



Distribution expansion of a tropical fish species *Elops smithi* (Elopiformes: Elopidae) in the southwestern Atlantic Ocean

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Abstract: Understanding the response of the organisms to climate alterations is one of the central goals of biology and ecology studies. Particularly, ocean warming has profound consequences for the ecosystems globally. Body size, diet shifts, and geographical range distributions alterations (e.g. ocean tropicalization), are the most frequent reported responses. Particularly, the southern portion of the SWA is considered a hotspot of ocean warming and the presence of several tropical species has been reported from this region. In this work we studied the southward range expansion of a tropical fish species *Elops smithi*, which inhabits the western Atlantic Ocean. The species is frequently captured in the tropical and subtropical coast of the southwestern Atlantic Ocean (SWA), where it lives in sympatry with *E. saurus* in part of their distribution. *Elops smithi* is distributed in the north of South America and the whole Caribbean Sea, while *E. saurus* has a northern distribution, in the eastern coast of North America and Gulf of México. We studied the distribution expansion of *E. smithi* in the SWA using data from literature (from 1988 to 2019) and data collected between 2008-2022. We observed an increased frequency of the reports of *E. smithi* at latitudes higher than 33°S from its first record in 2008. We found specimens in a wide range of sizes, from leptocephalus larvae to adults (48 cm in standard length). Specimens were captured in a wide range of environmental conditions, sea surface temperature (11.5-26.8 °C) and salinity (1.5-32 psu), along 350 km of the Uruguayan coast. This suggests that the presence of the species is much more common than only sporadic occurrence associated with specific thermal anomalies. Additionally, we suggest revising the identification of records from *E. saurus* in the SWA, which probably belong to *E. smithi*, which only differ by vertebrae counts. We highlight the need to study the potential interactions of the arrived species with the native fauna, which is considered as an important consequence of climate change.

Key words: Ladyfish, climate change, small-scale fisheries, ocean tropicalization.

Expansión de la distribución de una especie de pez tropical *Elops smithi* (Elopiformes: Elopidae) en el suroeste del Océano Atlántico. Resumen: Comprender las respuestas de los organismos frente a las alteraciones climáticas es una de las metas centrales de los estudios en Biología y Ecología. El calentamiento oceánico en particular tiene profundas consecuencias para

los ecosistemas a escala global. Las respuestas más frecuentemente reportadas refieren a cambios en el tamaño corporal, dieta y rangos de distribución. La porción sur del Atlántico Sudoccidental (ASO) se considera un “punto caliente” en el calentamiento oceánico, y en esa región se ha reportado la presencia de varias especies tropicales. En este trabajo estudiamos la expansión del rango de *Elops smithi*, una especie de pez tropical que habita al Atlántico Occidental. Esta especie es capturada frecuentemente en costas del ASO tropical y subtropical, donde vive en simpatria con *E. saurus* en parte de su rango de distribución. *Elops smithi* se distribuye en el norte de Sudamérica y en la totalidad del Mar Caribe, mientras *E. saurus* tiene una distribución hacia el norte, en la costa Este de Norteamérica y Golfo de México. Estudiamos la expansión en la distribución de *E. smithi* en el ASO usando datos de la literatura (desde 1988 hasta 2019) y datos colectados entre 2008 y 2022. Observamos una frecuencia creciente de reportes de *E. smithi* a latitudes mayores de 33°S desde su primer registro en 2008. Encontramos especímenes en un amplio rango de tamaños, desde larva leptocephalus a adulto (48 cm de longitud estándar). Los especímenes fueron capturados en un amplio rango de condiciones ambientales, temperatura superficial del mar (11.5 – 26.8°C) y salinidad (1.5-32 psu) a lo largo de 350 km de costa uruguaya. Esto sugiere que la presencia de la especie es mucho más común que una cierta ocurrencia esporádica asociada a anomalías térmicas específicas. Además, sugerimos revisar la identificación de registros de *E. saurus* en el ASO, los que probablemente correspondan a *E. smithi*, y de los que sólo difieren en el número de vertebras, Resaltamos la necesidad de estudiar posibles interacciones entre la especie recientemente llegada y la fauna nativa, lo que se considera una consecuencia importante del cambio climático.

Palabras clave: Malacho, cambio climático, pesca en pequeña escala, tropicalización de océanos

Introduction

Disentangling and predicting the effect of global change are among the main concerns of current biology and ecology studies (Mc Carty 2001). Particularly, global warming plays a key role in the distribution of the species, restricting or expanding the range distribution of sensitive and tolerant species, respectively (Parmesan *et al.* 2003, Perry *et al.* 2005, Cheung *et al.* 2009, Sunday *et al.* 2012). Different alternative behaviours developed by the species to cope the climate change have been observed (Bellard *et al.* 2012). Organisms can disperse to suitable regions expanding their range of distribution from areas that are no longer favourable. In this context, latitudinal and altitudinal changes have been reported for more than 1000 species in terrestrial and aquatic ecosystems (Parmesan 2006). In marine ecosystems, climate change affects the latitudinal gradient of biodiversity at a global scale (Chaudhary *et al.* 2021, Sydeman *et al.* 2021). Likewise, tropical oceans have increased their temperature by 1-2 °C over the past 100 years (Hoegh-Guldberg 1999). An increased rate of ocean warming alters, either directly or indirectly, the distribution, abundance, and life history traits of marine species (Poloczanska *et al.* 2016, Pauly & Cheung, 2018). Temperature is the main factor affecting the geographic distribution of fish species; the low and high latitudes geographic ranges of a

fish species may represent the upper and lower thermal tolerances, respectively (Sunday *et al.* 2012, Ninawe *et al.* 2018). According to this, as a response to climate change, marine fish species would change their distributions following their temperature preferences (Perry *et al.* 2005). This was particularly observed in temperate regions of the northern (Graham & Harrod 2009, Osland *et al.* 2021) and southern hemispheres (Cheung *et al.* 2012). However, the response of marine fish species from the South Western Atlantic Ocean (SWA), has being poorly explored (Perry *et al.* 2005). Evidence of climate change, particularly ocean warming in the SWA, have been frequently reported (Ortega *et al.* 2012, Manta *et al.* 2018, Franco *et al.* 2020, 2022, Li *et al.* 2022). In particular, the oceanic region of southern Brazil, Uruguay, and Argentina is considered one of the largest marine warming hotspots worldwide (Hobday & Pecl 2014). In this sense, based on high resolution models, Popova *et al.* (2016) have projected a surface temperature (SST) increase of 3°C of sea to the end of the century.

Ocean warming promote geographical range expansion of tropical and subtropical herbivorous fishes into temperate zones; this increase in fish herbivory may aggravates the reduction of algae (e.g. kelps) reported worldwide (Vergés *et al.* 2014, Vergés *et al.* 2016). A reduction in fish body size is

also expected with ocean warming (Daufresne *et al.* 2009, Ikpewe *et al.* 2021). However, it is difficult to disentangle the effects of climate and overfishing, because both might have a similar response on fish size. Another stressor related to global change are biological invasions, recognized as one of the main causes of homogenization of biota (Sala *et al.* 2000). The interaction between all these factors and others, such as ocean waters circulation changes, may influence the distribution of marine species (Vergés *et al.* 2014, Wilson *et al.* 2016). The expansion of the distribution of tropical marine species has been defined in the context of a phenomenon called “tropicalization” of marine ecosystems (Vergés *et al.* 2016). The occurrence of tropical and sub-tropical species has been locally reported along the temperate SWA coasts (e.g. Segura *et al.* 2009, Barneche *et al.* 2009, Solari *et al.* 2010, Laporta *et al.* 2021).

The ladyfish *Elops* spp. (Elopidae) is a teleost of the series Elopomorpha, an ancient lineage diagnosed primarily by the leptocephalus larvae (Nelson 2016). Seven species are currently recognized for the genus, of which two occur in the Western Atlantic. Smith (1989) originally recognized two morphs for populations of *Elops saurus* and McBride *et al.* (2010) determined one of them as a separate species, named *Elops smithi*. Taxonomy of the group is complex and poorly understood (Nelson *et al.* 2016); both species can be physically distinguished only by vertebrae count (centra) in adults and juveniles and by myomere counts during larvae stages (McBride *et al.* 2010). The Southern Ladyfish, *Elops smithi* (75-78 centra), occurs in the western Atlantic Ocean, from the northern coast of South America to the Caribbean Sea, throughout the Bahamas, and the eastern coast of the United States of America, and southwestern Gulf of Mexico; also it have been reported from Northern Brazil to the Argentinian Patagonia (McBride *et al.* 2010, Lucena & Carvalho Neto 2012, Sousa *et al.* 2019, 2021, Bovcon *et al.* 2022). The Northern Ladyfish *Elops saurus* (79-87 centra) occurs from the Yucatan Peninsula, throughout the Gulf of Mexico and along the eastern coast of North America up to Massachusetts (McBride & Horodysky 2004, McBride *et al.* 2010). Adults inhabit continental shelf waters and are offshore spawners, whereas juveniles are most common in estuarine and adjacent coastal areas (Santos-Martínez & Arboleda 1993, McBride & Horodysky 2004).

The conservation status of *E. smithi* was categorized as data deficient (Adams *et al.* 2014),

who proposed the exploitation of the species, habitat degradation, and water quality deterioration as the main threats and identified the need for information about life history, demographics, and harvest levels (Adams *et al.* 2014). Over the last years, individuals of *E. smithi* have been reported southern to the described species distribution (Lucena & Carvalho Neto 2012, Sousa *et al.* 2019, 2021, Bovcon *et al.* 2022). However, it is not clear if these can be considered sporadic records or the signal of a geographic expansion.

In this context, the aim of this work was to study the distribution expansion of *E. smithi* in the SWA from an ecological perspective including a review of published records of the species in the region, as well as new records documented during the present study. Additionally, we analysed a time series of the SST during the study period. We hypothesize that ocean warming is the driver for the geographic range expansion of *E. smithi* and the increased records in their southernmost distribution.

Materials and methods

Study site and data collection: The study area included the southwestern Atlantic Ocean (from 0° to 45° S) (Fig. 1). Several sources of information were used to study the spatial-temporal variation in the distribution expansion of *E. smithi*. We used specimens and data collected by the Small Scale Fisheries Monitoring Programs conducted by the Dirección Nacional de Recursos Acuáticos (DINARA, MGAP) in the Uruguayan Atlantic coast and in the coastal brackish lagoons (Santana & Fabiano 1999, Laporta *et al.* 2018). We additionally included individuals deposited the Fish Collection of Facultad de Ciencias (Universidad de la República, Uruguay; Institutional code ZVCP) and in the Montevideo Natural History Museum (Institutional code MHNM).

Additionally, a literature review was performed using “*Elops*” and “ladyfish” as keywords in Google Scholar. All the records containing *Elops* spp. information were included in the analysis. The obtained information was included in a map of occurrence of *Elops* (Fig.1), using QGIS software. Finally, specimens collected by artisanal fishermen that operate from Montevideo (Uruguay) with bottom gill nets were also considered.

Morphometric and meristic counts: Vertebral counts of 13 specimens were done from X-radiographs of individuals preserved in collections, and from filleted and scraped carcasses of fresh individuals. Vertebrae were counted from the first centrum next

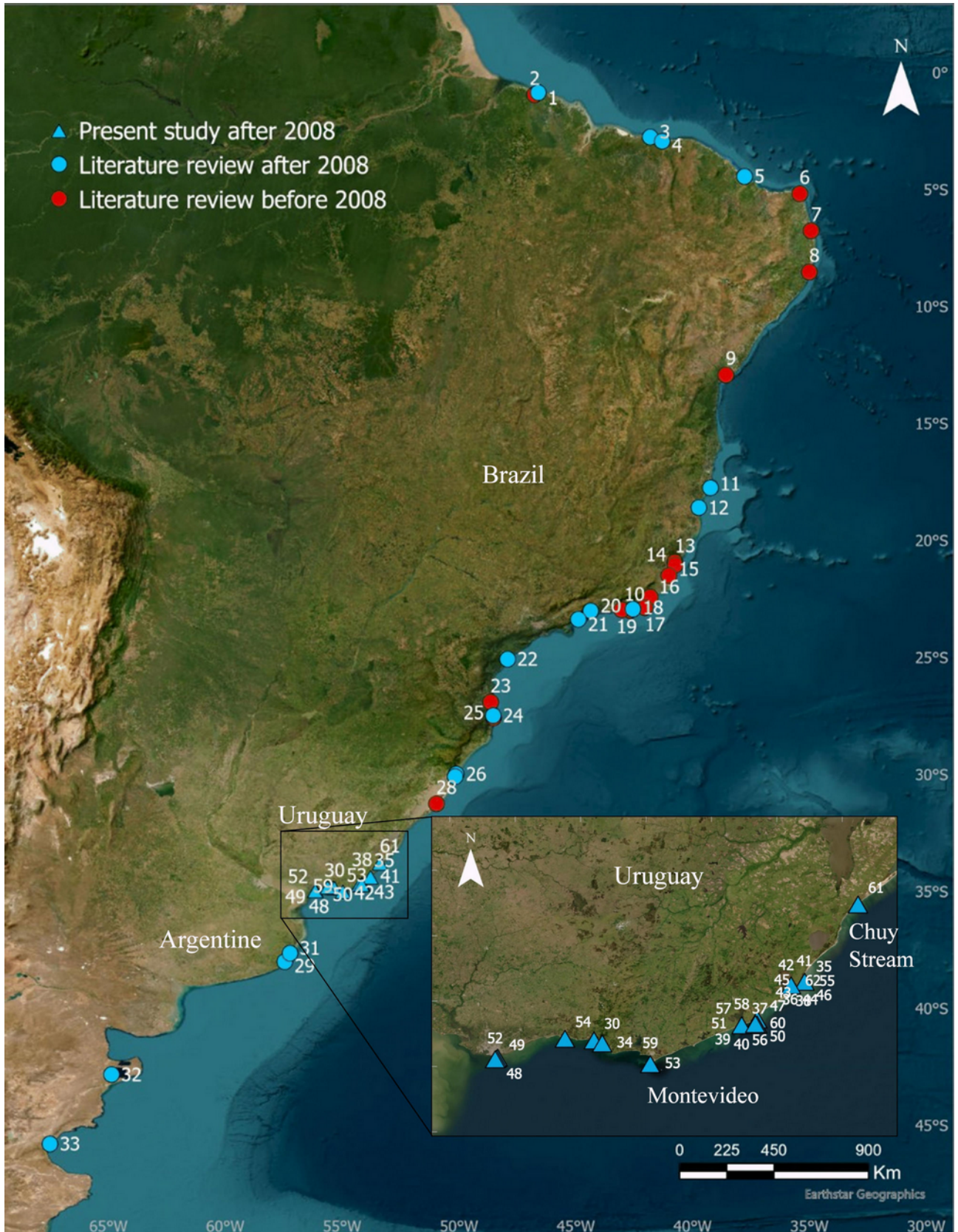


Figure 1. Map including the records from literature used in the literature review (circles) and for the data collected during the present study (triangles). Data collected before 2008 were presented in red and after this year in light blue. Numbers correspond to the references in Table 1.

to the cranium to terminal of the first centrum next to the cranium to terminal of the vertebral column, following McBride *et al.* (2010) (see Supporting information, Fig S2). For a subsample of 15 individuals, morphometrics measures and meristic counts were done following McBride *et al.* (2010). Measurements and counts includes: Dorsal fin rays (D), Anal fin rays (A), Pectoral fin rays (P1), Pelvic fin rays (P2), Lower gill rakers (GR l), Upper gill rakers (GR u), Lateral line scales (LL), Branchiostegal rays (B), Standard length (SL), Fork length (FL), Total length (TL), Head length (HL), Orbital diameter (OD), Lower jaw length (LJL), Head width at gills (HWG). We analysed the length-weight relationship using the individuals from this work, in order to determine the growth type of the species and to compare with published data.

Environmental variables: Sea surface temperature and salinity data were collected *in situ* for most of the catch events using a portable YSI EcoSense EC300-A in the context of the Environmental Variables Programme carried out by DINARA (Santana & Fabiano 1999, Santana *et al.* 2022). When data was not possible to be collected, we used punctual satellite SST for each day of collection from the NOAA ERDDAP online repository for the study duration period (<https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST41.html> - accessed on 28 November 2022).

Results

Records of present study and from literature: Data were obtained from scientific literature and field

collections for 63 *Elops* spp. (Fig 1, Table 1). Publications prior to 2010 did not differentiate between the two *Elops* species. We recorded a total of 39 individuals in approximately 350 km of the Uruguayan coast, from Montevideo (Río de la Plata Estuary) to the estuary of the Chuy river (Atlantic Ocean coast) from 2008 to 2022 (Fig. 1, Table 1). The records from Uruguay were confirmed as *E. smithi* based on vertebrae counts (Fig. 2).

We reported an increased frequency of the records of the species in higher latitudes of SWA after 2008. We found the presence of specimens in a wide range of sizes, from leptocephalus larvae of 5.1 cm to specimens of 48 cm SL, indicating the presence of adults and juveniles. Individuals were collected in a variety of environments: ocean, estuaries, and brackish coastal lagoons (Table 1). In the literature review we found a total of 31 articles containing information about catches of *Elops* spp. in the SWA along a latitudinal gradient from 0°51'S to 45°47'S from northern Brazil to Argentina between 1988 and 2019 (Table 1). When we merged data collected in the literature review and data collected during this work, we found a pattern with the position (latitude) and the year of each record (Fig 3). The records at lower latitudes (<31° S) were found in a wide range of time (from 1988-2018); however, records at higher latitudes (>33° S) were found in a narrower range of years (2008-2022) (Fig 3). In this context, it is important to highlight the lack of Elopiformes in classical systematic lists of fish species for the region such as Menni *et al.* (1984) and Nion *et al.* (2002).



Figure 2. X-Radiograph (upper panel) and fresh specimen (lower panel) of the Southern Ladyfish *Elops smithi* (ZVCP 15423) captured in 2020 in Arroyo Chuy, Rocha, Uruguay. Photograph: Javier Duarte.

Table 1. Information about the records used in the literature review and for the data collected during this study, including date and species, position (latitude and longitude), size range and average \pm standard deviation of standard-length SL or total length TL (cm) and abundance (number of individuals), habitat, references, temperature ($^{\circ}$ C) and salinity when available. Note that the literature review data were ordered starting by low latitude, while the data collected during this study were ordered by date of capture.

N ^o	Species	Date	Latitude	Longitude	Size (abundance)	Env	Reference	SST	Sal
1	<i>E. smithi</i>	2018	0°51'34.34"S	46°36'24.31"W		O	Sousa et al., 2021	na	na
2	<i>E. smithi</i>	2007-2008	0°56'47.10"S	46°45'25.20"W		O/E	Sousa et al., 2019	na	na
3	<i>E. saurus</i>	2016-2017	2°44'57.21"S	41°49'1.03"W	12.9-30.5 TL	E	Santos et a., 2020	na	na
4	<i>E. saurus</i>	2014-2015	2°55'42.00"S	41°18'26.15"W	136,6 (5)		de Mello et al., 2021	na	na
5	<i>E. saurus</i>	2015	4°26'1.85"S	37°46'30.99"W	25 \pm 2		Moura et al., 2018	na	na
6	<i>E. saurus</i>	2003-2013	5°11'12.12"S	35°24'53.98"W		O	Júnior et al., 2015	na	na
7	<i>E. saurus</i>	2011-2015	6°45'57.28"S	34°55'37.88"W	17.3 \pm 3.6	E	Medeiros et al., 2016	na	na
8	<i>E. smithi</i>	2011-2012	8°31'13.24"S	35° 0'15.58"W	5,5 - 2 (67)	O	Barboza de Camargo 2013	na	na
9	<i>E. saurus</i>	2003 -2005	12°55'2.12"S	38°34'38.33"W	-	O	Soares, et al., 2011	na	na
10	<i>E. saurus</i>	1993-2001	13° to 23°S		16.2-36.3 (16)	O	Frota et al., 2004	na	na
11	<i>E. saurus</i>	2008-2009	17°45'7.73"S	39°14'29.98"W	462.5 \pm 14.4 (3)	E	Giglio and Freitas 2013	na	na
12	<i>E. smithi</i>	2012-2013	18°35'44.07"S	39°44'8.56"W	30-32	E	Bolzán 2014	na	na
13	<i>E. saurus</i>	2003-2004	20°55'30.34"S	40°45'18.71"W	-	O	Pinheiro et al., 2015	na	na
14	<i>E. saurus</i>	1996-1998	21° 2'34.27"S	40°44'30.33"W	1.85 kg	O	Godoy et al., 2002	na	na
15	<i>E. saurus</i>	1996-2017	21°30'20.68"S	41°1'12.73"W			Lima et al., 2021	na	na
16	<i>E. smithi</i>	1993-2001	22°24'56.51"S	41°49'7.42"W	29.6 \pm 5.6 (91)	O	Sánchez et al., 2018	na	na
17	<i>E. saurus</i>	1994	22°52'12.10"S	42° 2'32.25"W			Saad, 2003	na	na
18	<i>E. saurus</i>	2011	22°55'41.83"S	42°32'46.58"W	3.6–16.0 (117)		Franco et al., 2014	na	na
19	<i>E. saurus</i>	2006	22°57'49.04"S	43° 2'29.04"W		E	Fortes et al., 2014	na	na
20	<i>E. saurus</i>	2014-2015	23°0'5.355''S	44°21'17.628''W	28 – 49 (50) TL		Celestino and Alves 2016	na	na
21	<i>E. sp</i>	2014-2016	23°21'38.55"S	44°53'18.69"W		O	Fernandes 2016	na	na
22	<i>E. saurus</i>	2009-2010	25° 3'46.94"S	47°54'49.62"W	Larvae	O	del Favero and Dias 2013	na	na
23	<i>E. saurus</i>	2000-2005	26°54'46.93"S	48°38'42.64"W		E	Branco et al., 2011	na	na
24	<i>E. saurus</i>	2010-2011	27°28'32.99"S	48°32'0.61"W			Ribeiro et al., 2014	na	na
25	<i>E. saurus</i>	1988	27°34'23.10"S	48°31'5.73"W	173-208	E	Cattani et al., 2020	na	na
26	<i>E. saurus</i>	2014-2015	29°58'35.91"S	50° 7'14.51"W		E	Santos et a., 2018	na	na
27	<i>E. smithi</i>	2010	30°05'12"S	50° 09'50"W	Larvae	O	de Lucena, 2012	na	na
28	<i>E. saurus</i>	2001	31°14'59.08"S	50°57'56.05"W		E	Loebmann et al. 2005	na	na
29	<i>E. saurus</i>	2011	37°59'25.56"S	57°27'31.49"W	40 (1) TL	O	Milessi et al., 2012	na	na
30	<i>E. smithi</i>	2010	34°47'29.17"S	55°23'55.42"W	Larvae	E	Machado et al., 2012	na	na
31	<i>E. smithi</i>	2019	37°38'S	57°14'W	39.2-65.0 (3) TL	O	Bovcon et al., 2022	na	na
32	<i>E. smithi</i>	2019	42°49'S	64°52'W	39.2-65.0 (3) TL	O	Bovcon et al., 2022	na	na
33	<i>E. smithi</i>	2013	45°47'S	67°30'W	39.2-65.0 (3) TL	O	Bovcon et al., 2022	na	na
34	<i>E. smithi</i>	1/3/2008	34°48'50.98"S	55°20'7.60"W	36.9	E	This study	20.8	na
35	<i>E. smithi</i>	16/12/2008	34°20'35.76"S	53°47'18.15"W	Larvae 5.1	E	This study	23.0	32.0
36	<i>E. smithi</i>	16/12/2008	34°20'35.76"S	53°47'18.15"W	Larvae 5.3	E	This study	23.0	32.0
37	<i>E. smithi</i>	21/6/2010	34°40'31.17"S	54°16'9.46"W	43	E	This study	13.1	6.4
38	<i>E. smithi</i>	21/2/2011	34°20'35.76"S	53°47'18.15"W	7.32	E	This study	26.8	31.6
39	<i>E. smithi</i>	21/4/2014	34°40'31.17"S	54°16'9.46"W	31.4	E	This study	15.5	13.9
40	<i>E. smithi</i>	17/6/2014	34°40'31.17"S	54°16'9.46"W	31.2	E	This study	11.5	12.4
41	<i>E. smithi</i>	11/3/2015	34°20'35.76"S	53°47'18.15"W	*21	E	This study	25.3	1.5
42	<i>E. smithi</i>	20/3/2015	34°20'35.76"S	53°47'18.15"W		E	This study	24.2	2.7
43	<i>E. smithi</i>	9/4/2015	34°20'35.76"S	53°47'18.15"W	20.5	E	This study	22.5	9.2
44	<i>E. smithi</i>	9/4/2015	34°20'35.76"S	53°47'18.15"W	19.5	E	This study	22.5	9.2
45	<i>E. smithi</i>	28/4/2015	34°20'35.76"S	53°47'18.15"W	20.2	E	This study	18.8	16.1
46	<i>E. smithi</i>	28/4/2015	34°20'35.76"S	53°47'18.15"W	16.5	E	This study	18.8	16.1
47	<i>E. smithi</i>	9/8/2015	34°37'53.48"S	54° 9'0.77"W	47.0	O	This study	16.5	31.3
48	<i>E. smithi</i>	18/8/2015	34°55'22.59"S	56° 8'6.65"W	(1)	E	This study	13.9	na
49	<i>E. smithi</i>	26/8/2015	34°55'51.69"S	56° 8'37.64"W	(4)	E	This study	14.0	na
50	<i>E. smithi</i>	31/3/2016	34°40'12.41"S	54° 9'3.95"W	38.9	O	This study	21.0	20.6
51	<i>E. smithi</i>	13/5/2016	34°40'31.17"S	54°16'9.46"W	50.0	E	This study	13.0	8.8
52	<i>E. smithi</i>	23/8/2016	34°56'9.57"S	56° 9'14.10"W	(9)	E	This study	12.6	na
53	<i>E. smithi</i>	26/8/2017	34°58'21.16"S	54°58'5.56"W	*34	O	This study	15.6	na
54	<i>E. smithi</i>	19/10/2017	34°46'44.16"S	55°37'12.70"W		E	This study	17.5	na
55	<i>E. smithi</i>	21/4/2018	34°20'35.76"S	53°47'18.15"W		E	This study	22.1	9.7
56	<i>E. smithi</i>	3/5/2018	34°40'31.17"S	54°16'9.46"W	56.0	E	This study	19.1	17.0

57	<i>E. smithi</i>	4/5/2018	34°40'31.17"S	54°16'9.46"W	*48	E	This study	19.1	17.0
58	<i>E. smithi</i>	4/5/2018	34°40'31.17"S	54°16'9.46"W	*45	E	This study	19.1	17.0
59	<i>E. smithi</i>	30/3/2019	34°58'21.16"S	54°58'5.56"W	*40	O	This study	20.6	na
60	<i>E. smithi</i>	6/6/2019	34°39'58.06"S	54°9'53.95"W	*27	O	This study	16.0	28.1
61	<i>E. smithi</i>	1/11/2020	33°45'7.74"S	53°22'47.49"W	31	E	This study	20.2	29.5
62	<i>E. smithi</i>	24/2/2022	34°22'14.36"S	53°53'30.66"W	14 StL	E	This study	22	3.6
63	<i>E. smithi</i>	16/3/2022	34°22'14.36"S	53°53'30.66"W	18 TL	E	This study	25	10.5

N°: number of individuals; na; data not available; Env: environment, O: ocean, E: estuary; SST: sea surface temperature (°C) (in bold data from satellite); Sal: salinity (psu).

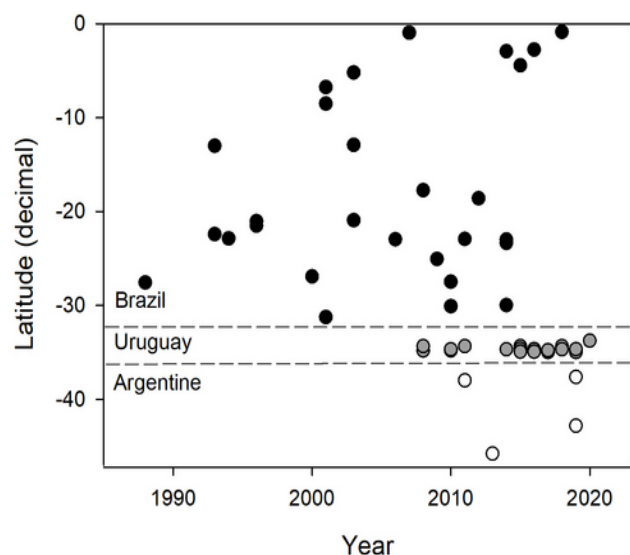


Figure 3. Relationship between latitude in decimal and year of collection including all the records from Brazil (black dots, 28 records), Uruguay (grey dots, 31 records) and Argentina (white dots, 4 records), dotted lines represent an approximation of the geographic limit of the countries.

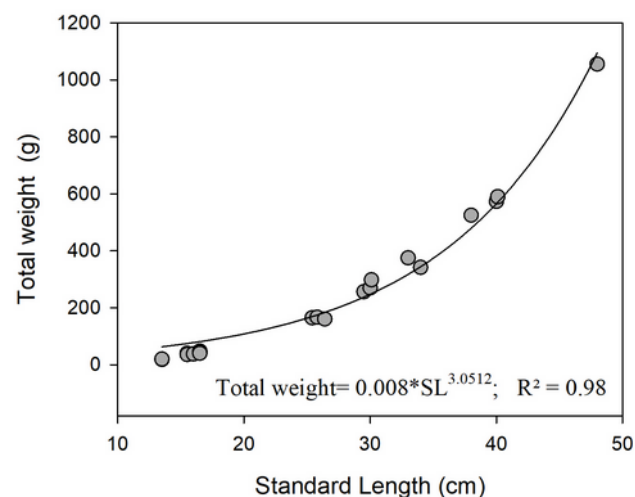


Figure 4. Standard length (cm) vs total weight (g) relationship of the Southern Ladyfish *Elops smithi* including adults and juveniles (22 individuals) captured in the Uruguayan coast of the Atlantic Ocean and in the Río de la Plata estuary.

The length weight relationship including juveniles and adults captured during this study showed a positive allometric growth (Fig. 4) (Total weight = $0.008 * (\text{Standard length})^{3.05}$; $R^2 = 0.99$; $p < 0.001$, mean SL: 26.5 ± 10.7 , range: 13.5 – 48 cm, n: 22). The individual meristic, morphometric measures, and vertebrae count from X-ray images are shown in Table 2. X-ray images and pictures of the collected specimens are presented in Appendix 1 and 2. Specimens captured during this work were observed in a wide range of environmental conditions, SST (11.5-26.8 °C) and salinity (1.5-32 psu) along 350 km of the Uruguayan coast (Table 1).

Discussion

Based on the results from published records in the literature and individuals collected during this study, we reported the southward expansion of the distribution of *Elops smithi* in the SWA. We found a latitudinal trend of the records (Fig. 3), within a wide range of years (1988- 2018) at low latitudes (Atlantic coasts of Brazil); while, for latitudes higher than 34° S (Atlantic coasts of Uruguay and Argentina) the records of the species were reported only after 2008. *Elops smithi* typically has a tropical distribution being abundant in warm waters in latitudes below 31° S (see Table 1 and references therein). However, in recent years the reports of this species became more frequent in the Atlantic coasts of Uruguay and Argentina with several individuals reported (Fig. 1, Table 1). The southernmost record was recently reported in three locations of the Argentinean coast (Bovcon *et al.* 2022).

The absence of physical barriers in the oceans determines that the distribution of the species is affected by their preferences for environmental conditions (Vergés *et al.* 2014). The increase of water temperature in temperate regions determine a reduction of an environmental filter for tropical and subtropical fish species, increasing the presence of these species in higher latitudes (Barneche *et al.* 2009). This represents a contribution to understanding the response of marine fish species from SWA to ocean warming (Perry *et al.* 2005).

Table 2. Selected meristic characters and morphometric measurements (mm) for the voucher specimens of *Elops smithi* proposed by McBride *et al.* 2010. Abbreviations of characters: Vert. (number of vertebrae), D (Dorsal fin rays), A (Anal fin rays), (t) total and (p) principal, P1 (pectoral fin rays), P2 (pelvic fin rays), GR (gillrakers), (l) lower or (u) upper, LL (lateral line scales), B (branchiostegal rays). SL (standard length), FL (fork length), TL (total length), HL (head length), OD (orbit diameter, LJL (lower jaw length), HWG (head width at gills). No data = nd.

Lot#	Vert	D (t)	D (p)	A (t)	A (p)	P1	P2	GR		LL	B	SL	FL	TL	HL	OD	LJL	HWG
								(l)	(u)									
ZVCP 8601	78	28	20	27	18	17	17	14	9	117	34	30.1	nd	36.9	80.3	14.9	45.7	32.7
ZVCP 15423	76	27	21	16	12	17	12	13	8	116	32	25.4	27	31	61.6	13.4	34.5	24.3
ZVCP 15438	76	29	24	21	14	17	14	16	10	113	31	34	36.3	43.5	81.4	17.5	51.7	32.2
ZVCP 15438	75	28	24	22	15	17	14	14	8	115	34	29.5	32	38	72.5	14.8	43.4	27.7
ZVCP 15438	75	31	23	20	15	16	14	15	8	111	32	33	35.5	41.5	83.0	17.6	49.7	31.7
ZVCP 15438	76	29	25	20	14	17	13	14	8	117	28	25.8	27.8	32	65.5	13.8	37.4	24.9
ZVCP 15439	75	na	23	na	na	16	12	13	8	112	31	32.6	35.5	41	77.1	16.5	46.8	29.6
ZVCP 15439	75	na	23	na	14	16	14	15	8	116	30	32.4	35	41.5	78.2	17.1	47.6	29
-	na	29	23	19	14	18	14	14	8	114	29	40.1	43.6	50.1	93.7	20.1	56.2	37.2
-	na	33	22	18	15	17	13	14	8	109	29	38	40.3	47	85.9	19.2	53.4	36.9
MHNM 4651	77	27	23	na	14	16	14	8	15	117	32	16	17	19.5	40.2	7.7	24.1	14.6
MHNM 4652	76	26	23	na	15	18	14	8	14	115	30	16.5	18	20.5	41	9.5	25.8	16.6
MHNM 4653	76	26	22	18	15	15	13	8	14	110	29	15.5	16.5	19.5	42.1	8.6	25.0	15.9
MHNM 4653	76	na	20	na	13	17	14	7	14	112	29	16.5	17	20.2	42.1	8.3	24.0	16
MHNM 4654	77	na	21	na	13	16	15	8	15	114	31	13.5	14	16.5	39.9	7.3	11.6	12.3

ZVCP: Zoología de Vertebrados Colección de Peces; MHNM: Museo Nacional de Historia Natural, Montevideo; na: data not available.

Ortega and Martínez (2007) reported an increased sea surface temperature for SWA, which was recently confirmed by Ortega *et al.* (2012, 2016). These data support the hypothesis that the Río de la Plata estuary and the SWA region is a warming hotspot (Hobday & Pecl 2014).

McBride *et al.* (2010) proposed a segregation of the two species, with *E. saurus* restricted to the north and *E. smithi* to the south, based exclusively on vertebrae counts. Consequently, before 2010 all the individuals found in the SWA were reported as *E. saurus*. However, after 2010 most of the studies found in the literature still continued recording as *E. saurus* without vertebrae counts. In this sense, we suggest the need to review the identification of the *Elops* individuals in the SWA, due to the difficulty to separate both species using external characteristics. Meristic and vertebrae count are typically negatively affected by temperature during development (Lindsey and Arnason, 1981; Ramler *et al.* 2014). Thus, a latitudinal pattern is expected for this variable with higher counts at higher latitude. However, in the case of *E. smithi* in the SWA the opposite pattern was observed, with lower counts in the colder south.

Sousa *et al.* (2019; 2021) recorded *Elops smithi* for northern Brazil. The authors presented evidence based on myomere counts from larvae and molecular analysis, and suggested that this species has been reported incorrectly as *Elops saurus* in the SWA. We agree with this idea and suggest that the

records of *Elops saurus* south to the Caribbean Sea should be revised, as, for example, the record by Milessi *et al.* (2012) (37°59'S; 57°27'W). The southernmost record of *E. smithi*, identified based on vertebrae counts, was recently reported (45°47'S; 67°30'W) by Bovcon *et al.* (2022). However, the identifications of most of the records included in this literature review were based on external characteristic which is not conclusive to separate both species.

We found a positive allometric relation for *E. smithi* as previously observed for *Elops* in central and south Brazil (Frota 2004, Franco *et al.* 2014).

The Río de la Plata estuary is influenced by the convergence of the warm Brazilian and the cold Malvinas currents (Combes & Matano 2014, Piola *et al.* 2018). In accordance, the occurrences of tropical and sub-tropical species were previously reported in this region (e.g. Segura *et al.* 2009, Solari *et al.* 2010, Laporta *et al.* 2021, 2024). Temperature anomalies produced by warm circulation events had been suggested to explain the occurrence of tropical fish species in this area. Recently, a subtropical fish (*Orthopristis ruber*) was reported at higher latitudes, mainly due to positive SST anomalies in the SWA shelf (Laporta *et al.* 2021). However, the presence of *E. smithi* is recurrent and persistent during the last two decades in the Uruguayan coast. The oldest record for Uruguay was a juvenile captured in 2008. This record could be interpreted as a vagrant individual that appeared at high latitudes due to a

particular temperature anomaly such as in the above-mentioned study. However, during that same year, two leptocephalus larvae were collected in Arroyo Valizas, Rocha municipality. Two years later a leptocephalus larvae was found in Arroyo Solís Chico estuary, (Machado *et al.* 2012). This suggests that the species also might be spawning in these latitudes or perhaps they can be transported a very long distance southward from more equatorial spawning site. Leptocephali have a very long larval duration, tarpon average about 25 days, bonefish about 55 days, and *Elops* spp. several months (McBride & Horodysky 2004, Adams *et al.* 2014).

Recently, the continuous records of several individuals of a wide range of sizes, widespread along the Uruguayan coast from 2014 to 2022, indicate that the species, although in low numbers, is now permanently present in the area. All these results suggest that the occurrence of *E. smithi* in Uruguay is not occasional and is becoming a resident fish species in Uruguayan waters. In this context, we expect an increase in frequency and abundance of *Elops smithi* in the Uruguayan and Argentinean waters under the scenario of ocean warming (IPCC, 2013). In this regard, we suggest an evaluation of the potential interaction of this new arrived species with the native fauna and its consequences for the trophic web. This kind of alterations in species interactions as consequence of climate change are considered more important than the direct physiological effects of changing environmental conditions (Vergés *et al.* 2016). One important consideration is the potential negative interaction with commercial fish species that inhabit the area and uses estuaries for reproduction and recruitment. A key example that would require monitoring is the potential interaction with *Micropogonias furnieri*, which is one of the main captured species by the artisanal and commercial fisheries in Atlantic coasts (Pereira *et al.* 2009).

Ethical statement

Samples for the present investigation were collected by artisanal and recreational fishermen, then did not require approval by an Ethical Committee.

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