A new species of western Atlantic lizardfish (Teleostei: Synodontidae: *Synodus*) and resurrection of *Synodus bondi* Fowler, 1939, as a valid species from the Caribbean with redescriptions of *S. bondi, S. foetens* (Linnaeus, 1766), and *S. intermedius* (Agassiz, 1829)

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Abstract—Western Atlantic synodontid species were studied as part of an ongoing effort to reanalyze Caribbean shorefish diversity. A neighbor-joining tree constructed from cytochrome *c* oxidase I (COI) data revealed 2 highly divergent genetic lineages within both *Synodus intermedius* (Agassiz, 1829) (Sand Diver) and *S. foetens* (Linnaeus, 1766) (Inshore Lizardfish). A new species, *Synodus macrostigmus*, is described for one of the *S. intermedius* lineages. *Synodus macrostigmus* and *S. intermedius* differ in number of lateral-line scales, caudal pigmentation, size of the scapular blotch, and shape of the anterior-nostril flap. *Synodus macrostigmus* and *S. intermedius* have overlapping geographic and depth distributions, but *S. macrostigmus* generally inhabits deeper water (>28 m) than does *S. intermedius* and is known only from coastal waters of the southeastern United States and the Gulf of Mexico, in contrast to those areas and the Caribbean for *S. intermedius*. *Synodus bondi* Fowler, 1939, is resurrected from the synonymy of *S. foetens* for one of the *S. foetens* genetic lineages. The 2 species differ in length and shape of the snout, number of anal-fin rays, and shape of the anterior-nostril flap. *Synodus bondi* and *S. foetens* co-occur in the central Caribbean, but *S. bondi* otherwise has a more southerly distribution than does *S. foetens*. Redescriptions are provided for *S. intermedius, S. foetens*, and *S. bondi*. Neotypes are designated for *S. intermedius* and *S. foetens*. A revised key to *Synodus* species in the western Atlantic is presented.

The aulopiform lizardfish family Synodontidae is represented in the western Atlantic by 3 genera: *Synodus* (5 species recognized before this study)*, Saurida* (4)*,* and *Trachinocephalus* (1). Lizardfishes are benthic predators in numerous ecosystems, including coral reefs, estuaries, and reef structure or sandy bottom areas on continental shelves (Anderson et al., 1966; Cressey, 1981; Randall, 2009). Once thought to occupy a mid-trophic position and employ a sit-and-wait predation strategy, adult lizardfishes now are known to occupy a high trophic position—apex in some systems—as active hunters feeding primarily on other predatory fishes (Cruz-Escalona et al., 2005).

Despite having no commercial value as food fishes, *Synodus* spp. and *Saurida brasiliensis* (Largescale Lizardfish) are caught as bycatch in shrimp-trawl fisheries in the western Atlantic, accounting for 1.5% and 1.8% of total-catch biomass in the Gulf of Mexico and North Carolina,[1]

respectively (Jeffers et al., 2008; Manjarrés et al., 2008). Populations of *Synodus foetens* (Linnaeus, 1766) (Inshore Lizardfish) are estimated to be at fully exploited levels as bycatch in Gulf of Mexico shrimp-trawl fisheries (Garcia-Abad et al., 1999; Wells, 2007; Jeffers et al., 2008). Proper management and ecological investigation of commercially fished species require an accurate understanding of species diversity. For example, Collette et al. (1978) discovered that the Caribbean and Brazilian populations of the commercially important *Scomberomorus maculatus* (Spanish Mackerel) constitute a distinct species, which they named *S. brasiliensis* (Serra). Without this systematic study, populations of *S. brasiliensis* would still be managed under the same plan as *S. maculatus*.

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[1] Brown, K. 2009. Interstate fisheries management program implementation for North Carolina. Job 3: characterization of the near-shore commercial shrimp trawl fishery from Carteret County to Brunswick County, North Carolina. Southeast Fisheries Science Center, Miami, FL, 29 p. [Available online from http://www.sefsc.noaa.gov/sedar/download/SEDAR20-ASMFC-DW09.pdf?id=DOCUMENT]

Scientists have periodically investigated the systematics of synodontids since Linnaeus (1758) described *Esox synodus* in the mid-18th century. Throughout the 19th century, researchers described 17 *Synodus* species in the western Atlantic (Anderson et al., 1966; Meek, 1884; Norman, 1935). In the most recent comprehensive treatments of western Atlantic lizardfishes (Anderson et al., 1966; Russell, 2003), 5 species of *Synodus* have been recognized. Ongoing research to evaluate diversity of the Caribbean ichthyofauna with DNA barcoding (Hebert et al., 2003) and traditional morphological investigation have led to the recent discovery of many new cryptic fish species and the resurrection of several formerly synonymized ones in what were thought to be well-studied taxa (Baldwin and Weigt, 2012; Baldwin et al., 2009, 2011; Tornabene et al., 2010; Victor, 2007, 2010). In the course of the present work, discrepancies were revealed between barcode data and the currently accepted species classification of western Atlantic *Synodus* lizardfishes. Specifically, each of 2 *Synodus* species, *S. intermedius* (Agassiz, 1829) (Sand Diver) and *S. foetens* comprise 2 distinct cytochrome *c* oxidase I (COI) lineages.

The purpose of this study was to reconcile genetic lineages with the nominal species of western Atlantic *Synodus*. Through comparative morphological study, our first goal was to determine if the "extra" genetic lineages correspond with morphologically distinct species and, if so, to assess whether they represent previously synonymized or undescribed species. Herein, we resurrect and redescribe *Synodus bondi* Fowler, 1939, from the synonymy of *S. foetens* and describe *S. macrostigmus* as a new species distinct from *S. intermedius*. We establish neotypes for *S. intermedius* and *S. foetens* and redescribe both species. We discuss preliminary evidence of population structure within *S. foetens*, *S. synodus* (Red Lizardfish), *Saurida brasiliensis*, and *Trachinocephalus myops* (Snakefish) and species-level genetic structure within *Synodus poeyi* (Offshore Lizardfish). Finally, we provide a revised key for the 7 species of *Synodus* found in the western Atlantic.

Materials and methods

Specimens for genetic analysis were collected in Tobago (Trinidad and Tobago), Turks and Caicos Islands, the Bahamas, Curaçao, Belize, North Carolina, South Carolina, and Florida. Type material and additional specimens from other localities were examined from ANSP, MCZ, UF, FSBC, KU, and USNM (institutional abbreviations are listed at http://www.asih.org/node/204, accessed February 2012). Specimens examined are listed in appropriate species sections or in the Appendix.

Specimens were collected with the use of quinaldine sulfate, rotenone, or a pole spear during snorkeling or scuba diving, as well as by bottom trawling and hook and line fishing. For most specimens, field protocol involved taking digital photographs of fresh specimens

to document living color patterns, and subsequently a small sample of tissue from the trunk musculature for genetic analysis. Voucher specimens were fixed in 10% formalin and ultimately preserved in 75% ethanol for archival storage.

Measurements were taken to the nearest 0.1 mm with Mitutoyo digital calipers (Mitutoyo Corp., Japan[2]). Measurements and counts follow Hubbs and Lagler (1964) and Randall (2009), except as noted below. Length of the anterior-nostril flap was measured from the posterior tip of the anterior nostril to the distal end of the flap when depressed. For the *S. intermedius* group only, the length of the scapular blotch was measured on an anterior–posterior axis at its greatest expanse. For the *S. foetens* group only, the width of the adipose lid was measured as the maximum distance between the bony orbit and distal edge of the lid.

Numbers of vertebrae and dorsal-, anal-, pectoral-, and caudal-fin rays were counted from digital radiographs or preserved specimens. Scales flanking the dorsal- and anal-fin bases are half the size of other trunk scales and are reported as half-scales.

Tissue samples were stored in saturated salt buffer (Seutin et al., 1990). DNA was extracted from up to approximately 20 mg minced, preserved tissue through an automated phenol: chloroform extraction on an Autogenprep965 DNA extraction system (Autogen, Holliston, MA) using the mouse tail tissue protocol to a final elution volume of 50 µL. In the polymerase chain reaction (PCR), 1 µL of extracted DNA was used in a 10 µL reaction with 0.5 U BioLine (Bioline USA, Inc., Boston, MA) Taq polymerase, 0.4 µL 50 mM $MgCl_2$, 1 µL 10× buffer, 0.5 µL 10 mM deoxyribonucleotide triphosphate, and 0.3 µL 10 µM each primer FISH-BCL (5′-TCAACYAATCAYAAAGATATYGGCAC) and FISH-BCH (5′-TAAACTTCAGGGTGACCAAAAAATCA). The PCR theromcycle protocol was: 1 cycle of 5 min at 95°C; 35 cycles of 30 s at 95°C, 30 s at 52°C, and 45 s at 72°C; 1 cycle of 5 min at 72°C; and a hold at 10°C. PCR products were purified with ExoSAP-IT (Affymetrix, Santa Clara, CA) with 2 µL 0.2× enzyme and incubated for 30 min at 37°C. The reaction was then inactivated for 20 min at 80°C. Sequencing reactions were performed with 1 µL of this purified PCR product in a 10 µL reaction that contained 0.5 µL primer, 1.75 µL BigDye reaction buffer (Life Technologies Corp., Carlsbad, CA), and 0.5 µL BigDye in the thermal cycler for 30 cycles of 30 s at 95°C, 30 s at 50°C, 4 min at 60°C, and then were held at 10°C after completion of cycles. These sequencing reactions were purified with MultiScreen-HV plates (MAHVN4550; EMD Millipore Corp., Billerica, MA) according to the manufacturer's instructions and stored dry until analyzed. Sequencing reactions were analyzed on an Applied Biosystems 3730XL automated DNA sequencer (Life Technologies Corp.), and sequence trace

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[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

files were exported into Sequencher, vers. 4.7 (Gene Codes Corp., Ann Arbor, MI). With the Sequencher program, ends were trimmed from the raw sequences until the first and last 10 bases contained fewer than 5 base calls with a confidence score (phred score) lower than 30. After trimming, forward and reverse sequences for each specimen were assembled. Each assembled pair was examined and edited by hand, and each sequence was checked for stop codons. Finally, the consensus sequence (655 bp) from each contig was aligned and exported in a NEXUS file format with PAUP* software, vers. 4.0 beta 10 (sensu Swofford, 2003).

MEGA software, vers. 5.05, (Tamura et al., 2011) was used to generate a distance matrix of Kimura 2-parameter distances (Kimura, 1980) of genetic sequence similarity, from which a neighbor-joining tree (Saitou and Nei, 1987) was constructed. The neighbor-joining tree is not intended to reflect phylogenetic relationships. The label for each entry on the tree is our DNA number, and we include that number in the material examined sections and figure captions. Abbreviations used in DNA numbers reflect geographical location, expedition name, or institutions that provided COI sequences or specimens for genetic analysis: BAH=Bahamas; BLZ=Belize; CUR=Curaçao; FCC=Florida Cape Canaveral (specimens were from east coast of Florida); FWRI=Florida Fish and Wildlife Research Institute (specimens were from deep waters of the Gulf of Mexico); FDA=Food and Drug Administration (specimens are from Alabama, collected by the FDA; specimens held at National Museum of Natural History, Smithsonian Institution [USNM]); KU=Kansas University Fish Collection (specimens are from Belize); MOC=*Miguel Oliver* Caribbean (specimens are from deep water off Central America); SC=South Carolina; SMS=Smithsonian Marine Station at Ft. Pierce, Florida (specimens are from east coast of Florida); TCI=Turks and Caicos; TOB=Tobago. COI sequences are deposited in GenBank (accession numbers in text). GenBank numbers for COI DNA sequences of type material, when sequences are available, are provided in the appropriate species sections. Photos were taken with a Fujifilm (Fujifilm Corp., Tokyo) or Nikon (Nikon Corp, Tokyo) digital camera or a Zeiss digital camera in a Zeiss Discovery V20 dissecting microscope (Carl Zeiss AG, Oberkochen, Germany). Photo credits are given only for images taken by individuals other than the authors.

Results

To generate genetic distances, 79 COI sequences of Synodontidae from numerous western Atlantic localities were used. From these genetic distances, a neighbor-joining tree was constructed. Intra- and interspecific divergences are tabulated in Table 1. To show the neighbor-joining tree on a single page, 23 sequences were then eliminated (Fig. 1). Removal of the sequences had no effect on tree topology. Our data set

includes all 10 previously recognized species of western Atlantic Synodontidae—5 species of *Synodus,* 4 species of *Saurida,* and *Trachinocephalus myops.* Specimens originally identified as *Synodus intermedius* and *S. foetens* constitute 4 genetic lineages, 2 of which represent *S. intermedius* (Agassiz, 1829) and *S. foetens* (Linnaeus, 1766). One of the remaining lineages represents *Synodus bondi* Fowler, 1939, a species that Anderson et al. (1966) relegated to the synonymy of *S. foetens.* The fourth lineage represents a new species. Herein, we describe the new species, redescribe *S. intermedius, S. foetens,* and *S. bondi*, and designate neotypes for *S. intermedius* and *S. foetens.* Percentages in parentheses throughout their descriptions represent mean values for all specimens examined.

Synodus macrostigmus Frable, Luther, and Baldwin, new species
Proposed English common name: Largespot Lizardfish
Figures 1, 2A, 3 (A and B), and 4, Tables 1–3

Holotype

UF 182810 (formerly, FSBC 020548), 189 mm standard length (SL), off Panama City, Florida, 29°16′59.95′N, 85°53′12.94′W, 71–73 m, sta. 097, NMFS-Pascagoula Deepwater Pelagics Survey, 1 November 2007, Coll: M. M. Leiby.

Holotype COI sequence

GenBank sequence JX519377, UF 182810 (formerly FSBC 020548), DNA number FWRI 20548b.

Paratypes

UF 182811 (formerly, FSBC 020548), 1 specimen, 192 mm SL (paratopotype), same locality data as for holotype; UF 182812 (formerly FSBC 020596), 5 specimens, 145–185 mm SL, off St. Petersburg, Florida, 28°8′44.41′N, 84°38′56.29′W, 75–77 m, sta. 123, NMFS-Pascagoula Deepwater Pelagics Survey, 5 November 2007, Coll: M. M. Leiby; USNM 358546, 1 specimen, 205 mm SL, Yellowtail Reef, Alabama, 29°33′28.08′N, 87°27′42.12′W, 68 m, sta. USGS-AE-9701-080, USGS Pinnacle Project, 12 August 1997.

Paratype COI sequences

GenBank sequences JX519376 and JX519380, UF 182811 and UF 182812, respectively, DNA numbers FWRI 20548a and 20596, respectively.

Additional material (not DNA vouchers)

Alabama: UF 29771, 5; Florida (Gulf of Mexico): UF 29818, 1; UF 46974, 1; UF 121816, 1; UF 123421, 2; UF

Table 1

Average percent divergence in cytochrome *c* oxidase I (COI) among species of *Synodus* (Sy.), *Saurida* (Sa.), and *Trachinocephalus* (T.) in the western Atlantic. Divergences between *Synodus macrostigmus* and *S. intermedius*, between *S. foetens* and *S. bondi*, and between the 2 lineages of *S. poeyi* are highlighted in bold. N/A=not available.

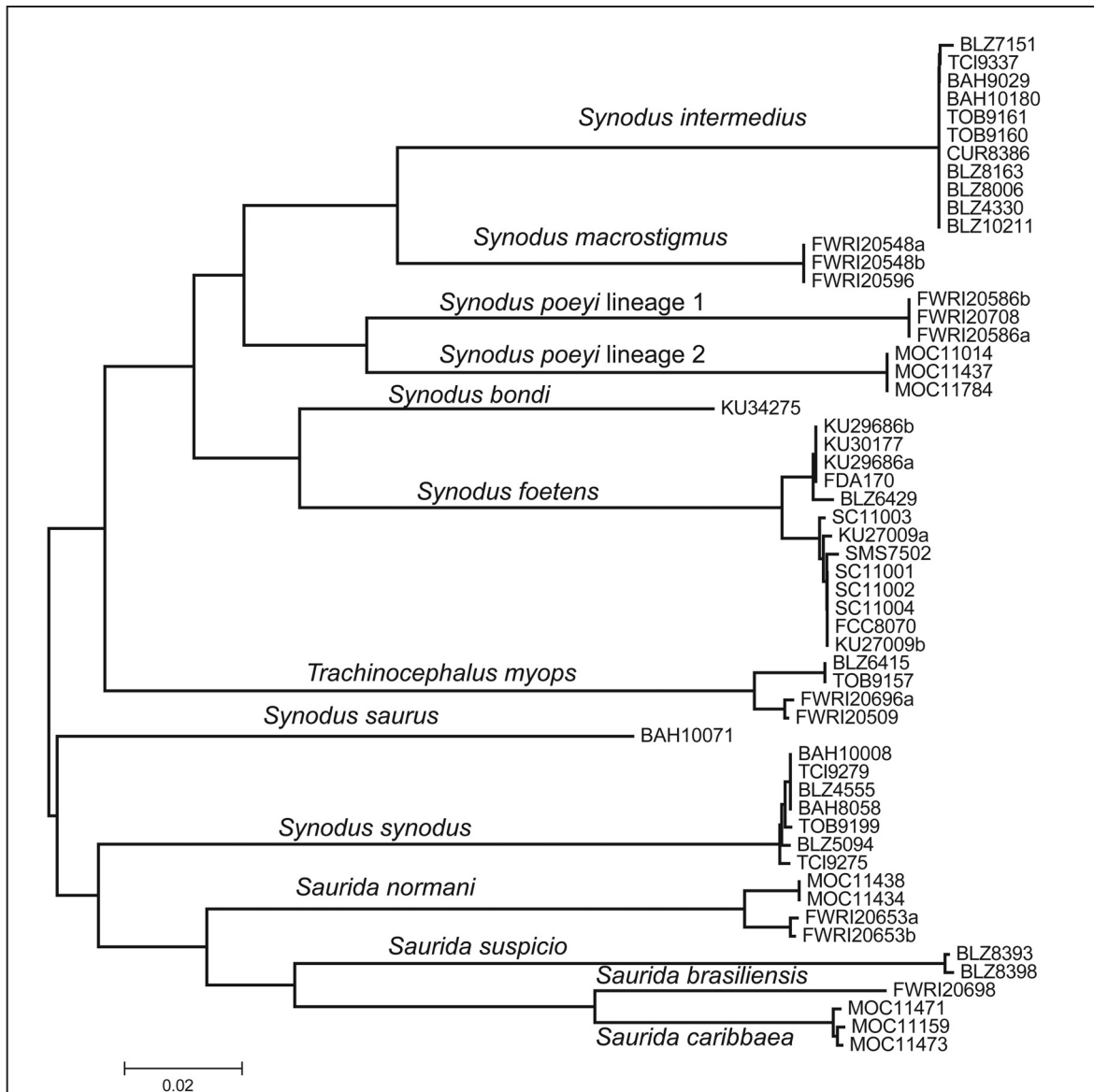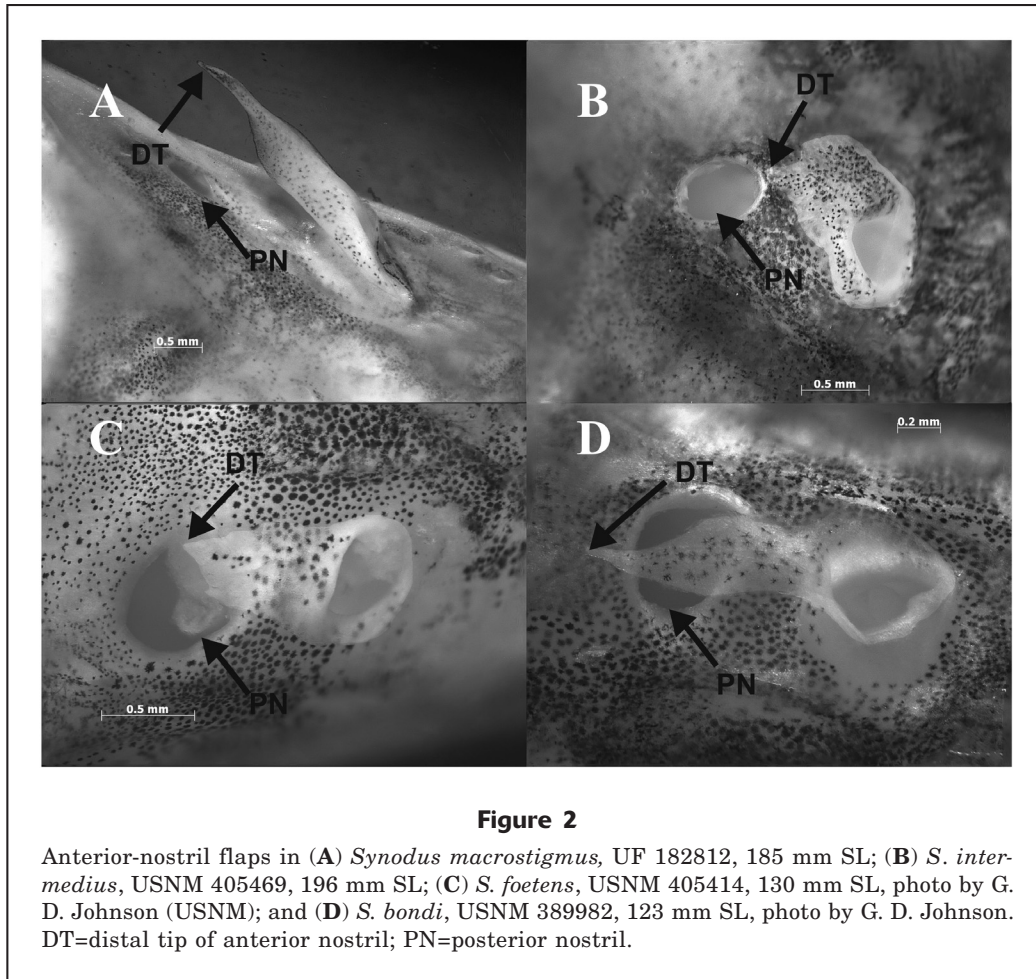|	*Sa. brasiliensis*	*Sa. caribbaea*	*Sa. normani*	*Sa. suspicio*	*Sy. bondi*	*Sy. foetens*	*Sy. intermedius*	*Sy. macrostigmus*	*Sy. poeyi 1*	*Sy. poeyi 2*	*Sy. saurus*	*Sy. synodus*	*T. myops*
Sa. brasiliensis n=1	N/A												
Sa. caribbaea n=3	0.09	0.00											
Sa. normani n=4	0.21	0.20	0.01										
Sa. suspicio n=2	0.20	0.21	0.23	0.00									
Sy. bondi n=1	0.25	0.24	0.24	0.27	N/A								
Sy. foetens n=13	0.27	0.26	0.26	0.31	**0.16**	0.01							
Sy. intermedius n=15	0.27	0.26	0.25	0.26	0.21	0.23	0.00						
Sy. macrostigmus n=3	0.24	0.22	0.24	0.27	0.18	0.21	**0.16**	0.00					
Sy. poeyi 1 n=3	0.26	0.24	0.26	0.27	0.21	0.23	0.26	0.23	0.00				
Sy. poeyi 2 n=3	0.25	0.22	0.22	0.22	0.21	0.23	0.21	0.17	**0.18**	0.00			
Sy. saurus n=1	0.22	0.22	0.24	0.21	0.19	0.23	0.26	0.22	0.24	0.22	N/A		
Sy. synodus n=26	0.25	0.25	0.25	0.23	0.23	0.26	0.26	0.23	0.25	0.24	0.23	0.00	
T. myops n=4	0.28	0.27	0.26	0.26	0.24	0.23	0.27	0.27	0.25	0.27	0.23	0.26	0.01

Figure 1

Neighbor-joining tree derived from 56 cytochrome *c* oxidase I sequences, showing genetically distinct lineages of Synodontidae in the western Atlantic. Abbreviations for DNA numbers are BAH=Bahamas; BLZ=Belize; CUR=Curaçao; FCC=Florida Cape Canaveral (specimens were from east coast of Florida); FWRI=Florida Fish and Wildlife Research Institute (specimens were from deep waters of the Gulf of Mexico); FDA=Food and Drug Administration (specimens are from Alabama, collected by the FDA-specimens held at National Museum of Natural History, Smithsonian Institution [USNM]); KU=Kansas University Fish Collection (specimens are from Belize); MOC=*Miguel Oliver* Caribbean (specimens are from deep water off Central America); SC= specimens collected off South Carolina; SMS=Smithsonian Marine Station at Ft. Pierce, Florida (specimens are from east coast of Florida); TCI=Turks and Caicos; TOB=Tobago.

146801, 1; UF 146657, 3; UF 152128, 7; UF 154795, 7; UF 169896, 1; UF 119194, 2; UF 123425, 2; UF 29799, 6; UF 147265, 1; UF 147286, 2; Florida (Atlantic): UF 111202, 5; Georgia: UF 123372, 1; UF 137046, 1; USNM 315754, 1; South Carolina: USNM 315532, 1; Mexico: UF 136960, 2; UF 136965, 1; USNM 18800, 3.

Diagnosis

A species of *Synodus* differentiated from its congeners by the following combination of characters: dorsal-fin rays 11 or 12 (rarely 11); anal-fin rays 11; total caudal rays 41–42; dorsal segmented caudal rays 9; ventral

Figure 2

Anterior-nostril flaps in (**A**) *Synodus macrostigmus,* UF 182812, 185 mm SL; (**B**) *S. intermedius*, USNM 405469, 196 mm SL; (**C**) *S. foetens*, USNM 405414, 130 mm SL, photo by G. D. Johnson (USNM); and (**D**) *S. bondi*, USNM 389982, 123 mm SL, photo by G. D. Johnson. DT=distal tip of anterior nostril; PN=posterior nostril.

segmented caudal rays 10; dorsal procurrent caudal rays 12; ventral procurrent caudal rays 10–11; pelvic-fin rays 8; pectoral-fin rays 11 or 12; total vertebrae 47–49, modally 49; predorsal vertebrae 12 or 13; pored lateral-line scales 45–48; median predorsal scales 12 or 13; scale rows on cheek 4–6; eye large, 4.5–6.9% SL (16.7–24.7% head length [HL]); anterior nostril flap long, tapering distally and extending over posterior nostril when depressed, length of flap 2.7–4.9% HL; snout blunt in dorsal view; pelvic-fin length 21.6–25.2% SL. Caudal fin with dark pigment on anterior end of fork and posterior portion of ventral caudal lobe; dorsal caudal lobe pale with light pigment on posterior margin; shoulder with large, ovoid, black scapular blotch, length 14.2–19.0% HL; 6–9 dark bars on trunk; in life, adults gray to olive with unevenly distributed orange-yellow stripes along body.
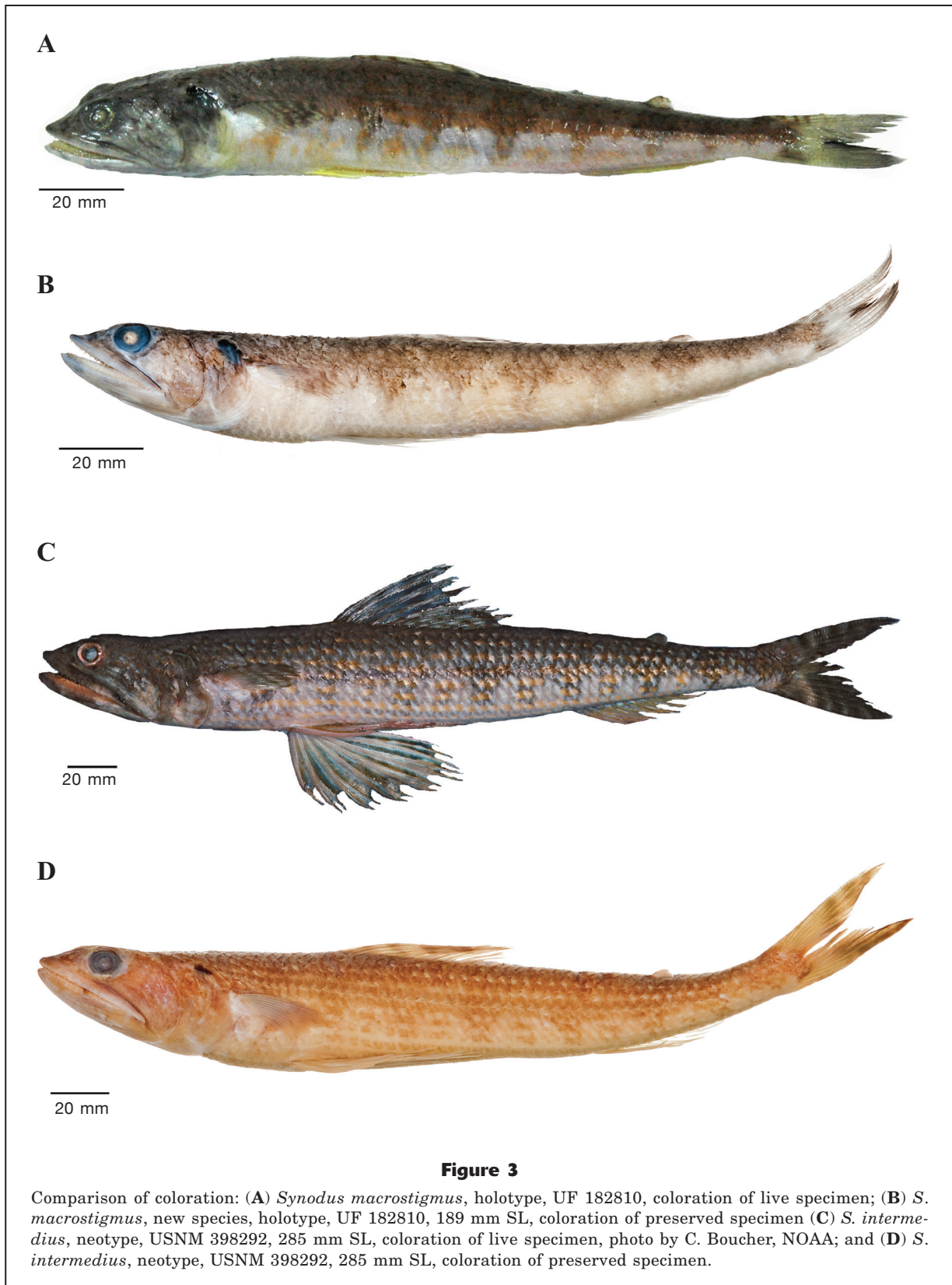
Description

Description based on 52 specimens, 67.0–212.0 mm SL. Counts and measurements of holotype given in Table 2. Frequency distribution of pored lateral-line scales given in Table 3.

Dorsal-fin rays 11–12, rarely 11; anal-fin rays 11; total caudal-fin rays 41–42; dorsal segmented caudal rays 9; ventral segmented caudal rays 10; dorsal procurrent caudal rays 12; ventral procurrent caudal rays 10–11; pelvic-fin rays 8; pectoral-fin rays 11 or 12; total vertebrae 47–49, modally 49; predorsal vertebrae 12 or 13; scales ctenoid; pored lateral-line scales 45–48, modally 47; median predorsal scales 15 or 16; scales above lateral line to dorsal-fin base 3.5; scales below lateral line to anal-fin base 4.5.

Body elongate and cylindrical; depth at pelvic-fin origin 9.3–13.8% SL (12.1%); depth at anal-fin origin 8.3–10.7% SL (9.6%); caudal-peduncle depth 4.4–5.7% SL (5.1%); body width at dorsal-fin origin 11.2–15.3% SL (13.1%); HL 24.2–29.0% SL (26.3%); snout length 5.6–7.4% SL (6.4%) and 21.7–26.5% HL (24.3%); orbit diameter 4.5–6.9% SL (5.5%) and 16.7–24.7% HL (20.8%), orbit with bony ridge extending over anterodorsal margin; interorbital width 2.8–4.3% SL (3.6%) and 9.5–15.3% HL (13.8%).

Predorsal length 37.8–43.6% SL (40.4%); prepelvic length 32.2–36.5% SL (34.3%); preanal length 67.6–72.5% SL (70.4%); preadipose length 75.7–82.1% SL (79.3%); dorsal-fin base 15.0–18.2% SL (16.5%), longest

Figure 3

Comparison of coloration: (**A**) *Synodus macrostigmus*, holotype, UF 182810, coloration of live specimen; (**B**) *S. macrostigmus*, new species, holotype, UF 182810, 189 mm SL, coloration of preserved specimen (**C**) *S. intermedius*, neotype, USNM 398292, 285 mm SL, coloration of live specimen, photo by C. Boucher, NOAA; and (**D**) *S. intermedius*, neotype, USNM 398292, 285 mm SL, coloration of preserved specimen.
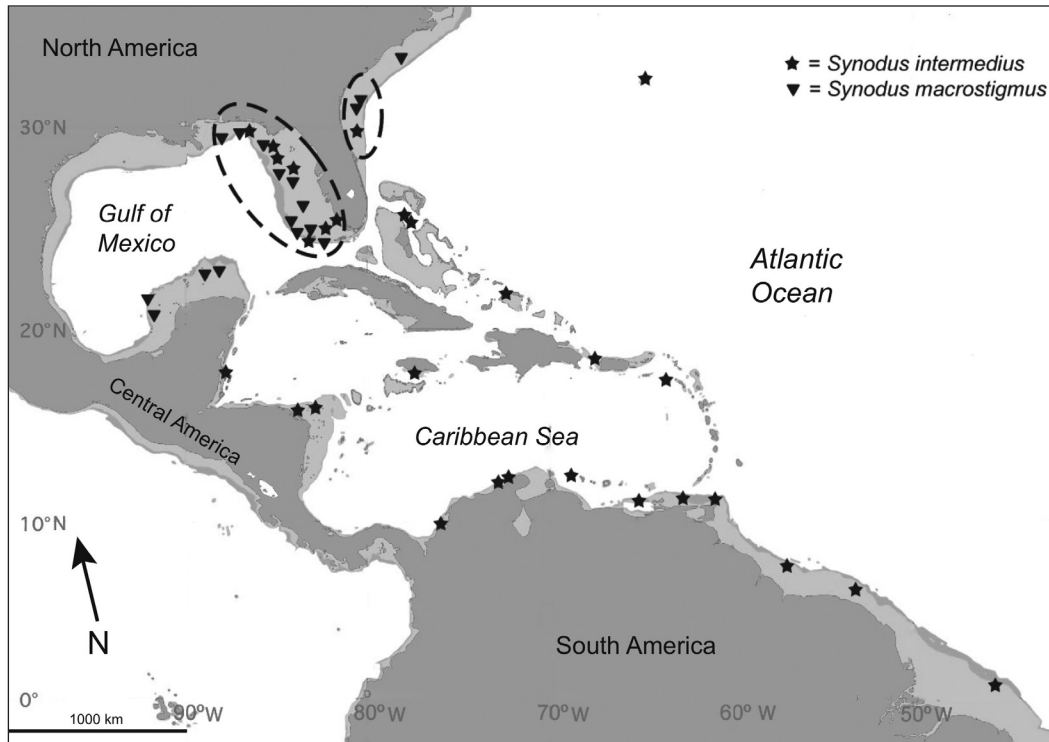
Figure 4

Distribution map *Synodus intermedius* and *S. macrostigmus,* new species. Symbols indicate sampling localities, not individual specimens. Dashed-line ovals highlight area of overlap in distribution of these species. Map by Robert Myers (Coral Graphics), reprinted with permission.

dorsal-fin ray 15.2–17.0% SL (16.1%); anal-fin base 13.0–15.5% SL (14.3%), longest anal-fin ray 6.9–9.4% SL (7.7%); pectoral-fin length 12.5–14.7% SL (13.5%); pelvic-fin length 21.6–25.2% SL (23.3%); caudal-peduncle length 9.9–16.7% SL (13.4%), caudal-fin length 16.5–21.5% SL (19.1%), ventral caudal lobe slightly longer than dorsal lobe.

Upper jaw slightly shorter than lower jaw, mouth oblique, forming an 8° angle with the horizontal body axis; upper-jaw length 13.7–17.6% SL (15.9%) and 55.8–63.8% HL (60.3%). Teeth thin, needlelike; upper jaw with 2 rows of teeth, teeth in inner row longer than teeth in outer row; lower jaw with 3 rows of teeth, size of teeth increasing medially, outer row covered by lips; posterior teeth in both jaws directed slightly anteriorly. Palatine with 3–4 rows of depressible teeth, teeth directed posteromedially. Tongue with 5 rows of posteriorly directed teeth, largest near anterior tip. Anterior nostril on level with median axis of orbit; posterior nostril same size and situated slightly dorsal to anterior nostril; anterior nostril with large, leaf-shaped flap that tapers distally, length of flap when depressed 0.8–1.2% SL (1.0%) and 2.7–4.9% HL (3.8%); anterior portion of posterior nostril occluded by basal rim of flap (Fig. 2A); posterior nostril without flap.

Cheek with 4–6 rows of large scales, modally 6; opercle with vertical row of 5–6 scales on anterior margin and several scales posteriorly; predorsal scales extending anteriorly to a position approximately one orbit diameter posterior to eye; interorbital region naked. Dorsal and anal fins each flanked basally by 10–12 half scales, remainder of dorsal and anal fins without scales; large, diamond-shaped scales covering pelvic-fin base, remainder of pelvic fin and pectoral fin without scales; 6 rows of body scales extending onto base of caudal fin; upper and lower caudal lobes each with a single, enlarged, horizontally elongate scale.

Coloration

Before preservation (Fig. 3A) Head and dorsal half of trunk gray to greenish brown, ventral half of trunk pale; 6–8 dark brown markings along length of trunk laterally, at least some of them resembling wide crosses that are widest along lateral midline; markings on left and right portions of trunk connected to one another across dorsal midline to form saddles; trunk also with several thin orange-yellow stripes dorsally, stripes thicker or broken into orange blotches ventrally; groove above maxilla with stripe of black pigment from below anterior edge of orbit to posterior end of jaw; posterior edge of branchiostegal membrane pale yellow; scapular region with large black blotch of pigment partially hidden by operculum, length 3.8–4.9% SL (4.3%) and

Table 2

Counts and proportional measurements of the holotype and paratypes of *Synodus macrostigmus*, new species, and neotype of *S. intermedius*. Standard length present in millimeters; other measurement values in percentages of standard length; values in parentheses are percentages of head length.

	Synodus macrostigmus Holotype UF 182810	*Synodus macrostigmus* Paratopotype UF 182811	*Synodus macrostigmus* Paratype UF 182812	*Synodus macrostigmus* Paratype UF 182812	*Synodus macrostigmus* Paratype UF 182812	*Synodus macrostigmus* Paratype UF 182812	*Synodus macrostigmus* Paratype UF 182812	*Synodus macrostigmus* Paratype USNM 358546	*Synodus intermedius* Neotype USNM 398292
Standard length	189.0	192.0	185.0	149.0	162.0	172.0	156.0	205.0	285.0
Vertebrae	49	49	48	49	47	49	49	47	49
Dorsal-fin rays	12	12	12	12	11	12	12	12	12
Anal-fin rays	11	11	11	11	11	11	11	11	11
Pectoral-fin rays	12–12	12–12	12–11	12–12	12–12	11–12	12–12	11–11	13–13
Pelvic-fin rays	8–8	8–8	8–8	8–8	8–8	8–8	8–8	8–8	8–8
Caudal-fin rays	41	41	41	40	41	40	41	41	43
Pored lateral-line scales	47	48	47	46	47	46	47	48	51
Predorsal scales	15	15	15	Missing	Missing	15	14	16	17
Cheek scales	6	6	6	6	6	Missing	6	6	7
Body depth (pelvic origin)	11.0	11.9	9.7	12.7	11.6	10.7	9.3	12.3	15.1
Body depth (anal origin)	9.8	10.3	8.8	9.7	9.5	8.6	8.3	9.4	10.2
Caudal-peduncle depth	5.0	5.6	4.8	4.9	5.3	4.4	4.7	5.1	6.1
Body width	14.0	13.0	13.0	13.5	14.0	12.2	12.5	13.5	15.6
Head length	24.2	24.4	24.8	25.4	25.8	24.6	25.5	26.1	26.9
Snout length	5.7 (23.7)	5.6 (23.0)	5.9 (23.8)	6.1(23.9)	5.6 (21.7)	5.8 (23.4)	6.4 (24.9)	6.5 (24.9)	6.0 (22.8)
Nostril-flap length	0.9 (3.9)	1.2 (4.9)	1.0 (4.1)	1.0 (4.1)	1.1 (4.1)	1.2 (4.9)	0.9 (3.7)	1.1 (4.4)	0.4 (2.2)
Orbit diameter	5.0 (20.5)	5.1 (20.7)	5.3 (21.6)	6.0 (23.5)	5.9 (22.8)	5.8 (23.4)	5.5 (21.5)	5.3 (20.4)	3.6 (16.4)
Interorbital width	3.7 (15.3)	3.7 (15.3)	3.7 (14.8)	3.8 (13.9)	3.5 (13.5)	3.5 (14.2)	3.3 (12.8)	3.8 (14.7)	4.6 (17.5)
Upper-jaw length	15.2 (62.3)	14.8 (60.4)	15.2 (61.2)	15.5 (61.0)	14.6 (56.7)	13.7 (55.8)	15.9 (62.1)	15.5 (59.3)	16.2 (59.4)
Scapular-blotch length	4.1 (17.0)	4.6 (18.8)	3.9 (14.8)	3.8 (14.8)	4.2 (16.1)	4.2 (16.9)	4.0 (15.6)	4.3 (16.5)	2.4 (10.4)
Predorsal length	38.7	37.8	40.1	39.9	39.6	39.5	39.2	40.0	40.8
Preanal length	68.8	70.3	70.3	67.6	69.8	69.2	69.9	71.7	71.1
Preadipose length	76.7	78.1	75.7	77.2	80.2	80.2	78.8	79.5	83.2
Prepelvic length	34.4	35.3	32.2	33.0	35.7	33.3	33.8	35.2	34.4
Dorsal-fin base	16.5	15.2	15.0	16.7	15.6	15.0	15.3	17.5	17.2
Longest dorsal ray	16.0	16.8	15.5	16.2	15.2	16.2	15.6	15.7	17.2
Anal-fin base	14.7	14.8	13.8	15.3	14.0	13.3	13.0	14.4	15.5
Longest anal ray	7.8	7.5	7.4	7.7	broken	7.1	9.4	7.7	9.6
Pectoral-fin length	13.1	13.0	13.4	12.5	13.2	12.9	12.8	14.2	13.1
Pelvic-fin length	22.6	24.7	21.8	23.0	21.6	23.5	24.9	23.3	26.2
Caudal-peduncle length	14.1	16.7	15.6	15.2	15.3	9.9	10.4	11.3	15.7
Caudal-fin length	19.0	18.4	19.0	20.0	21.5	20.1	16.5	18.7	17.5

Table 3

Frequency distributions of counts of pored lateral-line scales in *Synodus macrostigmus*, new species (*n*=51), and *S. intermedius* (*n*=52).

	Pored lateral-line scales							
	45	46	47	48	49	50	51	52
Synodus macrostigmus	4	12	27	8	–	–	–	–
Synodus intermedius	–	–	–	–	7	16	23	6

14.2–19.0% HL (16.4%); dorsal fin not erect in available photographs (Fig. 3A), but depressed fin pale yellow with oblique rows of dark pigment; adipose fin pale with at least one dark marking dorsally; pectoral fin pale with approximately 6 wavy, irregular bars of dark brown pigment; pelvic fins bright yellow; anal fin yellow; center of caudal fin (at anterior end of fork) and posterior portion of ventral caudal lobe dark gray to brown; dorsal caudal lobe pale with light, dusky pigment on posterior margin; dorsal caudal lobe with 2–3 small brown bars on procurrent rays.

In preservative (Fig. 3B)   Trunk tan to light brown dorsally, pale ventrally; dark markings along trunk present but faded in some specimens; black pigmentation on scapular region, head, and caudal fin (described in the previous paragraph) easily visible; barring on pectoral fin indistinct.

Etymology

Synodus macrostigmus is named for its large, black scapular blotch. The species name is a Latinized conjunction of the Greek *macros*, meaning large or long, and *stigma,* meaning brand or mark.

Distribution

The holotype and paratypes are from the northeastern Gulf of Mexico off the coast of Florida from depths of 71–75 m. Additional specimens of this species, previously identified as *S. intermedius* in museum collections, are from the northern Gulf of Mexico off Alabama and Florida, Yucatan Mexico, and Atlantic coast off Georgia and South Carolina. All specimens were collected at depths below 28 m. The specimens from the deepest known collection, UF46974, are from the Gulf Coast of Florida at 194 m.

Synodus intermedius (Agassiz, 1829)
English common name: Sand Diver
Figures 1, 2B, 3 (C and D), and 4, Tables 1–3

Saurus intermedius Agassiz *in* Spix and Agassiz, 1829:81, pl. 44. Type locality: "Brazil;" described

from specimen, 216 mm in total length in the Museo Monacensi, current whereabouts unknown; neotype herein designated, USNM 398292.
Saurus anolis Valenciennes in Cuvier and Valenciennes, 1850:483. Type localities: Martinique, Guadeloupe, and Bahia, Brazil; 2 types—MNHN A.8611, 390 mm, and MNHN B.1022, 400 mm.
Synodus cubanus Poey, 1876:143. Type locality: Cuba; one type—375 mm, current whereabouts unknown.

Holotype

No types known.

Designation of neotype

Agassiz (in Spix and Agassiz, 1829) described *Saurus intermedius* from a single specimen collected off Brazil (Kottelat, 1988). The original description is brief and provides little information to separate this species from a general *Synodus* body plan with the exception of the mention of transverse barring on the trunk, 55 mucous canal scales in the lateral line, a projected snout, and 12 pectoral- and anal-fin rays. The number of pored lateral-line scales is higher than the numbers observed in our study (49–52 scales); however, specimens of *S. intermedius* are known to have up to 55 lateral-line scales (Anderson et al., 1966; Anderson and Gehringer, 1975). The number of anal-fin rays (12) is also greater than the number we observed (11). This difference might be explained by a deep bifurcation in the last anal-fin ray that makes it appear to be 2 separate rays. The deep split is noted to result in miscounting (Anderson et al., 1966). There is no mention of caudal pigmentation or a scapular blotch.

Subsequent descriptions of *S. intermedius* by Günther (1864), Poey (1868), and Meek (1884) all included diagnostic features, such as a scapular blotch and caudal barring. Günther (1864) expressed frustration over the lack of diagnostic information in the original description. Kottelat (1988) was unable to locate the original type of *Saurus intermedius*. It may have been stored at the Zoologische Staatssammlung Munchen (ZSM), but the entire Spix and Agassiz collection housed there was destroyed in World War II (Kottelat,

1988). Or, it may be housed in the Museum d'Histoire Naturelle de Neuchâtel (MHNN), in Switzerland, where it has not been located. A color illustration of the holotype was published in Spix and Agassiz (1829, plate 44). The body shape, pigmentation, and barring on the caudal fin depicted in this illustration match those characters in later descriptions of *Saurus intermedius* and *Synodus intermedius* and in specimens recognized herein as *S. intermedius*. In light of our discovery of the similar *S. macrostigmus*, designation of a neotype is appropriate to clarify the taxonomic status of *S. intermedius*. We designate USNM 398292 from Brazil as a topologically equivalent neotype. We examined specimens of *Synodus intermedius* from Brazil and numerous localities in the Caribbean, and we found no significant morphological differences.

Note on authorship

Although *Synodus intermedius* was formally described in Spix and Agassiz (1829), Kottelat (1988) determined that Agassiz was the sole author of this name and the description was subsequently incorporated into this text. According to priority, the authorship of *S. intermedius* has been changed from (Spix and Agassiz, 1829) to (Agassiz, 1829) following the adopted format for other species described by Agassiz in the same work, including *Saurus longirostris* (Reis et al, 2003).

Neotype

USNM 398292, 285.0 mm SL, off northeastern Brazil, 0°13 48.00 N, 44°49 47.99 W, 62–64 m, sta. 67, Oregon II, 16 May 1975, field number BBC 1631, Coll: B. B. Collette.

Additional material

(DNA numbers and GenBank accession numbers for specimens that are vouchers are given in parentheses following catalog numbers). Florida: UF 146453, 3; UF 174147, 2; UF 234684, 1; UF 111225, 2; UF 116648, 5; UF 176286, 1; UF 152825, 1; UF 154795, 3; UF 152128, 3; UF 176286,1; UF 29818, 4; USNM 38711, 1; USNM 35045, 1; Puerto Rico: UF 234199, 2; Bahamas Islands: USNM 405474, 1; USNM 405461 (BAH 9029: JX519387), 1; USNM 405462 (BAH 10043: JX519402), 1; USNM 405463 (BAH 10180: JX519386), 1; USNM 405464 (BAH 10181: JX519366), 1; Belize: USNM 327555, 1; USNM 404211 (BLZ 10211: JX519367), 1; USNM 405465 (BLZ 7151: JQ841412), 1; USNM 405468 (BLZ 8163: JQ841835), 1; USNM 405469 (BLZ 8006: JQ841836), 1; Bermuda: USNM 368585, 1; USNM 385983, 1; Brazil: USNM 398292, 1; Colombia: UF 123373, 1; UF 137038, 3; USNM 384339, 1; Curacao: USNM 405470 (CUR 8386: JQ842339), 1; French Guiana: UF 211584, 1; Guyana: UF 137049, 3; Honduras: UF 136971, 1; UF 123383, 1; Jamaica: UF 123615, 1;

UF 231377, 5; Saba, Leeward Islands: UF 207329, 2; Tobago, Trinidad and Tobago: USNM 405471 (TOB 9160: JQ843084), 1; USNM 405472 (TOB 9090: JQ843082), 1; UF 123378, 1; Turks and Caicos: USNM 405473, 1; Venezuela: UF 224467, 4; UF 123377, 1.

Diagnosis

A species of *Synodus* differentiated from its congeners by the following combination of characters: dorsal-fin rays 11–12; anal-fin rays 11; total caudal rays 40–42; dorsal segmented caudal rays 9; ventral segmented caudal rays 9–10; dorsal procurrent caudal rays 11–12; ventral procurrent caudal rays 9–10; pelvic-fin rays 8; pectoral-fin rays 11–13; total vertebrae 49–52, modally 50; pored lateral-line scales 49–52, modally 51; median predorsal scales16 or 17; scale rows on cheek 6–8; HL 15.2–28.4% SL (26.6%); orbit diameter 3.6–6.4% SL (4.7%) and 13.4–22.5% HL (17.2%); interorbital width 2.8–5.3% SL (4.3%) and 10.1–19.4% HL (15.9%); flap on anterior nostril small and broad, length 1.5–3.6% HL (2.4%); snout triangular in dorsal view; pelvic-fin length 23.1–26.7% SL (24.9%). In preservative, 3 to 6 dark bars on caudal fin spanning upper and lower lobes; a small, rectangular-shaped, black scapular blotch (length 5.1–12.2% HL, mean 8.4%); 9 to 13 dark bars on trunk; in life, adults tan to olive and with unevenly distributed yellow stripes along body.

Description

Description based on 51 specimens, 59.2–285.0 mm SL. Counts and measurements of neotype given in Table 2. Frequency distribution of pored lateral-line scales given in Table 3.

Dorsal-fin rays 11–12; anal-fin rays 11; total caudal-fin rays 40–42; dorsal segmented caudal rays 9; ventral segmented caudal rays 9–10; dorsal procurrent caudal rays 11–12; ventral procurrent caudal rays 9–10; pelvic-fin rays 8; pectoral-fin rays 11–13; total vertebrae 49–52, modally 50; predorsal vertebrae 12 or 13; scales ctenoid; pored lateral-line scales, 49–52, modally 51, although counts of up to 55 have been reported (Anderson et al., 1966; Anderson and Gehringer, 1975); median predorsal scales15–17; scales above lateral line to dorsal-fin base 3.5; scales below lateral line to anal-fin base 4.5.

Body cylindrical; depth at pelvic-fin origin 12.4–16.3% SL (14.1%); depth at anal-fin origin 8.7–11.7% SL (10.2%); caudal-peduncle depth 5.1–6.2% SL (5.7%); body width at dorsal-fin origin 9.7–16.2% SL (14.2%); HL 24.5–28.4% SL (26.6%); snout length 6.0–7.3% SL (6.7%) and 22.0–27.5% HL (24.7%), snout triangular in dorsal view; orbit diameter 3.6–6.4% SL (4.7%) and 13.4–22.5% HL (17.2%), orbit with bony ridge extending over anterodorsal margin; interorbital width 2.8–5.3% SL (4.3%) and 10.1–19.4% HL (15.9%).

Predorsal length 38.0–43.5% SL (41.0%); prepelvic length 33.4–37.9% SL (35.0%); preanal length 69.2–

76.4% SL (72.2%); preadipose length 75.5–84.5% SL (80.2%); dorsal-fin base 13.9–19.4% SL (16.8%), longest dorsal-fin ray, usually third, 14.5–20.0% SL (17.0%); anal-fin base 12.7–15.9% SL (14.2%), longest anal-fin ray, usually second, 7.7–10.7% SL (9.1%); pectoral-fin length 12.1–14.0% SL (13.1%); pelvic-fin length 23.1–26.7% SL (24.9%); caudal-peduncle length 8.5–19.4% SL (14.9%), caudal-fin length (only measured in 19 specimens because many specimens had damaged caudal fins) 16.1–22.5% SL (19.4%), ventral caudal lobe slightly longer than dorsal lobe.

Mouth terminal, upper jaw slightly oblique, forming an 8° angle with the horizontal body axis; upper-jaw length 14.7–18.1% SL (16.4%) and 53.9– 64.2% HL (60.4%). Teeth needlelike; upper jaw with 2 rows of teeth, teeth in inner row longer than teeth in outer row; lower jaw with 3 rows of teeth, size of teeth increasing medially, outer row covered by lips; posterior teeth in both jaws directed slightly anteriorly. Palatine with 3–4 rows of depressible teeth, teeth directed posteromedially. Tongue with 5 rows of posteriorly directed teeth, largest near anterior tip. Anterior nostril on level with median axis of orbit; posterior nostril same size and situated slightly dorsal to anterior nostril; anterior nostril with small, spade-shaped flap, length of flap when depressed 0.4–1.0% SL (0.6%) and 1.5–3.6% HL (2.4%); anterior nostril flap does not reach posterior nostril (Fig. 2B); posterior nostril without flap.

Cheek with 6–8 rows of large scales, modally 7; opercle with vertical row of 6–8 scales on anterior margin and several scales posteriorly; predorsal scales extending anteriorly to a position approximately one orbit diameter posterior to eye; interorbital region naked. Dorsal and anal fins each flanked basally by 10–12 half scales, remainder of dorsal and anal fins without scales; large, diamond-shaped scales covering pelvic-fin base, remainder of pelvic fin and pectoral fin without scales; 5–7 rows of body scales extending onto base of caudal fin; upper and lower caudal lobes each with a single, enlarged, horizontally elongate scale.

Coloration

Before preservation (Fig. 3C)   Head and dorsal half of trunk gray-green to brown, ventral half of trunk pale; specimens more than 200 mm SL with 9–13 dark brown bars along length of trunk laterally, bars more faint in smaller specimens and resemble wide crosses that are widest along lateral midline; markings on left and right portions of trunk connected to one another across dorsal midline to form saddles; trunk with several thin, golden-yellow stripes dorsally, with stripes becoming disrupted near lateral midline and forming distinct stripes again ventrally; groove above maxilla with stripe of black pigment from below anterior edge of orbit to posterior end of jaw; posterior edge of branchiostegal membrane yellow; scapular region with small rectangular black blotch of pigment partially hidden by operculum, length 1.4–3.3% SL (2.3%) and 5.1–12.2% HL (8.4%); dorsal fin yellow-brown with multiple oblique rows of dark pigment; adipose fin brown; pectoral fin translucent with 4–5 diagonal bars of dark brown pigment; pelvic fins golden-yellow with darker pigment between rays; anal fin yellow; caudal fin light brown with 3–5 rows of dark pigmentation spanning both lobes, posterior fringes of fin dark brown.

In preservative (Fig. 3D)   Trunk tan to light brown dorsally, pale ventrally; dark markings along trunk present but faded in some specimens; black pigmentation on scapular region and jaw easily visible; barring on caudal fin less distinct in older specimens; barring on dorsal fin faded and pigmentation on pectoral and pelvic fins indistinct.

Distribution

Synodus intermedius was described originally from "the inlets and river outflows of Brazil" (Agassiz in Spix and Agassiz, 1829). The species also occurs widely throughout the western Atlantic. Specimens examined in this study are from Bermuda, the Gulf of Mexico, and the eastern coasts of the United States, Puerto Rico, Saba, Leeward Islands, Belize, Venezuela, Colombia, French Guiana, Guyana, Brazil, and Trinidad and Tobago (Fig. 4). Specimens are known from depths up to 183 m, but most specimens have been collected at depths <60 m.

Comparisons of *Synodus macrostigmus, S. intermedius,* and congeners

The anterior-nostril flap in *S. macrostigmus* is significantly larger (2.7– 4.9% HL, mean 3.8%) than that flap of *S. intermedius* (1.5–3.6% HL, mean 2.4%) and tapers distally (ends more abruptly in *S. intermedius*—Fig. 2, A and B). *Synodus macrostigmus* on average possesses a larger orbit diameter (20.8% versus 17.2% HL) and more narrow interorbital (width 13.8% versus 15.9% HL). It possesses a more blunt snout than does *S. intermedius* (Fig. 3, A–D) and has fewer lateral-line scales (45–48, modally 47, versus 49–52, modally 51, in *S. intermedius*) (Table 3). Dark pigment on the caudal fin in *S. macrostigmus* is restricted primarily to the center of the fin and ventral lobe, whereas *S. intermedius* has a distinctive banded pattern with 3 to 6 bars. The scapular blotch in *S. macrostigmus* is much larger and more ovoid than the miniscule, rectangular marking in *S. intermedius*, mean length of blotch 16.4% HL in *S. macrostigmus* and 8.4% HL in *S. intermedius*.

Additional fresh specimens of the new species are needed to verify differences in color patterns, but, in available material, *S. macrostigmus* has orange lateral stripes and markings on the trunk and *S. intermedius* has yellow stripes (Fig. 3, A and C). Specimens of *S. intermedius* more than 200 mm SL also appear to have more vertical bars along the trunk (9–13) than do large specimens of *S. macrostigmus* (6–8). Finally, *S. macrostigmus* has not been collected at depths shal-

lower than 28 m, whereas nearly half of the specimens of *S. intermedius* examined are from those depths. *Synodus macrostigmus* generally inhabits deeper waters (mean depth 96.5 m) than does *S. intermedius* (mean depth 49.3 m), but they co-occur at many depths. For example, 4 specimens of *S. intermedius* and 1 specimen of *S. macrostigmus* (UF 29818) were collected in a single trawl off Florida.

From their congeners, *S. macrostigmus* and *S. intermedius* can be differentiated from *S. poeyi* by anterior dorsal-fin rays that do not extend beyond the distal tips of succeeding rays when the fin is depressed and from *S. saurus* (Bluestripe Lizardfish), *S. bondi, S. foetens*, and *S. synodus* in having fewer lateral-line scales (45–48 in *S. macrostigmus,* 55 or more in the other species).

Remarks

Two previously described species are currently recognized as synonyms of *Synodus intermedius* (Agassiz, 1829): *Saurus anolis* (Valenciennes in Cuvier and Valenciennes, 1850) and *Synodus cubanus* Poey, 1876. Valenciennes described *Saurus anolis* in 2 brief paragraphs in Cuvier and Valenciennes (1850), but he did not mention a scapular blotch and compared the specimens only with *S. synodus*. Type material was deposited in the Muséum National d'Histoire Naturelle (MNHN) in Paris; 2 syntypes exist in this material, one dried (MNHN A-8611) and one in alcohol (B-1022) (Bertin and Estève, 1950). The wet specimen appears to be *S. intermedius* on the basis of caudal barring and remnants of a miniscule scapular blotch. Diagnostic features are not discernible on the dried syntype.

Albert K. L. G. Günther purportedly synonymized *Saurus anolis* with *Synodus intermedius* before 1868 (Poey, 1868); however, no published reference has been located. Meek (1884) recognized *Saurus anolis* as valid in his systematic review of Synodontidae in the western Atlantic, but he stated the original description is "so insufficient that no certain identification can be made" (Meek, 1884: 134). Anderson et al. (1966) listed *Saurus anolis* as a synonym of *Synodus intermedius* without providing discussion. We concur with Meek's assessment of the original description but recognize *Saurus anolis* as a synonym of *Synodus intermedius* on the basis of features of one of the MNHN *Saurus anolis* syntypes.

The second synonym*, Synodus cubanus,* was described as having caudal barring, yellow body stripes, short pelvic fins, and a scapular spot (Poey, 1876). The description was based on a 375-mm-SL specimen from Cuba, but the whereabouts of this specimen are unknown. Jordan (1884) identified a specimen from Florida (USNM 35045) as Poey's *S. cubanus*, but he noted that it matches the description of *S. intermedius* by previous authors (e.g., Günther, 1864). Our examination of USNM 35045 revealed a small scapu-lar marking typical of *S. intermedius* and diagnostic morphological features, such as 51 lateral-line scales. We agree that *S. cubanus* Poey, 1876, is a synonym of *S. intermedius.*

Synodus foetens (Linnaeus, 1766)
English common name: Inshore Lizardfish
Figures 1, 2C, 5 (A and B), and 6, Tables 1, 4, and 5

Salmo foetens Linnaeus, 1766: 513 (12th ed.). Description based on Catesby, 1743; specimens sent by Dr. Alexander Garden of Charleston, South Carolina; no types designated.

Osmerus albidus Lacepède, 1803: 229. Name given in list and based on descriptions by Catesby and Linnaeus. Type locality: South Carolina; no types designated.

Coregonus ruber Lacepède, 1803: 243. Name given in list and based on description by Plumier. Type locality: Martinique; no types designated.

Esox salmoneus Mitchill, 1815: 442. Type locality: New York Bay; described from specimens, 203–229 mm in total length; no types designated.

Saurus longirostris Agassiz *in* Spix and Agassiz, 1829: 80, pl. 43. Type locality: Brazil; described from specimens, 178–216 mm in total length; current whereabouts unknown.

Saurus mexicanus Cuvier, 1829: 314. Type locality: Gulf of Mexico; no types designated.

Saurus spixianus Poey, 1860: 304. Type locality: Cuba; one type—MCZ 6884, 330 mm.

Holotype

No types known.

Designation of neotype

Linnaeus (1766) described *Salmo foetens* from material collected off the coast of South Carolina. Type material is not present in known collections of Linnaean specimens (Wheeler, 1985; 1991), and, although the original description is vague, it indicates the presence of 12 anal-fin rays. We believe that the genetic lineage of "*Synodus foetens*" in our data set that comprises specimens with 12 anal-fin rays is *Synodus foetens* (Linnaeus, 1766); the type locality of *Salmo foetens* provides corroborative evidence, because several specimens in our *Synodus foetens* lineage are from South Carolina. To stabilize the taxonomic status of *Synodus foetens* and distinguish it from *S. bondi*, formerly considered a synonym of *S. foetens* but resurrected herein (see entry for *S. bondi* below), we establish a neotype for *S. foetens.* We have selected USNM 405413 as the neotype on the basis of its collection off the type locality, South Carolina.

Neotype

USNM 405413, 205 mm SL, South Carolina, 32°47′34.80′N, 79°39′46.80′W, 10 m, Sta. 20110526, 17 October 2011, Coll: P. Webster.

Neotype COI sequence

GenBank sequence JX519368, USNM 405413 (neotype), DNA number SC 11001

Additional material

(DNA numbers for specimens that are vouchers are given in parentheses following catalog numbers). Alabama: USNM 398343 (FDA 170: JX519375), 1; USNM 358612, 6; Georgia: UF 143583, 1; Florida: KU 29686 (KUIT 3949: JX519400, KUIT 3950: JX519401), 2; UF 177024, 1; UF 177327, 3; UF 177249, 1; USNM 160462, 3; USNM 57123, 1; USNM 38710, 1; USNM 405452, 15; USNM 405450 (SMS 7502: JQ842743), 1; USNM 405451(FCC 8070: JQ841978), 1; Louisiana: UF 99242, 2; USNM 185713, 2; Mississippi: UF 137002, 3; Maryland: USNM 125789, 1; New Jersey: USNM 399108, 1; USNM 395747, 1; North Carolina: KU 27009 (KUIT 1127: JX519409, KUIT 1128: JX519410), 2; UF 5239, 3; UF 77354, 2; UF 178337, 9; South Carolina: UF 44476, 2; UF 39667, 1; UF 39650, 6; USNM 25998, 2; USNM 405414 (SC11002: JX519369, SC11003: JX519370), 2; USNM 405475 (SC11004: JX519371), 1; USNM 405449, 2; Texas: KU 30177 (KUIT 5069: JX519411), 1; UF 54575, 10; Bahamas Islands: UF 200425, 1; Belize: BLZ 6429: JQ841024 (tissue only), 1; Bermuda: USNM 337726, 3; Cuba: MCZ 6884, 1; USNM 331820, 1; Jamaica: UF 123664, 1; St. Martin, Leeward Islands: UF 205900, 1; Mexico: UF 125765, 1; UF 123640, 1; UF 7108, 1; UF 123660, 1; Puerto Rico: UF 137023, 1.

Diagnosis

A species of *Synodus* distinguished from all congeners by the following combination of characters: dorsal-fin rays 10–12, rarely 10; anal-fin rays 11–13, rarely 11; pectoral-fin rays 11–13; total caudal-fin rays 40–41; dorsal segmented caudal rays 9–10; ventral segmented caudal rays 9; dorsal procurrent caudal rays 11–12; ventral procurrent caudal rays 11; vertebrae 59–62; lateral-line scales 59–63, modally 60; predorsal scales 20–30; scale rows above the lateral line to dorsal-fin base 5.5–6.5; HL 23.5–28.0% SL; snout long and triangular (length 6.0–8.3% SL, mean 6.8%, and 24.5–31.9% HL, mean 27.1%), tip slightly rounded; anterior-nostril flap broad and triangular, length 1.7–3.9% HL (3.0%); orbit diameter 3.3–5.3% SL (3.9%) and 11.6–20.1% HL (15.6%); interorbital area wide (width 9.2–18.5% HL, mean 14.6%); adipose lid around orbit narrow (width 1.9–5.2% HL, mean 3.5%); dorsal-fin base 9.2–12.7% SL, mean 11.3%, equal in length to or shorter than anal-fin base (9.6–14.7% SL, mean 12.1%); posterior

tip of pectoral fin not extending to pelvic-fin origin; color in preservation: trunk dark tan to brown dorsally, paler ventrally; 6–8 dark, vertical cross-shaped markings along trunk in specimens <100 mm SL, crosses disappearing or becoming indistinct dark patches in larger specimens; dark pigment present along posterior margin of ventral portion of upper caudal-fin lobe and along entire posterior margin of lower lobe, sometimes extending onto main portion of ventral lobe; dorsal half of adipose fin dark; in life, adults olive to tan.

Description

Description based on 52 specimens, 58.7–380.0 mm SL. Counts and measurements of neotype given in Table 4. Frequency distribution of anal-fin rays given in Table 5.

Dorsal-fin rays 10–12, rarely 10; anal-fin rays 11–13, rarely 11; total caudal-fin rays 40–41; dorsal segmented caudal rays 9–10; ventral segmented caudal rays 9; dorsal procurrent caudal rays 11–12; ventral procurrent caudal rays 11; pectoral-fin rays 11–13, pelvic-fin rays 8; total vertebrae 59–62; predorsal vertebrae 17–19; scales ctenoid; pored lateral-line scales 59–63, modally 60; median predorsal scales 20–30; scale rows above the lateral line to dorsal-fin base 5.5–6.5; scales below lateral line to anal-fin base 6.5.

Body cylindrical and elongate; depth at pelvic-fin origin 7.5–14.2% SL (11.8%); depth at anal-fin origin 6.2–10.5% SL (8.4%); caudal-peduncle depth 4.5–5.7% SL (5.1%); body width at dorsal-fin origin 8.7–14.2% SL (11.3%); HL 23.5–28.0% SL (25.2%); snout length 6.0–8.3% SL (6.8%) and 24.5–31.9% HL (27.1%), snout long and pointed, tip rounded in dorsal view; orbit diameter 3.3–5.3% SL (3.9%) and 11.6–20.1% HL (15.6%), orbit with bony ridge extending over anterodorsal margin and with narrow adipose lid on its posterior edge, adipose lid width 0.5–1.3% SL (0.9%) and 1.9–5.2% HL (3.5%); interorbital region wide, width 2.3–5.2% SL (3.7%) and 9.2–18.5% HL (14.6%).

Predorsal length 41.2–48.7% SL (44.6%); prepelvic length 32.1–40.3% SL (37.1%); preanal length 71.9–80.1% SL (76.0%); preadipose length 77.3–86.1% SL (81.5%); dorsal-fin base 9.2–12.7% SL (11.3%), longest dorsal-fin ray, usually third, 13.0–16.5% SL (15.0%); anal-fin base 9.6–14.7% SL (12.1%), longest anal-fin ray, usually third, 6.7–9.9% SL (8.3%); pectoral-fin length 10.9–13.7% SL (12.0%); pelvic-fin length 17.7–22.6% SL (20.1%); caudal-peduncle length 8.8–14.0% SL (10.8%), caudal-fin length (only measured in 27 specimens because many specimens had damaged caudal fins) 14.1–19.5% SL (17.1%), caudal lobes generally same length.

Mouth terminal, upper jaw slightly oblique, forming a 10° angle with the horizontal body axis, upper jaw extending anterior to lower jaw; upper-jaw length 13.3–17.2% SL (15.5%) and 55.0–65.2% HL (61.1%). Teeth needlelike; upper jaw with 2 rows of teeth, teeth in inner row longer than teeth in outer row; lower jaw with 3 rows of teeth, size of teeth increasing medially,

Table 4

Counts and proportional measurements of the holotype and paratype of *Synodus bondi* and the neotype of *S. foetens*. Standard length presented in millimeters; other measurement values in percentages of standard length; values in parentheses are percentages of head length.

	Synodus bondi Holotype ANSP 68634	*Synodus bondi* Paratype ANSP 68635	*Synodus foetens* Neotype USNM 408413
Standard length	220.0	155.9	205.0
Vertebrae	60	–	62
Dorsal-fin rays	13	12	14
Anal-fin rays	10	10	12
Pectoral-fin rays	13–12	14–13	14–14
Pelvic-fin rays	8–8	8–8	8–8
Caudal-fin rays	42	42	42
Pored lateral-line scales	60	59	62
Predorsal scales	24	23	28
Cheek scales	6	6	7
Body depth (pelvic origin)	12.0	10.5	13.2
Body depth (anal origin)	10.8	8.8	8.5
Caudal-peduncle depth	6.0	5.9	5.4
Body width	13.2	12.1	11.8
Head length	25.7	24.7	25.3
Snout length	7.7 (30.0)	6.5 (26.3)	7.3 (28.9)
Nostril-flap length	0.8 (3.1)	0.7 (2.7)	0.6 (2.5)
Orbit diameter	3.2 (12.4)	3.4 (13.6)	3.7 (14.5)
Adipose-lid width	1.2 (4.7)	1.1 (4.6)	0.8 (3.1)
Interorbital width	4.3 (16.6)	3.8 (15.5)	3.7 (14.5)
Upper-jaw length	16.2 (62.9)	15.3 (62.0)	15.5 (61.4)
Predorsal length	44.4	44.1	43.6
Preanal length	77.3	76.4	74.7
Preadipose length	81.8	81.4	79.0
Prepelvic length	36.6	37.5	36.2
Dorsal-fin base	12.8	11.9	11.4
Longest dorsal ray	16.2	16.1	15.0
Anal-fin base	11.0	11.0	12.2
Longest anal ray	9.5	8.5	8.2
Pectoral-fin length	11.8	11.6	12.3
Pelvic-fin length	18.4	18.7	20.5
Caudal-peduncle length	10.7	13.9	9.4
Caudal-fin length	18.0	20.3	16.7

outer row covered by lips; posterior teeth in both jaws directed slightly anteriorly. Palatine with 3–4 rows of depressible teeth, teeth directed posteromedially. Tongue with 5 rows of posteriorly directed teeth, largest near anterior tip. Anterior nostril on level with median axis of orbit; posterior nostril same size and situated slightly dorsal to anterior nostril, nostrils almost on dorsal surface of snout; anterior nostril with small, triangular flap, length of flap when depressed 0.4–1.0% SL (0.8%) and 1.7–4.0% HL (3.0%); anterior nostril flap reaches center of posterior nostril when depressed (Fig. 2C); posterior nostril without flap.

Cheek with 7 rows of large scales, opercle with 3–5 vertical rows of 9–10 scales on anterior margin; predorsal scales extending anteriorly above anterior mar-

gin of preopercle; interorbital region naked. Dorsal and anal fins each flanked basally by 8–10 half scales, remainder of dorsal and anal fins without scales; 3 large, diamond-shaped scales covering pelvic-fin base, pelvic-fins flanked by a row of 4–6 half-scales laterally, remainder of pelvic fin and pectoral fin without scales; 7–9 rows of body scales extending onto base of caudal fin; upper and lower caudal lobes each with a single, enlarged, horizontally elongate scale.
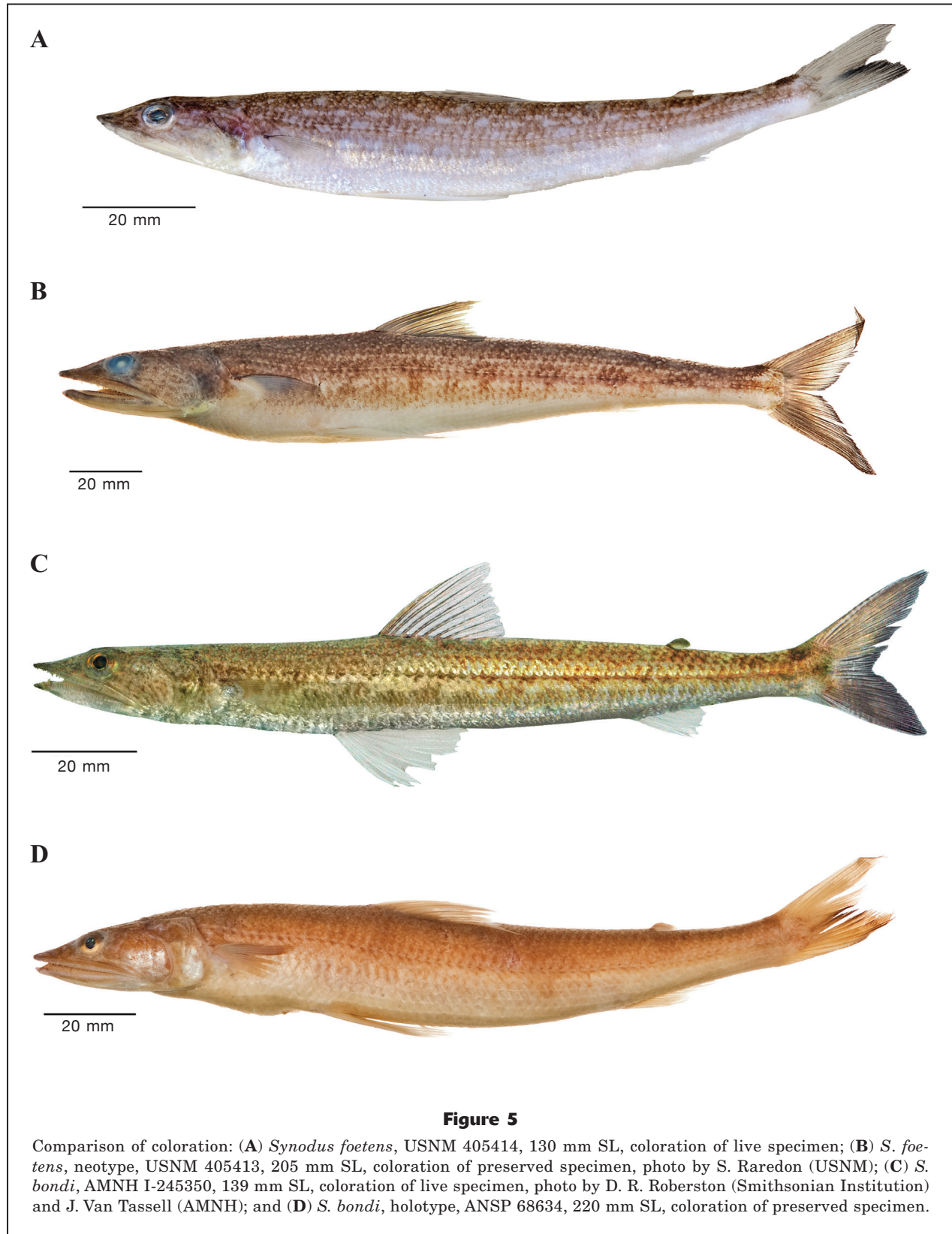
Coloration

Before preservation (Fig. 5A)   Head and dorsal half of trunk olive to brown, ventral half of trunk pale; 6–8 dark, vertical, cross-shaped markings along trunk in specimens <100 mm SL, with crosses disappearing or becoming indistinct dark patches in larger specimens; rows of light spots extending laterally over trunk; groove above maxilla with stripe of black pigment from anterior edge of orbit to posterior end of jaw; posterior edge of branchiostegal membrane pale yellow; dorsal fin brown with translucent membrane between rays; adipose fin tan with dark dorsal edge; pectoral fin translucent with dark pigment on dorsal edge; pelvic fin translucent to pale yellow; anal fin pale; dark pigment present along posterior margin of ventral portion of upper caudal-fin lobe and along entire posterior margin of lower lobe, sometimes extending onto main portion of ventral lobe.

In preservative (Fig. 5B.)   Trunk dark tan to brown dorsally, paler ventrally; dark markings in small speci-

Table 5

Frequency distributions of counts of anal-fin rays in *Synodus bondi* (*n*=46) and *S. foetens* (*n*=52).

	Anal-fin rays			
	10	11	12	13
Synodus bondi	12	32	2	–
Synodus foetens	–	2	35	15

Figure 5
Comparison of coloration: (**A**) *Synodus foetens*, USNM 405414, 130 mm SL, coloration of live specimen; (**B**) *S. foetens*, neotype, USNM 405413, 205 mm SL, coloration of preserved specimen, photo by S. Raredon (USNM); (**C**) *S. bondi*, AMNH I-245350, 139 mm SL, coloration of live specimen, photo by D. R. Roberston (Smithsonian Institution) and J. Van Tassell (AMNH); and (**D**) *S. bondi*, holotype, ANSP 68634, 220 mm SL, coloration of preserved specimen.
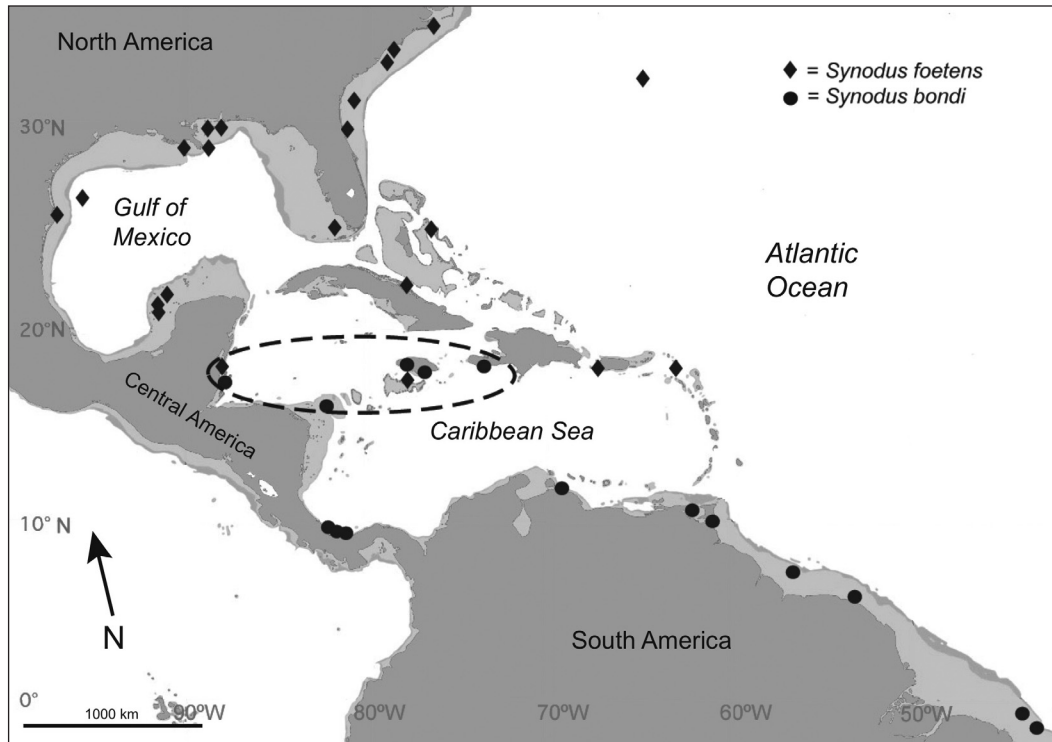
Figure 6

Distribution map of *Synodus foetens* and *S. bondi*. Symbols indicate sampling localities, not individual specimens. Dashed-line oval highlights area of overlap in distribution of these species. Map by Robert Myers (Coral Graphics), reprinted with permission.

mens faded; black pigmentation on jaw, pectoral, and adipose fin easily visible; dark caudal-fin pigmentation less distinct in larger specimens (>280 mm SL).

Distribution

Synodus foetens was originally described from South Carolina (Linnaeus, 1766). Additional specimens examined span the mid- and south-Atlantic coast of the United States: New Jersey, Maryland, North Carolina, South Carolina, Georgia, and Florida; the Gulf of Mexico: Alabama, Mississippi, Louisiana, Texas, and Mexico; Bermuda; Bahamas; Cuba; Jamaica; Puerto Rico; and St. Martin in the Leeward Islands. One larval specimen was collected in Belize (Fig. 6).

Synodus bondi Fowler, 1939
Proposed English common name: Sharpnose Lizardfish
Figures 1, 2D, 5 (C and D), and 6, Tables 1, 4, and 5

Holotype

ANSP 68634, 220 mm SL, Kingston, Jamaica, field number JB35-K-1, Jan 1935, Coll: J. Bond.

Paratype

ANSP 68635, 156 mm SL, Kingston, Jamaica, field number JB35-K-1, Jan 1935, Coll: J. Bond.

Additional material

(DNA numbers for specimens that are vouchers are given in parentheses following catalog numbers). Belize: KU 34275 (KUIT 5804: JX519392), 1; UF 137041, 8; USNM 300454, 1; USNM 328256, 1; Brazil: UF 213980, 1; UF 123639, 6; French Guiana: UF 211687, 1; Guyana: UF 123665, 1; Haiti: USNM 133666, 1; Honduras: UF 123637, 1; Jamaica: UF 5191, 1; USNM 38538, 1; USNM 32076, 1; Panama: UF 75450, 1; UF 75707, 1; USNM 390121, 3; USNM 389847, 2; USNM 389982, 7; Tobago, Trinidad and Tobago: UF 123636, 3; Venezuela: UF 123656, 1; UF 123659, 1; USNM 405447, 1.

Diagnosis

A species of *Synodus* distinguished by the following combination of characters: dorsal-fin rays 11–12; anal-fin rays 10–12, rarely 12; pectoral-fin rays 12–14; total caudal-fin rays 42; configuration of caudal-fin rays always 12 dorsal procurrent caudal rays + 10 segmented dorsal rays + 9 segmented ventral rays + 11 ventral

procurrent rays; total vertebrae 56–60, modally 59; lateral-line scales 57–60, modally 60; predorsal scales 23–25; scales above the lateral-line to dorsal-fin base 5.5 or 6.5; HL 22.4–26.7% SL (25.2%); snout very long and triangular (length 6.3–9.1% SL, mean 7.3%, and 26.3–37.2% HL, mean 29.0%), tip sharply pointed; anterior nostril with long, narrow flap that tapers to a filament distally, length 2.6–5.3% HL (3.4%); orbit diameter 2.8–4.9% SL (3.5%) and 11.1–19.0% HL (13.8%); interorbital width 10.4–16.9% HL (15.5%); thick adipose lids on anterior and ventral margins of orbit (width 3.4–7.4% HL, mean 4.8%); dorsal-fin base 10.5–13.0% SL, mean 11.9%, usually longer than anal-fin base (9.6–12.7% SL, mean 11.0%). In preservative, body dark gray to reddish brown above the lateral axis, pale below; a few lateral stripes darker than background color sometimes present along length of body; no vertical bars on trunk; dark pigmentation present on margins of caudal fin, usually extending onto main portion of ventral lobe; dorsal half of adipose fin dark. Body pale green to tan in life.

Description

Description based on 45 specimens, 55.3–279.0 mm SL. Counts and measurements of type specimens given in Table 4. Frequency distribution of anal-fin rays given in Table 5.

Dorsal-fin rays 11–12; anal-fin rays 10–12, rarely 12; total caudal-fin rays 42; configuration of caudal-fin rays in all specimens examined: 12 dorsal procurrent caudal rays + 10 segmented dorsal rays + 9 segmented ventral rays + 11 ventral procurrent rays; pectoral-fin rays 12–14; pelvic-fin rays 8; total vertebrae 56–60, modally 59; predorsal vertebrae 15–18; scales ctenoid, lateral-line scales 57–60, modally 60; predorsal scales 23–25; scales above the lateral-line to dorsal-fin base 5.5 or 6.5; scales below lateral line to anal-fin base 6.5.

Body cylindrical and elongate; depth at pelvic-fin origin 8.8–15.9% SL (11.8%); depth at anal-fin origin 5.7–10.8% SL (8.9%); caudal-peduncle depth 3.5–6.5% SL (5.6%); body width at dorsal-fin origin 10.5–14.2% SL (12.7%); HL 22.4–26.7% SL (25.2%); snout length 6.3–9.1% SL (7.3%) and 26.3–37.2% HL (29.0%), snout long and triangular, tip pointed in dorsal view; orbit diameter 2.7–4.9% SL (3.5%) and 11.1–19.0% HL (13.8%), orbit with bony ridge extending over anterodorsal margin and with wide adipose lid on its posterior edge, adipose lid width 0.8–1.9% SL (1.2%) and 3.4–7.4% HL (4.8%); interorbital width 2.7–4.5% SL (3.9%) and 10.4–16.9% HL (15.5%).

Predorsal length 40.9–45.8% SL (43.9%); prepelvic length 35.0–41.5% SL (38.6%); preanal length 75.0–81.3% SL (77.7%); preadipose length 80.0–86.4% SL (82.4%); dorsal-fin base 10.5–13.0% SL (11.9%), longest dorsal-fin ray, usually third, 14.0–17.2% SL (15.5%); anal-fin base 9.6–12.7% SL (11.0%), longest anal-fin ray, usually third, 7.0–9.6% SL (8.5%); pectoral-fin length 11.0–13.2% SL (11.9%); pelvic-fin length 15.9–21.2% SL (18.8%); caudal-peduncle length 7.9–14.4% SL (12.1%), caudal-fin length (only measured in 31 specimens because many specimens had damaged caudal fins) 15.7–20.3% SL (17.6%), caudal lobes generally same length.

Mouth terminal, upper jaw slightly oblique, forming an 8° angle with the horizontal body axis, upper jaw extending anterior to lower jaw; upper-jaw length 14.6–17.0% SL (15.9%) and 58.0–70.1% HL (62.9%), lower jaw with fleshy nub at symphysis. Teeth needle-like; upper jaw with 2 rows of teeth, teeth in inner row longer than teeth in outer row; lower jaw with 3 rows of teeth, size of teeth increasing medially, outer row covered by lips; posterior teeth in both jaws directed slightly anteriorly. Palatine with 3–4 rows of depressible teeth, teeth directed posteromedially. Tongue with 4–5 rows of posteriorly directed teeth, largest near anterior tip. Anterior nostril slightly ventral to median axis of orbit; posterior nostril same size and situated slightly dorsal to anterior nostril; anterior nostril with long, narrow flap that tapers to a filament distally, length when depressed 0.7–1.4% SL (0.9%) and 2.6–5.3% HL (3.4%); anterior nostril flap extending beyond posterior nostril when depressed (Fig. 2D); posterior nostril without flap.

Cheek with 6 rows of large scales, opercle with 2 vertical rows of 7–9 scales on anterior margin and several scales posteriorly; predorsal scales extending anteriorly above anterior margin of preopercle; interorbital region naked. Dorsal fin flanked basally by 10–12 half-scales, anal fin flanked by 8–10 half-scales, remainder of dorsal and anal fins without scales; 3 large, diamond-shaped scales covering pelvic-fin bases, pelvic fins flanked laterally by 6 half-scales, remainder of pelvic fin and pectoral fin without scales; 7 rows of body scales extending onto base of caudal fin; upper and lower caudal lobes each with a single, enlarged, horizontally elongate scale.

Coloration

Before preservation (Fig. 5C)   Head and dorsal half of trunk olive to golden-brown, ventral half of trunk pale; cross-shaped markings dispersed along trunk in specimens <100 mm SL, those markings not present in larger specimens; rows of light spots present on central region of trunk, spots darker in some specimens; groove above maxilla with stripe of black pigment from posterior edge of orbit to posterior end of jaw; dorsal-fin rays brown with translucent membrane between rays; adipose fin opaque, dorsal half dark; pectoral fin translucent with a few darker spots; pelvic fins translucent to pale yellow; anal fin pale; dark pigmentation present on margins of caudal fin, usually extending onto main portion of ventral lobe.

In preservative (Fig. 5D) Trunk dark orange-tan to brown dorsally, paler ventrally; dark markings in small specimens faded; lines on trunk faded or no longer visible; dark pigmentation on jaw and adipose fin visible; dark caudal-fin pigmentation less distinct in larger specimens (>280 mm SL).

Distribution

The holotype and paratype of *S. bondi* were collected off Kingston, Jamaica. Additional specimens of *S. bondi,* previously identified as *S. foetens,* are known from Jamaica, Haiti, Belize, Honduras, Panama, Trinidad and Tobago, Brazil, French Guiana, Guyana, and Venezuela. On the basis of the material examined, the distribution of this species is concentrated in the southern portions of the Caribbean (Fig. 6). No specimens currently are known from the United States, Mexico, Bahamas, or Bermuda.

Comparisons of *Synodus foetens, S. bondi,* and congeners

Synodus bondi was synonymized with *S. foetens* under the reasoning that "comparison of the type and paratype with specimens of *S. foetens* removes all doubt that *S. bondi* is identical to *S. foetens*" (Anderson et al., 1966: 73). The *S. foetens* discussed by Anderson et al. (1966) is undoubtedly the lineage we have identified as *S. foetens* because a majority of the specimens they examined possess 12–13 anal-fin rays and are from the United States and northern Caribbean. Anderson et al. (1966) noted that the apparent differences in counts between *S. foetens* and *S. bondi* for lateral-line scales and scale rows above the lateral line recorded by Fowler (1939) are incorrect. Their re-examination of the paratype of *S. bondi* revealed the presence of 60 (as opposed to Fowler's 54) lateral-line scales and 5 (instead of Fowler's 6) rows of scales above the lateral line. However, those counts were non-diagnostic in Fowler's species description, and additional reasoning for the synonymy was not provided.

Synodus bondi is, in fact, morphologically distinct from *S. foetens.* The snout of *S. bondi* ends in a sharper point than does the snout of *S. foetens* (Fig. 5) and is significantly longer (mean 29.0% HL in *S. bondi,* compared with 27.1% HL in *S. foetens*). The anterior-nostril flap in *S. bondi,* on average, is slightly longer than that flap in *S. foetens* (3.4% and 3.0% HL, respectively); however, the flap in *S. bondi* is narrow and tapers to a filament distally but in *S. foetens* is broad and triangular (Fig. 2, C and D). The upper jaw is longer in *S. bondi* than in *S. foetens*, 58.0–70.0% HL (63.0%) versus 55.0–65.2% HL (61.1%). The adipose lids surrounding the dorsal and ventral margins of the orbit are wider in *S. bondi* (mean 4.8% HL) than in *S. foetens* (mean 3.5% HL), making the orbit look superficially smaller in *S. bondi*. *Synodus bondi* usually possesses fewer anal-fin rays than does *S. foetens*

(10–12, usually 10 or 11, versus 12 or 13); as a result, the dorsal-fin base is usually longer than the anal-fin base in *S. bondi* (the opposite is true in *S. foetens*). In addition, the configuration of caudal-fin rays in *S. bondi* is consistently 12+10+9+11 in specimens examined, but it is more variable in *S. foetens* and other *Synodus* species. Finally, although the geographic ranges of these 2 species overlap in a swath across the central Caribbean, *S. bondi* otherwise has a more southern Caribbean distribution relative to *S. foetens,* which occurs northward to New York (Fig. 6).

Synodus bondi and *S. foetens* are distinguished from *S. synodus* by having a sharply pointed snout, pectoral fins that do not extend beyond the base of the pelvic fins, higher numbers of predorsal scales (20–30 versus 15–18), and no dark spot on the upper jaw. *Synodus bondi* and *S. foetens* differ from *S. saurus* by having 5 or 6 complete scale rows above the lateral line versus 3 and a snout that is longer than the diameter of the orbit. Finally, *S. bondi* and *S. foetens* are differentiated from *S. poeyi, S. intermedius*, and *S. macrostigmus* by having more than 55 lateral-line scales.

In the original description of *S. bondi*, Fowler (1939) noted that the type specimens have dark pigment on the isthmus and posterior margins of the branchiostegals. We did not observe this pigment in the ANSP types or additional material, but it may have faded in preservative. We have not examined fresh material beyond photographs.

Remarks

Although numerous synonyms exist for *Synodus foetens, S. bondi* is the only name that can be definitively associated with the additional genetic lineage of "*S. foetens*" in our material. Two nominal species, *Osmerus albidus* (Lacepède, 1803) and *Coregonus ruber* (Lacepède, 1803), were described only in brief paragraphs and lack known type material. The only diagnostic feature given in the original description for *C. ruber* is that it has a rounded snout. Based on the snout shape and lack of information of type material, neither name is applicable to specimens recognized herein as *S. bondi*. Mitchill (1815) described *Esox salmoneus* from New York without designating any type material. On the basis of the type locality, it is clear that this name also is not applicable to our *S. bondi* material. Cuvier (1829) described *Saurus mexicanus* from small, transparent specimens from the Gulf of Mexico without designating type material. These specimens were most likely larvae or small juveniles, but there is not enough detail in the original description to identify them to species. Agassiz (in Spix and Agassiz 1829) briefly described *Saurus longirostris* on the basis of 2 specimens from Brazil (deposited at ZSM) that have a short anal fin that comprises 12 rays and a very pointed snout. Kottelat (1988) was unable to find the type material of *Saurus longirostris* at ZSM or MHNN, and their whereabouts

Key to the western Atlantic species of *Synodus*

This key is modified from a provisional key for Synodontidae constructed by Russell (2003).

1a   Scales in lateral line 43 to 52..   2
1b   Scales in lateral line 54 to 65..   4
2a   Dorsal fin with anterior rays extending to, or usually beyond, tips of succeeding rays
      when depressed; lower jaw ending in fleshy knob; no black scapular blotch on shoulder
      under gill cover.. ***Synodus poeyi***
2b   Dorsal fin with anterior rays not extending beyond, but occasionally extending to, tips
      of succeeding rays when depressed; lower jaw rounded anteriorly, without fleshy knob;
      black scapular blotch present on shoulder under gill cover   3
3a   Caudal fin with 3–5 dark bars spanning both lobes; pored scales in lateral line 49–52;
      scapular blotch small and rectangular (length <12% HL); anterior-nostril flap broad and
      short, not tapering significantly posteriorly and not extending beyond posterior nostril
      when depressed.. ***Synodus intermedius***
3b   Caudal fin without prominent dark bars but with dark pigment on lower lobe; pored
      scales in lateral line 45–48; scapular blotch large and ovoid (length >14% HL); anterior-
      nostril flap large, tapering posteriorly and extending beyond posterior nostril when
      depressed .... ***Synodus macrostigmus*** new sp.
4a   Three rows of complete scales between lateral line and base of dorsal fin .... ***Synodus saurus***
4b   Four to 6 rows of complete scales between lateral line and base of dorsal fin....................................   5
5a   Snout rounded and blunt, its length less than diameter of eye; anal-fin base much
      shorter than dorsal-fin base; tip of pectoral fin extending well beyond base of pelvic fin;
      dark spot present on tip of upper jaw; predorsal scales 15 to 18................................. ***Synodus synodus***
5b   Snout triangular and pointed, its length greater than diameter of eye; anal-fin base
      slightly shorter to longer than dorsal-fin base; tip of pectoral fin falling short of or just
      reaching pelvic-fin base; no dark spot on tip of upper jaw; predorsal scales 20 to 30   6
6a   Anal-fin rays usually 10 or 11 (rarely 12); dorsal-fin base as long as or longer than anal-fin
      base; adipose lids around orbit thick; tip of snout sharply pointed; anterior-nostril flap
      narrow and tapering to filament distally; species currently known from off Central and
      South America, Jamaica and Haiti.. ***Synodus bondi***
6b   Anal-fin rays usually 12 or 13 (rarely 11); dorsal-fin base usually shorter than anal-fin
      base (rarely same length); adipose lids around orbit narrow; tip of snout not sharply
      pointed, slightly rounded; anterior-nostril flap broad and triangular, not tapering to
      filament; species currently known from New York south to the Leeward Islands, the
      Gulf of Mexico, and Belize .... ***Synodus foetens***

are unknown. Kottelat (1988) did find a specimen at MHNN collected off Brazil about the same time as Spix and Agassiz's (1829) *Saurus longirostris* (MHNN 793), which may be a syntype. However, as noted by Kottelat (1988), the length of that specimen does not match the lengths of *S. longirostris* recorded in the original description or in Agassiz's notes. Although this specimen could be the same one described by Fowler (1939) as *S. bondi* on the basis of its pointed snout, short anal fin, and collection locality (as noted previously, *S. bondi* is also known from Brazil), it would be imprudent to resurrect this name based on a specimen that may or may not be a primary type. Finally, we examined the holotype of another synonym, *Saurus spixianus* Poey, 1860 (MCZ 6884) and found that it has 13 anal-fin rays, a rounded snout, and morphometrics similar to those of *S. foetens*. Our observations, therefore, corroborate the synonymy of *Saurus spixianus* with *S. foetens*.

Discussion

Molecular variation

Our DNA barcoding analysis of Synodontidae in the Atlantic (Fig. 1) revealed 13 highly divergent lineages (average divergence in COI among lineages: 20.2%, range: 9.0–30.7%). Morphological examination of voucher specimens indicated that 10 of the lineages correspond to the following previously described species: *Saurida brasiliensis, S. caribbaea* (Smallscale Lizardfish)*, S. normani* (Shortjaw Lizardfish)*, S. suspicio* (Suspicious Lizardfish)*, Synodus foetens, S. intermedius, S. poeyi, S. saurus, S. synodus,* and *Trachinocephalus myops*. Of the additional 3 lineages, 2 represent morphologically distinct species originally identified as *S. intermedius* and *S. foetens*. We describe *S. macrostigmus* for the former and resurrect *S. bondi* for the latter. The thirteenth lineage in the data set represents specimens from deep

water off Central America originally identified as *S. poeyi* (*Synodus poeyi* lineage 2 in Fig. 1). That lineage is 17.9% divergent from *S. poeyi* specimens from the Gulf of Mexico (*Synodus poeyi* lineage 1 in Fig. 1).

A comprehensive study of *S. poeyi* from throughout its range, similar to this study conducted for *S. intermedius* and *S. foetens*, should help clarify the taxonomy of that species and likely will result in the recognition of a new species or one resurrected from synonymy. Preliminary investigation of *Synodus synodus* and *Saurida brasiliensis* from Cape Verde (not included in Fig. 1) reveal approximately 5–6% divergences in COI from western Atlantic *Synodus synodus* and *Saurida brasiliensis,* indicating deep population structure or potential cryptic species in those lizardfish lineages. Initial investigation of some Pacific lizardfish species (genetic data not included in this article) indicates that *Trachinocephalus myops* from the Philippines is highly divergent in COI from western Atlantic *T. myops*—a finding that sheds doubt on the current circumtropical distribution of *T. myops* and the monotypy of *Trachinocephalus*. Further investigation of this genus worldwide is needed to evaluate species diversity.

The intrageneric genetic variation in COI in western Atlantic *Synodus* and *Saurida* is high compared to the variation observed for other marine fishes that have been analyzed. Ward et al. (2005) found the average intrageneric variation in 207 species of Australian fishes to be 9.93%, and Hubert et al. (2008) found an average 8.30% intrageneric distance for 193 species of Canadian freshwater fishes. Average intrageneric divergence in western Atlantic synodontids (20.5%) exceeds even the average intergeneric distance of 16.6% calculated by Kartavtsev (2011) for animal species in general. Interspecific and intergeneric distances are similar in western Atlantic synodontids (Table 1). Large divergences likely reflect older speciation events, but the factors that drive lizardfish evolution are unknown.

Geographic and population variation

Although a species phylogeny for synodontids is needed to hypothesize sister-group relationships and examine patterns of speciation in this family, we note that morphologically and genetically similar species, such as *S. foetens* and *S. bondi* or *S. intermedius* and *S. macrostigmus*, exhibit different geographical and, sometimes, depth distributions. *Synodus foetens* and *S. bondi* have nearly distinct geographical distributions (Fig. 6). *Synodus foetens* occurs off the East Coast of the United States, in the Gulf of Mexico, and in the central Caribbean; *S. bondi* occurs in coastal Central and South America northward to Haiti. The distribution for these species overlaps in Belize and eastward to Jamaica and Haiti (Fig. 6).

Having largely disjunct distributions that overlap in the central Caribbean is a pattern congruent with distributions observed in other predatory fish genera, such as *Scomberomorus* (mackerels) and *Rhizoprion-*

odon (sharpnose sharks). In *Scomberomorus*, *S. maculatus* occurs off the East Coast of the United States, in the Gulf of Mexico, and in the northern and northwestern Caribbean, whereas *S. brasiliensis* occurs in the southern and central Caribbean (Collette et al., 1978; Banford et al., 1999). These 2 species overlap off northern Central America and potentially in the southern Gulf of Mexico. Similarly, *Rhizoprionodon terraenovae* (Atlantic Sharpnose Shark) inhabits the Gulf of Mexico, northern Caribbean, and East Coast of the United States, whereas the closely related species, *R. porosus* (Caribbean Sharpnose Shark), occurs off South and Central America. These 2 species may overlap in the central Caribbean (Springer, 1964; Compagno et al., 2005). *Synodus foetens* and *S. bondi* do not appear to have different depth preferences because both species inhabit depths between the surface and 95 m.

The geographic distributions of *Synodus macrostigmus* and *S. intermedius* overlap (Fig. 4). *S. macrostigmus* is known from the eastern and southern Gulf of Mexico and East Coast of the United States, whereas *S. intermedius* inhabits the eastern Gulf of Mexico, East Coast of the United States, Bermuda, Bahamas, and the Caribbean. These overlapping distributions are similar to the distributions observed in 2 genetic lineages of the goby, *Bathygobius soporator* (Frillfin Goby), by Tornabene et al. (2010). Those authors did not describe the lineages as separate species because no morphological differences were found to corroborate the genetic data, but Tornabene and Pezold (2011) noted that the *B. soporator* lineages could represent recent divergence and ongoing speciation in the western Atlantic. However, because the genetic divergence was observed in mitochondrial DNA alone, they could not rule out the possibility of deep coalescence.

Unlike the gobies, *S. intermedius* and *S. macrostigmus* are morphologically distinct, and they exhibit different depth preferences. Although *S. macrostigmus* primarily inhabits depths below 28 m (mean 96.5 m), *S. intermedius* is found typically at shallower depths (mean 49.3 m). However, *S. intermedius* has a broad depth distribution and has been collected in deep water along with *S. macrostigmus* (i.e., UF29818). Further investigation is needed to ascertain possible reproductive barriers in the evolutionary history of these species and whether or not ecological speciation (e.g., Rocha et al., 2005) could have played a role.

The neighbor-joining tree (Fig. 1) also reveals evidence of population structure in some species. For example, *S. foetens* specimens from the Gulf of Mexico differ in COI by 1.2% from a specimen in Belize, and Caribbean specimens of *Trachinocephalus myops* differ genetically by 1.6% from 2 deepwater Gulf of Mexico specimens. Finally, within *Saurida normani*, specimens from the Gulf of Mexico differ from Central American specimens by 1.7%. Additional material and genetic analyses are needed to describe the population structure of western Atlantic lizardfishes.

Fisheries concerns

Globally, some synodontids are commercially important as food fishes. *Trachinocephalus myops*, *Synodus synodus*, *Saurida tumbil* (Greater Lizardfish), and *Harpadon nehereus* (Bombay Duck) are targeted throughout the Mediterranean, Indian Ocean, and Southeast Asia (Raje et al., 2004; Ghosh et al., 2009; Xu et al., 2011). In the western Atlantic, synodontid species are encountered almost exclusively as bycatch in recreational and commercial fisheries. As a result, they have received little attention from fisheries researchers and managers despite their role as significant fish predators in various ecosystems (Sweatman, 1984; Cruz-Escolano et al., 2005). As mentioned previously, *S. foetens* makes up 1.5–2.0% of shrimp-trawl biomass and is usually among the 10 most prevalent finfish encountered by shrimp trawlers in the Gulf of Mexico, Caribbean, and off the southeastern United States.[1] (Gutherz, 1987; Jeffers et al., 2008; Manjarrés et al., 2008). These studies also report collection of *S. intermedius* and *S. poeyi* in much smaller amounts.

Jeffers et al. (2008) found that *S. foetens* in the northern Gulf of Mexico has a very high instantaneous annual mortality related to bycatch in fisheries (F_b), ranging from 0.4–0.6/year, and estimated exploitation ratios (E) of 0.43–0.55. Exploitation ratios of more than 0.5 generally indicate heavy fishing pressure and potential for overexploitation (Gulland, 1977). These data indicate that, although *S. foetens* is not commercially targeted, it is still fully exploited as bycatch.

To date, only commercially targeted fish species have been evaluated quantitatively as bycatch in the northern Gulf of Mexico (Jeffers et al., 2008), and little is known about bycatch rates and their effects on populations for noncommercial species. Broad ecosystem-scale studies of the effects of bycatch are needed that include nontargeted but exploited species, such as lizardfishes. For such studies, as well as any management plans that might result from them, an accurate understanding of species diversity and distribution is essential. This study provides new insights into the systematics of lizardfishes in the western Atlantic that should be incorporated into future management plans and fisheries research programs.

Conclusions

The description of *Synodus macrostigmus* as a new species and the recognition of *S. bondi* as a valid species bring the total number of valid western Atlantic *Synodus* species to 7. The integration of molecular and morphological data greatly facilitated identification of the new species and recognition of *S. bondi* as valid. A thorough systematic revision of western Atlantic Synodontidae that incorporates both molecular and morphological data is needed, and it seems likely that additional new species may exist. Geographic variation and population structure within this group also warrant further study.

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Appendix: Comparative material of western Atlantic Synodontidae examined in this study

In the lists below, the following sequence is observed: first, catalog number; second, DNA number; and third, GenBank accession number (the latter two numbers are shown within parentheses).

Synodus synodus USNM 405415 (BAH 8058: JQ839916), USNM 405416 (BAH 8059: JQ839915), USNM 405417 (BAH 9028: JX519403), USNM 405418 (BAH 9030: JX519388), USNM 405419 (BAH 10008: JX519382), USNM 405420 (BAH 10009: JX519383), USNM 405421 (BAH 10010: JX519384), USNM 405422 (BLZ 4026: JQ840361), USNM 405423 (BLZ 4027: JQ840360), USNM 405424 (BLZ 4555: JQ840362), USNM 405425 (BLZ 5094: JQ840726), USNM 405426 (BLZ 5133: JQ840727), USNM 405427 (BLZ 5159: JQ840729), USNM 405428 (BLZ 5240: JQ840728), USNM 405429 (BLZ 5214: JQ840730), USNM 405430 (BLZ 5455: JQ840725), USNM 405431 (BLZ 6297: JQ841025), USNM 405432 (TCI 9275: JX519404), USNM 405433 (TCI 9276: JX519405), USNM 405434 (TCI 9277: JX519389), USNM 405435 (TCI 9278: JX519390), USNM 405436 (TCI 9279 JX519406), USNM 405437 (TCI 9576: JX519408), USNM 405438 (TCI 9645: JX519407), USNM 405439 (TCI 9646: JX519391), USNM 405440 (TOB 9199: JQ843085).

Synodus poeyi   FSBC 020586 (FWRI 20586a: JX519378, FWRI 20586b: JX519379), FSBC 020708 (FWRI 20708: JX519381), USNM 405441 (MOC 11014: JX519397), USNM 405442 (MOC 11437: JX519398), USNM 405443 (MOC 11784: JX519399).

Synodus saurus   USNM 405444 (BAH 10071: JX519385).

Saurida brasiliensis   FSBC 020698 (FWRI 20698).

Saurida caribbaea   USNM 405445 (MOC 11159: JX519372), USNM 405446 (MOC 11471: JX519373).

Saurida normani   FSBC 020653 (FWRI 20653a: JX519393), USNM 405453 (MOC 11434: JX519374), USNM 405454 (MOC 11438: JX519365).

Saurida suspicio   USNM 405455 (BLZ 8329 JQ841833), USNM 405456 (BLZ 8393: JQ841834), USNM 405457 (BLZ 8397: JQ841786), USNM 405458 (BLZ 8398: JQ841832).

Trachinocephalus myops   FSBC 020509 (FWRI 20509: JX519396); FSBC 020698 (FWRI 20698a: JX519394); USNM 405460 (BLZ 6415: JQ841030); USNM 405459 (TOB 9157: JQ843093); USNM 405459.