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Variations in Morphology and Coloration in the Black Hamlet, *Hypoplectrus nigricans* (Teleostei: Serranidae)

ALFONSO AGUILAR-PERERA *Department of Marine Sciences, University of Puerto Rico, Mayagüez, PR 00681-9013. aaguilar@cima.uprm.edu*

ABSTRACT.—Black hamlet (*Hypoplectrus nigricans*) was observed to vary in coloration and morphology in Puerto Rico, Mexico and Belize. *H. nigricans* from Puerto Rico exhibited a larger, grayish body (pectoral fins transparent), with long and pointed pelvic fins, and lunate caudal fin, while individuals from Mexico and Belize exhibited a smaller, darker body (including pectoral fins), with shorter and no pointed pelvic fins, and a truncated caudal fin. Occurrence of coloration and morphology variations of *H. nigricans* had not been previously noted, and this is the first record of such in the western Atlantic. Color variants are known for at least four species of *Hypoplectrus*; however, these variants appear to be sympatric in the same geographic region. In contrast, *H. nigricans* variants may be allopatric. Smaller, darker variants were not found in Puerto Rico, while larger, grayish variants were not found in Mexico or Belize. Reasons for the occurrence of geographically segregated *H. nigricans* variants are not fully understood, but a hypothesis that may explain it, still needing further testing, is ongoing speciation.

KEYWORDS.—hamlets, *Hypoplectrus*, reef fishes, Serranidae, fish coloration, speciation

The genus *Hypoplectrus* comprises a group of simultaneous hermaphroditic fishes (Fischer 1980), commonly known as hamlets, associated to coral reefs of the northwestern Atlantic (Böhlke and Chaplin 1993; Randall 1996). The northern limit of *Hypoplectrus* is Bermuda (Smith-Vaniz et al. 1999), while the southern is Venezuela (Domeier 1994; Heemstra et al. 2002), and it is absent from the southwestern Atlantic (Floeter and Gasparini 2000). Reviews on the genus have been provided by Thresher (1978), Fischer (1980), and the most recent and comprehensive by Domeier (1994). Species encompassing *Hypoplectrus* were distinguished solely on variations in coloration pattern, since they are morphologically similar. Thus, individuals with different color patterns were largely considered by ichthyologists as color variants of the first described species, *H. unicolor* Walbaum, 1792 (Graves and Rosenblatt 1980; Robins et al. 1986). Nonetheless, *Hypoplectrus* is now considered as comprised by several species based on slight differences in morphology and ecology (Randall and Randall 1960; Böhlke and Chaplin 1993; Domeier 1994).

At least ten species are recognized and described by ichthyologists, including: butter hamlet (*H. unicolor* Walbaum 1792), barred hamlet (*H. puella* Cuvier and Valenciennes 1828), yellowtail hamlet (*H. chlorurus* Cuvier and Valenciennes 1828), black hamlet (*H. nigricans* Poey 1852), golden hamlet (*H. gummigutta* Poey 1852), indigo hamlet (*H. indigo* Poey 1852), shy hamlet (*H. guttavarius* Poey 1852), yellowbelly hamlet (*H. aberrans* Poey 1868), blue hamlet (*H. gemma* Goode and Bean 1882), and masked hamlet (*H. providencianus* Acero and Garzon 1994). A recently reported species (*H. cf. maculiferus* Poey 1871, Heemstra et al. 2002), commonly known as bicolor hamlet, needs clarification and at least two more (Belizean blue hamlet and tan hamlet) remain undescribed (Heemstra et al. 2002). Recently, mtDNA studies revealed no genetic difference among at least nine hamlet species (García-Machado et al. 2004; Ramon

et al. 2003); however, another concurrent study revealed differences for at least five species (McCartney et al. 2003).

During a study of hamlets from southwestern Puerto Rico (Aguilar-Perera 2003), I collected specimens of black hamlet (*Hypoplectrus nigricans* Poey 1852). When identifying them, using descriptions of Domeier (1994) and Humman (2002), some morphological and coloration differences emerged when comparing such descriptions with those of Randall (1996). Thence, I proceeded to compare the specimens from Puerto Rico, which were similar to descriptions of Randall (1996), to other specimens of *H. nigricans* but from Mexico and Belize, Mesoamerican Barrier Reef System (MBRS), which were similar to descriptions of Domeier (1994) and photographs of Humman (2002). Therefore, I document herein the variations in morphology and coloration exhibited by *H. nigricans* from Puerto Rico and two locations in the MBRS.

In southwestern Puerto Rico, field work was conducted in coral reefs off La Parguera from September to December of 2000 and 2001. Underwater visual censuses and hamlet collections were carried out before noon (09:30-10:30 hrs) in randomly selected areas (Aguilar-Perera 2003). Of the 206 hamlets sighted, 22 were *H. nigricans*. In previous fieldwork, underwater visual censuses were carried out in coral reefs of northern Belize (Turneffe) in 1992 and in Mexico (southern Quintana Roo, Mexican Caribbean) in 1995. At each of these locations, at least 5 and 15 individuals of *H. nigricans* were sighted in randomly selected reefs during diurnal hours, respectively. At least 20 specimens were collected in Puerto Rico and 12 in Mexico (none from Belize due to logistic restrictions).

All specimens were measured to the nearest 0.1 mm, including: Total length (TL), standard length (SL), head length, eye diameter, body depth, snout length, caudal peduncle depth and upper-jaw; predorsal, prepectoral, prepelvic, and preanal lengths. In addition, some meristics such as, dorsal and pectoral fins, lateral line scales and gill raker counts, were recorded according to Randall (1996) and Heemstra and Randall

(1993). Specimens from Puerto Rico were frozen after capture to preserve coloration until examination and description were conducted; then, fixed in 10% formalin, preserved in 75% ethanol and maintained in the fish collection of the Department of Marine Sciences, University of Puerto Rico (Mayagüez) at Magueyes Island. Specimens from Mexico were fixed, preserved, and deposited in the fish collection of El Colegio de la Frontera Sur in Quintana Roo.

In the MBRS (Mexico and Belize), *H. nigricans* showed body and fins blackish to intense dark, pectoral fins with dark pigment (i.e., not transparent), and darkish eyes (like in *H. chlorurus*). Mean body size of 91.2 mm SL (N = 12) with a range of 83.7-99.5 mm SL (Table 1). Pelvic fins short and rounded, not reaching the third spine of anal fin, and truncated caudal fin with lobes not pointed. Fish were collected in coral reefs at depths no shallower than 10 m. In Puerto Rico, *H. nigricans* showed a body brownish to grayish with the anterior part of pelvic and anal fins intense blue and the pectoral fins completely transparent (i.e., no dark pigment), with long and pointed pelvic fins reaching at least the third spine of the anal fin. Caudal fin lunate with lobes pointed. First upper ray in pectoral fins slightly blackish and yellow eyes (no dark pigmentation, like *H. chlorurus*). Mean body size of 98.2 mm SL (N = 20) with a range of 68-115 mm SL (Table 1). Fish were collected in coral reefs at depths not exceeding 6 m.

Hypoplectrus nigricans from Puerto Rico differed in coloration and morphology compared to individuals from MBRS. According to Randall and Randall (1960) and Randall (1996), *H. nigricans* commonly differs from the other hamlet species (e.g., *H. unicolor*) in having a body brownish to grayish with very long pelvic fins reaching the fourth ray in the anal fin. In fact, descriptions of *H. nigricans* by Randall and Randall (1960) and Randall (1996) are similar to Poey's (1852) original description.

Variations of *H. nigricans* in morphology and coloration described in this work are evident when comparing the specimen's photographs of Randall (1996), Humman

TABLE 1. Morphometrics (in millimeters) and meristics of Black Hamlet (*Hypoplectrus nigricans*) variants from Mexico and Puerto Rico. Mean length in parenthesis.

Measurements and counts	Mexico	Puerto Rico
Number of fish	12	20
Depth occurrence	>10 m	<6 m
Morphometrics		
Total length	101.0-118.8	84.3-150.0
Standard length	83.7-99.5 (91.2)	68.0-115.0 (98.2)
Head length	33.7-40.0	26.2-43.8
Snout length	12.2-13.0	7.1-12.4
Upper jaw length	15.8-19.0	10.5-17.5
Body depth	39.0-48.2	28.8-55.9
Eye diameter	8.0-10.1	6.6-9.5
Caudal peduncle depth	11.2-13.0	8.9-15.5
Meristics		
Dorsal fin	X-15 (16)	X-15 (16)
Pectoral fin rays	12-13	13
Lateral scales	51-60	50-58
Total gill rakers	7(6) + 1 + 12 (13)	7(6) + 1 + 11 (12)

(2002), and Domeier (1994). While Randall (1996) did not remark on *H. nigricans* pectoral fins, in his photographs such fins appear as evidently transparent (i.e., no pigment). In contrast, Domeier (1994) described *H. nigricans* as having well pigmented (dark) pectoral fins, while Humann (2002) showed photographs of individuals with very dark pectoral fins.

In Puerto Rico, *H. nigricans* fits Randall's description but not that of Domeier's or Humann's. *H. nigricans* with dark pectoral fins and dark body were observed in coral reefs of the MBRS. Nonetheless, *H. nigricans* as described by Randall were not found in the MBRS. Such a difference in coloration and morphology between *H. nigricans* had not been previously noted in the region. While it is not ruled out the possibility that same variants, either Randall's or Domeier's, may be found in other locations within the northwestern Atlantic region (e.g., Florida, Cuba), it is still necessary to further document such evidence.

According to Domeier (1994), some population centers for *Hypoplectrus* species exist in the region, which are explained by historic and geographic isolation. Many species are rare outside their respective population center, and expatriates are explained through larval transport; however, the degree of transport is not high enough

to allow all species to occur sympatrically. According to this hypothesis, *H. nigricans* has its population center in Puerto Rico (Domeier 1994). However, if that was the case, Randall's variant (body grayish with no pigment in pectoral fins) and not Domeier's (dark body with dark pigment in pectoral fins) occurs in Puerto Rico.

Many fishes associated to coral reefs exhibit color variations along their life history. For example, the Coney grouper (*Cephalopholis fulva*) exhibits three coloration phases: red in deepwater, orange-brown or bicolor in shallow waters and xanthic (i.e., yellow) in shallow and deep waters (Townsend 1929; Heemstra and Randall 1993; Nemtsov et al. 1993). Other groupers, such as scamp (*Mycteroperca phenax*) and gag (*M. microlepis*), display a variety of color phases associated with social behavior (Gilmore and Jones 1992), while the speckled hind (*Epinephelus drummondhayi*) display color variations associated to ontogenetic phases (Ross 1988). Similarly, parrotfishes (Scaridae) have three basic color phases: brightly colored in terminal (adult) males, drab in intermediate (adult) males and females and pale coloration for juveniles (Barlow 1975).

Other *Hypoplectrus* species also exhibit color variations (Thresher 1978). *H. puella* has four variants: striped-barred, center-

spotted, solid-barred, and front barred. In the Bahamas, the center-spotted variant dominates, but occasionally the solid-barred and striped barred variants are also present. In the southern Caribbean and Florida, *H. unicolor* has two variations related to the presence or absence of the blue-ringed, nasal ocelli. In Jamaica, *H. chlorurus* exhibits three variations in body coloration (brown, black and bluish) (Domeier 1994). According to Domeier (1994), *H. aberrans* has two variants based on dorsal coloration (blue or brown), with the blue variant occurring in Puerto Rico and Virgin Islands. However, in Puerto Rico the dorsally brown variant occurs (Randall 1996), while the blue variant (which may be the referred *H. c.f. maculiferus* found in Central America, Heemstra et al. 2002) has not been recorded (Aguilar-Perera 2003).

While variants of *H. puella*, *H. unicolor*, and *H. chlorurus* are sympatric with respect to the other variants of the same species (Thresher 1978), *H. nigricans* variants appear to be allopatric. While the *H. nigricans* darker variant with pigmented pectoral fins occurred in the MBRS, the grayish-brownish variant with transparent pectoral fins occurred in Puerto Rico. It appears to be that observed *H. nigricans* variants do not coexist together in the same geographic location. Moreover, not only the color but also the morphology (pelvic fins and caudal fin) vary. Specimens from Puerto Rico were larger, with pointed and long pelvic fins compared to those from MBRS, while individuals in the latter region were smaller with short and rounded pelvic fins.

Coloration and morphological characteristics exhibited by *H. nigricans* variants in locations sampled were consistent, and I hypothesize that such variations may not be the result of hybridization, ontogenetic process or any reversible change in coloration pattern to adjust to the environment (i.e., camouflage), as this latter is the case in many serranid fishes (Smith 1971). In the MBRS, *H. nigricans* darker variant was not easily confounded with other hamlets, such as tan hamlet or Belizean blue hamlet. The former exhibits a tan-brown body with pectoral fins transparent, while the latter has

an intense blue body. Reasons for the occurrence of *H. nigricans* variants are not fully understood; however, further sampling covering a greater geographical area is needed to determine either a wide range in distribution or geographic segregation for each *H. nigricans* variant.

Another hypothesis still to be tested in regard to the presence of variants in *Hypoplectrus* would be the case of a very recent speciation due to ecological causes (Schluter 2001). Studies on comparative phylogeography (i.e., biology, genetics, and biogeography combined; e.g., Avise 2000) are strongly recommended to determine the phylogenetic and population genetic distinctiveness not only for *H. nigricans* variants but also for the ten species comprising the *Hypoplectrus* genus (and their variants also). Phylogeographic studies have elucidated the influence of barriers (i.e., distance, riverine outflow) on the population structure of some marine fishes (e.g., Acanthuridae) and degree of population separation (Rocha et al. 2002), and also the possibility of ecological speciation (Schluter 2001) in fishes associated to coral reefs (Rocha 2003).

Current status of *Hypoplectrus* species is even more complex than expected. Three recent genetic studies on mtDNA, comparing up to nine species, reached contrasting results in relation to differences among the putative species. Ramon et al. (2003), based on collections of nine species from Belize, Jamaica, and Florida, found no genetic differences among species. Similarly, García-Machado et al. (2004) found no differences among six species from Cuba. In contrast, McCartney et al. (2003) found differences among five species from Puerto Rico, Panama and Jamaica. None of these studies rule out the continued recognition of *Hypoplectrus* color "morphs" as distinct species and reach similar conclusions related to the possibility that *Hypoplectrus* has experienced a recent speciation, (433000 years; McCartney et al. 2003) as consequence of earlier isolations of populations due to changes in sea level.

For the resolution of the *Hypoplectrus* taxonomy, Ramon et al. (2003) recommend to

adopt a clear statement of the minimal criteria for the recognition of species, since color alone is not sufficient. Additional data from more geographic locations on assortative mating (McCartney et al. 2003), ecological differences in larval dispersal and recruitment, genetics of color morphology and development of color preferences (Ramon et al. 2003), and hybrid fertility and self-fertilization studies (García-Machado, et al. 2004) are needed to provide a better understanding of the population structure and evolutionary dynamics of *Hypoplectrus*.

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