Zootaxa 2346: 29–41 (2010)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

A new species of ladyfish, of the genus *Elops* (Elopiformes: Elopidae), from the western Atlantic Ocean

RICHARD S. MCBRIDE[1], CLAUDIA R. ROCHA[2], RAMON RUIZ-CARUS[1] & BRIAN W. BOWEN[3]

[1]*Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, 100 8th Avenue SE, St. Petersburg, FL 33701 USA. E-mail: richard.mcbride@noaa.gov; ramrc@tampabay.rr.com*

[2]*University of Texas at Austin - Marine Science Institute, 750 Channel View Drive, Port Aransas, TX 78374 USA. E-mail: crocha@mail.utexas.edu*

[3]*Hawaii Institute of Marine Biology, P.O. Box 1346, Kaneohe, HI 96744 USA. E-mail: bbowen@hawaii.edu*

Abstract

This paper describes *Elops smithi*, **n. sp.**, and designates a lectotype for *E. saurus*. These two species can be separated from the five other species of *Elops* by a combination of vertebrae and gillraker counts. Morphologically, they can be distinguished from each other only by myomere (larvae) or vertebrae (adults) counts. *Elops smithi* has 73–80 centra (total number of vertebrae), usually with 75–78 centra; *E. saurus* has 79–87 centra, usually with 81–85 centra. No other morphological character is known to separate *E. smithi* and *E. saurus*, but the sequence divergence in mtDNA cytochrome *b* (d = 0.023–0.029) between *E. smithi* and *E. saurus* is similar to or greater than that measured between recognized species of *Elops* in different ocean basins. Both species occur in the western Atlantic Ocean, principally allopatrically but with areas of sympatry, probably via larval dispersal of *E. smithi* by oceanographic currents.

Key words: allopatry, sympatry, vertebrae, mtDNA, meristics, Caribbean Sea, Gulf of Mexico

Resumen

Este trabajo describe *Elops smithi* y designa un lectotipo para la especie *E. saurus*. Estas dos especies de peces pueden separarse de las otras cinco especies de *Elops* por una combinación de los números de vértebras y branquispinas. Morfológicamente pueden distinguirse una de la otra sólo por el número de miomeros (larvas) o de vértebras (adultos). *Elops smithi* tiene 73–80 centra (número total de vértebras), usualmente con 75–78 centra; *E. saurus* tiene 79–87 centra, usualmente con 81–85 centra. Ningún otro carácter morfológico es conocido para separar *E. smithi* y *E. saurus*, pero la divergencia en la secuencia del citocromo *b* del mtDNA (d = 0.023–0.029) entre *E. smithi* y *E. saurus* es similar a, o mayor que aquella medida entre las especies reconocidas de *Elops* de océanos diferentes. Ambas especies se encuentran en el Océano Atlántico occidental, mayormente alopátricamente pero con áreas de simpatría probablemente originadas por la dispersión larval de *E. smithi* por corrientes oceanográficas.

Introduction

The ladyfishes or tenpounders (genus *Elops*) are widely distributed in tropical-subtropical, marine and coastal waters. Six species of *Elops* are recognized worldwide (Eschmeyer & Fong 2008), but the taxonomy of the group is poorly known and some authors recognize fewer species (Nelson 2006). Taxonomic uncertainty of *Elops* is exemplified by the ladyfish, *E. saurus*, currently recognized as the only species of *Elops* in the western Atlantic Ocean. A large collection (n = 440) of larvae from this area, revealed a bimodal distribution of myomere counts, which indicated that two morphs existed (Smith 1989). Smith identified *Elops saurus* as a high-count morph (79–86 total myomeres) and he assigned *Elops* sp. as a low-count morph (74–78 total myomeres). He also reported that the preanal myomere counts were distinct (76–80 v. 68–72, respectively). Although he found no additional morphological characters to diagnose *Elops* sp., he regarded these two

Accepted by M.R. de Carvalho: 14 Dec. 2009; published: 28 Jan. 2010

morphs as "so distinct they should probably be treated as separate species" (Smith 1989; see also Smith & Crabtree 2002).

Smith (1989) also noted that the two morphs had largely allopatric geographic distributions. The high-count morph is mostly distributed off the eastern coast of North America and in the Gulf of Mexico, whereas the low-count morph is mostly distributed off the northern coast of South America, throughout the Caribbean Sea and the Bahamas (Smith 1989; McBride & Horodysky 2004). There are, however, areas of sympatry, most notably along the eastern seaboard of the U. S., occurring as an apparent consequence of northerly larval transport of low-count larvae (Smith 1989; McBride & Horodysky 2004). Thus, the allopatric, latitudinal separation of each morph is interrupted by secondary contact via larval dispersal. Furthermore, McBride and Horodysky (2004) concluded that few of the low-count *Elops* in these northern areas survive beyond their first few years, so the potential for reproduction between morphs appears low. In this context, the allopatric distributions of two morphs can be maintained and may be evidence of two species despite pockets of sympatry.

Very little gene flow is necessary to maintain genetic similarity (Slatkin 1987), so the validity of these two morphs as separate species requires further consideration. In particular, the latitudinal gradient of myomeres and vertebral counts among *Elops* could simply be an intraspecific example of Jordan's rule, such that lower meristic counts develop at higher temperatures and lower latitudes (Jordan 1891; McDowall 2008). Recent work has, however, failed to support such an ecophenotypic hypothesis. When Obermiller and Pfeiler (2003) included a single specimen of *Elops* sp. in their phylogenetic analysis of the Elopomorpha, the genetic distance between this specimen and *E. saurus* was comparable to the distance between *E. saurus* and *E. hawaiiensis*, valid species that occur in different ocean basins.

Thus, the purpose of this study was to evaluate Smith's (1989) *Elops* sp. We examined specimens of *E. saurus* and *Elops* sp. using common morphological and meristic characters that have been used to distinguish the six species of *Elops* worldwide (*E. saurus*, *E. affinis*, *E. lacerta*, *E. senegalensis*, *E. machnata*, and *E. hawaiensis*; Whitehead, 1962). We also present mtDNA cytochrome *b* data to provide an independent assessment of evolutionary divergence and to provide a genotypic character on which to base our species description.

Materials and methods

Archived material was borrowed from various museums (Table 1). Institutional abbreviations follow those listed at http://www.asih.org/codons.pdf, with the acronym FSBC rather than the incorrect FDNR used for the State of Florida Ichthyology Collection. Other, non-type material used herein for scale counts (n = 25) or genetic analysis (n = 56) was collected as part of a statewide sampling program by the Florida Fish and Wildlife Conservation Commission (FWC); see McBride *et al.* (2001) and McBride and Horodysky (2004) for FWC collection methods.

Vertebral counts of museum specimens were taken from radiographs, counting from the first centrum that articulates with the basioccipital bone of the cranium to the two independent ural centra along the upturned terminal of the vertebral column, as was done by McBride & Horodysky (2004). Vertebral counts of non-type material not retained were made directly from filleted, steamed, and scraped carcasses (McBride & Horodysky 2004). Principal fin rays were counted following Hubbs and Lagler (1947) and presented along with total ray counts. Morphometrics follow Hubbs and Lagler (1947). These were made with dial calipers to the nearest 0.1 mm, except standard length (SL), fork length (FL) and total length, which were recorded to the nearest 1 mm on a measuring board.

Gill tissue from fresh or frozen fish was used as the source for DNA sequencing. Fish were sampled at several Florida locations, principally along the southeastern coast. Fish length was measured to the nearest mm SL or converted from the empirically derived equation SL = 0.941 × FL – 2.58. Tissue from the gill arch was excised and placed into saturated salt buffer (Amos and Hoelzel 1991).

Total genomic DNA was isolated via organic extraction (phenol:chloroform:isoamyl alcohol), precipitated with sodium acetate in a 95% ethanol solution, and resuspended in 100 µl TE (10 mM Tris and 1mM EDTA, pH 8.0). Using primers Cyb-09H (5'-GTGACTTGAAAAACCAC CGTTG-3'; Song *et al.* 1998) and Cyb-07L (5'-AATAGGAAGTATCATTCGGGTTTGATG-3'; Taberlet *et al.* 1992), we amplified approximately 700 base pairs (bp) of the mitochondrial cytochrome *b* gene with the polymerase chain reaction (PCR; Saiki *et al.* 1985). The amplification reaction mix for both fish morphs contained 3.0 mM $MgCl_2$, 20 nM of each primer, 17.5 nM of each dNTP, 0.40 µl of *Taq* DNA polymerase (Promega Inc., Madison WI), and 5.0 µl of 10x PCR buffer (Promega, Inc., Madison WI) in 50 µl total volume. PCR reactions used the following cycling parameters: initial 94° C denaturation and 72° C final extension (three minutes each), with an intervening 25 cycles of 30 seconds at 94° C, 1 minute at 52° C, and 1 minute at 72° C. Excess primers were removed with either 30,000 MW Ultrafree-MC centrifugal filter units (Millipore Corp., Bedford MA) or by simultaneous incubation of PCR reaction with exonuclease I and shrimp alkaline phosphatase (USB Corp., Cleveland OH).

DNA sequencing reactions with fluorescently labeled dideoxy terminators were conducted according to manufacturer's recommendations, and the labeled extension products were analyzed with ABI models 373A and 377 (PE Applied Biosystems, Foster City, CA) at the University of Florida Sequencing Core. Forward and reverse sequences were obtained in selected cases to assure the accuracy of nucleotide assignments. We aligned and edited resulting chromatograms using Sequencher ver. 3.0 (Gene Codes Corp., Ann Arbor, MI). Genetic distance (*d*) was calculated by Kimura's (1980) two-parameter method.

***Elops smithi*, new species**

Figure 1; Table 1

Elops saurus non Linnaeus 1766: Regan, 1909 (in part), Hildebrand, 1943 (in part); Bertin, 1944 (in part); Fowler, 1931; Gehringer, 1959 (in part); Whitehead, 1962 (in part); Hildebrand, 1963 (in part); Eldred and Lyons, 1966 (in part); Carles, 1967; Miller and Jorgenson, 1973 (in part), Santos-Martínez and Arboleda (1993). These studies examined what we recognize here as *E. smithi*, either in whole or in part, based on their reports of meristic values, sample locality, or both.

Elops sp.: Smith, 1989; Smith-Vaniz *et al.*, 1999; Obermiller and Pfeiler, 2003

FIGURE 1. *Elops smithi*, holotype, UF 45683, 303 mm SL, left lateral view.

Holotype. UF 45683, 303 mm SL, marine waters of Guyana, by trawl, 16 July 1967.

Paratypes. UF 45682, marine waters of Trinidad, 13 December 1967; GCRL 11950, 4, Commewijne River, Suriname, 14 October 1973; GCRL 12733, Gatun Locks, Canal Zone, Panama, 4 March 1974; UF 11269, 2, Tortuguero Lagoon, Costa Rica, August 1963.

Other museum material examined. *Elops saurus*: FSBC 00258, Florida, Pinellas County, 13 December 1957; FSBC 10270, Florida, Pinellas County, 15 December 1977; FSBC 12589, 3, Florida, Hillsborough County, 3 June 1983; GCRL 0345, Louisiana, 8 September 1959; GCRL 1938, Mississippi, 8 August 1966; UF 47036, Honduras, 26 April 1967; UF 105715, 2, Florida, Volusia County, 17 November 1972.

Diagnosis. *Elops smithi* is distinguished from *E. saurus* in the number of vertebrae (73–80, usually 75–78 versus 79–87, usually 81–85, respectively). According to McBride and Horodysky (2004), vertebrae counts in

the overlap range (79–80) occurred in only 94 of 3,255 (2.9%) specimens examined from the coasts of the Americas, the Bahamas, and the Caribbean islands.

As reported by Whitehead (1962) counts of gill rakers and total vertebrae can be used to separate all species of *Elops*. Western Atlantic *Elops*, now recognized as *E. smithi* and *E. saurus*, have lower gill raker counts (10–15 on the lower part of the first arch) than *E. affinis* (16–20) and *E. lacerta* (17–19). *Elops smithi* and *E. saurus* have higher vertebrae counts (> 72; see above for ranges) than *E. senegalensis* (67), *E. machnata* (63–64), and *E. hawaiensis* (68–70).

Description. Body elongate (head length 25–29% of SL) and slender (width 7.5–9.4% of SL). Mouth large (maxilla 56–60% of head length) and nearly terminal. Caudal fin deeply forked, with lobes equal. Principal dorsal-fin rays 19–20 (24–27 total); anal rays 12–13 (16–19 total); pectoral rays 17–18; pelvic rays 13–16; branchiostegal rays 30–34; gill rakers on lower arch 13–15 (total 21–23 excluding rudiments); lateral-line scales (102–118, but may be higher if specimen is found north of the Caribbean Sea [see below]); and 73–80 vertebrae (usually 75–78). Data for above description are from Table 1, Figure 2, and McBride and Horodysky (2004).

TABLE 1. Comparison of selected phenotypic characters for *Elops smithi* (top) and *E. saurus* (bottom). Abbreviations of meristic characters are: Vert. (total number of vertebrae), D (Dorsal fin elements [total (t) or principal (p)]), A (Anal fin elements [total (t) or principal (p)]), P1 (pectoral fin elements), P2 (pelvic fin elements), GR (gillrakers [lower (l) or upper (u)]), LL (lateral line scales), B (branchiostegal rays). Morphometric measurements are in mm; abbreviations used are: SL (standard length), FL (fork length), TL (total length), HL (head length), OD (orbit diameter, LJL (lower jaw length), HWG (head width at gills). *Indicates H for holotype, P for paratype, L for lectotype (data for *E. saurus* lectotype are from Linnaeus [1766]). No data = nd.

		Meristic characters										
Institution	Lot# (type*)	Vert.	D (t)	D (p)	A (t)	A (p)	P1	P2	GR(l)	GR(u)	LL	B
Elops smithi												
UF	45683 (H)	76	27	20	nd	13	17	14	14	9	108	32
UF	45682 (P)	76	27	20	17	12	17	14	13	9	116	33
UF	11269 (P)	75	26	20	nd	12	18	14	14	9	112	32
UF	11269 (P)	77	nd	20	nd	12	18	14	14	8	118	34
GCRL	12733 (P)	77	27	20	19	12	18	13	14	8	117	32
GCRL	11950 (P)	78	25	19	16	12	18	14	14	8	102	30
GCRL	11950 (P)	78	24	19	16	12	18	14	13	8	108	31
GCRL	11950 (P)	78	24	20	16	12	18	15	15	8	105	33
GCRL	11950 (P)	76	24	20	16	12	17	16	15	8	109	31
Elops saurus												
Linn. Soc.	90 (L)	nd	24	20	16	13	17	14	nd	nd	nd	30
UF	47036	84	nd	20	nd	13	17	14	14	9	119	30
FSBC	10270	84	24	20	18	13	18	14	13	8	120	32
GCRL	1938	84	26	21	18	12	18	15	13	8	123	30
GCRL	345	84	28	20	18	13	17	14	14	9	128	27
UF	105715	83	27	21	18	13	17	13	14	9	124	34
UF	105715	85	25	19	18	14	17	15	14	7	119	30
FSBC	258	85	24	21	17	12	18	14	14	8	123	32
FSBC	12589	84	27	21	17	12	19	14	14	8	121	29
FSBC	12589	85	27	20	18	13	18	14	14	8	122	33
FSBC	12589	84	28	20	17	13	17	13	14	8	119	29

continued.

		Morphometric characters						
Institution	Lot# (type*)	SL	FL	TL	HL	OD	LJL	HWG
Elops smithi								
UF	45683 (H)	303	329	388	80.4	15.2	45.6	24.4
UF	45682 (P)	504	548	604	127.4	25.5	71.2	39.6
UF	11269 (P)	424	452	528	120.2	26.6	71.0	39.0
UF	11269 (P)	362	393	469	96.2	19.3	57.7	29.5
GCRL	12733 (P)	440	473	568	114.8	22.8	65.0	41.3
GCRL	11950 (P)	204	213	264	57.2	11.2	33.3	15.4
GCRL	11950 (P)	160	172	207	45.6	9.4	26.1	12.2
GCRL	11950 (P)	171	187	220	48.2	9.5	28.5	13.6
GCRL	11950 (P)	172	188	222	48.2	9.7	28.0	15.7
Elops saurus								
Linn. Soc.	90 (L)	nd	480	nd	nd	nd	nd	nd
UF	47036	451	495	569	119.4	22.4	67.4	37.3
FSBC	10270	224	245	294	60.4	12.4	35.3	16.2
GCRL	1938	242	258	301	63.0	12.2	36.0	17.8
GCRL	345	258	278	331	66.5	11.4	38.8	21.2
UF	105715	226	246	292	63.4	13.2	36.7	18.8
UF	105715	201	215	257	56.3	11.3	31.7	15.0
FSBC	258	232	252	301	61.3	13.1	37.0	19.0
FSBC	12589	257	276	333	69.8	14.9	41.0	20.4
FSBC	12589	275	290	355	73.9	14.5	43.8	20.5
FSBC	12589	267	288	344	72.7	14.8	43.1	20.9

The larvae are of leptocephalus form, and the total myomere number of the leptocephalus equals that of total vertebrae (McBride & Horodysky 2004). Predorsal (61–66) and preanal (68–72) myomeres are also reliable characters for identifying premetamorphic leptocephali (Smith 1989). Others examining *Elops* from the Caribbean Sea have noted minor variations in these meristic characters (Carles 1967; Santos-Martínez and Arboleda 1993), indicating differences in counting methods or geographic variation.

Coloration. Living adults bright silver, particularly on sides; may be bluish-gray on back with yellowish hue on fins. Not as silvery in preservative.

Comparisons. We found no character other than counts of vertebrae that separates adult *E. smithi* from *E. saurus* (Table 1). Although lateral-line scale counts appeared to be a diagnostic character, the scales are formed late in larval development so this character is indicative of latitude where larval transformation occurs instead of where spawning occurred. To demonstrate this, it can be shown that lateral-line scale counts are distinct among *E. smith* and *E. saurus* that had not been dispersed outside their typical range (Table 1, Fig. 2A), but the lateral-line scale counts are not distinct among a test collection from the southern Indian River Lagoon, Florida, which included *E. smithi* that had presumably been dispersed from their spawning grounds (Fig. 2B). This disconnect can be explained because vertebral number is set during embryogenesis but scales are not developed until about 50 mm in the late metamorphic period (Gehringer 1959). Thus, lateral-line scale counts will be a misleading diagnostic character when measured from specimens collected within areas of sympatry. The leptocephalus larva, common to this genus, is associated with long-distance dispersal (McBride & Horodysky 2004), so scale counts may be problematic as a taxonomic character in other species of *Elops* as

well. In addition, the scales of these species are small and easily displaced, further confounding their use as a taxonomic character.

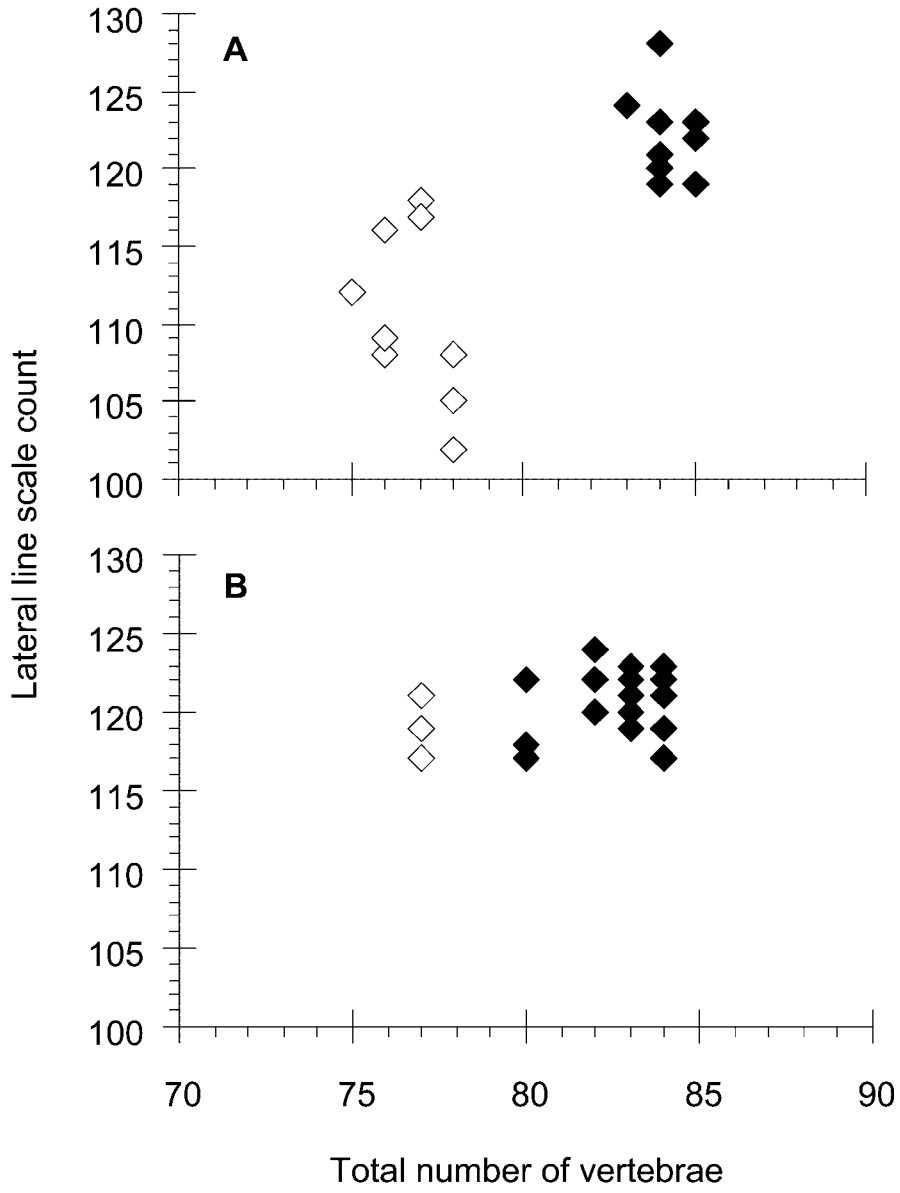

FIGURE 2. High (or low) counts of vertebrae do not always match to high (or low) counts of lateral line scales with *Elops smithi* (open symbols) and *E. saurus* (filled symbols). Two datasets are used here: (A) individuals from Table 1 (various collections), and (B) a single collection of 25 *Elops* collected March 30, 1998, in the southern Indian River Lagoon, Florida. See text for full explanation as to why we consider lateral-line scale counts to be a misleading diagnostic character.

Mitochondrial DNA sequence data provide an independent character for recognizing two species of *Elops* in the western North Atlantic. We observed 14 haplotypes in two primary lineages corresponding to *E. saurus* and *E. smithi* (Table 2). These sequences have been deposited in GenBank under accession numbers GQ183881 – GQ183882 (*E. saurus*, haplotypes A, B) and GQ183883 – GQ183894 (*E. smithi*, haplotypes C – N). The genetic difference (*d*) between the *E. saurus* haplotypes and the *E. smithi* haplotypes ranged from 0.023 to 0.029 (Fig. 3). Obermiller and Pfeiler (2003) reported a similar level of divergence between what we recognized as *E. smithi* and *E. saurus* (*d* = 0.021 with 12S and 16S rRNA mtDNA sequences). In addition, Obermiller and Pfeiler (2003) observed a similar level of divergence between *E. saurus* and *E. hawaiiensis* (*d* = 0.024), two recognized species that occupy different ocean basins.

TABLE 2. Data associated with fish used in the genetic analysis. Collection date and locale are listed, along with standard length (SL), and total number of vertebrae (Vert.). Fish are sorted as vertebrae morph (high vs. low-count) and haplotype. *Mismatches between phenotype and genotype are indicated with an asterisk. Locality codes are: IR = Indian River Lagoon (northern or southern regions of the lagoon), southeast Florida, CK = Cedar Key, west coast Florida, and FW = Fort Walton, panhandle Florida.

Date	Locale	SL (mm)	Vert.	Morph	Haplotype
6/17/1996	IR (North)	54	83	H	A
7/10/1996	IR (North)	130	85	H	A
7/10/1996	IR (North)	140	85	H	A
7/10/1996	IR (North)	141	84	H	A
7/10/1996	IR (North)	144	85	H	A
7/10/1996	IR (North)	147	84	H	A
7/10/1996	IR (North)	147	85	H	A
7/10/1996	IR (North)	155	79	H	A
7/10/1996	IR (North)	177	84	H	A
10/15/1997	CK	230	86	H	A
10/15/1997	CK	234	83	H	A
8/29/1996	FW	244	84	H	A
1/3/2001	IR (South)	246	82	H	A
6/8/2000	IR (North)	272	85	H	A
12/12/2000	IR (South)	280	83	H	A
7/12/2000	IR (North)	286	82	H	A
9/5/2000	IR (North)	303	83	H	A
2/7/2001	IR (South)	312	80	H	A
9/11/2000	IR (North)	314	83	H	A
6/8/2000	IR (North)	321	83	H	A
12/12/2000	IR (South)	335	83	H	A
8/28/2000	IR (South)	351	83	H	A
2/3/2001	IR (North)	372	80	H	A
2/7/2001	IR (South)	376	86	H	A
12/12/2000	IR (South)	393	83	H	A
12/12/2000	IR (South)	467	83	H	A
11/2/2000	IR (North)	498	83	H	B
12/12/2000	IR (South)	200	83	H	E*
6/18/1996	IR (North)	51	79	H	N*
11/2/2000	IR (North)	222	76	L	A*
12/12/2000	IR (South)	313	77	L	A*
11/6/1997	IR (South)	328	77	L	A*
5/28/2000	IR (South)	332	74	L	A*
12/12/2000	IR (South)	350	75	L	A*
6/17/1996	IR (North)	75	77	L	C
3/30/1998	IR (South)	305	77	L	C
7/10/1996	IR (North)	110	78	L	D

continued next page

TABLE 2. (continued)

Date	Locale	SL (mm)	Vert.	Morph	Haplotype
6/18/1996	IR (North)	39	78	L	E
6/18/1996	IR (North)	40	78	L	E
6/17/1996	IR (North)	49	77	L	E
3/30/1998	IR (South)	213	77	L	E
6/8/2000	IR (North)	282	78	L	E
12/12/2000	IR (South)	315	75	L	E
6/18/1996	IR (North)	69	78	L	F
6/18/1996	IR (North)	41	77	L	G
6/17/1996	IR (North)	54	77	L	H
6/17/1996	IR (North)	68	76	L	H
2/9/2000	IR (South)	200	77	L	H
11/20/1997	IR (South)	277	77	L	H
6/18/1996	IR (North)	48	77	L	I
12/12/2000	IR (South)	183	75	L	I
7/10/1996	IR (North)	79	77	L	J
1/3/2001	IR (South)	200	77	L	K
6/8/2000	IR (North)	286	75	L	L
2/22/2000	IR (North)	250	77	L	M
7/10/1996	IR (North)	129	78	L	N

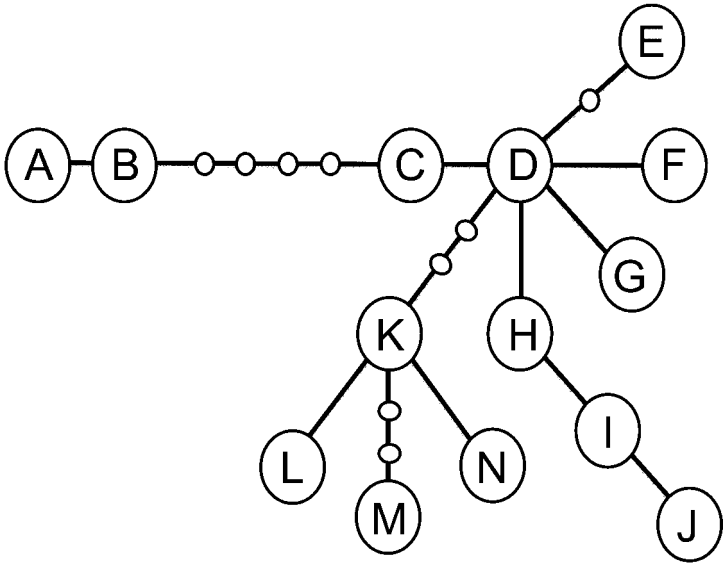

FIGURE 3. There were 14 haplotypes of *Elops* in two primary lineages in the western North Atlantic (see Table 2 for data source). Separation between haplotypes occurs by a single base pair substitution, or, if more than one, the number of dots (plus one) placed between each haplotype. Haplotypes A and B are *E. saurus*; haplotypes C-N are *E. smithi* (Table 2).

Although the mtDNA data presented here and data presented previously by Obermiller and Pfeiler (2003) indicate two evolutionary lineages, the mtDNA character was not absolutely diagnostic. In seven of 56 specimens (12.5%), there was a mismatch between classification based on genetics and that on morphology (Table 2). Five of these individuals had morphology similar to *E. smithi* but haplotypes in the *E. saurus*

lineage, and two had the reverse. These mismatches may indicate ecophenotype plasticity within species, hybridization, or retention of ancestral polymorphisms. All three phenomena have been documented in fishes (see Rocha *et al.* 2007). The sympatric sturgeons *Scaphirhynchus albus* and *S. platorynchus* share mtDNA haplotypes because of their recent speciation and hybridization (Campton *et al.* 2000). The marine angelfishes *Centropyge argi* and *C. aurantonotus* are sister species that share haplotypes despite diagnostic differences in coloration (Bowen *et al.* 2006). And the Atlantic bluefin tuna (*Thunnus thynnus*) has haplotypes derived from both Pacific bluefin (*Thunnus orientalis*) and albacore (*Thunnus alalunga*; Alvarado Bremer *et al.* 2005). Surveys of multiple nuclear loci have resolved these phenomena in other species and could profitably be applied to *Elops*. Nonetheless, given these genetic results, it is unlikely that we are observing an intraspecific, or population-level, genetic phenomenon, so we reject the hypothesis that *E. smithi* and *E. saurus* are ecophenotypes.

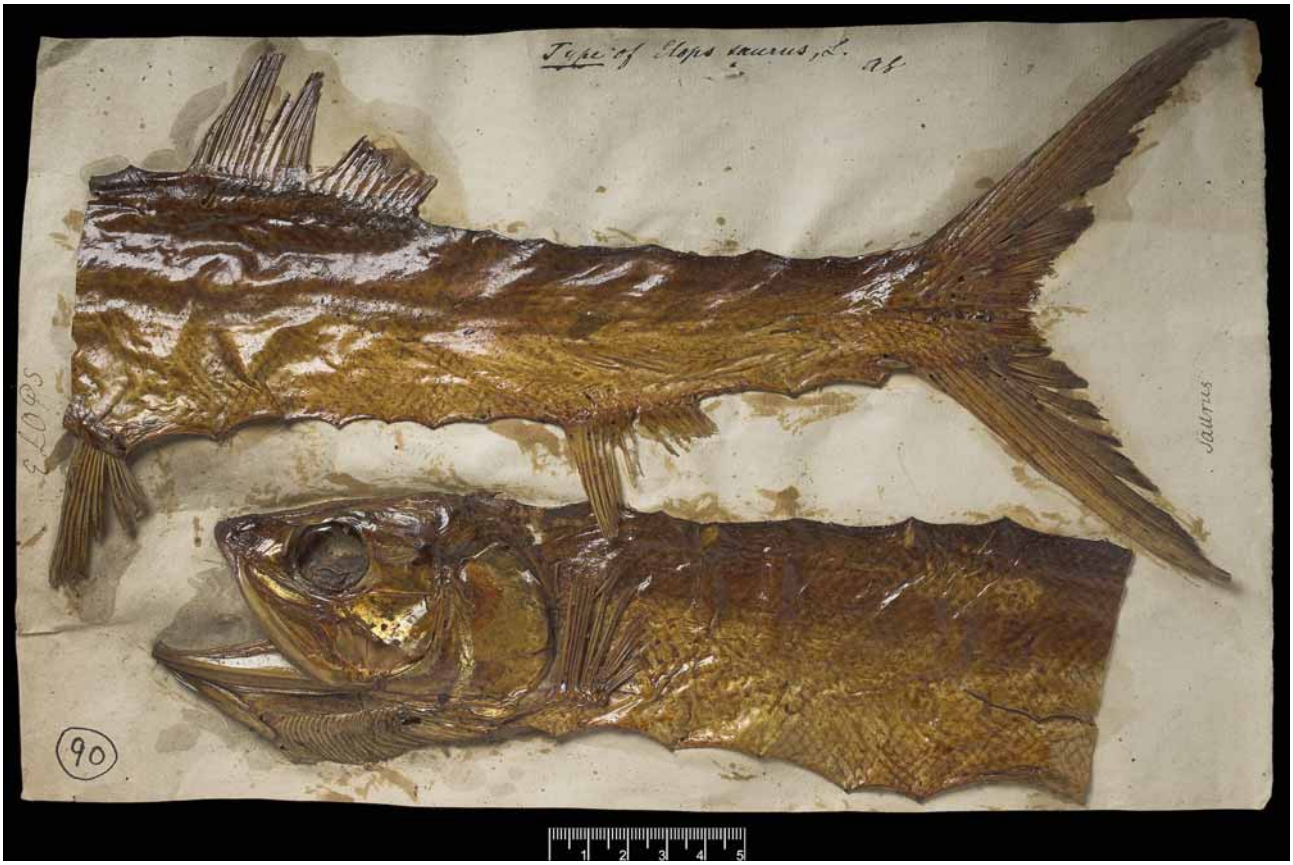

FIGURE 4. Photograph of the lectotype for *Elops saurus* (Linnean Society of London 90 [half-skin, 2 pieces]). See text for discussion of this specimen. The scale bar has increments in mm and is numbered at 1 cm intervals. Photo by P. Hurst (copyright, Natural History Museum [London])

Distribution. *Elops smithi* occurs along the northern coast of South America, in the Caribbean Sea, and throughout the Bahamas; it also occurs sympatrically with *E. saurus* in the Gulf of Mexico and along the eastern seaboard of North America (Smith 1989; see McBride & Horodysky [2004] for distribution maps of larvae, juveniles and adults). In addition, there are two records of *Elops* from Bermuda (Linton 1907) although no resident population has been found there (Smith-Vaniz *et al.* 1999). Only one specimen is available, a 181 mm SL fish (BAMZ 1990-083-037) with 73 vertebrae; this apparently represents a waif from the population inhabiting the Caribbean (Smith-Vaniz *et al.* 1999).

Elops smithi is found in a wide range of salinities. Mature adults and early-life-history stages are found in offshore, marine habitats, where spawning presumably occurs (Gehringer 1959; Santos-Martínez & Arboleda 1993; McBride & Horodysky 2004). Transforming larvae and subadults are found throughout estuaries, as far up as the oligohaline zone, as well as in hypersaline lagoons (Carles 1967; McBride *et al.* 2001; McBride & Horodysky 2004).

Etymology. The specific epithet honors David G. Smith, of the Smithsonian Institution, for his thoroughness in examining leptocephali of *Elops* to reveal that two morphs were present. We recommend the vernacular name Malacho, which is already used for *Elops* in several countries bordering the Caribbean basin.

Discussion

When Linnaeus (1766; p. 518) named *E. saurus*, he examined one specimen and referred to two previously published illustrations, one from Sloane (1725) and the other from Browne (1756). These three specimens are regarded by Eschmeyer and Fong (2008) as syntypes, although only the one directly examined by Linnaeus is surviving. Further complicating this, vertebrae counts were not reported for any of the syntypes, so we cannot reevaluate their taxonomic identity.

The two illustrated but 'lost' syntypes are both from Jamaica. Based on such a collection locality, they were undoubtedly *E. smithi*. However, the description in Sloane is very vague (mostly shape and color), and, to add to the confusion, Linneaus erroneously cites the pages and figure as p. 284 and tab. 251, fig. 1, which appears to be a lizardfish (Synodontidae), instead of p. 282 and tab. 250, fig. 1. The description and illustration in Browne (p. 452, tab. 46, fig. 2) appears to be of a leatherjack (Carangidae). In both cases, Linnaeus may have been referring to species with names resembling the trivial name for *E. saurus* (i.e., *Saurida* or *Oligoplites saurus*). Thus, the correct nomenclature for these lost syntypes is in doubt until each specimen is found and reexamined.

The only specimen Linnaeus (1766) appears to have examined was from "Carolina" (U.S.A.), collected by Garden. This specimen is archived as a dried skin (Hildebrand 1963); it is cataloged as Linnean Society of London 90 (half-skin, 2 pieces) (Table 1; Fig. 4). Vertebral counts were not included by Linnaeus (1766), and vertebrae are lacking from this specimen. Nonetheless, we accept that this specimen is the high-count morph (i.e., *E. saurus*), as postulated by Smith (1989) and Smith and Crabtree (2002). To be specific, *E. smithi* can occur offshore of the Carolina coast but it is rare there. Smith (1989) found both *E. saurus* and *Elops* sp. (= *Elops smithi*) in waters offshore of Virginia, just north of the Carolinas, but 98% of the larvae he examined were *E. saurus*. McBride and Horodysky (2004) also report that *Elops* offshore of the Carolinas and farther north were overwhelmingly *E. saurus*. Therefore, we designate Linnean Society of London 90 (half-skin, 2 pieces) as the lectotype for *E. saurus*.

It is not surprising that the taxonomy of the genus *Elops* has been incompletely understood, despite several reviews of the genus dating back to Regan (1909), given the overall morphological similarity of the various species. Ladyfishes belong to the taxonomic subdivision Elopomorpha, a group of ancient teleost lineages united primarily by the leptocephalus larvae (Nelson 2006). Morphological conservatism is a common feature within these basal lineages, most notably in bonefishes and eels. Bonefishes (Family Albulidae, genus *Albula*) were classified until recently as two or three species, but now appear to include at least ten species (Bowen *et al.* 2007; Hidaka *et al.* 2008). Vertebrae counts of other species of *Elops* may continue to reveal interesting variation because few fish have been examined to date. Many taxonomic studies of *Elops* (e.g., Whitehead 1962) examined less than 20 specimens per species, and at the extreme, the published vertebrae count for *E. senegalensis* is based on a single specimen (Hildebrand 1943). Hence, there may be even more species of *Elops* awaiting discovery.

In terms of possible subpopulation structure, we note much higher mtDNA diversity in *E. smithi* (N = 27; 12 haplotypes) than *E. saurus* (N = 29; 2 haplotypes), despite nearly equal sample sizes. Intraspecific genetic diversity is a function of many factors including mutation rate, natural selection, and fluctuations in abundance, but in stable conditions is primarily influenced by population size, with larger populations having higher genetic diversity (Kimura 1983). Given the large geographic ranges of both species, it is not immediately clear to us that *E. smithi* should be more numerous or have higher diversity. Perhaps the distribution of *E. saurus* in higher latitudes has resulted in population crashes in response to glacial cycles, with corresponding loss of genetic diversity (Lecomte *et al.* 2004). Additional genetic analyses, including nuclear DNA loci, would be informative to resolve the demographic history of both species.

The mtDNA data presented here were only meant to test whether the morphological differences were accompanied by genetic separations, but the results are suggestive of phylogeographic or phylogenetic relationships among species of *Elops*. For phylogeographic analysis, we would need to survey specimens from throughout the ranges of both species. Phylogenetically, Obermiller and Pfeiler (2003) identify *E. saurus* and *E. smithi* (designated *Elops* sp. in their paper) as separate species because the distance between these taxa in corresponding mtDNA sequences ($d = 0.021$) is equivalent to or higher than the distance between either *E. saurus* or *E. smithi* and two congeners in the Pacific, *E. affinis* or *E. hawaiensis* ($d = 0.010 – 0.024$). If this observation holds (the eastern Atlantic *E. senegalensis* and *E. lacerta* are not yet included in phylogenetic surveys), then speciation within the *E. saurus-E. smithi* complex may be another example of evolutionary divergence without strong vicariant barriers (parapatry). The distribution of these two species is similar to that of the wrasse *Halichoeres bivittatus*, which contains two evolutionary lineages corresponding to subtropical and tropical habitats (Rocha *et al.* 2005). The larvae of the tropical form drift into subtropical habitats, but they fare poorly there, and most do not survive to reproduce (L.A. Rocha, pers. comm.). Likewise, McBride and Horodysky (2004) found that larval cohorts of the tropical *Elops smithi* regularly enter the waters of continental North America but fare poorly there, nearly disappearing over 1–2 years. In the case of *E. saurus* and *E. smithi*, ecological specialization in tropical and subtropical habitats may be a foundation for speciation.

Acknowledgements

We greatly appreciate the encouragement of D. G. Smith, of the Smithsonian Institution's Division of Fishes, to pursue this research. Florida specimens were generously contributed by D. Adams, R. McMichael, J. Whittington, and other field biologists at the Florida Fish and Wildlife Conservation Commission (FWC). Material used was borrowed from: the FWC-Fish and Wildlife Research Institute's collections (FSBC); the Florida Museum of Natural History (UF); and the Gulf Coast Research Laboratory Museum (GCRL). R. E. Matheson, D. G. Smith, and W. Eschmeyer provided taxonomic advice. J. Maclaine assisted with Fig. 4. A. Horodysky, F. Stengard, A. Bass and S. Karl provided logistic support. R. E. Matheson, L. Rocha, and D. G. Smith provided valuable comments on a previous manuscript. Genetic studies were supported by grants from the National Science Foundation (DEB-9727048 and OCE-0453167). We thank all of the above.

References

Alvarado Bremer, J.R., Viñas, J., Mejuto, J., Ely, B. & Pla, C. (2005) Comparative phylogeography of bluefin tuna and swordfish: the combined effects of vicariance, secondary contact, introgression, and population expansion on the regional phylogenies of two highly migratory pelagic fishes. *Molecular Phylogenetics and Evolution*, 36, 169–187.

Amos, B. & Hoelzel, A.R. (1991) Long-term preservation of whale skin for DNA analysis. *Report of the International Whaling Commission* 13, 99–103.

Bertin, L. (1944) La distribution mésogéenne des *Elops*. *Compte Rendu Sommaire des Seances. Societe de Biogeographie, Paris*, 21, 17–23.

Bowen, B.W., Karl, S.A. & Pfeiler, E. (2007) Resolving evolutionary lineages and taxonomy of bonefishes (*Albula* spp.). *In*: Ault, J.S. (Eds.), *Biology and Management of the World Tarpon and Bonefish Fisheries*. CRC Press, Boca Raton, FL USA, pp. 147–154.

Bowen, B.W., Muss, A., Rocha, L.A. & Grant, W.S. (2006) Shallow mtDNA coalescence in Atlantic pygmy angelfishes (genus *Centropyge*) indicates a recent invasion from the Indian Ocean. *Journal of Heredity*, 97, 1–12.

Browne, P. (1756) The Civil and Natural History of Jamaica. Selbstverl., London. Available from http://www.botanicus.org/title/b12073179 (accessed 30 April 2009)

Campton, D.E., Bass, A.L., Chapman, F.A. & Bowen, B.W. (2000) Genetic distinction of pallid, shovelnose, and Alabama sturgeon: emerging species and the US endangered species act. *Conservation Genetics*, 1, 17–32.

Carles, C.A. (1967) Datos sobre la biología del banano *Elops saurus* Linnaeus (Teleostomi: Elopidae). *Instituto Nacional De La Pesca Cuba, Contribución* No. 27, 1–53.

Eldred, B. & Lyons, W.G. (1966) Larval ladyfish, *Elops saurus* Linnaeus 1766, (Elopidae) in Florida and adjacent waters. *Florida Department of Natural Resources, Marine Research Laboratory, Leaflet Series*, IV, Part 1, No. 2,

unpaginated.
Eschmeyer, W.N. & Fong, J.D. (2008) Species by Family/subfamily in the Catalog of Fishes. Available from http://research.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp (accessed 30 April 2009)
Fowler, H.W. (1931) Fishes obtained by the Barber Asphalt Company in Trinidad and Venezuela in 1930. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 83, 391–410.
Gehringer, J.W. (1959) Early development and metamorphosis of the ten-pounder *Elops saurus* Linnaeus. *Fishery Bulletin, U. S.*, 59, 618–647.
Hidaka, K., Iwatsuki, Y. & Randall, J.E. (2008) A review of the Indo-Pacific bonefishes of the *Albula argentea* complex, with a description of a new species. *Ichthyological Research*, 55, 53–64.
Hildebrand, S.F. (1943) Notes on the affinity, anatomy, and development of *Elops saurus* Linnaeus. *Journal of the Washington Academy of Sciences*, 33, 90–94.
Hildebrand, S.F. (1963) Family Elopidae. *Memoir Sears Foundation for Marine Research Number I. Fishes of the Western North Atlantic. Part Three.* Sears Foundation for Marine Research, Yale Univ., New Haven, pp. 111–131.
Hubbs, C.L. & Lagler, K.F. (1947) Fishes of the Great Lakes Region. Cranbrook Institute of Science, Bloomfield Hills, Michigan, 186 pp.
Jordan, D.S. (1891) Relations of temperature to vertebrae among fishes. *Proceedings of the United States National Museum*, 14, 107–120.
Kimura, M. (1980) A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16, 111–120.
Kimura, M. (1983) The Neutral Theory of Molecular Evolution. Cambridge University Press, Cambridge.
Lecomte, F.L., Grant, W.S., Dodson, J.J., Rodriguez-Sanchez, R. & Bowen, B.W. (2004) Living with uncertainty: genetic imprints of climate shifts in East Pacific anchovy (*Engraulis mordax*) and sardine (*Sardinops sagax*). *Molecular Ecology*, 13, 2169–2182.
Linnaeus, C. (1766) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I, [Regnum animale]. [Pars I]. Holmiae: Impensis Direct. Laurentii Salvii. Available from http://gallica.bnf.fr/ark:/12148/bpt6k99004c.r=Systema+naturae.langEN (accessed 30 April 2009)
Linton, E. (1907) Notes on parasites of Bermuda fishes. *Proceedings of the United States National Museum*, 33, 85–126.
McBride, R.S. & Horodysky, A.Z. (2004) Mechanisms maintaining sympatric distributions of two ladyfish (Elopidae: *Elops*) morphs in the Gulf of Mexico and western North Atlantic Ocean. *Limnology and Oceanography*, 49, 1173–1181.
McBride, R.S., MacDonald, T.C., Matheson, R.E., Rydene, D.A. & Hood, P.B. (2001) Nursery habitats for ladyfish, *Elops saurus*, along salinity gradients in two Florida estuaries. *Fishery Bulletin, U. S.*, 99, 443–458.
McDowall, R.M. (2008) Jordan's and other ecogeographical rules, and the vertebral number in fishes. *Journal of Biogeography*, 35, 501–508.
Miller, G.L. & Jorgenson, S.C. (1973) Meristic characters of some marine fishes of the Western Atlantic Ocean. *Fishery Bulletin, U. S.*, 71, 301–312.
Nelson, J.S. (2006) Fishes of the World (4th Edition). John Wiley & Sons, New York, 601 pp.
Obermiller, L.E. & Pfeiler, E. (2003) Phylogenetic relationships of elopomorph fishes inferred from mitochondrial ribosomal DNA sequences. *Molecular Phylogenetics and Evolution* 26, 202–214.
Regan, C.T. (1909) A revision of the fishes of the genus *Elops*. *Annals and Magazine of Natural History Series 8* 3, 37–40.
Rocha, L.A., Craig, M.T. & Bowen, B.W. (2007) Phylogeography and the conservation of coral reef fishes. *Coral Reefs*, 26, 501–512.
Rocha, L.A., Robertson, D.R., Roman, J. & Bowen, B.W. (2005) Ecological speciation in tropical reef fishes. *Proceedings of the Royal Society of London Series B*, 272, 573–579.
Saiki, R.K., Scharf, S., Faloona, F., Mullis, K.B., Horn, G.T., Ehrlich, H.A. & Arnheim, N. (1985) Enzymatic amplification of beta-globin genomic sequences and restriction site analysis for diagnosis of sickle-cell anemia. *Science*, 230, 1350–1354.
Santos-Martínez, A. & Arboleda, S. (1993) Aspectos biológicos y ecológicos del macabí *Elops saurus* Linnaeus (Pisces: Elopidae) en la Cienaga Grande de Santa Marta y costa adyacente, Caribe Colombiano. *Anales del Instituto de Investigaciones Marinas de Punta de Betín*, 22, 77–96.
Slatkin, M. (1987) Gene flow and the geographic structure of natural populations. *Science*, 236, 787–792.
Sloane, H. (1725) Voyage to the Islands Madera, Barbados, Nieves, S. Christophers and Jamaica with the Natural History of the Herbs and Trees, Four-footed Beasts, Fishes, Birds, Insects, Reptiles & c. of the Last of Those Islands. Vol. II. Benjamin Motte, London. Available from http://www.botanicus.org/title/b12082429 (accessed 30 April 2009)
Smith, D.G. (1989) Order Elopiformes; Families Elopidae, Megalopidae, and Albulidae: Leptocephali. *Memoir Sears Foundation for Marine Research. Number I. Fishes of the Western North Atlantic. Part Nine. Volume Two*. Sears Foundation for Marine Research, Yale Univ., New Haven, pp. 961–972.

Smith, D.G. & Crabtree, R. (2002) Order Elopiformes, Elopidae, Tenpounders (ladyfishes). *In*: Carpenter, K.E. (Ed.), *The Living Marine Resources of the Western Central Atlantic. Volume 2: bony fishes part 1 (Acipenseridae to Grammatidae). FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5*. Food & Agricultural Organization, Rome, pp. 679–680.

Smith-Vaniz, W.F., Collette, B.B. & Luckhurst, B.E. (1999) Fishes of Bermuda: History, Zoogeography, Annotated checklist, and Identification Keys. *American Society of Ichthyologists and Herpetologists Special Publication No. 4*. American Society of Ichthyologists and Herpetologists, 424 pp.

Song, C.B., Near, T.J. & Page, L.M. (1998) Phylogenetic relations among percid fishes as inferred from mitochondrial cytochrome b DNA sequence data. *Molecular Phylogenetics and Evolution*, 10, 343–-353.

Taberlet, P., Meyer, A. & Bouvet, J. (1992) Unusually large mitochondrial variation in populations of the blue tit, *Parus caeruleus*. *Molecular Ecology*, 1, 27–36.

Whitehead, P.J.P. (1962) The species of *Elops* (Pisces: Elopidae). *Annals and Magazine of Natural History Series 13*, 5, 321–329.