



Hypoplectrus liberte, a new and endangered microendemic hamlet from Haiti (Teleostei: Serranidae)

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Abstract

The hamlets of the genus *Hypoplectrus* comprise a species flock of about 20 species found on coral reefs of the tropical western Atlantic Ocean, distinguished by complex color patterns and sharing mitochondrial DNA haplotypes within the Caribbean Sea (Gulf of Mexico and Florida-centered species are about 3% divergent in the COI marker). The species show a variety of biogeographic patterns, from widespread common species to relatively rare species limited to small parts of the Greater Caribbean region. We describe here a distinctive striped morph of barred hamlet, apparently limited to Fort-Liberté Bay in northeastern Haiti, as the new species *Hypoplectrus liberte*. The bay is relatively large and isolated, with a long and narrow opening. The markings of the new species differ from the widespread Caribbean Barred Hamlet, *Hypoplectrus puella*, to a similar degree as the two recently described allied northern species, which both have divergent mtDNA sequences. The marking pattern of the new species is more conspicuous and less colorful than the widespread *H. puella*, perhaps an adaptation to more turbid waters (also true for the Gulf of Mexico and Florida species). The mtDNA COI sequence of the new species is the same as that of the other species in the Caribbean species flock. This unusual microendemic species should be an invaluable subject for studying the microevolution of a species radiation. With the tiny population and the vulnerability of Fort-Liberté Bay to development and habitat degradation, this new species represents a critical extinction risk.

Key words: new species, Striped Hamlet, taxonomy, ichthyology, systematics, coral-reef fishes, evolution, endemism, phylogeography.

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Introduction

The hamlets of the genus *Hypoplectrus* comprise a species flock of small and colorful seabasses (Serranidae) native to Caribbean coral reefs (Fischer 1980, Domeier 1994, Heemstra *et al.* 2002, Williams *et al.* 2006, Puebla *et al.* 2011). Their highly varied color patterns are explained mostly by aggressive mimicry of other colorful and innocuous reef fishes by the predatory hamlets (Randall & Randall 1960, Thresher 1978, Randall 2005). Although some species are wide-ranging and occur sympatrically in the Greater Caribbean, several species have been described recently with relatively narrow ranges within the region (Acero & Garzon-Ferreira 1994, Del Moral Flores *et al.* 2011, Lobel 2011, Victor 2012). At present, Eschmeyer *et al.* (2018) list 18 valid species. We describe an additional species here with the smallest range, a single bay in northeastern Haiti, about 10 km across, and discuss the evolutionary implications of this particularly extreme form of microendemism.

The species flock of Caribbean hamlets represents a difficult phylogenetic puzzle that challenges some of our preconceptions of the species concept and has been a source of angst among fish taxonomists for decades. There is an argument over whether to name the morphs as “good” species, since there is a small degree of documented hybridization and, in some cases, intermediate color patterns do occur. Second only to the striking radiation of cichlids in the Rift Lakes of East Africa, the hamlets provide a remarkable case-study of the complexities of the grey zone between populations, morphotypes, subspecies, and species (Victor 2015). The results are important to understanding speciation mechanisms that produce a proliferation of very different phenotypes, especially in sympatry (McCartney *et al.* 2003, Ramon *et al.* 2003, Puebla *et al.* 2007, 2008, 2011, Aguilar-Perera & González-Salas 2010, Holt *et al.* 2011). Part of the paradigm of these species flocks as early radiations of partially interbreeding morphotypes is the apparent genetic uniformity within the species complex, with complex patterns of fine differentiation in certain nuclear genes (Puebla *et al.* 2014). In the case of the hamlets, the northern species in the Gulf of Mexico, Yucatán, and South Florida do diverge substantially in mtDNA sequences, more than 3% in the COI marker (Victor 2012, Tavera & Acero 2013). This indicates that, in some cases at least, there are major barriers to gene flow. Further progress on understanding the genetic changes underlying these early stages in speciation in this species flock doubtless will be forthcoming from genome studies presently underway at present (e.g. Puebla *et al.* 2014, Picq *et al.* 2016).

Background

In 2013, the Haitian government designated the Parc National des Trois Baies or Three Bays National Park Marine Protected Area (MPA) on the northeast coast of Haiti, encompassing the three bays of Limonade, Caracol, and Fort-Liberté, as well as the lagoon Lagon aux Boeufs, an area of 75,618 ha (Kramer *et al.* 2016). The Nature Conservancy was contracted by the Inter-American Development Bank (IDB) to assist the Ministry of Environment (MDE) of Haiti by conducting a biological inventory of the marine and coastal resources of the Park and developing a biodiversity database (Kramer *et al.* 2016). A total of 183 species of marine fishes were identified within the Park waters, including an undescribed hamlet species that was recorded only within Fort-Liberté Bay.

Materials and Methods

Specimens were collected under MDE permit from Fort-Liberté Bay, Haiti, by the junior author in 2015 using nets and spear. Type specimens are deposited at the Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA (UF) and the National Museum of Natural History, Washington, D.C., USA (USNM). Surveys of marine fish biodiversity in the bay comprised 7 man-hours of underwater surveying, while outside the bay, surveys were conducted for 23h 58m (by D. Grenda and K.W. Marks).

A 652-bp segment (the “barcode” marker) was amplified from the 5' region of the mitochondrial cytochrome c oxidase (COI) gene using a variety of primers (Ivanova *et al.* 2007). DNA extractions were performed with the NucleoSpin96 (Machery-Nagel) kit according to manufacturer specifications under automation with a Biomek NX liquid-handling station (Beckman-Coulter) equipped with a filtration manifold. PCR amplifications were

performed in 12.5 µl volume including 6.25 µl of 10% trehalose, 2 µl of ultra pure water, 1.25 µl of 10× PCR buffer (10 mM KCl, 10 mM (NH₄)₂SO₄, 20 mM Tris-HCl (pH8.8), 2 mM MgSO₄, 0.1% Triton X-100), 0.625 µl of MgCl₂ (50 mM), 0.125 µl of each primer (0.01 mM), 0.0625 µl of each dNTP (10 mM), 0.0625 µl of *Taq* DNA polymerase (New England Biolabs), and 2 µl of template DNA. The PCR conditions consisted of 94°C for 2 min., 35 cycles of 94°C for 30 sec., 52°C for 40 sec., and 72°C for 1 min., with a final extension at 72°C for 10 min. Specimen information and barcode sequence data from this study were compiled using the Barcode of Life Data Systems (Ratnasingham & Hebert 2007, Ward *et al.* 2009). The sequence data is publicly accessible on BOLD and GenBank. Measurements were made by digital dial calipers and the measurements are presented as values for the holotype followed by the range for the paratypes in parentheses.

Hypoplectrus liberte, n. sp.

Striped Hamlet
Mero Rayado

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Figures 1 & 2A.

Holotype. UF 239538, 84.1 mm SL, Haiti, Baie de Fort-Liberté, off Fort St. Joseph, 19.677°, -71.843°, 9 m depth, K.W. Marks & D. Grenda, 30 August 2015.

Paratypes. UF 239539, 2 specimens, 75.5–87.7 mm SL, same data as holotype, K.W. Marks & S.A. Pea, 4 September 2015; USNM 444944, 80.6 mm SL, same data, 4 September 2015.

Diagnosis. A species of *Hypoplectrus* with a black stripe from eye to base of caudal fin, interrupted by white iridescent lines on head and broken on rear body and caudal peduncle into three discrete black spots centered just above lateral line; lower half of head and body pale.

Description. Dorsal-fin elements X,14 (X,14); anal-fin elements I,7 (I,7); pectoral-fin rays 14 (13–14), upper two and lower two unbranched, uppermost ray short, up to third of fin length, lowermost ray short, up to half fin length; pelvic-fin rays I,5, all rays branched; caudal fin with 15 (15) branched and 20 (21) segmented rays and 3 (2–3) visible dorsal procurrent rays and 2 (2–3) visible ventral procurrent rays; total gill rakers on first arch, including rudiments, 7 upper (6–7)+13 (13–15) lower=20 total (19–22).



Figure 1. *Hypoplectrus liberte*, fresh holotype, UF 239538, 84.1 mm SL, Fort-Liberté Bay, Haiti (K.W. Marks).

Body wide and broadly oval, maximum body depth at about third dorsal-fin-spine origin 37 (37–41)% SL and compressed, side-to-side width 15 (13–14)% SL (measured just forward of pectoral-fin base); predorsal length (oblique) 44 (41–43)% SL; preanal length (oblique) 67 (67–68)% SL; prepelvic length (oblique) 40 (40–44)% SL; caudal-peduncle depth 13 (12–13)% SL, caudal-peduncle length (dorsal, horizontal span) 10 (10–11)% SL, (ventral, horizontal span) 17 (15–17)% SL; lateral line complete, curving in an arch over pectoral fin becoming straight on caudal peduncle.

Head large, length 39 (37–40)% SL; dorsal head profile smooth and mostly straight, rising sharply from terminal tip of jaw (lower lip) to dorsal-fin origin; eyes large and round, horizontal orbital diameter 24 (23–27)% HL, pupil pear-shaped, pointing forward; interorbital space flat and relatively narrow, minimum bony-interorbital width 17 (14–16)% HL; snout sharply pointed and short, length 12 (11–13)% SL or 31 (30–32)% HL (oblique); upper preopercular margin about vertical with a rounded angle to lower limb, serrations on both limbs, curved spines along lower arm (about 10–15), small, regular, and straight (about 30–40) on vertical arm; interopercular, subopercular, and opercular margin with fine serrations or smooth; three flat opercular spines behind eye, upper inconspicuous, middle largest. Anterior nostril a short tube, posterior nostril a flat oval opening with a diameter about distance to anterior nostril.

Mouth large, upper jaw ending at a vertical between mid-pupil and rear of eye, oblique length 46 (45–51)% HL; rear end of maxilla expanded; teeth small to moderately-sized and caniniform, stout and fixed, lining upper and lower jaws in irregular multiserial rows, largest in upper jaw laterally near front of jaw. Tongue long, relatively narrow, and spatulate. Gill rakers on first arch finely serrated, upper limb with one long raker followed by spiny short nubs, lower limb with longest at about angle, grading down to nubs anteriorly, longest raker about length of gill filaments (about pupil height in length).

Dorsal fin single and long-based without notch between spinous and soft portions, last ray split to base; dorsal-fin base 56 (54–56)% SL; first dorsal-fin spine 5 (4–5)% SL, second dorsal-fin spine 9 (8)% SL, third dorsal-fin spine 14 (12–14)% SL, last dorsal-fin spine 15 (13–14)% SL; first dorsal-fin soft ray 14 (14–16)% SL; longest dorsal-fin soft ray (about 7th) 16 (15–17)% SL; anal fin short and broadly rounded, last ray split to base, anal-fin base 19 (18)% SL; first anal-fin spine 6 (5–6)% SL; second anal-fin spine 12 (12)% SL, third anal-fin spine 14 (13–14)% SL, longest anal-fin soft ray (penultimate) 17 (17–18)% SL; pectoral-fin length 28 (29)% SL; pectoral-fin base 6 (6)% SL; pelvic-fin spine length 13 (14–15)% SL, longest pelvic-fin ray (second) 23 (23–24)% SL; caudal fin slightly forked, caudal-fin length 24 (25–26)% SL.

Scales small and ctenoid, extending over body and head including cheek and operculum, sparing snout, interorbital, cranium, and underside of head; small scales extend up median fin membranes, about one-third of soft dorsal fin and most of length of first to second or third soft anal-fin membranes; about 50 (47–52) pored scales in lateral line from uppermost operculum to edge of hypural plate, 3 or 4 more on fin base, about 70 lateral scale rows (counted above lateral line), about 12 scale rows between base of first dorsal-fin spine and lateral line (not counting tiny scales on fin base).

Color in life. (Figs. 1 & 2A) An overall pale background on body and head as well as fins, with a prominent mid-lateral thick black stripe from behind eye to lateral line at level of anal-fin origin, where stripe breaks up and continues as three separated black spots, slightly above and overlapping posterior lateral line, last spot on caudal peduncle smaller and more vertical. White to bluish iridescent lines ringing eye and then in vertical position in a series behind eye, prominently interrupting black stripe; vertical whitish lines continue closely arrayed across body creating jagged edges to black stripes and spots. Bluish spots on snout and a bright blue spot on operculum above level of pectoral-fin base. Fins translucent and mostly unmarked, except dorsal and anal fins with a thin blue edge and pelvic fins bluish or dusky.

Color in alcohol. Specimens in ethanol retain only shades of brown described for live color, but include diagnostic dark stripe and spots. Breaks in dark stripe behind eye formed by whitish iridescent vertical lines remain prominent. Preserved specimens develop faint dusky extensions of stripe ventrally, in pattern of other barred hamlet species, but in all cases stripe is obvious. Pelvic fins can be dusky or dark.

Genetic results. Tissue samples from the holotype and 3 paratypes yielded 3 mitochondrial DNA COI haplotypes within the large lineage comprising all the Caribbean Sea hamlet species sequenced to date (excluding Florida, tip of Yucatán, and the Gulf of Mexico). The haplotype of the holotype (GenBank accession number

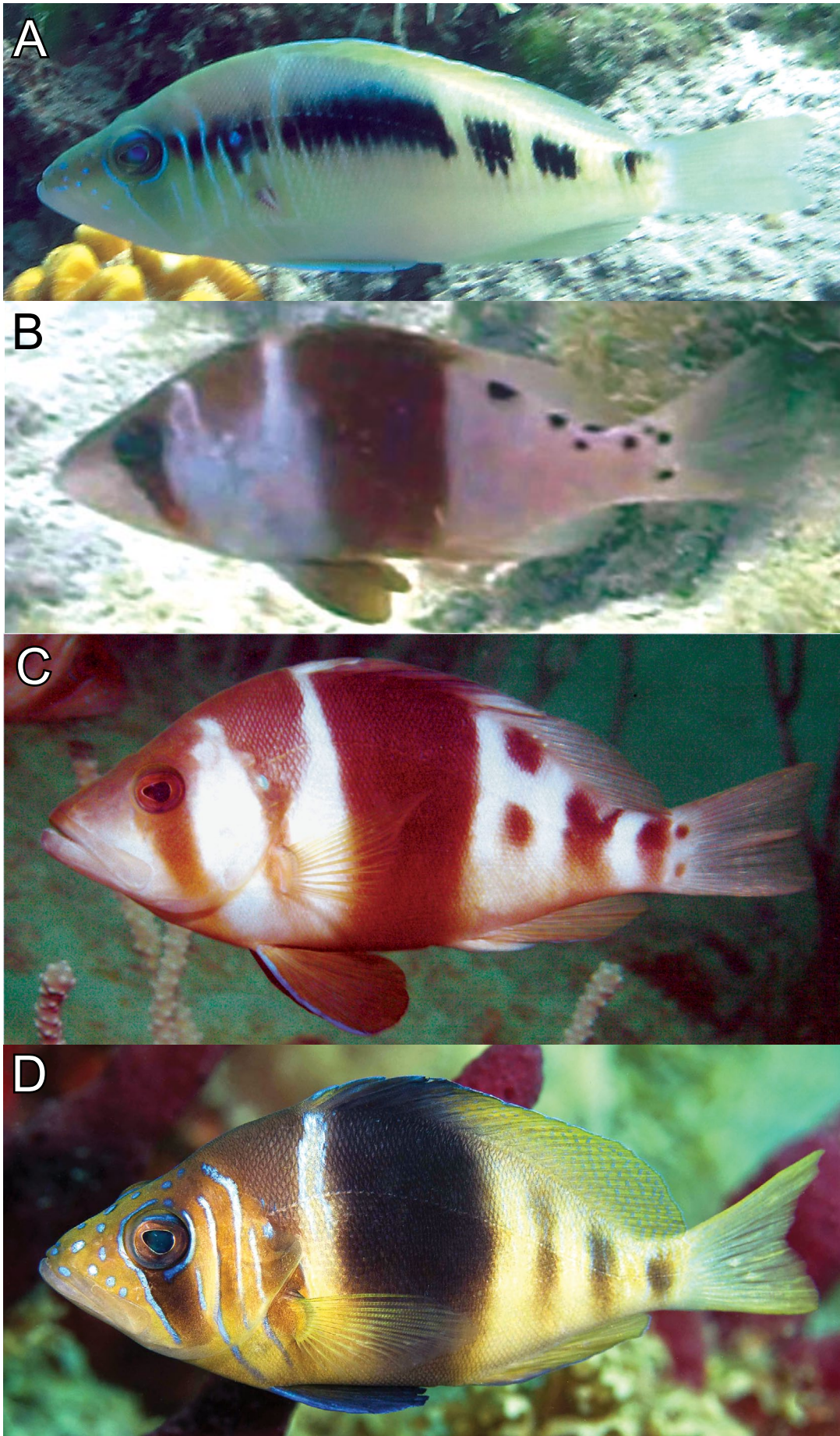


Figure 2. The barred hamlet species-complex: A) *Hypoplectrus liberte*, Fort-Liberté Bay, Haiti (K. W. Marks); B) *H. ecosur*, Yucatán, Mexico (B. Carlson); C) *H. floridae*, S. Florida (M. Kovach); D) *H. puella*, St. Vincent (R. Whitworth).



Figure 3. Type location for *Hypoplectrus liberte*, Fort-Liberté Bay, Haiti: map of Hispaniola (above) and map of Fort-Liberté Bay with Fort-Liberté town indicated; X= the collection location at 19.677°, -71.843° (Google Earth).

KU986285) was shared with specimens of several hamlet species from Bermuda, Florida, Bahamas, Cuba, Puerto Rico, Belize, Panama, and Curaçao; the second haplotype (paratypes KU986298 and KU986293) with specimens from Belize and Panama, and the third paratype (KU986282) was a close unique haplotype.

Etymology. The specific epithet is a noun in apposition named for the type location.

Distribution and habitat. The new species is thus far known only from the Fort-Liberté Bay in northeastern Haiti (Fig. 3). It is common in the shallow waters of the bay. Barred Hamlets surveyed by the junior author outside of the bay have normal markings for *H. puella*, and, notably, there are a few normally marked *H. puella* present in the bay as well. The surveys also recorded other hamlet species within the bay, i.e. *H. guttavarius* (Shy Hamlet),

H. indigo (Indigo Hamlet), *H. nigricans* (Black Hamlet), and *H. unicolor* (Butter Hamlet). The habitat is shallow inshore seagrass and coral reef with a muddy bottom, high turbidity, extensive algal growth, low live-coral cover, and abundant sponges (Kramer *et al.* 2016).

Comparisons. The live markings are distinctive and distinguish the new species from all other hamlets. The most diagnostic marking is the lateral black stripe, a pattern not present on any other hamlet, but frequent in many other reef fishes. Other hamlets often show bar patterns, but never stripes. An occasional individual of *H. puella* does have some intensification of the mid-portion of the bars on the body, but the broad darker area on the anterior body is below the lateral line vs. much of the stripe above the lateral line in *H. liberte*. Compared to other barred hamlets, *H. liberte* also differs by having a completely pale lower half of the head and body.

There are no well-documented meristic differences among the barred hamlet species complex (and, debatably, among all hamlet species) and morphometric differences listed among hamlets in general are compromised by small samples, large allometric variations, and observer variation in measuring definitions and techniques. Larger series and a wider range of sizes would be needed to evaluate if there are any reliable differences.

Remarks. The most interesting aspect of the diagnostic markings on *H. liberte* is that they are more contrasting and in smaller patches than the markings on *H. puella* (Figs. 1 & 2). Instead of a relatively uniform barring, *H. liberte* has a prominent dark stripe from the eye rearward, broken into distinct dark spots against a pale background on the rear half of the body. The fish can then intensify the dark spots and whiten the background to make the markings highly visible even in murky and low-light conditions (see video list below). Both northern barred hamlet species, *H. ecosur* and *H. floridae*, also have developed more contrasting markings on the rear half of the body, but in different and presumably independently derived patterns (Fig. 2). Instead of intensifying a lateral stripe, *H. ecosur* has intensified small dark spots along the dorsal margin and the two colon-like spots on the base of the caudal fin and *H. floridae* has intensified a dark rear spur at the top of the fifth bar and the two spots on the base of the caudal fin, as well as breaking the fourth bar into two dark portions. Notably, *H. ecosur* can intensify the contrast of the rear body pattern in life producing a strikingly contrasted appearance (see video list below), somewhat similar to that shown by *H. liberte*.

The development of more contrasted marking patterns in these isolated populations, and particularly the fact that all three patterns are different and thus can be considered independently derived, argues that there is significant natural selection driving these populations to diverge as different species. It is clearly not coincidental that the locations of these species are known to have more turbid conditions with lower visibility than typical Caribbean coral reefs, i.e. Fort-Liberté Bay in Haiti and Gulf of Mexico waters on both the Yucatán Peninsula (*H. ecosur*; newest records from Zarco-Perelló *et al.* 2014) and the Florida Middle Grounds, where the main population of *H. floridae* likely occurs. Turbidity has been discussed as a factor controlling relative abundances of hamlet species in Puerto Rico (Hench *et al.* 2017), and its role in structuring the community of hamlets and its potential microevolutionary effects deserve additional investigation. A somewhat analogous situation has been documented for coral-reef fishes in the Marquesas Islands of the SE Pacific Ocean, where more turbid conditions have promoted rapid disruptive selection and a proliferation of local endemic species closely related to widespread Indo-Pacific siblings (and often with different bright colors), with species splits occurring in less than 0.5 Ma (Gaither *et al.* 2015).

Visibility is especially important in the mating system of hamlets, which pair up and spawn in the reduced light of dusk, in an intricate dance during which egg-trading by hermaphrodites occurs (see example in Fig. 4). Since both partners have eggs and sperm to contribute, and the cost of eggs is far higher than sperm, cheating can only be prevented by each partner anteing up repeatedly during a spawning event (Fischer 1987). In a situation where the behavior of the partner is important, pairing is critical, and staying together in low visibility is imperative, there would be very strong selection for being more visible in turbid waters by developing more prominent contrasting markings. This selection pressure would clearly put more subtly marked or colorful individuals at a disadvantage and strongly select against hybridization, thus disruptive selection would strongly promote speciation in these local populations.

Fort-Liberté Bay is extremely vulnerable and the population of *H. liberte* may well be exceptionally small, hundreds to a few thousand individuals. Although now part of the Three Bays National Park Marine Protected Area, the bay has been proposed as a deepwater port development site in the recent past (e.g. <http://www.sbe>).

be/en/page/112/port-development-feasibility-study-haiti). Extensive deforestation of the protective mangrove forests in the area, overfishing of fishes of all sizes, and widespread agriculture and commercial development in the surrounding region threaten the existence of corals and the associated fish fauna in the bay. The conservation status of the new species is critical and immediate evaluation and priority for conservation measures are imperative.

Photographic material:

Video of *H. liberte* at Fort-Liberté, Haiti, by Kenneth W. Marks:

<http://doi.org/10.5281/zenodo.1064133>

Video of *H. ecosur* at Contoy Island, Yucatán, Mexico, by Bruce Carlson:

<http://doi.org/10.5281/zenodo.1009193>

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Figure 4. Mating pair in the Barred Hamlet, *Hypoplecterus puella*, in Dominica (C.J. Estapé).

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