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Discovery of a Distinctive Spotted Color Pattern in the Cuskeel *Neobythites unicolor* (Teleostei, Ophidiidae) Based on Underwater-Vehicle Dives, with New Records from the Southern and Eastern Caribbean

Franz Uiblein[1], Jørgen G. Nielsen[2], Carole C. Baldwin[3], Andrea M. Quattrini[4], and Ross Robertson[5]

***In situ* images and/or collection of seven specimens by underwater-vehicle dives at 269–609 m depth off Curaçao, Dominica, and Puerto Rico (S, E, and NE Caribbean) revealed new records and a previously unknown, distinctive color pattern for the cuskeel *Neobythites unicolor* (Ophidiidae). Species identification was based on detailed comparisons with earlier studied type and non-type material using morphometric, meristic, and otolith-form characters. A revised color description is provided based on images of live specimens *in situ* in their habitat, shortly after capture, and after preservation. Live and fresh specimens of *Neobythites unicolor* show a large number of distinctive, dark, rounded or irregularly shaped spots distributed dorsally on head, dorsal portion of body, and on the dorsal fin. This color pattern fades when fish are frozen, and it is completely lost during preservation over several years. The available images of fresh color patterns indicate an increase in spot size with fish size. In addition, some of the quantitatively examined morphometric and otolith characters of museum specimens show positive allometry. No geographic variation in color patterns could be detected. Although the Curaçao population is separated from all other known populations of *N. unicolor* by at least 650 km, the only population difference found was a slightly lower pectoral-fin ray count for the four specimens collected off Curaçao. An updated distribution map is provided correcting for an erroneous record in the inner Gulf of Mexico from which *N. unicolor* appears to be completely absent. While the spotted color pattern described here is unique among the 54 species of *Neobythites*, a similar pattern occurs in two other genera of the subfamily Neobythitinae, *Sirembo* and *Spottobrotula*. Further requirements to more fully understand the color diversity and related biology, ecology, and evolution in the species-rich genus *Neobythites* are emphasized.**

COLOR patterns in live or freshly collected fishes may provide important information about taxonomic distinction, systematic relationships, life history, and ecology. Many fish species change color due to intrinsic or environmental conditions, while others have quite different color patterns for larvae, juveniles, and adults of each sex. Variation such as this needs to be considered when using color patterns for taxonomic purposes. In addition, dramatic color changes may happen during or after collection with various sampling devices and particularly during or after fixation during the curation of specimens for scientific collections. Long-term preservation of fish specimens may lead to partial or complete loss of color patterns, which confounds proper diagnoses in species descriptions (e.g., Maciolek, 1977; Baldwin et al., 2009; Uiblein et al., 2017; Uiblein and Nielsen, 2018).

The cuskeel genus *Neobythites* is the most diverse ophidiid genus with 54 valid species (Uiblein and Nielsen, 2018). Members of this genus are commonly found at 100–800 m depth on the lower part of the shelf and the upper part of the slope of subtropical and tropical areas of all oceans, except for the eastern Atlantic. Many species of *Neobythites* have distinct color patters that are diagnostically important (Uiblein and Nielsen, 2005). However, in many cases the original descriptions of species of *Neobythites* were based entirely on preserved specimens, and there was no information on fresh color patterns. One example is the species *Neobythites unicolor*, which was described based on museum specimens that had been preserved for nine years after being collected in the Caribbean (north of 16°N), the Gulf of Mexico, and adjacent areas of the tropical NW Atlantic. The species name *"unicolor"* emphasized the rather uniform pale body color and lack of dark pigment markings, such as dark eyespots or ocelli, bands, bars, or stripes, which occur in preserved specimens of many other species of *Neobythites* found in the Caribbean (Nielsen, 1999; Nielsen et al., 2009) and elsewhere (Uiblein and Nielsen, 2005, 2018, 2019).

During recent underwater-vehicle dives in the southern and eastern Caribbean using a human-occupied mini-submersible and two remotely operated vehicles (ROVs), seven conspicuously colored ophidiid specimens were encountered at 269–609 m depth. Four of those specimens were photographed and/or videotaped *in situ,* and five were collected, photographed, subsequently preserved, and included in the USNM fish collection. After detailed analyses of meristic, body-form, and otolith-shape characters, color patterns, and comparisons with types and previously known non-type material, the first two authors of the paper identified the seven specimens as *N. unicolor*.

Here we provide a taxonomic account of *N. unicolor* with an updated diagnosis along with a detailed redescription of coloration that reveals substantial differences in color patterns among live, freshly collected, and preserved specimens, as well as size-related differences. Four of the five submersible-collected specimens are from Curaçao, representing the first records of *N. unicolor* for the southern

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Caribbean. Because Curaçao is relatively remote from all other localities of the species, we compared those specimens with the northern population regarding possible geographic differentiation. The findings are discussed with respect to inter- and intraspecific variation in coloration and morphology in *Neobythites*, the occurrence of similar color patterns in other, closely related fish taxa, and the need for a more complete coverage of fresh color information in *Neobythites*. Furthermore, this study highlights the importance of utilizing submergence technologies for obtaining *in situ* imagery of deep-sea fishes.

MATERIALS AND METHODS

In situ sampling and post-dive processing.—For *in situ* photographs and collection of specimens, the submersible *Curasub* (https://www.substation-curacao.com) was employed during various field periods with dives off Curaçao, southern Caribbean (2011–2014), and off Dominica, eastern Caribbean (2016) as part of the Smithsonian Institution's Deep Reef Observation Project—DROP (Fig. 1). *In situ* photographs during dives were made with a Nikon D80 digital camera, equipped with a 60 mm macro lens in a deep-water aluminum housing, a flash, and a laser pointer to assist framing of each photograph. Fish specimens were collected using the fish anesthetic quinaldine dissolved in ethanol that was pumped from a reservoir through a tube attached to one hydraulic arm of the sub and a suction hose (that uses the same pump as the anesthetic-delivery apparatus) attached to the other arm. The suction tube empties into a vented plexiglass cylinder attached to the outside of the sub.

During each of five *Curasub* dives, a single specimen of *N. unicolor* was collected. At the surface, each specimen was measured, photographed, tissue sampled (muscle biopsy from right side, for genetic analysis), and preserved in 10% formalin. In some instances, pending scientist availability, specimens were frozen in seawater before being processed in the lab. Finally, all specimens were preserved in 75% ethanol and accessioned into the USNM fish collection.

For documentation of color patterns and their variation depending on treatment conditions, we examined five specimens. Two specimens from dives off Curaçao (USNM 431331, USNM 431721) were photographed both *in situ* and shortly after capture. One specimen from off Curaçao (USNM 433497) and one from off Dominica (USNM 440570) were photographed shortly after capture. One specimen from off Curaçao (USNM 422668) was frozen for some time before being defrosted and photographed. After preservation of the five specimens, each was photographed and the time since fixation recorded. For comparison with fish subject to long-term fixation, a paratype of *N. unicolor* (ZMUC P77940) was used. An overview of photographs obtained for respective treatment conditions is provided in Table 1.

In situ images of two additional specimens were obtained during two ROV dives, one in the Mona Passage off Puerto Rico and another in the Anegada Passage near the Virgin Islands (Table 1, Fig. 1). For this the ROV *Hercules* was tethered to the camera sled *Argus* and deployed from the EV *Nautilus* in October 2013, and the ROV *Deep Discoverer* (D2) was tethered to the camera sled *Seirios* and deployed from the NOAA RV *Okeanos Explorer* in April 2015. Both ROVs were equipped with high-definition cameras and paired lasers positioned 10 cm apart. Still images of the two encountered specimens were extracted from the video footage and included in the USNM collection for proper reference and accessibility.

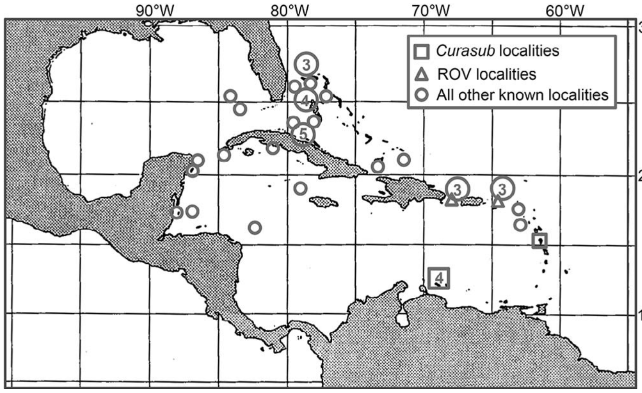

Fig. 1. Distribution of *Neobythites unicolor*. Localities of specimens encountered and collected by the *Curasub* submersible are indicated by squares; triangles indicate the two ROV stations with verified images of this species; circles indicate all localities of specimens studied by Nielsen (1999), slightly updated (see text). Enlarged symbols with numbers indicate multiple, closely overlapping localities.

Taxonomy and distribution studies.—Counts and measurements of 12 meristic, 14 body shape, and seven otolith characters were obtained and analyzed for the five submersible-collected specimens and 28 additional type and non-type specimens, following Uiblein and Nielsen (2018, 2019). All available photographs and/or video footage of the seven specimens encountered by underwater vehicles and those of the collected specimens were used for preparing the color description, considering three treatment conditions: *in situ*, shortly after capture, and after preservation. An updated distribution map was prepared to include the additional locality information considering the distribution information available from Nielsen (1999). During preparation of this study, a recheck of the original data sheets for three specimens of *N. unicolor* (USNM 309223) examined by Nielsen (1999) resulted in an updated locality for this lot, which is from SE of Florida instead of the NW Gulf of Mexico.

Institutional abbreviations follow Sabaj (2016). Other abbreviations are: SL = standard length, TL = total length; HT = holotype; PT = paratype.

Neobythites unicolor **Nielsen and Retzer, 1994**

Figures 1–5, Tables 1, 2

Neobythites unicolor Nielsen and Retzer, 1994: 993, fig. 2a; Nielsen, 1999: 354–358, figs. 11–13.

Holotype.—FMNH 69349, 90 mm SL, female, East Caribbean Sea, 17°38.5′N, 63°27′W, RV *Oregon*, Sta. 2633, bottom trawl, 348 m depth, 30 September 1959.

Paratypes.—(*n* = 8, 58–104 mm SL) FMNH 69348, 103 mm, female, East Caribbean Sea, 18°3′N, 67°27′W, RV *Oregon*, Sta. 2643, bottom trawl, 275–330 m depth, 5 October 1959; FMNH 69352, 82 mm SL, female, ZMUC P77940, 104 m SL, male, West Caribbean Sea, RV *Oregon*, Sta. 1868, bottom trawl, 320 m depth, 21 August 1957; FMNH 69354, 100 mm SL, female, East Caribbean Sea, 18°12′N, 67°18′W, RV *Oregon*, Sta. 2648, bottom trawl, 275 m depth, 6 October 1959; TCWC 4469.3, 58–89 mm SL, 2 females, West Caribbean Sea, 20°20.5′N, 89°19.4′W, MBI, Sta. 168, 10′ otter trawl, 240–267

Table 1. Image documentation for *Neobythites unicolor* encountered and partly collected by underwater vehicles and a paratype (PT) of this species used for comparisons, with information on treatment conditions under which the photographs were taken. *Dive number not recorded. **Photo from video footage.

				Treatment condition for photographs taken			
Collection number	Size (SL)	Dive	Locality	*In situ*	Shortly after collection	After long-term freezing	Time after fixation
USNM 422668	93 mm	MUV *Curasub* 13-nn*	off Curaçao	–	–	X	508 days
USNM 431331	94 mm	MUV *Curasub* 14-01	off Curaçao	X	X	–	211 days
USNM 431721	69 mm	MUV *Curasub* 14-15	off Curaçao	X	X	–	179 days
USNM 433497	38 mm	MUV *Curasub* 14-25	off Curaçao	–	X	–	95 days
USNM 440570	65 mm	MUV *Curasub* 15-29	off Dominica	–	X	–	460 days
USNM 444965	ca.10 cm	HI1305	near Virgin Islands**	X	–	–	–
USNM 444964	ca. 8 cm	EX1502L3-3	off Puerto Rico**	X	–	–	–
ZMUC P77940, PT	104 mm	–	W Caribbean Sea	–	–	–	57 years

m, 11 April 1976; TCWC 6207.2, 93 mm SL, female, 100 mm SL, Western Caribbean Sea, 20°26.3′N, 87°14.7′W, MBI, Sta. 167, otter trawl, 253–276 m depth, 11 April 1976.

Non-type material.—($n = 19$, 49–103 mm SL) MCZ 39257, 88 mm SL, female, off Cuba, 22°13′N, 81°10.5′W, RV *Atlantis,* Sta. 3319, 357–393 m depth, 4 April 1938; MCZ 39327, 93 mm SL, male, off Cuba, 22°49′N, 78°48′W, RV *Atlantis,* Sta. 3412, 430 m depth, 29 April 1938; MCZ 39396, 75 mm SL, male, off Cuba, 22°48′N, 79°9′W, RV *Atlantis,* Sta. 3422, 430 m depth, 30 April 1938; MCZ 41866, 72 mm SL, female, Gulf of Mexico, 25°8′N, 84°19′W, RV *Oregon,* Sta. 1026, 298 m depth, 19 April 1938; UF 202019, 93 mm SL, male, ZMUC P771190, 81 mm SL, female, off Cuba, 22°55′N, 79°16′W, RV *Oregon,* Sta. 1341, 439 m depth, 16 July 1955; UF 214148, 94 mm SL, female, 49 mm SL, male, ZMUC P771191, 84 mm SL, female, off Grand Bahama Is., 27°25′N, 78°41′W, RV *Gerda*, Sta. 251, 306–311 m depth, 5 February 1964; UF 230529, 78–103 mm SL, 1 female, 3 males, ZMUC P771189, 85 mm SL, female, Turks Is. Passage, 20°53.1′N, 71°36′W, RV *Pillsbury,* Sta. 1425, 737–787 m, 19 July 1971; USNM 309225, 73–99 mm SL, 1 female, 4 males, off Saba, 17°38.5′N, 63°27′W, RV *Oregon,* Sta. 2633, 40′ flat trawl, 348 m depth, 30 September 1959.

Submersible-collected specimens for this study.—($n = 5$, 38–94 mm SL) USNM 422668, 93 mm SL, off Curaçao, near aquarium, 12°04′59″N, 68°53′57″W, *Curasub* dive 13 nn (no dive and depth data), A. Schrier and B. Brandt, 2013; USNM 431331, 94 mm SL, female, same locality as above, *Curasub* dive 14-01, 305 m depth, C. C. Baldwin, D. R. Robertson, and B. Brandt, 17 March 2014; USNM 431721, 69 mm SL, off Curaçao, near Jan Thiel Bay, 12°04′59″N, 68°53′57″W, *Curasub* dive 14-15, 305 m depth, C. C. Baldwin, A. Schrier, and B. Brandt, 19 September 2014; USNM 433497, 38 mm SL, off Curaçao, near aquarium, 12°04′59″N, 68°53′56″W, *Curasub* dive 14-25, 269 m depth, found living inside a beer bottle, C. C. Baldwin, B. van Bebber, and C. Castillo, 9 December 2014; USNM 440570, 65 mm SL, off western coast of Dominica, 15°34′23″N, 61°28′28″W, *Curasub* dive 16-29, 289 m depth, A. Schrier and B. Brandt, 29 March 2016.

Unvouchered* in situ *photographs of ROV-encountered specimens.—($n = 2$, ca. 8–10 cm SL) USNM 444964 (Fig. 3C), ca. 8 cm SL, off Puerto Rico, Mona Passage, Pichincho plateau, 18°22.683′N, 67°46.781′W, dive EX1502L3-3, 415 m depth, 12 April 2015; USNM 444965 (Fig. 3A, B), ca. 10 cm SL, near Virgin Islands, Anegada Passage, Noroit Seamount, 18°05.967′N, 64°6.295′W, dive HI1305, 609 m depth, 14 October 2013.

Diagnosis.—One strong, sharp spine on hind margin of preopercle; dorsal-fin rays 96–101; anal-fin rays 80–86; pectoral-fin rays 24–30; precaudal vertebrae 12; total vertebrae 56–61; pseudobranchial filaments 2–3; long gill rakers on anterior arch 12–14; head length 21.5–24.0% SL; pelvic-fin length 16–22% SL, pelvic-fin rays almost reaching anus; orbit length 4.9–5.8% SL, 20.5–26.5% head length, and 2.1–2.4 times in upper-jaw length; longest gill filament 0.9–2.0% SL and 4.1–8.3% head length.

Color in life.—Body and head light gray, covered dorsally and above and behind belly with rounded, sometimes irregularly shaped and/or interconnected gray to black spots; belly white; dorsal and anal fins pale gray, semi-hyaline, with white outermost margin and irregular spots at mid-fin and/or along fin base, pelvic fin pale white.

Color after capture.—Body and head pale reddish brown to brown; belly bluish silvery or pale gray; head dorsally and body above and behind belly with irregularly distributed dark-brown or black rounded spots; dorsal and anal fins pale brown, semi-hyaline, with outermost white margin, with or without dark-gray or black spots; pelvic fin pale. Color after preservation: rather uniformly yellowish, pale brown, or brown, with or without spots on body and dorsal and anal fins; belly gray, bluish, or black, with or without spots on body and dorsal and anal fins. Otolith length 5.3–6.7% SL; sulcus length 3.5–5.5% SL; and ostium height 16.5–25% sulcus length.

Color pattern description

In situ.—(Figs. 2A, E, 3) Entire body and head light gray, covered by rounded to oblong, sometimes connected, dark gray to black spots except for the white region below eye from snout to ventral part of belly (well visible in Figs. 2E, 3C); spots arranged irregularly and of variable size, smaller on head, on ventral half of body, and along posterior quarter of body, becoming larger dorsally to about orbit size above lateral line; several spots connect with each other on dorsal half of body from behind head to about mid-body, forming short stripes or more irregular "marbled" (Figs. 2A, 3) or u-shaped (Fig. 2E) patterns; several large spots along dorsal body margin extend onto dorsal-fin base; dorsal fin semi-

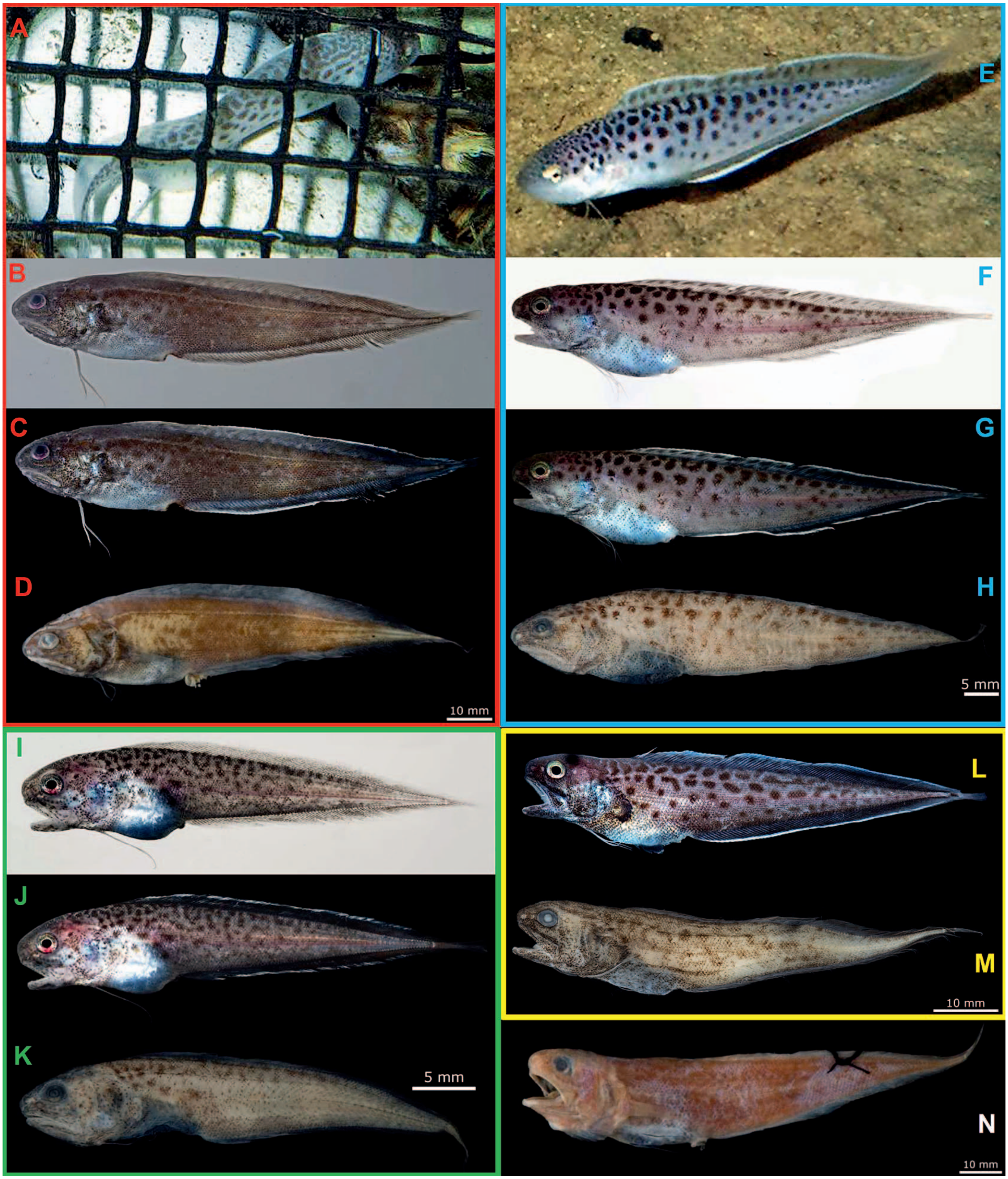

Fig. 2. *Neobythites unicolor* from off Curaçao (A–K) and from more northern (≥15°N) areas (L–N). (A–D, in red frame) USNM 432331, 94 mm SL; (A) *in situ* photograph, inside a grass-mat trap; (B, C) shortly after capture above two different backgrounds; (D) after preservation; (E–H, in blue frame) USNM 431721, 69 mm SL; (E) *in situ* photograph; (F, G) shortly after capture above two different backgrounds; (H) after preservation; (I–K, in green frame) USNM 433497, 38 mm SL; (I, J) shortly after capture above two different backgrounds; (K) after preservation; (L–M, in yellow frame) USNM 440570, 65 mm SL, from off Dominica; (L) shortly after capture; (M) after freezing and preservation; (N) ZMUC P77940, paratype, 104 mm SL, from NW Caribbean. Sources: (A, E) Carole Baldwin and Ross Robertson, courtesy of substation Curaçao; (B, C, F, G, I, J) Carole Baldwin and Ross Robertson; (D, H, K, M, N) Marcus Krag, ZMUC; (L) Chris Richards, Curaçao Sea Aquarium.

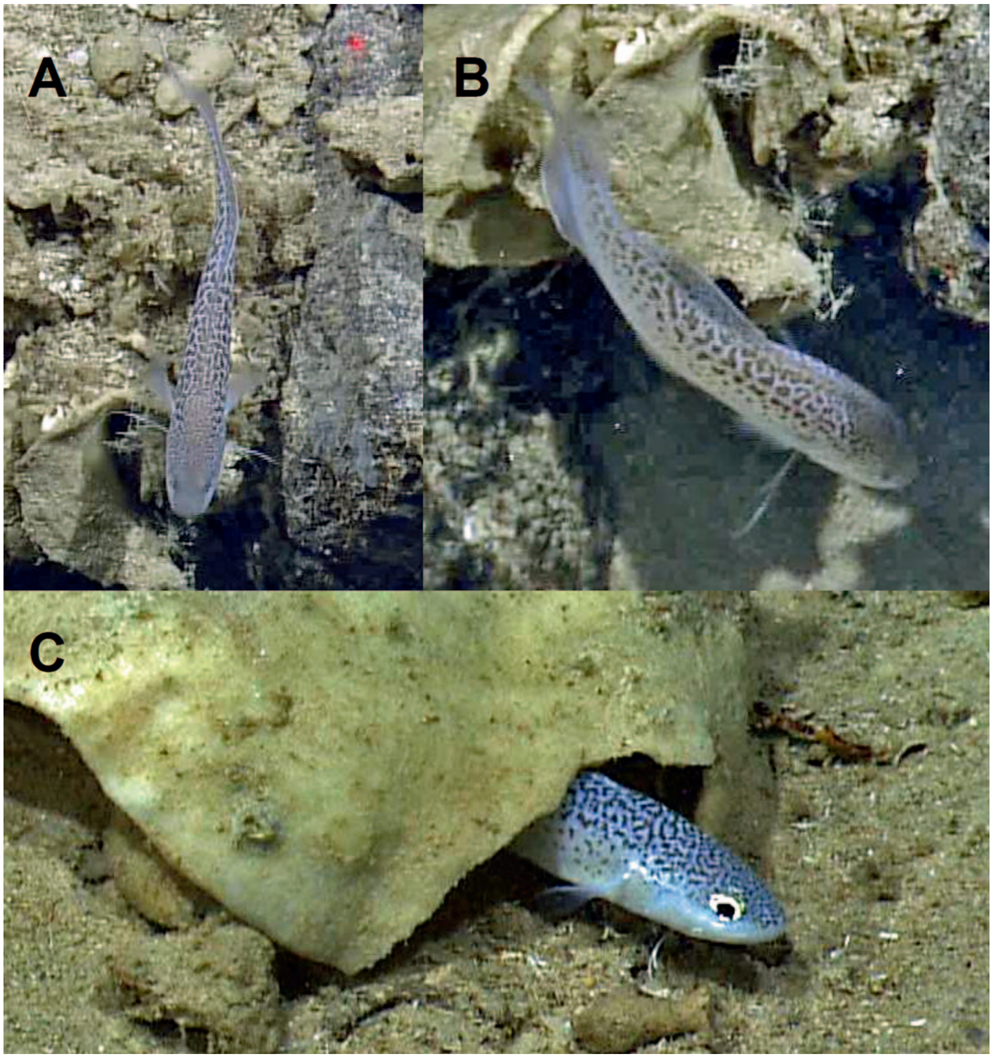

Fig. 3. *Neobythites unicolor* encountered during ROV dives (unvouchered photographs). (A, B) USNM 444965, ca. 10 cm SL, off Virgin Islands, Anegada Passage, Noroit Seamount (Ocean Exploration Trust and U.S. Geological Survey); (C) USNM 444964, ca. 8 cm SL, off Puerto Rico, Mona Passage, Pichincho plateau. (NOAA Okeanos Explorer Program).

hyaline to pale gray, with a contrasting white outer margin and numerous rounded dark-gray spots (e.g., 17 spots in Fig. 2E) of about half orbit-size along anterior two thirds of fin, with those spots positioned at mid-fin (Fig. 2B, C, F, G, L) and/or close to fin base (Figs. 2C, D, 3B); anal fin semi-hyaline pale gray with a white outer margin (Fig. 2E) and small gray spots along mid-fin (Figs. 1A, 2A); pelvic fins pale whitish, caudal and pectoral fins hyaline.

Shortly after capture.—(Fig. 2B, C, F, G, I, J, L) Body and head pale reddish brown to brown, covered rather densely (Fig. 2B, C) to more sparsely (Fig. 2F, G, I, J, L) with minute pale-gray to dark-gray scales; maxilla and nostrils pale; pupil black; belly and head ventrally behind eyes silvery blue or pale gray; lateral line either forming a thin pale stripe along first three quarters of body (Fig. 2B, C) or only faintly or not visible (other five images); vertebral column partly visible as weak brown (Fig. 1B, C) or more distinct reddish stripe (Fig. 1F, G, I, J, L); head from above eyes and body dorsally and above and behind belly region to caudal-fin base covered with at least 40 irregularly distributed dark-brown or black rounded spots of about half-orbit to orbit size; spots becoming larger dorsally, some extending onto dorsal-fin base; dorsal fin pale brown to semi-hyaline, with a contrasting white outer margin (visible only in photographs taken using a black background); dorsal fin with at least with ten dark-gray or black rounded spots arranged along middle of anterior two thirds of fin (Fig. 2F, G, L); dorsal-fin spots only weakly visible in Figure 2B, C or absent in Figure 2I, J; anal fin pale brown with weak brown stripe distally (best visible with pale background) and white outermost margin (only visible with black background); caudal fin hyaline pale brown, pectoral fins hyaline, pelvic fins pale.

After preservation.—(Fig. 2D, H, K, M, N) Body and head yellowish, pale brown, or brown, with either minute brown scales and differently sized, rounded or irregularly shaped gray or brown spots on posterior head and body (Fig. 2D, H, K, M), or lacking any distinct spotting pattern (Fig. 2N); belly gray, bluish, or black; maxilla and nostrils (when visible) pale; pupil dark blue or black; lateral line either forming a pale, at least partly visible stripe from behind head to posterior-most third of body (Fig. 2D, H, K, M) or not visible (Fig. 2N); dorsal fin pale semi-hyaline, either with rounded gray spots (Fig. 2H, K, M) or without spots (Fig. 2D, N); anal and caudal fins pale, pelvic fins (when visible) pale; pectoral fins hyaline.

Distribution, habitat, and size.—Widely distributed in the northern and north-central Caribbean, from the outer southeastern Gulf of Mexico and off southern Florida to Belize and Dominica (new record). South of 15°N only known from Curaçao, southern Caribbean (new record); no records from the inner Gulf of Mexico (see also Materials and

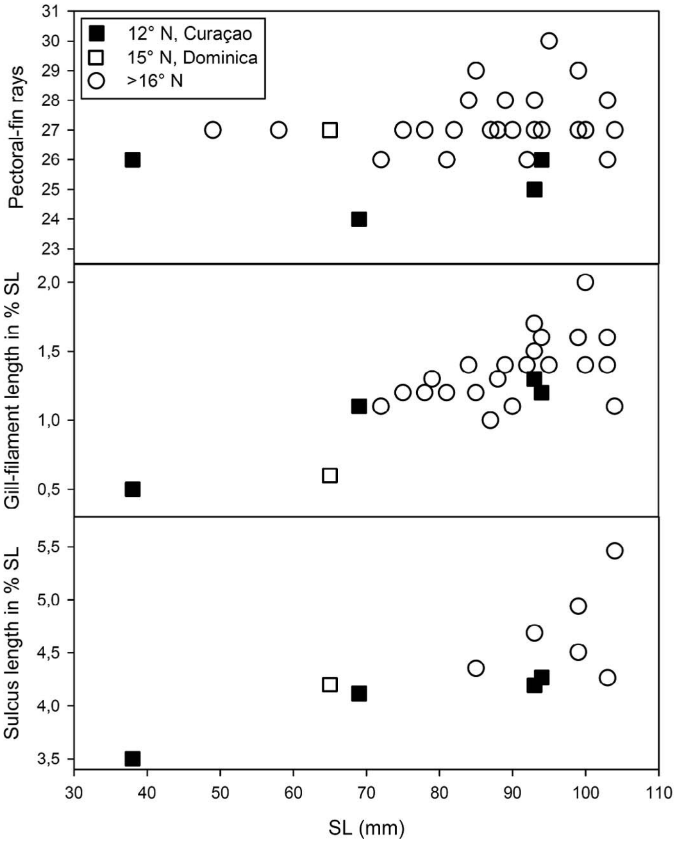

Fig. 4. Number of pectoral-fin rays, length of longest gill filament, and otolith sulcus length against SL in *Neobythites unicolor*.

Methods); depth: 183–937 m; encountered during underwater-vehicle dives on mixed or hard bottoms actively swimming close to crevices (Fig. 3A, B) or below or inside (Fig. 3C; Nielsen, 1999) glass sponges; maximum size 126 mm SL.

Comparisons

Size-related and population differences.—Several body-shape and otolith characters show positive allometry. These include gill-filament length and otolith-sulcus length (Fig. 4). Size-related variation occurs also in fresh color patterns. Among the four specimens that were photographed shortly after capture, the smallest fish (38 mm SL; Fig. 2I, J) has smaller and more tightly spaced spots compared to the three larger specimens (65–94 mm SL; Fig. 2B, C, F, G, L). Furthermore, in the largest specimen (Fig. 2A–C), the spots on the anterior and mid-parts of the body appear slightly larger in size than in the two intermediate-size specimens (Fig. 2E–G, L). Also, the spots are less conspicuous due to a darker body pigmentation in the largest specimen after capture (Fig. 2B, C). This loss of color contrast is, however, not evident when comparing the *in situ* photographs of this specimen with that of the intermediate-sized specimen (69 mm SL; Fig. 2A, E).

When comparing the four specimens collected off Curaçao with the other specimens from further north, the only difference that was found among all characters (including color patterns) is a slightly higher number of pectoral-fin rays (24–26 vs. 26–28; Fig. 4).

Interspecific differences.—*Neobythites unicolor* differs from the other six Caribbean congeners, *N. elongatus*, *N. gilli*, *N. marginatus*, *N. monocellatus*, *N. multidigitatus*, and *N. multi-*

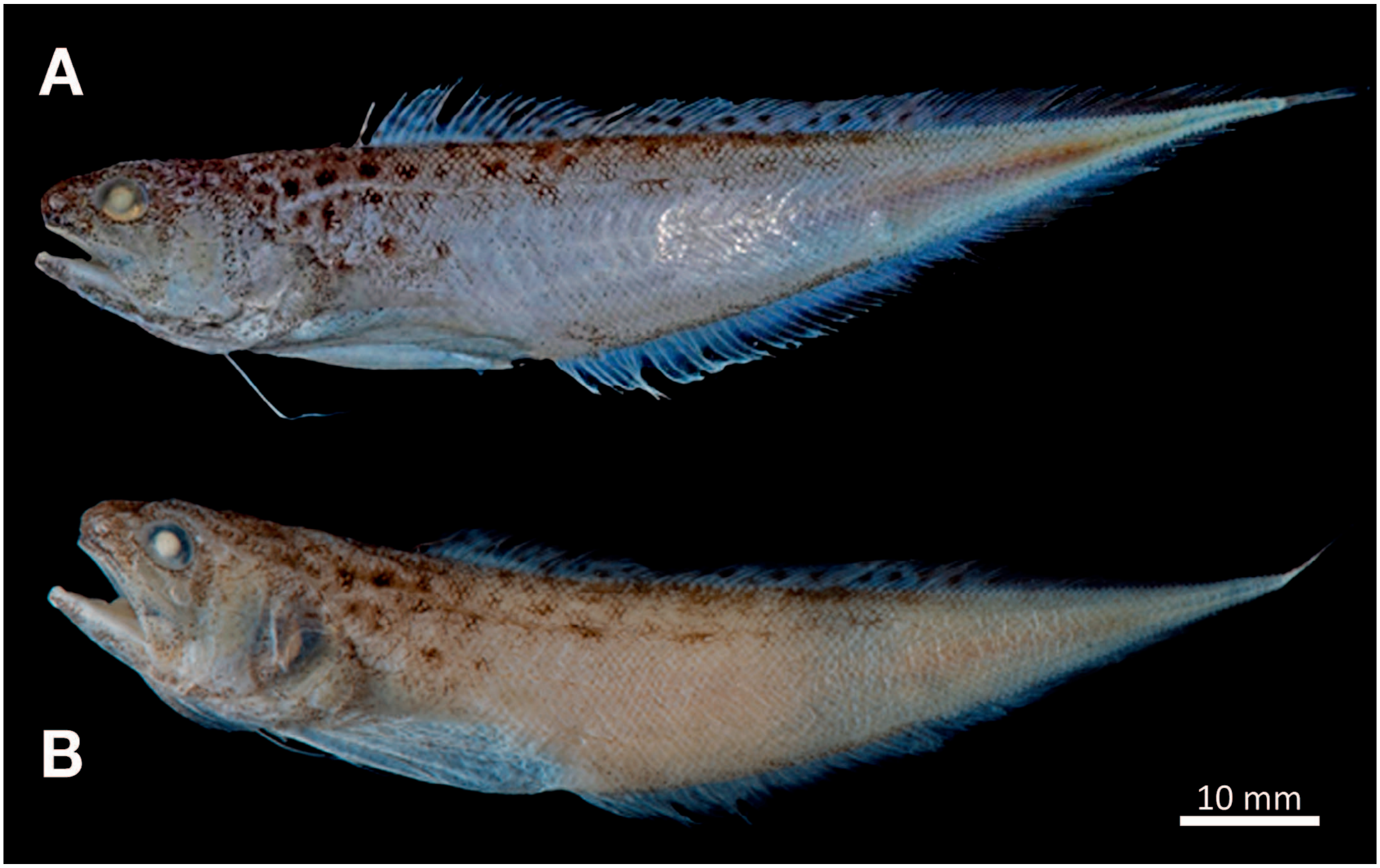

Fig. 5. *Neobythites unicolor*, USNM 422668, 93 mm SL, from off Curaçao; (A) after several months of freezing and subsequent defrosting (Carole Baldwin and Ross Robertson; mirror image); (B) after 508 days preservation (Marcus Krag).

Table 2. Quantitative meristic, morphometric, and otolith characters in *Neobythites unicolor*.

	Curaçao				Dominica	Types				Other specimens				All			
	Min	Mean	Max	*n*	*n* = 1	Min	Mean	Max	*n*	Min	Mean	Max	*n*	Min	Mean	Max	*n*
Standard length (SL in mm)	38.0	73.5	94	4	65	58	91.0	104	9	49.0	85.5	103	17	38.0	84.9	104	31
Meristic characters																	
Dorsal-fin rays	96	98.0	99	4	97	97	99.3	101	9	96	98.1	101	17	96	98.4	101	31
Caudal-fin rays	8	8.0	8	2	8	8	8.0	8	9	8	8.0	8	16	8	8.0	8	28
Anal-fin rays	81	82.8	84	4	85	82	83.7	86	9	80	82.8	85	17	80	83.1	86	31
Pectoral-fin rays	24	25.3	26	4	27	27	27.2	28	9	26	27.4	30	18	24	27.1	30	32
Precaudal vertebrae	12	12.0	12	4	12	12	12.0	12	9	12	12.0	12	19	12	12.0	12	33
Total vertebrae	57	57.5	58	4	61	57	58.3	59	9	56	58.0	60	17	56	58.1	61	31
Pseudobranchial filaments	2	2.7	3	3	2	2	2.2	3	9	2	2.3	3	19	2	2.3	3	32
Dorsal-fin origin above vertebra no.	5	5.3	6	4	5	5	5.0	5	9	5	5.0	5	19	5	5.0	6	33
Anal-fin origin below dorsal-fin ray no.	19	19.5	20	4	19	18	19.1	20	9	18	19.4	20	19	18	19.3	20	33
Anal-fin origin below vertebra no.	14	14.3	15	4	15	14	14.2	15	9	14	14.1	15	19	14	14.2	15	33
Developed gill rakers	12	13.0	14	3	12	12	12.9	13	9	12	12.8	14	19	12	12.8	14	32
Total gill rakers	23	23.0	23	1	—	19	20.4	22	7	19	20.7	23	19	19	20.7	23	27
Morphometric characters (in %SL)																	
Body depth at anal-fin origin	16.0	17.1	18.5	4	16.5	16.5	16.9	18.0	9	16.0	17.3	18.5	17	16.0	17.1	18.5	31
Head length (HL)	22.0	22.8	23.5	4	22.5	21.5	22.8	24.0	9	21.5	22.3	23.5	17	21.5	22.5	24.0	31
Postorbital distance	13.0	13.3	13.5	4	14.0		—		0	12.5	13.2	14.0	9	12.5	13.3	14.0	14
Orbit length	4.9	5.2	5.5	4	5.2	4.9	5.2	5.5	7	4.9	5.3	5.8	15	4.9	5.2	5.8	27
Upper-jaw length	11.0	11.9	12.5	4	12.0	11.5	12.0	12.5	7	11.0	11.9	12.5	16	11.0	12.0	12.5	28
Preanal distance	36.0	38.7	41.5	4	42.0	35.0	39.6	42.5	9	38.0	40.4	43.0	17	35.0	40.0	43.0	31
Predorsal distance	23.0	24.5	25.5	4	25.0	24.0	24.9	26.5	9	22.5	24.3	27.0	17	22.5	24.5	27.0	31
Pelvic-fin to anal-fin origin distance	19.5	22.9	26.5	4	23.5	21.5	23.0	24.0	7	22.0	23.5	25.5	17	19.5	23.3	26.5	29
Pelvic-fin length	16.0	17.4	19.0	4	18.0	17.0	19.6	22.0	9	16.0	19.5	22.0	15	16.0	19.2	22.0	29
Gill-filament length	1.3	1.4	1.6	4	0.9	1.1	1.5	2.0	7	1.1	1.5	1.7	16	0.9	1.5	2.0	28
Morphometric characters (in %HL)																	
Postorbital distance	56	58.4	61	4	62		—			56	59.0	61	9	56	59.1	62	14
Orbit length	22.5	22.8	24.0	4	23.0	20.5	22.6	24.0	7	21.5	23.6	26.5	15	20.5	23.2	26.5	27
Upper-jaw length	51	52.3	54	4	53.0	51	53.4	57	7	51	53.4	57	16	51	53.2	58	28
Gill-filament length	5.6	6.1	6.9	4	4.1	4.8	6.5	8.3	7	5.3	6.9	7.8	18	4.1	6.6	8.3	30
Orbit length in % upper-jaw length	41.5	43.7	47.0	4	43.5	41.0	43.0	46.0	6	41.5	43.5	47.5	14	41.0	43.4	47.5	25
Otolith characters (in %SL)																	
Otolith length	5.6	5.7	6.1	4	5.8	5.7	6.3	6.7	3	5.3	5.9	6.2	3	5.3	5.9	6.7	11
Otolith height	3.4	3.6	4.0	4	3.8	3.5	4.0	4.5	3	3.5	3.8	4.0	3	3.4	3.8	4.5	11
Sulcus length	3.5	4.0	4.3	4	4.2	4.3	4.8	5.5	3	4.4	4.6	4.9	3	3.5	4.4	5.5	11
Ostium length	2.0	2.6	2.8	4	2.6	2.6	3.1	3.8	3	2.6	3.0	3.5	3	2.0	2.8	3.8	11
Ostium height	0.6	0.8	0.9	4	0.9	0.8	0.9	1.0	3	0.7	1.0	1.2	3	0.6	0.9	1.2	11
Ostium height in % sulcus length	17.5	19.1	21.0	4	21.0	17.5	18.7	20.0	3	16.5	21.4	25.0	3	16.5	19.8	25.0	11
Ostium height in % ostium length	26.5	30.1	32.0	4	34.5	26.5	28.9	32.5	3	27.5	32.2	35.5	3	26.5	30.8	35.5	11

ocellatus, in the following combination of characters (Nielsen, 1999; Nielsen et al., 2009): a single, strong and sharp preopercular spine, 96–101 dorsal-fin rays, 80–86 anal-fin rays, 24–30 pectoral-fin rays, 12–14 long gill rakers on anterior arch, no ocelli on dorsal fin, and no long bands, bars, or stripes on body. Live or freshly caught *N. unicolor* differ from all congeners of which the fresh color is known by the presence of dark spots on its body and head.

Remarks.—Specimen USNM 422668 was frozen for a rather long period (Table 1) before being photographed. Its photograph after being thawed (Fig. 5) shows considerable bleaching of the color patterns on both head and body, with few dark spots retained on the dorsal, anterior part of the body and on the dorsal fin.

DISCUSSION

Our study reveals that the scientific name *N. unicolor* is not reflective of a distinctive pattern of pronounced dark spots that are apparent in living and freshly deceased specimens. Natural fish coloration is very often not or not entirely retained in scientific collections. Fresh color patterns may change considerably, fading or becoming completely lost during post-capture handling and preservation in formalin and then ethanol for long-term storage. This is especially true for natural chromatophore patterns formed by erythrophores and xanthophores, which disappear upon fixation in formalin (Gordon, 1931). However, color patterns that comprise melanophores (black or brown pigment) are often retained in specimens that have been preserved over longer time periods. In the genus *Neobythites,* melanistic pigment comprising dark eyespots, bands, bars, or stripes occurs in a large number of species, including in many preserved museum specimens (Uiblein and Nielsen, 2005). The absence of such patterns therefore has diagnostic relevance, especially if it allows separation of preserved specimens of similar and co-occurring species (Nielsen and Retzer, 1994; Nielsen, 1999).

The spotted color pattern of *N. unicolor* described herein is unique among the patterns of the 54 known members of the genus. Similar color patterns do however occur in two other genera of the subfamily Neobythitinae, *Sirembo* and *Spottobrotula* from the Indo-West Pacific. *Sirembo imberbis* and *Spottobrotula mahodadi* both have dark, rounded spots on the head, body, and the proximal part of the dorsal fin. In *Sirembo imberbis,* the spots are of rather similar size (relative to the size of the eye) to those in *N. unicolor* and have been retained in preserved specimens for 20 years (Nielsen et al., 2015). In *Spottobrotula mahodadi*, the spots are also of similarly relative size to those of *N. unicolor* and have been largely retained in the single type specimen for at least 44 years (Nielsen et al., 2015). Recently, photographs of two freshly deceased *Spottobrotula mahodadi*, which show the rounded, brown to black spots on the body and dorsal fin, have been published (Matsunuma et al., 2017). The spots on these individuals vary in size from smaller to larger than orbit diameter and show a rather scattered configuration pattern. To our knowledge, no fresh color images for *Sirembo imberbis* are currently available and *in situ* observations are lacking for both species.

The striking similarity of the spotted color pattern in fresh specimens of *N. unicolor*, *Sirembo imberbis*, and *Spottobrotula mahodadi* raises the question why the spots are not retained in preserved *N. unicolor* while they persist in the other two species? One possible reason may be species differences in melanophore-response characteristics when exposed to distinct preservatives. While numerous experimental studies have examined the effect of preservatives on shape, size, or weight of adult or subadult fishes (e.g., Shields and Carlson, 1996; Kristoffersen and Salvanes, 1998; Ajah and Nunoo, 2003; Martinez et al., 2013; Larochelle et al., 2016), differential loss of coloration through preservation has—to our knowledge—not been thoroughly investigated.

Our finding of an increase of spot size with larger fish size provides preliminary evidence for ontogenetic color change. No indications of geographic variation in color patterns have been discovered yet in *N. unicolor.* In order to examine possible intraspecific variation in spot size, configuration, or number among populations to further detail, comparative documentation from live or freshly collected specimens representative for both the entire size range and the overall distribution area of *N. unicolor* would be required.

Additional evidence for intraspecific phenotypic variation in *N. unicolor* comes from the morphological analysis. Positive allometry in otolith form as observed in this study has also been reported recently for *N. kenyaensis*, an ocellus-bearing species that occurs in the area from South Africa to Kenya (Uiblein and Nielsen, 2019). More comparative otolith data from other species of *Neobythites* and related genera are currently being gathered to better understand whether otolith form changes with size in a similar manner across a larger number of cuskeel species (see also, Uiblein and Nielsen, 2019).

Geographic variation in the morphology of *N. unicolor* is indicated by the slightly higher number of pectoral-fin rays in the Curaçao specimens, which are separated by at least 650 km from the northern and central Caribbean populations. More sampling and deep-water exploration in the southeastern and entire southern Caribbean, ideally including genetic analyses, is needed to understand whether the Curaçao population is indeed distinct.

As shown in the images taken by underwater vehicles, the spots of *N. unicolor* represent a rather contrasting, conspicuous color pattern that may still be visible in weakly illuminated depths such as the uppermost slope. In some cases strongly contrasting black-white color patterns may be visible to depths of 550 m depth (Clarke and Denton, 1961). Eyespots or ocelli have been hypothesized to be of functional significance until about 500 m depth (Uiblein and Nielsen, 2005). The contrast of the typical ocelli of *Neobythites*, which are much larger than the spots that form the color pattern of *N. unicolor*, is greatly enhanced by a white concentric ring surrounding the rounded, dark spot. Ocelli-bearing species of *Neobythites* occur mostly in the shallower part of the range of depths at which the genus occurs, and well above 500 m depth (Uiblein and Nielsen, 2005). *Neobythites unicolor*, however, occurs across a substantially wider depth range. The function of ocelli in *Neobythites* has been hypothesized to serve in deterring visually hunting predators, deflecting their attacks to less vital parts of the body, or assisting in social communication and species recognition (Uiblein and Nielsen, 2005, 2018). Whether the specific color pattern of *N. unicolor* serves any similar visual functions appears rather doubtful, as it is less conspicuous than the ocellar patterns and is borne by a species that ranges into much darker depths.

The use of underwater vehicles for the study of deep-water fauna has allowed many new insights in several research areas such as deep-water fish behavioral ecology and habitat selection (e.g., Uiblein, 2011; Uiblein et al., 2002, 2003, 2010), community ecology (e.g., Quattrini et al., 2015, 2017; Baldwin et al., 2018), and systematics (Baldwin and Robertson, 2013, 2014, 2015; Baldwin et al., 2016a, 2016b). For the genus *Neobythites* which includes many species that live below 200 m depth, only very few insights from underwater-vehicle encounters have been obtained so far. One earlier published example is the image-documented encounter during a dive with the submersible *Johnson Sea-Link II* of a *Neobythites marginatus* at 610 m depth off Puerto Rico referred to in Nielsen (1999). This image reveals a conspicuous dark-lined color pattern on unpaired fins and body that is only partly retained in preserved specimens. Certainly, additional deep-water exploratory initiatives are needed to more comprehensively document the range of color diversity in the species of *Neobythites*, and deep-water fishes in general, und use this information in updated taxonomic accounts and, eventually, in ongoing and future biological, ecological, and evolutionary research.

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