



Hypoplectrus espinosai sp. nov. (Teleostei: Serranidae), a new hamlet on coral reefs in the southwestern Gulf of Mexico

OSCAR PUEBLA^{1,2,3}, ALFONSO AGUILAR-PERERA^{4*}, MARTIN HELMKAMPF¹, D. ROSS ROBERTSON³, CARLOS J. ESTAPÉ⁵, ALLISON MORGAN ESTAPÉ⁵ & OMAR DOMÍNGUEZ-DOMÍNGUEZ⁶

¹Leibniz Centre for Tropical Marine Research (ZMT), Bremen, Germany

✉ martin.helmkamp@leibniz-zmt.de; <https://orcid.org/0000-0003-1995-9062>

²Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl von Ossietzky Universität Oldenburg, Germany

✉ oscar.puebla@uni-oldenburg.de; <https://orcid.org/0000-0001-9700-5841>

³Smithsonian Tropical Research Institute (STRI), Panama, Republic of Panama

✉ RossRobertsonDR@si.edu; <https://orcid.org/0000-0003-3972-149X>

⁴Departamento de Biología, Marina Universidad Autónoma de Yucatán, Mérida, Yucatán, México *alfaguilar@gmail.com

⁵197 Gulfview Dr., Islamorada, FL 33036, USA

✉ carlos.allison@me.com; <https://orcid.org/0000-0001-8540-9101>

✉ allison.carlos@me.com; <https://orcid.org/0000-0002-2279-8987>

⁶Laboratorio de Biología Acuática, Facultad de Biología, Universidad Michoacana de San Nicolás de Hidalgo, Morelia, Michoacán, México

✉ omar.dominguez@umich.mx; <https://orcid.org/0000-0001-9583-4443>

*Corresponding author: ✉ alfaguilar@gmail.com; <https://orcid.org/0000-0002-7579-2183>

Abstract

The hamlets (*Hypoplectrus* spp., Teleostei: Serranidae) are a group of small predatory reef-associated fishes endemic to the tropical northwestern Atlantic that are characterized by an exceptionally high diversification rate. Currently 18 species are recognized, with seven described or redescribed in the last 14 years. Here, we describe the Campeche Bank hamlet, *Hypoplectrus espinosai* sp. nov. As indicated by its common name, this species is distributed throughout the Campeche Bank in the southwest Gulf of Mexico. *Hypoplectrus espinosai* sp. nov. differs from two similar hamlets, the butter hamlet *H. unicolor* (Walbaum) and the Veracruz hamlet *H. castroaguirrei* Del Moral Flores, Tello-Musi & Martínez-Pérez in terms of geographic distribution and color pattern. Furthermore, phylogenetic and population genetic analyses based on whole-genome data from 68 individuals indicate that *H. espinosai* sp. nov. is genetically distinct from *H. unicolor* and *H. castroaguirrei*.

Key words: Gulf of Mexico, Campeche Bank, Serranidae, reef fishes, hamlets, *Hypoplectrus*

Introduction

The hamlets (*Hypoplectrus* spp., Perciformes: Serranidae) are small predatory reef-associated fishes endemic to the tropical northwestern Atlantic (Aguilar-Perera & González-Salas 2010; Holt *et al.* 2010). They belong to the genus *Hypoplectrus* (Gill), which currently includes 18 recognized species (Domeier 1994; Lobel 2011; Puebla *et al.* 2022). The hamlets are characterized by an exceptionally high diversification rate and low levels of genetic divergence among species (McCartney *et al.* 2003; Puebla *et al.* 2014; Hench *et al.* 2022). Nonetheless, they are recognized as species by the ichthyological community due to the stable differences in color pattern and geographic distribution among species, and the strong levels of assortative mating that are observed in sympatry (Fischer 1980; Domeier 1994; Puebla *et al.* 2007, 2012; Barreto & McCartney 2008).

Seven species have been described, or redescribed, in the last 14 years (Lobel 2011; Del Moral Flores *et al.* 2011; Victor 2012; Tavera & Acero 2013; Victor & Marks 2018; Puebla *et al.* 2022). These include a high proportion of microendemic *Hypoplectrus* species, notably the Maya hamlet (*H. maya* Lobel) in Belize, the Veracruz hamlet (*H. castroaguirrei* Del Moral Flores, Tello-Musi & Martínez-Pérez) and the Jarocho hamlet (*H. atlahua* Tavera &

Acero) in the southwestern Gulf of Mexico, the spotted hamlet (*H. ecosur* Victor) in the Yucatan Peninsula, the striped hamlet (*H. liberte* Victor & Marks) in Fort-Liberté Bay in Haiti, and the Florida hamlet (*H. floridae* Victor) in Southwest Florida. Reports of *H. floridae* in the southwestern Gulf of Mexico are likely to be *H. atlahua*, whose range of variation overlaps with *H. floridae*, particularly in *H. atlahua* juveniles (Robertson *et al.* 2019a). The high proportion of microendemic *Hypoplectrus* species is another consequence of their exceptionally high diversification rate, and these species often show higher levels of genetic divergence than more widely distributed *Hypoplectrus* species (Victor 2012; Tavera & Acero 2013; Moran *et al.* 2019; Helmkamp *et al.* under review).

Hamlets are essentially distinguished by their color patterns, which differ among species and are in large part genetically determined (Domeier 1994, Coulmance *et al.* 2023). Nonetheless, they show variation in color pattern within species, both within and between geographic locations. This variation has been documented in the barred hamlet *H. puella* (Cuvier) by Thresher (1978), in the black hamlet *H. nigricans* (Poey) by Aguilar-Perera (2004) and Lobel (2011), in *H. atlahua* and other hamlets by Robertson *et al.* (2019a), and in the bluelip hamlet *H. affinis* (Poey) by Puebla *et al.* (2022). For example, *H. puella* shows variation in barring pattern both within and between locations (Thresher 1978; Robertson *et al.* 2019a), and the yellowbelly hamlet *H. aberrans* (Poey) shows variation in the presence or absence of a spot on the side of the snout and another on the caudal peduncle (Puebla *et al.* 2022).

The butter hamlet *H. unicolor* (Walbaum) varies in terms of the presence or absence of a black spot on the snout, as well as the presence or absence and extent of a black saddle on the caudal peduncle (Williams *et al.* 2008; Fig. 1). *Hypoplectrus castroaguirrei*, which resembles the butter hamlet, also shows variation in the presence or absence of a spot on the snout and the extent of the black saddle on the caudal peduncle (Robertson *et al.* 2019a; Fig. 2). In addition, both species are variable regarding the presence or absence of a weak barring pattern and thin vertical pale blue lines throughout the body. Nevertheless, *H. castroaguirrei* is distinct from *H. unicolor* due to the presence of a black eye-mask, and it is restricted to the southwestern Gulf of Mexico where *H. unicolor* is not found.

A consistent variant that resembles *H. unicolor* and *H. castroaguirrei* was identified in coral reefs of the Campeche Bank in the southwestern Gulf of Mexico. The objectives of this study are to i.) assess the geographic distribution of this variant, ii.) evaluate whether it falls within or outside the color pattern variation that is observed in *H. unicolor* and *H. castroaguirrei*, iii.) determine whether it is genetically distinct from these hamlets, and iv.) if so, describe it as a new species.

Materials and methods

Study area. We focused on the Campeche Bank, which extends more than 200 km north of the Yucatan Peninsula, Mexico, in the southwestern Gulf of Mexico (Fig. 3). This region is characterized by specific oceanographic conditions (Belanger *et al.* 2012; Färber Lorda *et al.* 2019) and constitutes a distinct biogeographic subunit within the Northern Province of the Greater Caribbean (Robertson & Cramer 2014). Campeche Bank includes a dozen submerged banks and emergent reefs. The largest and easternmost reef complex is Alacranes Reef (Arrecife Alacranes), which is located 135 km off the Yucatan Peninsula and was established as a national park (Parque Nacional Arrecife Alacranes) in 1994 (Jordán-Dahlgren & Rodríguez-Martínez 2003). Alacranes Reef is a shallow-water, semi-elliptic reef platform (length and width 26.8 km and 14.6 km, respectively) rising above the continental shelf from depths of 50 m (Korniker & Boyd 1962; Bonet 1967; Jordán-Dahlgren & Rodríguez-Martínez 2003). The platform includes a long arcuate reef, which forms the windward side, a deeper and less sharply defined reef belt outlining the leeward margin, and a multitude of patch reefs of various shapes and sizes in the enclosed reef lagoon. The other reefs and banks in Campeche Bank, which vary in size, form, and degree of emergence, include Cayo Arenas, Banco Pera, Banco Nuevo, Triángulo Oeste, Triángulo Este, Banco Obispo Norte, Banco Obispo Sur, and Cayo Arcas (Fig. 3).

Fieldwork. We gathered data from expeditions in the Alacranes Reef (22°31'28.18" N, 89°42'44" W) by AA-P in 2009, in Cayo Arcas by DRR in August 2016 (Robertson *et al.* 2016), Cayo Arenas by DRR in May 2017, and Triángulo Oeste, Triángulo Este, Banco Obispo Norte, Banco Obispo Sur, Banco Nuevo, and Banco Pera by DRR and OD-D in September 2017 (Robertson *et al.* 2019b). Overall, more than 50 roving dive surveys were conducted by AA-P, DRR, and OD-D in daytime at depths of 5–30 m, recording the presence and abundance (uncommon, occasional, and common) of hamlets. Live hamlets were photographed in Alacranes Reef by AA-P in June 2009 and by CJE in August 2019. Voucher specimens were collected with a pole spear in coral reefs of Cayo Arcas by OD-D

and DRR. Fieldwork was led under research and collecting permits PPF/DGOPA-/2013, PPF/DGOPA-262-17, and PPF/DGOPA-025/23.

Labwork. Fin clips of collected hamlets were stored in 95% ethanol for genetic analysis. Voucher specimens were fixed in 10% formalin and then 70% ethanol and deposited in the Ichthyological Collection of the Laboratorio de Biología Acuática, Universidad Michoacana de San Nicolás de Hidalgo, Mexico (SEMARNAT registration number MICH-PEC-227-07-09). Morphometric measurements and meristic counts of all voucher specimens were taken following Lobel (2011) and Puebla *et al.* (2022) for consistency and comparison with previous measurements and meristic counts of other hamlet species. Measurements included total length (TL), standard length (SL) and head length (HL) in millimeters, body depth, body width, head length, snout length, orbit diameter, interorbital width, upper-jaw length, caudal-peduncle depth, caudal-peduncle length, predorsal length, prepelvic length, prepectoral length, length of dorsal-fin base, length of anal-fin base, length of longest dorsal spine, length of longest anal spine, length of longest anal ray, caudal-fin length, pectoral-fin length, and pelvic-fin length in % SL, and snout length, upper-jaw length, interorbital width, and orbit diameter in % HL. Meristic counts included the number of dorsal, anal, pelvic and pectoral spines and rays.

Sequencing. Genomic DNA was extracted from voucher specimens using MagAttract high-molecular-weight DNA extraction kits (Qiagen). Illumina DNA Prep libraries were prepared following the manufacturer's instructions and whole genomes were sequenced on the Illumina NovaSeq 6000 platform. In order to put the new species within a broader phylogenetic context with respect to *H. castroaguirrei* and *H. unicolor*, whole genomes from these two species were considered in addition to *H. floridae*, which belongs to a different mitochondrial lineage (Victor 2012). Two species of *Serranus* (see below), the genus most closely related to *Hypoplectrus* (Hench *et al.* 2022), were chosen as outgroups. A total of 68 genomes were considered, including three genomes of the new species from Cayo Arcas, 54 *H. unicolor* genomes from Panama, Belize, Honduras, the Florida Keys, Puerto Rico, and the southeastern coast of the Yucatan Peninsula (Quintana Roo, Mexico), two *H. castroaguirrei* genomes from the western Gulf of Mexico (Anton Lizardo, Veracruz, Mexico), three *H. floridae* genomes from the Florida Keys (USA), and six from *Serranus tortugarum* Longley and *S. tabacarius* (Cuvier) from Honduras and Panama (Fig. 3, Table S1). All these genomes were available from previous or ongoing studies (Hench *et al.* 2019, 2022; Coulmance *et al.* 2023; Helmkamp *et al.* under review; accession numbers in Table S1).

Genotyping. Samples were genotyped anew based on the *H. puella* reference genome (Hench *et al.* 2019) using GATK v4.1.9 (McKenna *et al.* 2010) as described previously (Hench *et al.* 2022). Mean coverage passed a 10x threshold for each sample and averaged 21x across all samples. Haplotype likelihoods were determined individually, and genotypes were called jointly along all 24 linkage groups (chromosomes). Only variant, bi-allelic sites present in at least 90% of samples were retained after passing various quality thresholds. Sites were additionally filtered regarding a minor allele count of at least 2, and a minimum physical distance of 5000 bp using VCFtools v0.1.16 (Danecek *et al.* 2011), which resulted in a final dataset of approximately 91,000 single nucleotide polymorphisms (SNPs).

Principal Component Analysis. Relationships among samples across all SNPs were visualized using a Principal Component Analysis (PCA) in R v4.3.3 (R Core Team 2024) with the R package adegenet v2.1.10 (Jombart & Ahmed 2011). This analysis was first performed at the species level, i.e., including samples from the new species, *H. castroaguirrei*, *H. unicolor*, and *H. floridae*. The PCA was then repeated with the new species and *H. unicolor* only to better visualize the relationships within this genetic subgroup.

Phylogenetic inference. The same dataset was converted from VCF to FASTA format and a maximum-likelihood phylogeny was reconstructed using two approaches. In the first approach, the optimal tree was calculated with RAxML-NG v1.2.0 from 40 starting trees under the GTGTR4+G model (Tavaré 1986; Kozlov *et al.* 2019) with Lewis' ascertainment bias correction (Lewis 2001). Branch supports were calculated as Transfer Bootstrap Expectations (Lemoine *et al.* 2018) based on 200 bootstrap replicates. The second approach employed a thorough Nearest Neighbor Interchange (NNI) search in IQ-TREE v2.2.5 (Minh *et al.* 2020) under the GTR model with Lewis' ascertainment bias correction (Lewis 2001) and 200 nonparametric bootstrap replicates.

Results

Distribution. The new species was observed throughout coral reefs off cays from the Campeche Bank. It was occasional in Alacranes Reef and Triángulo Este, and rare in Triángulo Oeste, Cayo Arenas, and Cayo Arcas. All the

white-colored hamlets recorded in the Campeche Bank corresponded to the new species that we detail below. The other similar hamlets, i.e., *H. unicolor* and *H. castroaguirrei*, were not found on these reefs. Conversely, the new species was not recorded outside of Campeche Bank (i.e., in the northern Gulf of Mexico and in the Caribbean Sea). Nevertheless, several other hamlet species were observed in the Campeche Bank, notably *H. aberrans*, *H. ecosur*, *H. gemma* Good & Bean, *H. guttavarius* (Poey), *H. indigo* (Poey), *H. nigricans*, *H. puella*, and *H. randallorum* Lobel.

Phenotypic variation. The caudal peduncle of the new species is entirely covered by a black saddle blotch, which extends over the posterior part of the body, and sometimes over the posterior part of the dorsal fin (Fig. 4). This character differentiates the new species from *H. unicolor*, where this blotch is less extensive and covers only part of the caudal peduncle (Fig. 1). Additionally, the black eye-mask that characterizes *H. castroaguirrei* (Fig. 2) is absent in the new species.



FIGURE 1. Phenotypic variation in the butter hamlet (*Hypoplectrus unicolor*). Note the variability in the extent of the black saddle blotch on the caudal peduncle, the presence or absence of this saddle and the snout spot, the occurrence of thin vertical lines (*f*), and faint vertical bars (*e*) on the body. *a*. Roatan, *b*. Florida Keys, *c*. Bonaire, *d*. and *e*. St. John (USVI), *f*. Bocas del Toro (Panama). Photographs by Carlos and Allison Estapé.



FIGURE 2. Phenotypic variation in the Veracruz hamlet (*Hypoplectrus castroaguirrei*). Note the variability in the extent of the black saddle blotch on the caudal peduncle, the presence or absence of the snout spot and a small spot at the base of the pectoral fin, the occurrence of thin vertical lines (b), and faint vertical bars (c) on the body. a. All photographs from Veracruz by Carlos and Allison Estapé.

Principal Component Analysis. The first axis of the PCA distinguished samples of *H. floridae* from those of *H. unicolor*, *H. castroaguirrei*, and the new species (Fig. 5a). The second axis differentiated *H. castroaguirrei* from the other samples, and the two axes together further differentiated the new species and two *H. unicolor* populations. A second PCA was conducted on the latter subsample to better visualize the relationships between the new species and *H. unicolor* (Fig. 5b). Here, the first two axes distinguished the new species, the *H. unicolor* population from the Florida Keys, and the *H. unicolor* population from Bocas del Toro (Panama) from the other *H. unicolor* populations.

Phylogenetic inference. The Maximum Likelihood phylogeny generated by RAxML based on more than 90,000 genome-wide SNPs is presented in Figure 6. In line with the previous whole-genome phylogenetic analysis (Hench *et al.* 2022), few nodes were resolved with high bootstrap support (>90% Transfer Bootstrap Expectation).

Notably, the new species was placed in a sister-group relationship with all *H. unicolor* populations except the population from the Florida Keys, rendering *H. unicolor* paraphyletic with respect to the new species. The new species, *H. castroaguirrei*, and *H. floridae* were each recovered as monophyletic with high support (> 90%). Within *H. unicolor*, only the Bocas del Toro (Panama) population formed a clade with at least moderate support (> 70%). The IQ-TREE phylogeny (Fig. S1) showed a similar topology, supporting only *H. floridae* (> 90% nonparametric bootstrap), *H. castroaguirrei* (> 90%), and the new species (> 70%) as monophyletic at the species level. The main difference between the trees concerned the relationship between *H. floridae* and *H. castroaguirrei*—they are sister species in the RAxML phylogeny, but *H. floridae* is the sister group to all other represented hamlets in the IQ-TREE phylogeny. Another difference is the new species is sister to a clade of all *H. unicolor* except those from Florida in the RAxML phylogeny (Fig. 6) vs. sister to a Florida clade of *H. unicolor* in the IQ-TREE phylogeny (Fig. S1). Considering the distinct geographic distribution, color pattern, and genetic divergence of the population from Campeche Bank, and how this compares to the variation between the other hamlet species, it is recognized as a new species, distinct from the two species it most closely resembles, *H. unicolor* and *H. castroaguirrei*.

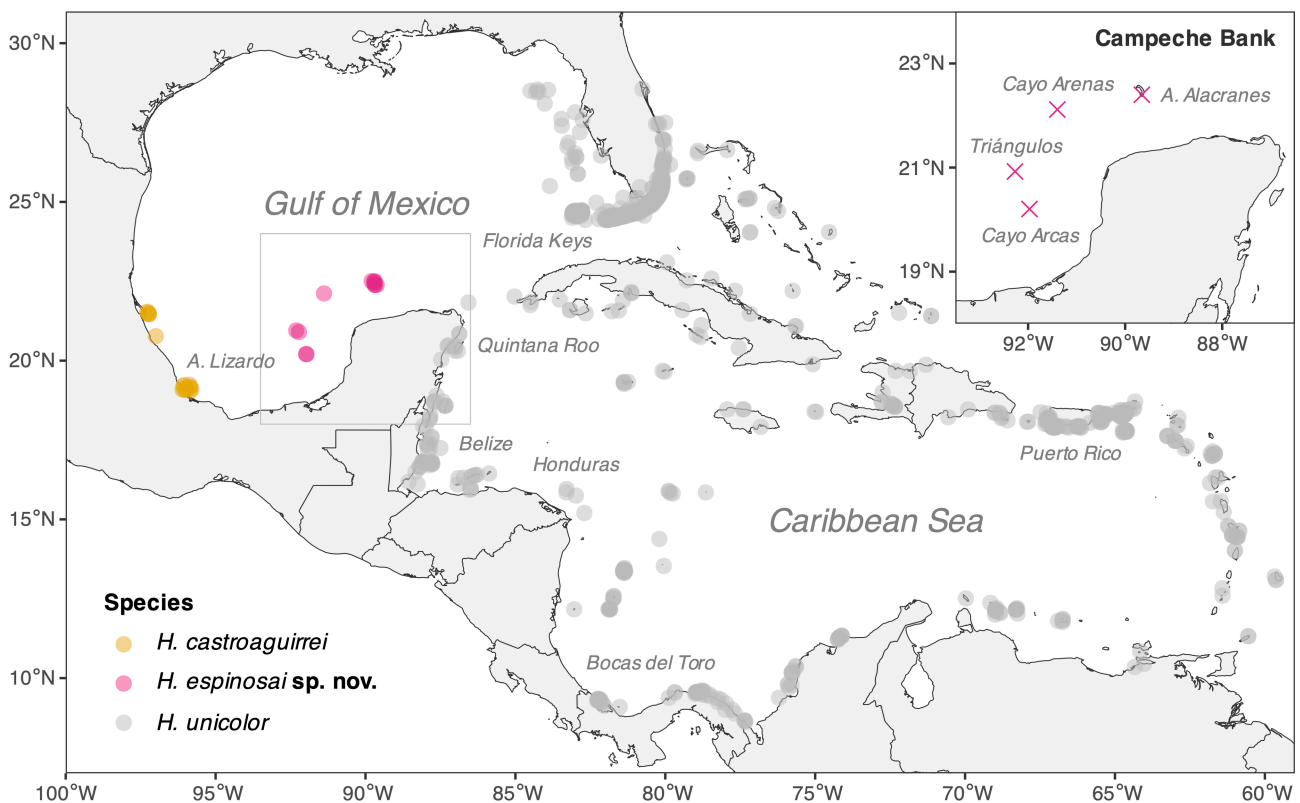


FIGURE 3. Distribution of *Hypoplectrus espinosai* sp. nov., *H. castroaguirrei*, and *H. unicolor* according to records from this study and the Shorefishes of the Greater Caribbean online information system (Robertson & Van Tassell 2023). The inset details the Campeche Bank area with four locations (×) where *H. espinosai* sp. nov. was recorded. A. Alacranes = Arrecife Alacranes, A. Lizardo = Anton Lizardo.

***Hypoplectrus espinosai* sp. nov. Puebla, Aguilar-Perera, Robertson & Domínguez-Domínguez 2025**

Zoobank LSID: urn:lsid:zoobank.org:act:975A80C9-4CA7-4C91-B8B6-506054C3CA66

English common name: Campeche Bank hamlet

Spanish common names: mero del Banco de Campeche (AFS), vaca del Banco de Campeche (FAO), hamlet del Banco de Campeche (vernacular)

Figure 4; Table 1

Holotype. UMSNH CPUM 14398 (specimen) and CTUM 62555 (tissue sample), 90.4 mm SL, Cayo Arcas, Campeche Bank, Campeche, Mexico (20°12'14"N, 91°58'15"W), 24 June 2018, reef, pole spear. Omar Domínguez-Domínguez, Xavier Madrigal Guridi, D. Ross Robertson, David Tafolla Venegas and Georgina Palacios Morales (European Nucleotide Archive accession number ERS20924495).



FIGURE 4. Phenotypic variation of *Hypoplectrus espinosai* sp. nov. A black saddle blotch covers the caudal peduncle and extends over the posterior part of the body, sometimes over the posterior border of the dorsal fin. Note the consistency of the thin vertical lines. Photographs from Alacranes reef by Carlos and Allison Estapé (*a, b, c, d*), Isai Dominguez Guerrero (*e*), and Alfonso Aguilar-Perera (*f*).

Paratypes. UMSNH CPUM 14404 (specimen) and CTUM 62571 (tissue sample), 97.6 mm SL, Cayo Arcas, Campeche Bank, Campeche, Mexico, 25 June 2018, reef, pole spear. Omar Domínguez-Domínguez, Xavier Madrigal Guridi, D. Ross Robertson, David Tafolla Venegas and Georgina Palacios Morales (European Nucleotide Archive accession number ERS20924502). UMSNH CPUM 14408 (specimen) and CTUM 62585 (tissue sample), 82.2 mm SL, Cayo Arcas, Campeche Bank, Campeche, Mexico (20°11'44"N, 91°57'34"W), 25 June 2018, reef, pole spear. Omar Domínguez-Domínguez, Xavier Madrigal Guridi, D. Ross Robertson, David Tafolla Venegas and Georgina Palacios Morales (European Nucleotide Archive accession number ERS20924506).

Diagnosis. *Hypoplectrus espinosai* sp. nov. is distinguished from all named congeners by coloration. Body white with thin vertical lines but no bars (or very faint). Black spot on snout surrounded by electric blue lines. Caudal peduncle entirely covered by black saddle blotch, which extends over posterior part of body, and sometimes over

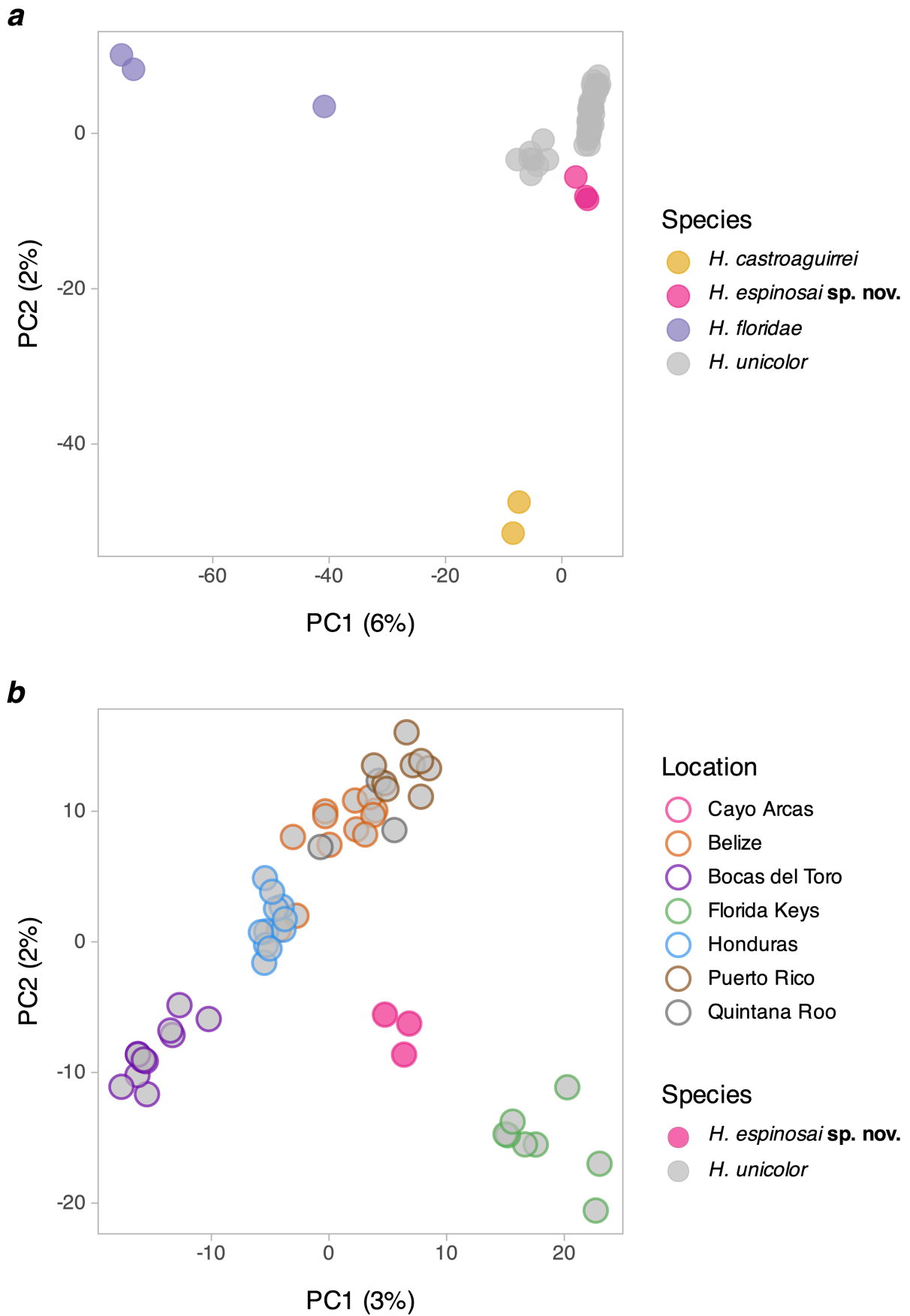


FIGURE 5. Principal Component Analysis (PCA) based on approximately 91,000 genome-wide SNPs, (a) with all samples, (b) *H. unicolor* and *H. espinosai* **nov. sp.** only.

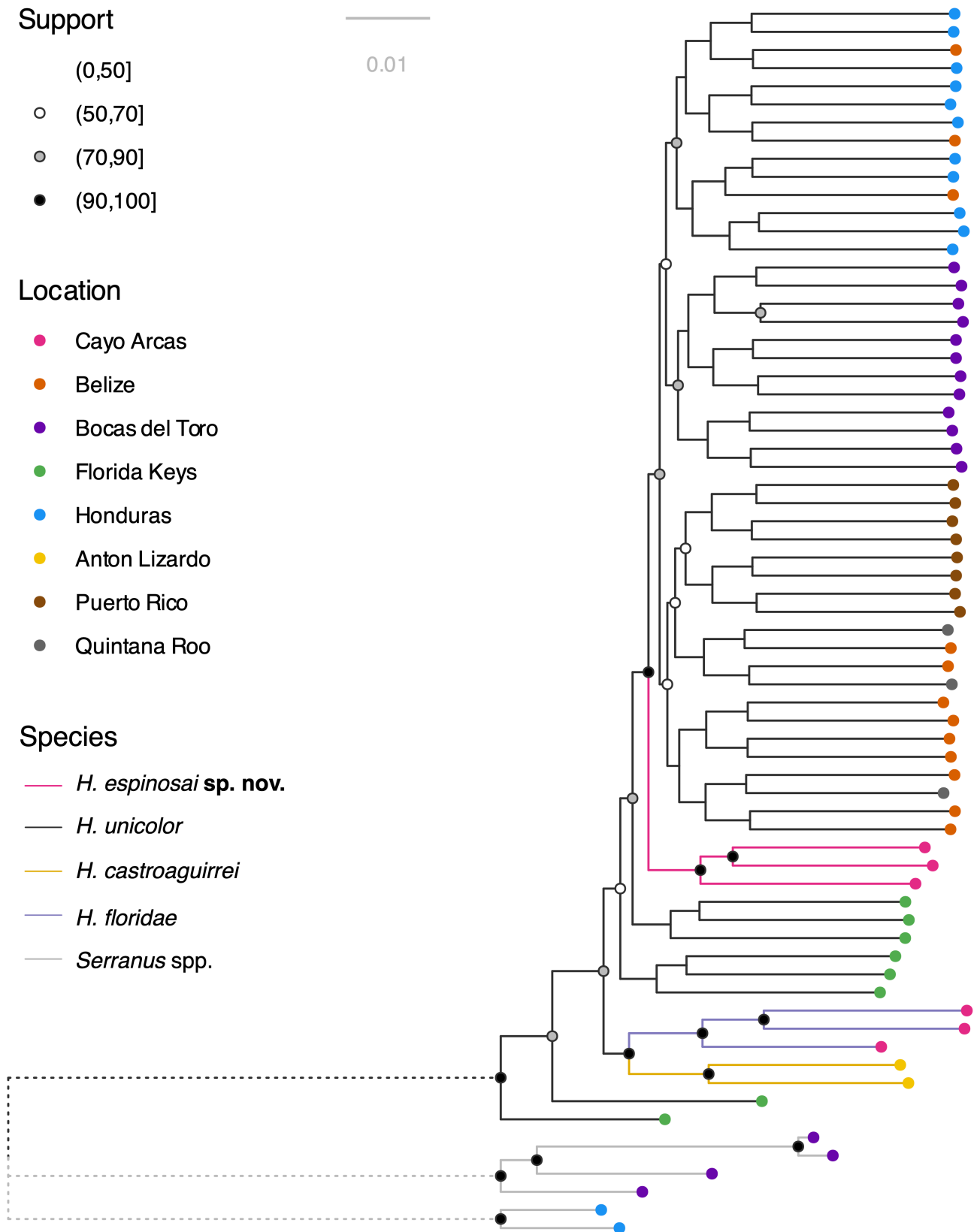


FIGURE 6. Optimal maximum likelihood phylogeny of *Hypoplectrus* species and populations in this study according to RAxML-NG (ln $L = -1824004.117034$). The analysis was based on approximately 91,000 genome-wide SNPs and the GTGTR4+G model including Lewis' ascertainment bias correction. The tree was rooted with three species in the genus *Serranus*. Support symbols at the nodes indicate Transfer Bootstrap Expectations based on 200 bootstrap replicates.

TABLE 1. Morphometric measurements (in millimeters) and meristic counts (in percentage of standard length) of *Hypoplectrus espinosai* **sp. nov.** in Cayo Arcas in the southern Gulf of Mexico.

	Holotype	Paratype	Paratype
	CPUM 14398	CPUM 14404	CPUM 14408
	CTUM 62555	CTUM62571	CTUM 62585
	Cayo Arcas	Cayo Arcas	Cayo Arcas
	Campeche Bank	Campeche Bank	Campeche Bank
	Mexico	Mexico	Mexico
Morphometrics			
Total length	113.1	120.4	100.2
Standard length	90.4	97.6	82.3
Head length	35.4	40.1	32.6
Percentage of standard length			
Body depth	45.6	44.7	42.3
Body width	12.5	16.2	13.2
Head length	39.2	41.1	39.6
Snout length	11.2	14.9	10.4
Orbit diameter	8.8	8.6	9.2
Inter-orbital width	6.8	7.3	7.2
Upper-jaw length	17.4	17.5	16.7
Caudal-peduncle depth	13.3	12.3	12.6
Caudal-peduncle length	12.7	11.9	8.5
Pre-dorsal length	44.6	43.2	41.8
Pre-pelvic length	40.2	45.0	40.3
Pre-pectoral length	37.8	41.8	39.2
Base of dorsal fin	56.6	53.9	53.7
Base of anal fin	19.9	19.5	21.4
Longest dorsal spine	16.0	15.2	13.6
Longest anal spine	13.6	13.4	13.5
Longest anal ray	17.4	17.4	17.5
Caudal-fin length	24.8	23.4	24.9
Pectoral-fin length	32.9	30.9	30.9
Pelvic-fin length	27.4	25.4	25.2
Percentage of head length			
Snout length	28.6	36.2	26.2
Upper-jaw length	44.5	42.5	42.3
Inter-orbital width	17.3	17.7	18.2
Orbit diameter	22.3	21.0	23.2
Meristics			
Dorsal fin	X, 15	X, 15	X, 15
Anal fin	III, 7	III, 7	III, 7
Pelvic fin	I, 5	I, 5	I, 5
Pectoral fin	13	13	13

posterior part of dorsal fin. Black saddle blotch is more extensive than in *H. unicolor*. Black eye-mask characteristic of *H. castroaguirrei* absent.

Description. The morphometric measurements and meristic counts of the holotype and paratypes are presented in Table 1. Dorsal X, 15; anal III, 7; pelvic I, 5; pectoral rays 13; mouth terminal. Morphometrics as percentage SL (mean, min–max): body depth 44.2% SL (42.3–45.6); body compressed, width 14.0 (12.5–16.2); head length 40.0 (39.2–41.1); snout length 12.2 (10.4–14.9); orbit diameter 8.9 (8.6–9.2); interorbital width 7.1 (6.8–7.3); upper-jaw length 17.2 (16.7–17.5); caudal-peduncle depth 12.8 (12.3–13.3); caudal-peduncle length 11.1 (8.5–12.7); predorsal length 43.2 (41.8–44.6); prepelvic length 41.8 (40.2–45.0); prepectoral length 39.6 (37.8–41.8); base of dorsal fin 54.7 (53.7–56.6); base of anal fin 20.3 (19.5–21.4); longest dorsal spine 14.9 (13.6–16.0); longest anal spine 13.5 (13.4–13.6); longest anal ray 17.4 (17.4–17.5); caudal-fin length 24.3 (23.4–24.9); pectoral fin length 31.6 (30.9–32.9); pelvic fin length 26.0 (25.2–27.4). Morphometrics as percentage HL (mean, min–max): snout length 30.3 (26.2–36.2); upper-jaw length 43.1 (42.3–44.5); interorbital width (17.7, 17.3–18.2); orbit diameter (22.3, 21.0–23.2). Body moderately deep, caudal fin truncate, pelvic fins elongate ovals with rounded tips.

Live coloration (Fig. 4). The body color ranges from white to pale grayish-white to pale brownish-white with ~15 thin vertical whitish to pale bluish-white lines that extend from the top of the body profile to near the bottom. The face is also white with thin vertical lines, but with a yellowish tint, particularly towards the anterior part (including the jaw). An eye-sized black spot is present on the snout. It is surrounded by electric blue lines that extend onto the forehead, around the eye, and onto the lower jaw and towards the rear corner of the opercle. The caudal peduncle is entirely covered by a black blotch, which extends over the posterior part of the body, and sometimes over the posterior edge of the dorsal fin. The pelvic and anal fins are yellow with a faint bluish tint on the leading edge. The pectoral and caudal fins are translucent. The dorsal fin is translucent, with irregular yellow markings.

Preserved coloration (Fig. S2). Light brown with an eye-sized black spot on the snout and a black saddle blotch covering the caudal peduncle and extending into the posterior part of the body.

Comparisons. *Hypoplectrus espinosai* **sp. nov.** is distinguished from its congeners by coloration. The most similarly colored hamlets are *H. unicolor* and *H. castroaguirrei*, which differ from *H. espinosai* **sp. nov.** most noticeably by a much less extensive caudal-peduncle black saddle blotch in both species and the presence of a strong black eye-mask in *H. castroaguirrei*. The range of morphometric measurements and meristic counts of the *H. espinosai* **sp. nov.** holotype and paratypes largely overlap with congeners. *Hypoplectrus espinosai* **sp. nov.** has body and fin shapes and sizes similar to the majority of its congeners, except for *H. gemma*, which also occurs in Campeche Bank and has a semilunate caudal fin, and an undescribed black-colored hamlet from the northeastern Caribbean that also has a semilunate caudal fin as well as pointed pelvic fins. The thin vertical lines on the body and face can also be present in *H. unicolor* (Fig. 1f) and *H. castroaguirrei* (Fig. 2b), but they are more pronounced and consistently present in *H. espinosai* **sp. nov.**

Etymology. We assign the species name *espinosai* **sp. nov.** in honor of Héctor Salvador Espinosa Pérez (1954–2022), a dedicated Mexican ichthyologist, founder of the Mexican Ichthyological Society and curator of the Mexican National Fish Collection. The common name refers to the geographic distribution of the species, the Campeche Bank off the north coast of the Yucatan Peninsula in the southwestern Gulf of Mexico, Mexico.

Behavior. Like its congeneric species, *Hypoplectrus espinosai* **sp. nov.** is diurnal and solitary. It was not observed displaying aggressive mimicry behavior as *H. unicolor* does in Panama (Puebla *et al.* 2007, 2018).

Ecology. *Hypoplectrus espinosai* **sp. nov.** is mostly associated with shallow coral-reef habitats at depth ranges between 1 m and 20 m. Maximum known size is 97.6 mm TL.

Geographic distribution. *Hypoplectrus espinosai* **sp. nov.** is distributed throughout coral reefs from the Campeche Bank in the southern Gulf of Mexico (Mexico), including coral reefs in the Alacranes Reef, Triángulo Este, Triángulo Oeste, Cayo Arenas, and Cayo Arcas. It has not been recorded far outside of the Campeche Bank, implying that it is likely endemic to this geographic area.

Discussion

This study corroborates the specificity of the fish fauna of the Campeche Bank in the southern Gulf of Mexico (Robertson & Cramer 2014). Our observations, and all the available data, indicate that *H. espinosai* **sp. nov.** is endemic to the Campeche Bank, and that the two most similar congeners, *H. unicolor* and *H. castroaguirrei*, do

not occur in the area, although several other hamlet species (*H. aberrans*, *H. ecosur*, *H. gemma*, *H. guttavarius*, *H. indigo*, *H. nigricans*, *H. puella*, and *H. randallorum*) are present on the same reefs as *H. espinosai* **sp. nov.** In this respect, the difference among the three species is clear-cut, with distinct and non-overlapping geographic distributions. Similarly, the examination of >650 live photographs of the three species from all over the Greater Caribbean indicates that phenotypic variation is largely non-overlapping among them, with a much more extensive caudal peduncle blotch and no eye-mask in *H. espinosai* **sp. nov.** In this regard we note that we did not observe individuals that are phenotypically intermediate (putative hybrids) between *H. espinosai* **sp. nov.** and any other hamlet species in the Campeche Bank. We note that Robertson *et al.* (2016, 2019b) and González-Gándara & Arias-González (2001) recorded *H. espinosai* **sp. nov.** as *H. unicolor* at those reefs because it was undescribed when those studies were conducted, but Robertson *et al.* (2016, 2019b) observed neither typical *H. unicolor* nor *H. castroaguirrei* on any of those reefs.

Furthermore, the phylogenetic and population genetic data showed that, although not deeply diverged, *H. espinosai* **sp. nov.** is nonetheless genetically distinct from *H. unicolor* and *H. castroaguirrei*. Principal Component Analysis and phylogenetic analyses revealed that *H. espinosai* **sp. nov.** is genetically more distant and less closely related to most populations of *H. unicolor* than those are to each other. The exception to this is the Florida Key population, which renders *H. unicolor* at least paraphyletic with respect to *H. espinosai* **sp. nov.** Notably, Hench *et al.* (2022) have already demonstrated that *H. unicolor* constitutes a highly variable polyphyletic assemblage, even when only considering populations from Panama, Belize, and Honduras. The placement of *H. espinosai* **sp. nov.** within *H. unicolor* (Figs. 6, S1) further corroborates the polyphyly of *H. unicolor* and does not preclude awarding species status to the Campeche Bank hamlet. Considering the genetic and phenotypic variation between the other named hamlet species (Lobel 2011; Hench *et al.* 2019, 2022; Puebla *et al.* 2022), the description of the Campeche Bank hamlet as a species is therefore justified.

This study also corroborates the occurrence of microendemic species in *Hypoplectrus* (*H. maya* in Belize, *H. castroaguirrei* and *H. atlahua* in the western Gulf of Mexico, *H. floridae* in Southwest Florida, *H. ecosur* in the Yucatan Peninsula, and *H. liberte* in Haiti) by adding another species to that group. These microendemic species tend to show increased levels of genetic distinctiveness compared to the other hamlets (Victor 2012; Tavera & Acero 2013; Moran *et al.* 2019; Helmkamp *et al.* under review), and this is also the case for *H. espinosai* **sp. nov.** It should nonetheless be noted that hamlets show unusually low levels of genetic divergence among species, which is due to their exceptionally rapid diversification (Hench *et al.* 2022). An in-depth discussion on why the hamlets should nonetheless be recognized and described as species is provided in Puebla *et al.* (2022).

An interesting result of our study is discovering the genetic distinctiveness of the *H. unicolor* population from the Florida Keys. Considering the lack of monophyly and phenotypic divergence among these populations, we interpret this pattern as evidence of within-species population genetic structure rather than a distinct species.

The biodiversity of non-commercial reef fishes remains poorly known in the southwestern Gulf of Mexico due to the lack of records for some species, particularly local endemics, and identification biases. For instance, in the case of labrid fishes from Alacranes Reef, the rainbow wrasse *Halichoeres pictus* (Poey) was considered for a long time to be present there, but, after careful examination, Aguilar-Perera & Tuz-Sulub (2009) found that it was *Halichoeres burekai* Weaver & Rocha (Mardi Gras wrasse), a new species from the Gulf of Mexico (Weaver & Rocha 2007). In the case of *Hypoplectrus*, many species occur in Alacranes Reef (Aguilar-Perera & González-Salas 2010, Robertson *et al.* 2016, 2019b). The blue hamlet (*H. gemma*), which was considered endemic to the Florida Keys (Domeier 1994) is common in Alacranes Reef (Aguilar-Perera & Tuz-Sulub 2010). More ichthyological work is needed in Alacranes Reef and the other cays such as Cayo Arenas, Cayo Arcas and Triángulos.

The International Union for Conservation of Nature (IUCN)'s Red List considers the *Hypoplectrus* species in different levels of biological conservation, with many of them classified as Least Concern (LC). However, it classifies *H. castroaguirrei* and *H. maya* as Endangered (Anderson *et al.* 2015; Moran & Puebla 2020), *H. liberte* as Critically Endangered (Robertson & Carpenter 2019), and *H. ecosur* and *H. atlahua* as Data Deficient (McEachran & Rocha 2015). *Hypoplectrus espinosai* **sp. nov.** could also be considered LC given the remoteness of its geographic distribution in coral reefs from the cays of Campeche Bank (more than 140 km from the coast of the Yucatan Peninsula). Conservation threats to *H. castroaguirrei*, *H. liberte*, and *H. maya* are related to climate-associated changes as well as coral-reef degradation and pollution due to the close proximity of their habitat to well-populated coastal areas.

Conclusions

A combined effort of scientists who worked in Campeche Bank on fishes associated with coral reefs noticed a hamlet that displayed a consistent color pattern that differs from its most similarly colored congeners, *H. unicolor* and *H. castroaguirrei*. This fish, now called the Campeche Bank hamlet, *Hypoplectrus espinosai* **sp. nov.**, is endemic to the cays of this region in the southern Gulf of Mexico, with no other geographic records so far. This hamlet not only differs in coloration but is also genetically distinct from *H. unicolor* and *H. castroaguirrei*.

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Supplementary Materials. The following supporting information can be downloaded at the DOI landing page of this paper:

FIGURE S1. Optimal maximum likelihood phylogeny of *Hypoplectrus* species, and populations, considered in this study according to IQ-TREE ($\ln L = -675689.891$). The analysis was based on approximately 91,000 genome-wide SNPs and the GTR+ASC model. The tree was rooted with three species in the genus *Serranus*. Support symbols at the nodes indicate nonparametric bootstrap estimates based on 200 replicates.

FIGURE S2. Preserved holotype UMSNH CPUM 14398 *Hypoplectrus espinosai* **sp. nov.** 90.4 mm SL, collected in Cayo Arcas, in the southern Gulf of Mexico (20°12'14"N, 91°58'15"W) on 24 June 2018.

TABLE S1. Fish species identity, collection date and location, and European Nucleotide Archive (ENA) accession numbers of samples used in this study. NA = precise coordinates and/or dates are unknown; Mex. = Mexico; Pan. = Panama.