20) of known specimens (Poey, 1875; Rodriguez-Pino, 1961).

The analysis of literature accounts of the habitat usage and spawning patterns of western Atlantic lutjanids indicated that one of the most likely species pairs to produce a natural hybrid through accidental fertilization is *L. synagris* and *O. chrysurus*. Both species inhabit and spawn in relatively shallow waters, often in association with reef structures (Randall, 1968; Allen, 1985; Grimes, 1987). Most western Atlantic lutjanids inhabit and probably spawn in waters much deeper than *Ocyurus* (C. R. Gilbert, pers. comm.), reducing the possibility of accidental hybridization. Erdman (1976) reported a spawning period near Puerto Rico from March to September for *Ocyurus*, overlapping with that of *L. synagris*. In Jamaica, both species overlapped in timing of spawning (Munro et al., 1973), with *Ocyurus* spawning year-round. Both species have a spawning period from March to late summer in Cuba (Piedra, 1969; Druzhinin, 1970; Claro and Reshetnikov, 1981), and juvenile recruitment data indicated nearly year-round spawning in Cuban waters (Garcia-Arteaga et al., 1990). In Trinidad, *L. synagris* spawned year-round with a March peak (Manickchand-Dass, 1987).

Discussion

The analyses presented in this paper support a hybrid origin for the fish described as *L. ambiguus.* The survey of museum collections and the literature provided fewer than 30 records for this taxon, most from tropical coastal waters. Although those specimens might represent a reproductively isolated species produced by hybridization, the rarity of *L. ambiguus* in collections indicates it is more likely the product of occasional hybridization. Rodriguez-Pino (1961) concluded her paper by emphasizing that *L. ambiguus* was an extraordinarily rare species. Were this a viable species, it would be remarkable for a brightly colored, edible-sized snapper to have escaped detection in waters heavily used by divers and fishermen. The fish might normally inhabit deeper waters inaccessible to fishermen, but the specimens examined lacked the coloration typical of deepwater snappers. Its apparent rarity may be best explained by a hybrid produced through accidental fertilization. The low incidence of hybrid marine fishes compared to the frequency of hybridization in freshwater fishes is well-documented (Hubbs, 1955; Schwartz, 1972, 1981), and is especially true in tropical marine waters (Hubbs, 1955). Coincident with the low frequency of marine fish hybridization is the rarity of such hybrid individuals (Hubbs, 1955).

Assuming that *L. ambiguus* is a hybrid, the data and analyses presented here support that it is an intergeneric hybrid between *L. synagris* and *Ocyurus chrysurus.* Neff and Smith (1979) discussed the problems with attempting to infer the parental species of natural hybrids in their criticism of Hubbs' Hybrid Index, in that use of the index requires a priori identification of the parental species and assumes uniform intermediacy of the physical characters of the hybrid. Hubbs (1955) stated that natural interspecific hybrids are almost always intermediate between the parental species in the characters in which they differ. This rule was generally confirmed by Neff and Smith's (1979) analysis of natural and laboratory-produced hybrids, although they demonstrated that variability in some hybrid characters may present problems of discrimination in hybrid identification.

I approached the problem of a priori designation of proposed parents for *L. ambiguus* through the elimination of species of *Lutjanus* as parents. Fin morphology and coloration of *L. ambiguus* strongly indicated *Ocyurus* as the other parent. The meristic data for the hybrid ruled out several *Lutjanus* spp., as did ecological information on habitat usage (Anderson, 1967; Allen, 1985; Bortone and Williams, 1986). The size at maturity of *L. ambiguus* pointed to the likelihood of the *Lutjanus* parent being one of the smaller species. None of the *L. ambiguus* specimens in collections exceeded 266 mm SL. Those with mature gonads examined by Rodriguez-Pino (1961) ranged from 169 to 366 mm TL. *L. synagris* is one of the most abundant, smaller species of western Atlantic *Lutjanus* (maximum size 356 mm, Randall 1968). Although data are scanty for spawning seasonality and spawning habitats of snappers, the analysis of existing information pointed to *L. synagris* as a most likely accidental partner for *Ocyurus* because of overlap in timing and place of spawning. Starck in Starck and Schroeder (1971) observed that gray snapper (*L. griseus*) seemed to spawn in groups that milled about actively over reef structures at dusk. If other snapper species employ broadcast spawning behavior, then the probability of accidental hybridization should be highest in species that share spawning habitats and seasons. The coloration of the fresh specimen I examined also showed the probable influence of *L. synagris.* Because species are usually less abundant towards the limits of their ranges, the probability of accidental hybridization through encounters of ripe individuals of the putative parents should be higher nearer the center of their sympatric distribution. All specimens of *L. ambiguus* have been taken in Florida and Caribbean waters where the putative parents are abundant (Fig. 3).

The results of the Hybrid Index analysis demonstrated the expected intermediacy of the characters of *L. ambiguus* compared to *O. chrysurus* and *L. synagris*. The plot of the principal component scores for specimens of the three taxa also showed the intermediacy and lack of overlap for specimens assigned to *L. ambiguus* (Fig. 2). The taxon *L. ambiguus* meets the criteria that characterize hybrid organisms—rarity, intermediacy in coloration and morphology, and occurrence sympatric with the putative parents. Another characteristic of hybrids beyond the scope of this study is abnormal gonadal development and high sterility in the F_1 generation related to problems of spermatogenesis (Hubbs, 1955). Most of the specimens I examined had been eviscerated or had the gonads disturbed so I cannot comment on their state. Poey (1875) remarked that the two individuals he described were hermaphrodites. Of the 18 specimens examined by Rodriguez-Pino, those with mature gonads showed no evidence of hermaphroditism. Of significance to the question of hybridism is Rodriguez-Pino's (1961) finding that the mature gonads of *L. ambiguus* were only one-third the size of mature gonads of *O. chrysurus* or *L. synagris,* possibly indicative of abnormal development. There are no data available on the fertility of specimens of *L. ambiguus.*

An obvious way of demonstrating the possibility of hybrid origin of *L. ambiguus* would be to artificially cross *Ocyurus* and *L. synagris* under controlled conditions, and to raise the progeny to a size where their characters could be compared to the descriptions of *L. ambiguus.* Fortunately, as this study was nearing completion, laboratory production of hybrid progeny of *Ocyurus* and *L. synagris* was accomplished (Domeier and Clarke, 1992). The progeny closely matched the description of Poey's (1875) specimens. Domeier and Clarke's (1992) results, in combination with the analyses reported in this paper, strongly support a hybrid origin for *L. ambiguus.* With the advances in marine aquaculture facilities and rearing techniques, it will now be possible to address the reproductive ability and genetics of this hybrid.

Hubbs (1955) presented numerous examples to illustrate the close collection between hybridization and phylogenetic relationships of the parental forms. As presently understood, *L. ambiguus* represents an intergeneric hybrid of the monotypic *Ocyurus* and the polytypic *Lutjanus.* Domeier and Clarke (1992) presented evidence for three hybrid forms resulting from crosses of *Ocyurus* and several *Lutjanus* spp. They concluded that *Ocyurus* may not be generically distinct from *Lutjanus,* especially when meristic similarities are also considered. The morphology of *Ocyurus* reflects its adaptation to a midwater, planktivorous lifestyle, in contrast to the benthic habits of most *Lutjanus* spp. A recent study of Indo-Pacific lutjanoids (Caesionidae) suggested that the morphology of those species, which are midwater planktivores, had diverged sufficiently to require separation from the immediate outgroups, the sub-families of lutjanid snappers (Carpenter 1990). Whether the magnitude of morphological adaptations of *Ocyurus* is great enough to demand generic separation will best be answered by comparing *Ocyurus* and other lutjanid species in intensive systematic and genetics studies. In the case of *L. ambiguus,* the production of viable progeny in natural and laboratory crosses of *O. chrysurus* × *L. synagris* demonstrates genetic compatability which must be considered in phylogenetic classification.

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Appendix 1. Morphometric measurements expressed as thousandths of the standard length, and selected meristic characters for *Lutjanus ambiguus*. Dash (—) indicates that specimen damage precluded accurate measurements

L. ambiguus	*USNM 13036*	*UMML 21923*	*AMNH 35999*	*UF 31652*	*AMNH 4494*	*AMNH 4793*	*MCZ 9951*	*Mean*	*STD*	*Coef. Var. (%)*
Standard length (mm)	192	266	249	201	215	253	198	224.86	28.12	12.51
Suborbital width	65	73	67	72	65	71	63	68.00	3.66	5.39
Maxillary length	139	143	143	142	130	127	138	137.43	5.97	4.35
Mandible length	176	174	183	180	169	170	—	175.33	5.02	2.86
Interorbital width	78	90	77	89	74	87	68	80.43	7.76	9.65
Body depth	332	—	344	379	330	352	332	344.83	17.17	4.98
Caudal peduncle depth	122	124	113	124	116	116	116	118.71	4.16	3.51
Pectoral-fin length	310	308	259	316	284	254	—	288.50	24.76	8.58
Anal-fin length	247	239	227	256	219	233	—	236.83	12.28	5.19
Middle caudal-ray length	166	176	145	176	158	166	—	164.50	10.74	6.53
Upper caudal-ray length	318	344	293	295	243	269	—	293.67	32.41	11.04
Lower caudal-ray length	297	303	276	282	—	277	—	287.00	10.97	3.82
2nd anal-spine length	75	69	81	87	79	67	—	76.33	6.90	9.03
Pelvic-fin length	225	212	201	226	200	210	198	210.29	10.75	5.11
Head length	364	365	384	373	367	356	359	366.86	8.64	2.36
Snout length	129	136	137	135	133	115	130	129.57	7.63	5.89
Upper gill rakers	8	7	11	8	10	7	8	8.43	1.40	16.61
Lower gill rakers	17	16	12	17	17	15	16	15.71	1.67	10.60
Total gill rakers	25	23	23	25	27	22	24	24.14	1.55	6.43