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Article



A review of the Caribbean hamlets (Serranidae, *Hypoplectrus*) with description of two new species

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Abstract

Thirteen species of the Western Atlantic genus *Hypoplectrus* (Serranidae) are currently recognized, two of which are described as new. *Hypoplectrus maya* n. sp. (Maya hamlet) is restricted to the coastal lagoon of the Meso-American Barrier Reef system in Belize. It is a solid iridescent blue, lacks nose spots and lacks black margins on fins. *Hypoplectrus randallorum* n. sp. (Tan hamlet) is found widely in the central and western Caribbean. Its color varies from light brown to tan and it has spots on the nose, at the base of the pectoral fin and occasionally on the upper part of the caudal peduncle. All identified species of *Hypoplectrus* are illustrated in live coloration along with examples of color variations in *H. nigricans* and *H. unicolor*. A historical review of *Hypoplectrus* is included with a discussion of issues concerning their taxonomy.

Introduction

The hamlets are small (max about 20cm SL) reef fishes found throughout the Caribbean (Randall 1968, Domeier 1994, Heemstra *et al.* 2002, Aguilar-Perera & Gonzalez-Salas 2010, Holt *et al.* 2010). They are predatory fish that feed on small crustaceans and tiny fishes (Randall 1967, Whiteman *et al.* 2007, Holt *et al.* 2008). Hamlets are simultaneous hermaphrodites, which broadcast spawn in the water column (Barlow 1975, Fisher 1980a, 1981, 1987; Lobel & Neudecker 1985). Individual fish maintain pair bonds and the paired fish exchange positions between mating bouts whereby they take turns spawning as male or female. Mating hamlets produce a unique sound while gametes are dispersed which may help to synchronize spawning (Lobel 1992, 2002). The fish also produce a very low amplitude pre-mating sound. Preliminary acoustic field recordings suggest that different hamlet species possibly produce different pre-mating sound patterns, although this has yet to be statistically validated (Lobel 1992).

On any given coral reef location in the tropical western Atlantic ocean, several hamlet species are typically sympatric, maintaining reproductive isolation with occasional hybridization (Barlow 1975, Fisher 1980a, 1981, Lobel and Neudecker 1985, Domeier 1994, Puebla *et al.* 2007). These fishes are intriguing both because of their hermaphroditic behavior as well as the possibility of their exhibiting sympatric speciation (e.g. Fisher 1980b, 1987; Charnov 1982, Rocha & Bowen 2008, Salzburger 2008). It has been proposed that the hamlets have evolved as aggressive mimics of non-predatory reef fishes (Randall & Randall 1960, Thresher 1978, Fisher 1980b, Randall 2005). This scenario of mimicry driving the evolution of hamlet species was reviewed by Puebla (2009).

Defining the species in the genus *Hypoplectrus* has been a classic taxonomic problem in ichthyology for decades. No clear morphological or meristic characters delineate the hamlet "species" except color patterns (Randall 1968, Fisher 1980b, Domeier 1994). Color pattern and geographic distribution appear to be reliable characters for defining the hamlet species (Randall 1968, Heemstra *et al.* 2002, Aguilar-Perera 2003, Puebla *et al.* 2007, Aguilar-Perera & Gonzalez-Salas 2010, Holt *et al.* 2010). Hamlets display strong mating preference for individuals of the same color pattern. However, the boundaries of the species as defined by color are confounded by occasional mixed matings and hybrids (Barlow 1975, Fisher 1980b, Rao & Lakshmi 1999). The results of these mixed mating are offspring with mixed coloration (Domeier 1984, Whiteman *et al.* 2007). Mating between same colored (i.e. species) hamlets produce offspring of the same color pattern as the parents (Domeier 1994). The difficulty of defining the hamlet species flock is similar to that found for African rift-lake cichlids (Puebla 2009). In this regard, the importance of using behavior for aiding in the definition of "evolutionary significant units" (Stauffer *et al.* 1995, 2002) is noteworthy. As in cichlids, the hamlet species flock is recently evolved with one estimate placing divergence at about 400,000 years ago (McCartney *et al.* 2003). Available evidence suggests that hamlets maintain segregation by behavioral mating preferences for like-colored mates. This behavior plus the biogeography of species distributions combined with recent genetic data supports the designation as species for the hamlet lineages defined by distinct color patterns (Domeier 1994, Heemstra *et al.* 2002, Ramon *et al.* 2003, McCartney *et al.* 2003, Puebla *et al.* 2007, 2009; Aguilar-Perera & Gonzalez-Salas 2010, Holt *et al.* 2010). Coloration coupled with biogeography has been used to similarly characterize the enigmatic species complexes in many other reef fishes (e.g Springer 1988, Randall and Bruce 1983, Randall & Edwards 1984, Randall & Pyle 2001a,b; Greenfield & Randall 2008, Baldwin *et al.* 2011).

Two new hamlet species are described in this paper based on color and biogeographic distribution. The "Tan" hamlet has been recognized in the literature for decades (Randall & Randall 1960, Thresher 1978, Graves & Rosenblatt 1980, Domeier 1994, Heemstra *et al.* 2002, Aguilar-Perera & Gonzalez-Salas 2010, Holt *et al.* 2010). It has a broad distribution including the Florida Keys, Puerto Rico, West Indies and Belize (Aguilar-Perera & Gonzalez-Salas 2010, Holt *et al.* 2010). The "Maya" hamlet was found in Belize by the author in 1993. It was probably the fish observed in Belize at Laughing Bird Cay by Domeier (1994), who reported it as *H. gemma*. Smith *et al.* (2003) referred to it as an undescribed species and reported on its distribution in the Pelican Cays, Belize. The Maya hamlet is known only from Belize. Both the "Tan" and the "Maya" hamlets were included in the taxonomic review by Heemstra *et al.* 2002 (as *Hypoplectrus* sp. "tan" and *Hypoplectrus* species "Belize", respectively).

Material and Methods

Type specimens of the new species of *Hypoplectrus* and additional specimens used for comparison have been deposited in the Museum of Comparative Zoology, Harvard University (MCZ) and the Bishop Museum (BPBM), Honolulu, HI.

Lengths of specimens are given as standard length (SL), measured from the median anterior point of the upper lip to the base of the caudal fin (posterior end of the hypural plate); body depth is measured at the origin of pelvic fins and body width at the axil of the pectoral fins (as viewed from the ventral side); head length (HL) is taken from the median anterior point of the upper lip to the posterior end of the opercular membrane; orbit diameter is the greatest fleshy diameter, and interorbital width the least fleshy width; snout length is measured from the median anterior point of the upper lip to the nearest fleshy edge of the orbit; upper-jaw length from the same anterior point to the posterior end of the maxilla; caudal-peduncle depth is the least depth, and caudal-peduncle length the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; lengths of spines and rays are measured to their extreme bases; caudal- and pectoral-fin lengths are the lengths of the longest ray; pelvic-fin length is measured from the base of the pelvic spine to the tip of the longest soft ray.

Data in parentheses in the descriptions apply to paratypes. Morphometric data in the descriptions are given as percentages of the standard length with range from minimum to maximum in parentheses.

X-rays were used for meristic counts and were prepared by Andrew Williston, Dept of Fishes, Museum of Comparative Zoology, Harvard University. All photographs of live fishes were photographed underwater in their habitat by the author.

Comparative material:

Specimens collected from Discovery Bay, Jamaica, July 1990, P. S. Lobel: n=4 *H. puella*, n=4 *H. indigo*, n=1 *H. nigricans*, n=1 *H. guttavarius*, n=2 *H. unicolor*. Specimens collected from Discovery Bay, Jamaica, April 1991, P. S. Lobel: n=6 *H. puella*. Specimens collected from Conch reef, Key Largo, Florida, Feb. 1992, P. S. Lobel: n=3 *H. gemma* & n=1 *H. puella*. Specimens collected from Glovers Atoll, Belize, July 1999, P. S. Lobel, L. K. Lobel & J. E. Randall; n=9 *H. nigricans*; n=2 *H. indigo*, n=1 *H.puella*, n=7 *H.unicolor*. Specimens collected from the Pelican Cays, Belize, July 1999, P. S. Lobel, L. K. Lobel & J. E. Randall; n=4 *H. puella*, n=1 *H. aberrans*.

Genetic sequence data for several of the type specimens and for specimens used for comparative material are deposited in GenBank and are available on the NIH Nucleotide database (<u>http://www.ncbi.nlm.nih.gov/nuccore/</u>).

The genetic data for these specimens were generated and reported by Ramon *et al.* 2003 (Accession numbers AY262168–AY262254). Voucher specimens are deposited in the MZC and are listed in Table 1 which shows the MCZ number and corresponding GenBank number.

MCZ number	GenBank	species	location	date
169216	AY262238	H. gemma	Florida	Feb-92
169217	AY262180	H. puella	Florida	Feb-92
169218	AY262239	H. gemma	Florida	Feb-92
169219	AY262240	H. gemma	Florida	Feb-92
169231	AY262204	H. nigricans	Glovers Atoll, Belize	Jul-99
169232	AY262205	H. nigricans	Glovers Atoll, Belize	Jul-99
169233	AY262192	H. indigo	Glovers Atoll, Belize	Jul-99
169236	AY262193	H. indigo	Glovers Atoll, Belize	Jul-99
169237	AY262186	H. puella	Glovers Atoll, Belize	Jul-99
169238	AY262230	H. unicolor	Glovers Atoll, Belize	Jul-99
169239	AY262231	H. unicolor	Glovers Atoll, Belize	Jul-99
169240	AY262233	H. unicolor	Glovers Atoll, Belize	Jul-99
169241	AY262234	H. unicolor	Glovers Atoll, Belize	Jul-99
169242	AY262206	H. nigricans	Glovers Atoll, Belize	Jul-99
169243	AY262207	H. nigricans	Glovers Atoll, Belize	Jul-99
169244	AY262208	H. nigricans	Glovers Atoll, Belize	Jul-99
169245	AY262209	H. nigricans	Glovers Atoll, Belize	Jul-99
169246	AY262210	H. nigricans	Glovers Atoll, Belize	Jul-99
169247	AY262211	H. nigricans	Glovers Atoll, Belize	Jul-99
169248	AY262212	H. nigricans	Glovers Atoll, Belize	Jul-99
169249	AY262235	H. unicolor	Glovers Atoll, Belize	Jul-99
169206	AY262168	H. puella	Jamaica	7-Jul-90
169207	AY262169	H. puella	Jamaica	7-Jul-90
169208	AY262170	H. puella	Jamaica	7-Jul-90
169209	AY262171	H. puella	Jamaica	7-Jul-90
169210	AY262187	H. indigo	Jamaica	7-Jul-90
169211	AY262188	H. indigo	Jamaica	7-Jul-90
169212	AY262189	H. indigo	Jamaica	7-Jul-90
169213	AY262190	H. indigo	Jamaica	7-Jul-90
169234	AY262199	H. nigricans	Jamaica	7-Jul-90
169235	AY262194	H. guttavarius	Jamaica	7-Jul-90
169214	AY262213	H. unicolor	Jamaica	7-Jul-90
169215	AY262214	H. unicolor	Jamaica	7-Jul-90
169220	AY262172	H. puella	Jamaica	14-17April-91
169221	AY262173	H. puella	Jamaica	14-17April-91
169222	AY262174	H. puella	Jamaica	14-17April-91
169223	AY262175	H. puella	Jamaica	14-17April-91
169226	AY262176	H. puella	Jamaica	14-17April-91
169228	AY262177	H. puella	Jamaica	14-17April-91
169205	AY262182	H. puella	Pelican Cayes, Belize	Jul-99
169229	AY262203	H. nigricans	Pelican Cayes, Belize	Jul-99
169230	AY262197	H. aberrans	Pelican Cayes, Belize	Jul-99

TABLE 1. Comparative specimens deposited in the MCZ, Harvard and GenBank.

Hypolectrus maya, n. sp.

(Figs. 1, 2; Tables 2, 3)

Hypoplectrus sp "Belize" Heemstra *et al.* 2002: page 1368. *Hypoplectrus* sp Smith *et al.* 2003 (Pelican Cays, Belize)

Holotype: MCZ 169196, 86.2 mm SL, Tunicate Cove, Pelican Cays, 7 Dec. 1997, 16^o 39.6' N, 88^o 11.1'W, 3m depth, reef and seagrass, spear, P. S. Lobel.

Paratypes: MCZ 169194, 73.5 mm SL, Tunicate Cove, Pelican Cays, 9 Dec. 2001, 3m depth, reef and seagrass, spear, P. S. Lobel; MCZ 169195, 87.2 mm SL, Tunicate Cove, Pelican Cays, 9 Dec. 2001, 3m depth, reef and seagrass, spear, P. S. Lobel; MCZ 169197, 70.0 mm SL, Tunicate Cove, Pelican Cays, 9 Dec. 2001, 3m depth, reef and seagrass, spear, P. S. Lobel; MCZ 169198, 86.0 mm SL, Tunicate Cove, Pelican Cays, 7 July 1999, 3m depth, reef and seagrass, spear, P. S. Lobel and J. E. Randall (GenBank AY262250);. MCZ 169199, 82.9 mm SL, Tunicate Cove, Pelican Cays, 7 July 1999, 3m depth, reef and seagrass, spear, P. S. Lobel and J. E. Randall (GenBank AY262251). MCZ 169200, 68.1mm SL, Tunicate Cove, Pelican Cays, 10 November 1994, 3m depth, reef and seagrass, spear, P. S. Lobel, photographed underwater (GenBank AY262249). MCZ 169201, 94.4 mm SL, collected with holotype. MCZ 169202, 57.6 mm SL, Tunicate Cove, Pelican Cays, 26 March 1997, 3m depth, reef and seagrass, spear, P. S. Lobel and J. E. Randall.



FIGURE 1. *Hypoplectrus maya*, paratype MCZ 169200, 68.1mm SL, Tunicate Cove, Pelican Cays, 10 November 1994, 3m depth, reef and seagrass.

Diagnosis: *H. maya* can be distinguished from congeners by its solid deep iridescent blue color and lack of black margins on fins (Figs. 1, 2). The only other similarly colored hamlet is the blue hamlet, *H. gemma*, from Florida and the Yucatan; it is distinguished by having dark black upper and lower margins on the caudal fin (Fig. 3).

Description: Dorsal X, 14 or 15; anal III, 6 or 7; dorsal and anal soft rays branched, the last to base; pectoral rays 13 or 14; pelvic I, 5; branched caudal rays 18 (17–20); vertebrae 23 (one specimen with 22), mouth terminal; tongue truncate.

The following morphometrics are given as percentages of the standard length (range, min–max): body depth 42.2% SL (40.2–44.0); body compressed, width 16.5 (14.5–19.4); head length 37.7 (35.9–39.9); snout length 11.6 (10.0–12.8); orbit diameter 9.1 (7.7–10.1); interorbital width 8.5 (7.3–9.8); upper jaw length 17.7 (16.6–18.8); caudal–peduncle depth 13.9 (12.3–16.1); caudal–peduncle length 17.4 (11.7–22.7); predorsal length 40.6 (20.5–47.3); preanal length 25.7 (21.0–35.4); prepelvic length 41.6 (36.9–46.4); base of dorsal fin 56.2 (52.5–59.2); longest dor-

sal spine 15.8 (14.3–17.0); base of anal fin 18.5 (13.7–22.6); longest anal spine 14.2 (13.3–14.7); longest anal ray 18.3 (16.2–9.8); caudal fin length 20.7 (14.2–26.6); pectoral fin length 28.9 (25.6–34.4); pelvic fin length 22.8 (20.6–24.3).



FIGURE 2. Hypoplectrus maya, Tunicate Cove, Pelican Cays, Belize.

	169196	169202	169200	169197	169194	169199	169198	169195	169201
Specimen	Holotype	Paratype							
SL, mm	86.2	57.6	68.1	70.0	73.5	82.9	86.0	87.2	94.4
Body depth	41.9	43.6	40.2	42.9	42.4	40.7	42.1	44.0	42.3
Body width	17.9	16.9	14.6	15.8	16.1	14.5	17.0	19.4	16.3
Head length	36.1	39.9	37.9	36.9	38.2	37.1	38.6	38.2	35.9
Snout length	11.5	11.7	10.0	12.1	10.9	12.5	11.9	11.2	12.8
Orbit diameter	7.7	10.1	9.7	8.2	8.4	9.7	9.8	8.6	9.5
Interorbital width	7.9	9.8	7.3	7.9	8.9	9.3	8.5	8.5	8.4
Upper-jaw length	16.6	18.8	17.2	18.4	17.2	17.5	18.3	18.1	16.6
Caudal peduncle depth	14.4	16.1	14.6	14.1	12.8	12.3	13.1	15.0	12.6
Caudal peduncle length	17.6	13.6	11.7	22.7	22.5	18.3	18.4	19.2	13.0
Predorsal length	40.8	47.3	44.5	46.0	20.5	40.3	41.5	43.4	41.5
Preanal length	21.0	24.4	21.1	21.8	23.5	35.4	30.6	25.1	28.5
Prepelvic length	46.4	41.3	40.6	42.4	38.2	36.9	39.4	43.4	45.6
Base of dorsal fin	55.9	53.0	58.0	56.8	59.2	52.9	58.5	58.7	52.5
Longest dorsal Spine	14.3	16.4	17.0	16.6	14.9	15.9	16.5	15.0	15.4
Base of anal fin	18.9	18.3	19.1	20.5	18.6	13.7	18.9	22.6	16.0
Longest anal Spine	14.1	damage	damage	14.1	14.1	14.7	14.6	14.4	13.3
Longest anal Ray	18.5	19.8	damage	18.5	19.2	19.0	18.5	16.2	17.0
Caudal fin length	14.2	23.5	20.2	21.5	16.5	21.2	23.9	18.7	26.6
Pectoral fin length	28.3	34.4	26.6	26.7	28.8	25.6	31.5	28.8	29.6
Pelvic fin length	23.4	24.3	24.3	20.9	22.9	20.6	23.8	22.5	22.7

TABLE 2. Proportional measurements of Hypoplectrus maya as percentage of SL. Listed by MCZ number.

The following characteristics are similar for all *Hypoplectrus* species. Body deep, compressed, the depth contained 2.1 to 2.4 times in standard length; dorsal fin with 10 spines and 14 to 16 soft rays, the interspinous fin membranes not incised or notched; no elongate dorsal spines; lateral-line scales 48 to 54; gradually arched anteriorly; gill rakers on first arch moderately long and slender, 6 to 8 on upper limb and 11 to 15 on lower limb; 7 branchiostegal rays; vertebrae 10 + 14; caudal fin truncate and moderately concave; pectoral fins elongated and rounded; pelvic fins rounded; pelvic fins reach to or beyond anus; upper jaw moderately protrusile; no scaly flap of skin joining upper part of pectoral-fin base to body; soft dorsal and anal fins mostly naked; jaw teeth distinct, small canines; vomer and palatines with villiform teeth arranged in rows; supramaxilla absent; teeth fixed (not depressible); posterior process of premaxilla broad and near tip of alveolar ramus; preopercle is angular and not expanded posteriorly, with serrae along the ventral and posterior margins and several small antrose serrae on the ventral margin near the angle; nostrils closer to the eye than to jaw; scales cover all body except that the snout and preorbital region is naked; scale type ctenoid.

Larval development of Hypoplectrus is described and illustrated in Richards 2006.

	169196 Holotype	169202 Paratype	169200 Paratype	169197 Paratype	169194 Paratype	169199 Paratype	169198 Paratype	169195 Paratype	169201 Paratype
Dorsal	X 15	X 14	X 15	X 15	X 15	X 14	X 15	X 14	X 15
Anal	III 7	III 7	III 7	III 6	III 7	III 6	III 7	III 7	III 7
Caudal	18	18	17	20	18	18	19	17	17
Pelvic	I 5	I 5	I 5	I 5	I 5	I 5	I 5	I 5	I 5
Pectoral	14	14	13	14	14	14	14	14	13
Vertebrae	23	23	22	23	23	23	23	23	des

TABLE 3. Meristic data for Hypoplectrus maya. Listed by MCZ number.

Coloration Live: Body a solid deep iridescent blue, darker above the lateral line. The pelvic, dorsal and anal fins are blue. Pectoral fin is clear. Caudal fin margin is blue and the rest is tinted blue (Figs 1, 2).

Coloration Preserved: Color in alcohol pale brown to blackish. Pectoral fin clear, other fins are opaque tan (Fig. 4).

Etymology: This species is named with the dual purpose to honor the Maya people of Belize and the author's daughter, Maya Rose Lobel.

Remarks: The Maya hamlet was discovered in 1993 in Belize in the Pelican Cays. I have documented its occurrence from the South Water Marine Reserve area at Wee Wee Cay southward throughout the Pelican Cays and to the Sapodilla Cays at the southern most margin of the Meso-Amercian Barrier Reef (MABR). The inner barrier reef system contains several fish and other species found only or predominately in the complex geography of mangrove cays and coral reefs (Smith *et al.* 2003, Lobel *et al.* 2009). We have not observed it on the ocean side of the MABR or at Glovers and Lighthouse Atolls. However, a single specimen of the Maya hamlet was found and collected by B. Birmingham in 2010 on the ocean side of the MABR off Alligator Cay (17°10.849'N 088° 2.978'W). This specimen and tissue samples are in the Neotropical Fish Collection at the Smithsonian Tropical Research Institute in Panama (O. Puebla pers. comm.).

The other similarly colored hamlet is *H. gemma*; it is distinguished by having dark upper and lower margins on the caudal fin (Figure 3). The Florida Blue hamlet, *H. gemma*, has for many years only been known from Florida. Recently, it was found in the Alacranes Reef platform off the northern Yucatan Penninsula, Mexico (Aguilar-Perera & Tuz-Sulub 2010). Domeier (1994) noted finding *H. gemma* in Belize at Laughing Bird Cay but we suspect that he actually observed *H. maya*.

One hypothesis for hamlet evolution is that they are aggressive mimics of other fishes (review by Puebla 2009). One possible model species for *H. maya* could be the pomacentrid fish, *Chromis cyanea*, which does occur in the same habitat but is rare there. *H. maya* is often found among the mangrove roots that grow over shallow seagrass beds. Growing on the roots is the bright blue tunicate, *Clavelina puerto-secensis*, which can be quite abundant in this habitat. The colors of *H. maya* and the tunicate are quite similar and perhaps another possibility is that this hamlet has evolved camouflage coloration against this tunicate. This would confer an advantage when ambushing small prey. *H. maya* has been observed (personal observation) on several occasions attacking small silversides (*Jenkinsia lamprotaenia*) which form diurnal aggregations among the mangrove roots.



FIGURE 3. Hypoplectrus gemma, Conch Reef, Florida Keys.



FIGURE 4. Hypoplectrus maya, holotype MCZ 169196, preserved specimen.

Hypoplectrus randallorum n. sp.

(Figs. 5, 6; Tables 4, 5)

Hypoplectrus sp "tan", Randall & Randall 1960, Thresher 1978, Domeier 1994 *Hypoplectrus* sp "tan", Heemstra *et al.* 2002: page 1368.

Holotype: MCZ 169250, 80.6 mm SL, Carrie Bow Cay, Belize, ridge east of cay at 16^o 48.2' N, 88^o 4.5'W, 18 m depth, reef, spear, 6 June 1993, J. E. Randall.

Paratypes: BPBM 35766, 70.9 mm SL, collected, with holotype. MCZ 169203 91.4 mm SL, Glovers Atoll, 10 m depth, ocean side reef, spear, 21 July 1999, P. S. Lobel and J. E. Randall (GenBank AY262253). MCZ 169204, 70.9 mm SL collected with MCZ 169203, (GenBank AY262252).

Diagnosis: The tan hamlet is distinguished from its congeners by coloration. Its body is uniformly light brown to tan colored. It possesses distinct nose spots, a spot at the base of the pectoral fin and a caudal peduncle spot.

Description: Dorsal X, 15; anal III, 7; dorsal and anal soft rays branched, the last to base; pectoral rays 14; pelvic I,5; branched caudal rays 17 or 18; vertebrae 23 or 24.

The following morphometrics are given as percentages of the standard length (range, min–max): body depth 45.6% SL (44.2–47.0); body compressed, width 16.6 (16.0–17.8); head length 39.8 (38.5–41.5); snout length 11.3 (10.3–12.2); orbit diameter 10.0 (9.6–10.4); interorbital width 8.9 (7.6–11.0); upper jaw length 17.7 (16.2–18.9);

caudal-peduncle depth 14.0 (13.6-14.2); caudal-peduncle length 11.8 (9.9-13.8); predorsal length 43.3 (42.4-46.4); preanal length 22.1 (16.8-26.9); prepelvic length 42.8 (40.7-44.9); base of dorsal fin 55.4 (49.8-57.7); longest dorsal spine 16.7 (16.1-17.3); base of anal fin 18.8 (16.5-20.7); longest anal spine 14.6 (13.9-15.6); longest anal ray 18.2 (15.3-20.4); caudal fin length 22.8 (21.4-25.9); pectoral fin length 32.1 (31.9-32.4); pelvic fin length 25.9 (22.4-28.6).



FIGURE 5. *Hypoplectrus randallorum*, paratype: MCZ 169203, 91.4 mm SL, Glovers Atoll, 10 m depth, ocean side reef, spear, 21 July 1999, P. S. Lobel and J. E. Randall.



FIGURE 6. Hypoplectrus randallorum, Belize.

Other characteristics similar to congeners as described above.

Coloration Live: Trunk dark to light brown, head more tan colored. The belly, fins and head can sometimes have a faintly yellowish hue. Pectoral fins clear. Distinct nose spots present on nasal area, a dark spot present at base of pectoral fin and a dark spot present on the upper part of caudal peduncle. The size and intensity of spots can vary (Figs. 5, 6).

Coloration Preserved: Uniformly light brown color. Caudal fin is clear and other fins are pigmented. Spots on nose, pectoral fin base and upper part of caudal peduncle remain visible in preservative (Fig. 7).

Etymology: Named in honor of Helen and John E. Randall, who first recognized the tan hamlet as a possible new species in their 1960 paper. The ending *"orum"* refers to "of man (men) and woman (women)". J. E. Randall collected the holotype.

Remarks: The "Tan Hamlet" has long been recognized as "another hamlet" by Randall & Randall 1960, Thresher 1978, Domeier 1994, Heemstra *et al.* 2002, Ramon *et al.* 2003, Aguilar-Perera 2004, Nelson 2004, Williams *et al.* 2006, Aguilar-Perera & Gonzalez-Salas 2010, Holt *et al.* 2010, Kells & Carpenter 2011). It is wide-

spread in the western Caribbean from the West Indies to Central America (Heemstra *et al.* 2002, Aguilar-Perera & Gonzalez-Salas 2010, Holt *et al.* 2010). Although its body coloration can sometimes be dark, *H. randallorum* differs from the black hamlet by having nose spots. There are several variants of the black hamlet, *H. nigricans* that differ in the coloration of their fins and slightly in some body proportions (Aguilar-Perera 2004). Puebla *et al.* (2008) proposed, based on DNA data, that *H. nigricans* may actually represent several different lineages that have independently evolved from an ancestral *H. puella* stock during multiple evolutionary events. Three different color variants of *H. nigricans* that have been described by Aguilar-Perera (2004) are shown in Fig. 7.



FIGURE 7. Hypoplectrus randallorum. Holotype MCZ 169250, preserved specimen.

	169250	BPBM 35766	169203	169204	
Specimen	Holotype	Paratype	Paratype	Paratype	
SL, mm	80.6	70.9	91.4	71.86	
Body depth	45.4	46.0	47.0	44.2	
Body width	16.0	16.1	17.8	16.6	
Head length	40.3	39.1	41.5	38.5	
Snout length	12.2	10.6	12.2	10.3	
Orbit diameter	10.2	10.4	9.8	9.6	
Interorbital width	8.2	8.7	11.0	7.6	
Upper-jaw length	18.0	17.6	18.9	16.2	
Caudal peduncle depth	13.6	13.9	14.2	14.2	
Caudal peduncle length	11.5	13.8	11.9	20.1	
Predorsal length	42.4	42.5	46.4	46.0	
Preanal length	25.5	16.8	26.9	19.1	
Prepelvic length	40.7	41.8	43.6	44.9	
Base of dorsal fin	56.7	57.7	57.3	49.8	
Longest dorsal Spine	16.4	17.2	16.1	17.3	
Base of anal fin	19.4	20.7	18.7	16.5	
Longest anal spine	14.7	14.2	13.9	15.6	
Longest anal ray	20.4	18.7	18.2	15.3	
Caudal fin length	21.6	21.4	25.9	22.1	
Pectoral fin length	32.1	31.9	32.2	32.4	
Pelvic fin length	26.7	28.6	25.8	22.4	

TABLE 4. Proportional measurements of Hypoplectrus randallorum. Listed by MCZ and BPBM number

	169250	BPBM 35766	169203	169204
Specimen	Holotype	Paratype	Paratype	Paratype
Dorsal	X 15	X 15	X 15	X 15
Anal	III 7	III 7	III 7	III 7
Caudal	17	17	18	17
Pelvic	I 5	I 5	I 5	I 5
Pectoral	14	14	14	13
Vertebrae	23	24	23	n/a

TABLE 5. Meristic data for Hypoplectrus randallorum. Listed by MCZ and BPBM number.

Ecology: Hamlets are predators of small benthic shrimp, crabs, mysids, stomatopods and tiny fishes (Randall 1967). In one study (Randall 1967), fishes constituted between 10 to 44.2% of hamlet's food items with *H. nigricans* having the highest percentage of fishes in its diet. One specimen of *H. randallorum* (70.2 mm SL) collected 8 July 1990 on reefs off the Discovery Bay Marine Laboratory in Jamaica had a freshly consumed cleaner goby, *Elacatinus evelynae* (16.5 mm SL) in its stomach content (personal observation). I have also observed hamlets attack and consume *Elacatinus* spp in Belize both in the field and in an aquarium. Randall (1967) reported that a Nassau grouper, *Epinephalus guttatus* had eaten one *H. puella*.

Discussion

Walbaum (1792) described the first hamlet species, H. unicolor, as a member of the genus Perca. Cuvier (1828) described H. puella and H. chlorurus and reclassified them into the genus Plectropoma. Poey, working primarily in Cuban waters, described H. indigo (Poey 1851), H. gummigutta (Poey 1851), H. nigricans (Poey 1852), and H. guttavarius (Poey 1852). In 1861, Gill defined the new genus Hypoplectrus for these fishes but did not add any new species. Soon after, Poey described H. aberrans (Poey 1868) and H. maculiferus (Poey 1871). Goode and Bean (1882) described H. gemma from Florida. The most recent description of a new Hypoplectrus was H. providencianus by Acero & Garzon-Ferreira (1994). These eleven species are currently defined by color pattern (Heemstra et al. 2002). Seven of these species are found in US and Mexico waters and were listed by Nelson et al. 2004 as valid species. This decision reversed the earlier position from the 1980 edition of the "Common and scientific names of fishes from the United States, Canada and Mexico" (Nelson et al. 1980) in which all Hypoplectrus species were considered as one species under the oldest name, H. unicolor. The 1980 consolidation of species was based mainly on early isozyme analyses, which did not reveal any difference among the color morphs (Graves & Rosenblatt 1980). That hamlets were possibly color variants of a single species was initially suggested by the first underwater observations of their mating behavior, which indicated that the different species would occasionally hybridize (Barlow 1975). The decision by Nelson et al. (2004, page 227) for a reversal back to recognizing the color-morphs as species was substantially based upon the behavioral study by Domeier (1994). Domeier demonstrated experimentally that the color forms breed true and that mixed mating produced hybrid color mixes. It has been widely observed that hamlets mate assortatively by color-pattern and that hybrid matings are rare (Fisher 1980a,b, Lobel & Neudecker 1985, Lobel 1992, Domeier 1994, Thresher 1978, Whiteman & Gage 2007, Barieto & McCarthy 2007, Puebla et al. 2007).

While early genetic data did not separate species (Graves and Rosenblatt 1980), recent data suggest some degree of genetic isolation between geographically separated populations although this is not an absolute pattern (Ramon *et al.* 2003, Garcia-Machado *et al.* 2004, McCartney *et al.* 2003, Puebla *et al.* 2008, 2009). The recent genetic data also suggest some sorting by color, however, the species are recently diverged and therefore very similar genetically. Two of the hamlets separate distinctly from congeners genetically: *H. indigo* (McCartney *et al.* 2003, Ramon *et al.* 2003) and *H. gummigutta* (Puebla *et al.* in press). *H. gemma* is distinct from *H. puella* (Barretto & McCartney 2007). *H. nigricans* sorts into multiple lineages based on fin coloration and morphology (Aguilar-Perera 2004). Divisions in *H. nigricans* are supported by genetic variability as well (Puebla *et al.* 2008). Rare hybridization occurs and this obscures genetic distinctiveness between the species (Domeier 1994, Ramon *et al.*

2003, Puella *et al.* 2008). Thus, the current genetic data suggests multiple lineages of hamlets sorted by coloration although the genetic differences are small. The same type of systematic problem is evident for other fishes as well, particularly the African rift-lake cichlids (Puebla 2009). The consensus of biologists who have examined the issue of the hamlet flock is that the application of species terminology to describe these fishes by color is consistent with current taxonomic practices (Randall 1968, Fisher 1980, Domeier 1994, Acero & Garzon-Ferrera 1994, Heemstra *et al.* 2002, McCartney *et al.* 2003, Aguilar-Perera 2003, 2004; Garcia-Machado *et al.* 2004, McEachran & Fechhelm 2005, Puebla *et al.* 2007, 2008; Whiteman *et al.* 2007, Aguilar-Perera & Gonzalez-Salas 2010, Holt *et al.* 2010).

The recognized species of hamlets now totals 13. These are H. aberrans (Fig. 10), H. chlorurus (Fig. 11), H. gemma (Fig. 3), H. gummigutta (Fig. 12), H. guttavarius (Fig 13), H. indigo (Fig 14), H. maya (Fig. 1,2), H. nigricans (Fig. 8), H. maculiferus (Fig. 15), H. puella (Fig. 16), H. providencianus (Fig. 17), H. randallorum (Fig. 5, 6), and H. unicolor (Fig. 9). There are some other hamlet color-morphs which vary, too subtlely to be clearly distinguished at this time. There are 4 variants of H. puella (Thresher 1978), 2 variants of H. unicolor (Domeier 1994), 3 variants of H. chlorurus (Domeier 1994), 2 variants of H. aberrans (Domeier 1994), and 3 variants of H. nigricans (Fig. 7, Aguilar-Perera 2004). Individuals of H. unicolor are occasionally observed that have a double caudal spot but this represents individual variation and is not a fixed trait in a population (Fig. 9, Williams et al. 2008). A taxonomic key to the species including the two new species described herein is in Heemstra et al. 2002. Maps of the hamlet species distributions are in Heemstra et al. 2002, Aguilar-Perera & Gonzalez-Salas 2010 and Holt et al. 2010. These distributions should be considered with some caution as the databases contain errors (Robertson 2008). A map of the distributions for *H. maya* and *H. randallorum* is shown in Figure 18. I defined the tan hamlet, H. randallorum, as having nose spots and a spot at the base of the pectoral fin which was also recognized by Randall and Randall 1960 and by Domeier 1994. There is the other light tan colored hamlet (Figure 8b), which was shown in photographs and referred to as "tan hamlet" by Williams et al. 2008 and Holt et al. 2010. Puebla et al. (in press) referred to this one as the "tan type 2". As mentioned above, this "tan type 2" (Figure 8b) is one of the morphs in the *H. nigicans* complex and this clade will require further research in order to define its taxonomy.



FIGURE 8. Color variations in *H. nigricans*. The notable difference is the coloration of the pectoral fin. A) Jamaica, B) Jamaica, C) Belize.



FIGURE 9. A mated pair showing the normal *H. unicolor* spot pattern on the caudal peduncle (lower right) and an individual with the double spot (upper). This was a mating pair, Discovery Bay, Jamaica.



FIGURE 10. H. aberrans, Jamaica.



FIGURE 11. H. chlorurus, St. Croix.



FIGURE 12. H. gummigutta, Jamaica.



FIGURE 13. H. guttavarius, Jamaica.



FIGURE 14. H. indigo, Belize.



FIGURE 15. H. maculiferus, St Barth's.



FIGURE 16. H. puella, Belize.



FIGURE 17. H. providencianus, Jamaica.



FIGURE 18. Distribution of the Maya hamlet, *Hypoplectrus maya*, and the Tan hamlet, *H. randallorum*. Based on photographic and sight records in Randall & Randall 1960, Domeier 1994, Ramon *et al.* 2003, Lobel *et al.* 2009, Puebla *et al.* in press and from <u>www.fishdb.co.uk</u> photos # 1084 and 1204. The Tan hamlet will likely be found in other locations but must be distinguished from the "tan type 2".

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Literature cited

- Acero, P. & Garzon-Ferreira, J. (1994)Descripcion de una especie nueva de Hypoplectrus (Pisces:Serranidae) del Caribe Occidental y comentarios sobre las especies Colombianas del genero. *Boletin de Investigaciones Marinas y Costeras*, 23, 5– 14.
- Aguilar-Perera, A. (2003) Abundance and distribution of hamlets (Teleostei: Hypoplectrus) in coral reefs off southwestern Puerto Rico: support for the multiple-species hypothesis. *Caribbean Journal of Science*, 39, 147–151.
- Aguilar-Perera, A. (2004) Variations in morphology and coloration in the black hamlet, *Hypoplectrus nigricans* (Teleostei: Serranidae). *Caribbean Journal of Science*, 40, 150–154.
- Aguilar-Perera, A. & González?Salas, C. (2010) Distribution of the genus *Hypoplectrus* (Teleostei: Serranidae) in the Greater Caribbean Region: support for a color?based speciation. *Marine Ecology*, 31, 375–387.
- Aguila-Perera, A. & Tuz-Sulub A.N. (2010) Scientific Note *Hypoplectrus gemma* (Teleostei, Serranidae) is not endemic to southern Florida waters. *Pan-American Journal of Aquatic Sciences*, 5, 143–146.
- Baldwin, C.C., Castillo, C.I., Weigt, L.A. & Victor, B.C. (2011) Seven new species within western Atlantic Starksia atlantica, S. lepicoelia, and S. sluiteri (Teleostei, Labrisomidae), with comments on congruence of DNA barcodes and species. ZooKeys, 79, 21–72.
- Barlow, G.W. (1975) On the sociobiology of some hermaphroditic serranid fishes, the hamlets, in Puerto Rico. *Marine Biology*, 33, 295–300.
- Barreto, F.S. & McCartney, M.A. (2007) Extraordinary AFLP fingerprint similarity despite strong assortative mating between reef fish color morphospecies. *Evolution*, 62, 226–233.
- Charnov, E.L. (1982) The Theory of Sex Allocation. Princeton University Press, Princeton, NJ. 355pp.
- Cuvier, G.G. (1828) Histoire naturelle des poissons. Paris, France. (Reprint A. Asher. & Co., Amsterdam, Holland).551pp

Domeier, M.L. (1994) Speciation in the serranid fish Hypoplectrus. Bulletin of Marine Science, 54, 103-141.

- Garcia-Machado, E., Chevalier Monteagudo, P.P. & Solignac, M. (2004) Lack of mtDNA differentiation among hamlets (*Hypoplectrus*, Serranidae). *Marine Biology*, 144, 147–152.
- Goode, G.B. & Bean, T.H. (1882) Descriptions of twenty-five new species of fish from the southern United States and three new genera, *Letharcus, Ioglossus*, and *Chriodorus*. *Proceedings of the United Stations National Museum*, 5, 412–437.
- Fischer, E.A. (1980a) The relationship between mating system and simultaneous hermaphroditism in the coral reef fish, *Hypoplectrus nigricans* (Serranidae). *Animal Behaviour*, 28, 620–633.
- Fischer, E.A. (1980b) Speciation in the hamlets (Hypoplectrus, Serranidae)-a continuing enigma. Copeia, 4, 649-659.
- Fischer, E.A. (1981) Sexual allocation in a simultaneously hermaphroditic coral reef fish. The American Naturalist, 117, 64-82.
- Fischer, E.A. (1987) Mating behavior in the black hamlet—gamete trading or egg trading? *Environmental Biology of Fishes*, 18, 143–148.
- Graves, J.E. & Rosenblatt, R.H. (1980) Genetic-relationships of the color morphs of the serranid fish *Hypoplectrus unicolor*. *Evolution*, 34, 240–245.
- Greenfield, D.W. & Randall, J.E. (2008) *Eviota tigrina*, a new goby from Tonga (Telostei: Gobidae). *Proceedings of the California Academy of Sciences*, 59, 497–501.
- Heemstra, P.C., Anderson Jr, W.D. & Lobel, P.S. (2002) Serranidae; Groupers (seabasses, creolefish, coney, hamlets, anthines, and soapfishes), 1308–1369, *In* Carpenter, K.E. (ed.), The living marine resources of the Western Central Atlantic. Volume 2: Bony fishes, part 1 (Acipenseridae to Grammatidae). *FAO Species Identification Guide for Fishery Purposes* and *American Society of Ichthyologists and Herpetologists Special Publication No. 5.*, FAO, Rome, Italy, 601–1374.
- Holt, B.G., Emerson, B.C., Newton, J., Gage, M.J.G. & Côté, I.M. (2008) Stable isotope analysis of the *Hypoplectrus* species complex reveals no evidence for dietary niche divergence. *Marine Ecology Progress Series*, 357, 283–289.
- Holt, B.G., Côté, I.M. & Emerson, B.C. (2010) Signatures of speciation? Distribution and diversity of Hypoplectrus (Teleostei: Serranidae) colour morphotypes. *Global Ecology and Biogeography*, 19, 432–441.
- Kells, V. & Carpenter, K. (2011) A Field Guide to Coastal Fishes from Maine to Texas. John Hopkins Press, Baltimore, MD. 446pp
- Lobel, P.S. (1992) Sounds produced by spawning fishes. Environmental Biology of Fishes, 33, 351–358.
- Lobel, P.S. (2002) Diversity of fish spawning sound and the application of passive acoustic monitoring. *Bioacoustics*, 12, 286–289
- Lobel, P.S. & Neudecker, S. (1985) Diurnal periodicity of spawning activity by the hamelt fish *Hypoplectrus guttavarius* (Serranidae). *The Ecology of Coral Reefs, NOAA Symposia Series for Undersea Research*, 3, 71–86.
- Lobel, P.S., Rocha, L. & Randall, J.E. (2009) Color phases and distribution of the western Atlantic labrid fish, *Halichoeres* socalis. Copeia, 1, 171–174.
- McCartney, M.A., Acevedo, J., Heredia, C., Rico, C., Quenoville, B., Bermingham, E. & McMillan, W.O. (2003) Genetic mosaic in a marine species flock. *Molecular Ecology*, 12, 2963–2973.
- McEachran, J.D. & Fechhelm, J.D. (2006) Fishes of the Gulf of Mexico, Volume 2: Scorpaeniformes to Tetraodontiformes. University of Texas Press, Austin, Texas. 1004pp
- Nelson, J.S., Crossman, E.J., Espinosa-Perez, H., Findley, L.T., Gilbert, C.R., Lea, R.N. & Williams, D.J. (2004) Common and scientific names of fishes from the United States, Canada and Mexico, 6th ed. American Fisheries Society, Special Publication 29, Bethesda, MD. 386pp

Poey, F. (1852) Memorias sobre la historia natural de la Isla de Cuba. Havana, Cuba. Publisher, Place, 463pp

Poey, F. (1868) Synopsis piscium cubensium. Catalogo razonado de los peces de la Isla de Cuba. *Repertorio fisiconatural de la Isla de Cuba*, 2, 279–484.

- Puebla, O., Bermingham, E., Guichard, F. & Whiteman, E. (2007) Colour pattern as a single trait driving speciation in *Hypoplectrus* coral reef fishes? Proceedings of the Royal Society B: *Biological Sciences*, 274, 1265–1271.
- Puebla, O., Bermingham, E. & Guichard, F. (2008) Population genetic analyses of *Hypoplectrus* coral reef fishes provide evidence that local processes are operating during the early stages of marine adaptive radiations. *Molecular Ecology*, 17, 1405–1415.
- Puebla, O. (2009) Ecological speciation in marine v. freshwater fishes. Journal of Fish Biology, 75, 960–996.
- Puebla, O., Bermingham, E. & Guichard, F. (2009) Estimating dispersal from genetic isolation by distance in a coral reef fish (*Hypoplectrus puella*). *Ecology*, 90, 3087–3098.
- Puebla, O., Bermingham, E. & Guichard, F. (in press) Pairing dynamics and the origin of species. *Proceedings of the Royal Society* B (2011).
- Ramón, M.L., Lobel, P.S. & Sorenson, M.D. (2003) Lack of mitochondrial genetic structure in hamlets (*Hypoplectrus* spp.): recent speciation or ongoing hybridization? *Molecular Ecology*, 12, 2975–2980.
- Randall, J.E. (1967) Food habits of reef fishes of the West Indies. Studies of Tropical Oceans, 5, 665-847.
- Randall, J.E. (1968) Caribbean reef fishes. TFH Publications, Neptune City, NJ.318pp
- Randall, J.E. (2005) A review of mimicry in reef fishes. Zoological Studies, 44, 299-328.
- Randall, J.E. & Bruce, R. (1983) The parrotfishes of the subfamily Scarinae of the western Indian Ocean with a description of 3 new species. *Ichthyological Bulletin of the J.L.B Smith Institute of Ichthyology*, 47, 1–39.
- Randall, J.E. & Edwards, A. (1984) A new labrid fish of the genus *Thalassoma* from the Pitcairn Group, with a review of related Indo-Pacific species. *Journal of Aquariculture and Aquatic Sciences*, 4, 13–22.
- Randall, J.E. & Pyle, R.L. (2001) Four new serranid fishes of the anthiine genus *Pseudanthias* from the South Pacific. *Raffles Bulletin of Zoology*, 49, 19–34.
- Randall, J.E. & Pyle, R.L. (2001) Three new species of labrid fishes of the genus *Cirrhilabrus* from the islands of the tropical Pacific. *Aqua*, 4, 89–98.
- Randall, J.E. & Randall, H.A. (1960) Examples of mimicry and protective resemblance in tropical marine fishes. Bulletin of Marine Science, 10, 444–480.
- Rao, K.S. & Lakshmi, K. (1999) Cryptic hybridization in marine fishes: significance of narrow hybrid zones in identifying stable hybrid populations. *Journal of Natural History*, 33, 1237–1259.
- Richards, W.J. (ed.) (2006) Early Stages of Atlantic Fishes An Identification Guide for the Western Central North Atlantic, Taylor and Francis Group, Boca Raton, FL. 2640pp
- Rocha, L.A. & Bowen, B.W. (2008) Speciation in coral-reef fishes. Journal of Fish Biology, 72, 1101–1121.
- Robertson D. R. (2008) Global biogeographic databases on marine fishes: caveat emptor. *Diversity and Distributions*, 14, 891–892.
- Salzburger, W. (2008) To be or not to be a hamlet pair in sympatry. *Molecular Ecology*, 17, 1397–1399.
- Smith, C.L., Tyler, J.C., Davis, W.P., Jones, R.S., Smith D.G. & Baldwin, C.C. (2003) The fishes of the Pelican Cayes, Belize, Central America. *Atoll Research Bulletin*, 497, 1–88.
- Springer, V.G. (1988) The Indo-Pacific blenniid fish genus Ecsenius. Smithsonian Contributions to Zoology, 465, iv 134.
- Stauffer Jr, J.R., Bowers, N.J., McKaye, K.R. & Kocher, T.D. (1995) Evolutionarily signification units among cichlid fishes: the role of behavioral studies. *American Fisheries Society Symposium*, 17, 227–244.
- Stauffer Jr, J.R., McKaye, K.R. & Konings, A.F. (2002) Behaviour: an important diagnostic tool for Lake Malawi cichlids. *Fish and Fisheries*, 3, 213–224.
- Thresher, R.E. (1978) Polymorphism, mimicry, and evolution of hamlets (*Hypoplectrus*, Serranidae). Bulletin of Marine Science, 28, 345–353.
- Walbaum, J.J. (1792) Petri Artedi sueci genera piscium. In quibus systema totum ichthyologiae proponitur cum classibus, ordinibus, generum characteribus, specierum differentiis, observationibus plurimis. Redactis speciebus 242 ad genera 52. Ichthyologiae pars III. Petri Artedi renovai, Greifswald, Germany. 732pp
- Whiteman, E.A., Côté, I.M. & Reynolds, J.D. (2007) Ecological differences between hamlet (*Hypoplectrus*: Serranidae) colour morphs: between-morph variation in diet. *Journal of Fish Biology*, 71, 235–244.
- Whiteman, E.A. & Gage, M.J.G. (2007) No barriers to fertilization between sympatric colour morphs in the marine species flock *Hypoplectrus* (Serranidae). *Journal of Zoology*, 272, 305–310.
- Williams, E.H., Bunkley-Williams, L.R., Rogers, C.S. & Fenner, R. (2006) New geographic records of Hamlets, *Hypoplectrus* spp. (Serranidae), in the Caribbean. *Revista de Biología Tropical*, 54, 171–173.
- Williams, E.H., Bunkley-Williams, L.R., Rogers, C.S. & Fenner, R. (2008) Color correction of a publication error in the tan hamlet and the second occurrence of a potentially inheritable character the butter hamlet (Perciformes: Serranidae). *Revista de Biologia Tropical*, 56, 289–292.