

NEW MULTIPLE RECORDS OF THE BLUNTHEAD PUFFER *SPHOEROIDES PACHYGASTER* (MÜLLER & TROSCHEL, 1848) ALONG THE WESTERN MEDITERRANEAN COASTS AND REASSESSMENT OF ITS BIOGEOGRAPHY

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ABSTRACT. – Five individuals of the blunthead puffer *Sphoeroides pachygaster* were caught along the Algerian coast during the first quarter of 2014 and five other specimens were observed on the Mediterranean coasts of France between 1995 and 2017. These records highlight the wider spread of this thermophilic species in the Mediterranean. Until now, the Sicily Strait was considered as a central core from which the population has spread in different directions, including on French coasts. However, reports along the Algerian coasts presuppose a different dynamic, which consists of an entry via the Strait of Gibraltar of new individuals from the Atlantic. Some arguments are advanced here to support this hypothesis and to reassess the species' biogeography in the Mediterranean Sea.

INTRODUCTION

Tetraodontidae, named ‘puffers’ for their capability of inflation by intake of water or air, are circumtropical, littoral, medium-sized fish inhabiting the oceans worldwide (Shipp, 1974). They include 29 genera and 200 species, among which 10 species are found in the Mediterranean Sea (Froese & Pauly 2019).

Among the Tetraodontidae, the genus *Sphoeroides* is distinguished from other genera by a single lateral line on the side of the body, a truncated or rounded caudal fin (rarely slightly concave) and two nostrils easily visible on each side of the snout. Spines are most often present on the back and belly skin. This genus includes 22 species (Froese & Pauly 2019), two of which are reported in the Mediterranean as exotic species: *S. marmoratus* (Lowe, 1838), the Guinean puffer, and *S. pachygaster* (Müller & Troschel, 1848), the blunthead puffer. *Sphoeroides spengleri* (Bloch, 1785), originally reported by Reina-Hervás *et al.* (2004), is regarded as a misclassification of *S. marmoratus* (Zenetos *et al.* 2005).

The blunthead puffer *S. pachygaster* is distributed circumglobally in tropical and temperate waters. It presents a widespread amphi-atlantic distribution. Along the western Atlantic coast, the species is reported from New England to southern Brazil (Golani *et al.* 2002). Along the eastern Atlantic coast, the species is reported from south of the Gibraltar Strait, off Morocco (Séret & Opic 1981),

to the Gulf of Guinea (Blache *et al.* 1970, Shipp 1990), and probably to South Africa (Smith & Heemstra 1986).

S. pachygaster is also reported from Irish waters (Wheeler & Van Oijen 1985), the Bay of Biscay (Quéro *et al.* 1998), and Portugal (Albuquerque 1954-1956). Outside the Atlantic Ocean, the species is also reported from the Indian and the Pacific Ocean (Froese & Pauly 2019).

Most of the puffers are inshore fishes, but the blunthead puffer is a relatively benthopelagic deepwater species, with a depth range of 50-480 m, or more usually 50-250 m (Froese & Pauly 2019). To date, it is not known whether the Mediterranean *S. pachygaster* may be poisonous, but it is well known that tetrodotoxin is found in fishes of the order Tetraodontiformes (Mosher *et al.* 1964), and among these, the most toxic species belong to the genus *Lagocephalus*. However, no proof of poisonous flesh has been reported for the Mediterranean specimens of *S. pachygaster* (Streftaris & Zenetos 2006). In addition, most of the catches are discarded at sea (*e.g.* Ragonese & Morara 2012), thus reducing the risk of poisoning for humans. However, proper toxicological studies would be appropriate and investigations into the possible commercial exploitation of Mediterranean populations would be welcome.

In the Mediterranean, *S. pachygaster* was reported for the first time in the Balearic Islands in 1979 (Oliver 1981), followed by Moreno & Roca (1984) (Table III). It is considered as one of the 100 worst invasive species

(Streftaris & Zenetos 2006). The "core" of the Mediterranean population seems to be located in the Strait of Sicily (Lipej *et al.* 2013).

This paper reports 10 new records of the blunthead pufferfish *S. pachygaster* along the Algerian and French Mediterranean coasts. We also provide an overview of its spatial distribution in the Mediterranean as a basis for reassessing its biogeography and discussing its spread dynamic.

MATERIALS AND METHODS

Between February 9th and April 14th 2014, five individuals of blunthead *S. pachygaster* were caught in five different localities along the Algerian coasts, from Mostaganem in the west ($35^{\circ}56'0''N, 0^{\circ}5'0''E$) to Collo in the east ($37^{\circ}0'23.4''N, 6^{\circ}33'39.24''E$). Four specimens were caught by trawl net and one by gillnet (Table I). All were identified in accordance with Shipp (1990).

In France, in 1995 an individual was trawled off Saintes-Marie-de-la-Mer (Quignard JP comm pers). In October 2006, two individuals (ca. 15 cm TL) were trawled to the south of La Ciotat ($43^{\circ}09'30''N, 5^{\circ}36'40''E$) at 100 m depth and identified as *S. pachygaster* by the head of the Monaco Museum Aquarium, Dr Pierre Gilles, but they were not preserved. On 9th May 2014, one ca. 30 cm TL individual was fished by angling at night in shallow water in Antibes harbor ($43^{\circ}35'17''N, 7^{\circ}07'37''E$). The fishers were not able to identify the fish. So they took a picture of the fish and released it. The same individual was observed dying on the surface of the harbor the following day by a professional fisherman, who caught it. Finally, in October 2017, one individual (32 cm TL, 550 g) was trawled to the south of La Ciotat at 100-110 m depth and identified by one of the authors (PF; Fig. 1C).

All the individuals caught from Algeria were weighed to the nearest gram and measured to the nearest millimeter. One of them (N° 3; Fig. 1A) was photographed, preserved in 5% formaldehyde and deposited in the Ichthyological collection of the National Centre for Research and Development of Fisheries and Aquaculture (CNRDPA) at Bou-Ismail (Algeria). Morphometric measurements and meristic counts were recorded on only three individuals (1, 3 and 5).

RESULTS

All the Algerian specimens had an inflatable body, a large and extremely blunt head, papillary lips, and heavy jaws forming a beak of two teeth in both upper and lower jaws, forming a dental plate with entire cutting edge. The skin is completely smooth and



Fig. 1. – Blunthead pufferfish *Sphoeroides pachygaster* caught in: (A) waters off Mostaganem bay (Algeria) on March 20th 2014 (19.7 cm TL), (B) harbor of Antibes (France) on May 9th 2014 (ca 30 cm TL), (C) waters off La Ciotat (France) on October 17th 2017 (32 cm TL).

lacking scales, spines and body plates. The lateral line on both sides is convoluted. The dorsal fin is single and placed behind midpoint and opposite the similar-shaped anal fin. The pelvic fins are absent and the caudal fin is truncated. The eyes are large and oval with a flat interorbital space. The color is greyish on the dorsal surface with brownish spots, the belly whitish pale grey and the caudal and dorsal fins bases are dark. All morphometric mea-

Table I. – Characteristics of catches of *Sphoeroides pachygaster* carried out on Algerian coasts.

N°	Locality	Date	Depth (m)	TL (cm)	TW (g)	Fishing gear
01	Tipasa	09/02/2014	–	19.0	187	Gillnet
02	Bouharoune	23/02/2014	–	13.1	80	Trawl
03	Mostaganem	20/03/2014	–	19.7	185	Trawl
04	Al Aouana	19/03/2014	–	26.0	450	Trawl
05	Collo	14/04/2014	110	18.0	140	Trawl

Table II. – Morphometric measurements, meristic counts and weights carried out on three individuals of *Sphoeroides pachygaster* caught in Algerian waters (% TL values are in brackets).

Specimens	1	3	5
Metric measurements (mm)			
Total length	19.0	19.7	18.0
Standard length	16.5 (86.8)	16.5 (83.7)	14.5 (80.5)
Fork length	–	–	16.8 (93.3)
Head length	6.0 (31.5)	6.5 (32.9)	5.8 (32.2)
Orbit height	0.8 (4.2)	0.9 (4.5)	0.6 (3.3)
Orbit width	1.4 (7.3)	1.3 (6.5)	1.2 (6.6)
Interorbital space	2.2 (11.5)	2.5 (12.6)	2.5 (13.8)
Preorbital length	3.0 (15.7)	3.1 (15.7)	2.4 (13.3)
Postorbital length	4.1 (21.5)	4.5 (22.8)	6.6 (36.6)
Internarial space	1.3 (6.8)	1.9 (9.6)	1.2 (6.6)
Width of gill opening	2.2 (11.5)	1.6 (8.1)	–
Prepectoral length	6.5 (34.2)	7.0 (35.5)	5.3 (35.3)
Predorsal length	12.0 (63.1)	12.5 (63.4)	–
Preanal length	13.0 (68.4)	13.7 (69.5)	11.1 (61.6)
Anus-anal fin	1.0 (5.2)	0.7 (3.5)	0.3 (1.6)
Dorsal fin length	1.9 (10)	1.4 (7.1)	1.2 (6.6)
Dorsal fin base length	0.7 (3.6)	0.8 (4.0)	0.4 (2.2)
Anal fin length	1.7 (8.9)	1.1 (5.5)	1.7 (9.4)
Anal fin base length	0.9 (4.7)	0.4 (2.0)	0.6 (3.3)
Pectoral fin length	1.7 (8.9)	2.0 (10.1)	2.7 (15.0)
Width of pedunculum	1.0 (5.2)	1.0 (5.0)	0.7 (3.8)
Meristic counts			
Dorsal finrays	7	7	8
Anal finrays	9	8	8
Pectoral finrays	13	14	14
Weight (g)			
	187	185	140

surements and meristic counts are summarized in Table II. According to the available photographs, the French individuals fished at Antibes in 2014 (Fig. 1B) and La Ciotat in 2017 (Fig. 1C) share the same morphological characteristics.

This morphology and color patterns fit the previous descriptions of *S. pachygaster* (e.g. Tortonese 1986, Jardas & Pallaoro 1996, Ragonese *et al.* 1997, Golani *et al.* 2002 Psomadakis *et al.* 2008, Giordano *et al.* 2012). The meristic counts (Table II) are consistent with values reported by other authors in the Mediterranean (Hemida *et al.* 2009, Cherif *et al.* 2010, Giordano *et al.* 2012, Lipej *et al.* 2013).

DISCUSSION

In Algeria, *S. pachygaster* was reported by Hemida *et al.* (2009) close to Annaba (an adult male, 33 cm TL, 650 g TW). All the new individuals recorded here were

caught to the west of Annaba and are the second confirmed set of sightings in Algeria (Table III). Along the French Mediterranean coast, *S. pachygaster* was previously reported on one single occasion in 1991 off Sète, in the Gulf of Lion (Quignard & Raibaut 1993). No other record has been reported apart from the four observations of 1995, 2006 and 2014.

In the Mediterranean, Lipej *et al.* (2013) listed 55 records of *S. pachygaster* between 1979 and November 2012. Since this review, *S. pachygaster* has been reported in Libya (Bazairi *et al.* 2013, Shakman *et al.* 2017), in Syria (first record; 4 individuals on 14 September 2012, Rahman *et al.* 2014), in Calabria, Italy (1 individual; Visentin & Borg 2014), in Malta (14 immature individuals in 3 years; Visentin & Borg, 2014), in Spain (one individual fished, and photographed, off Alicante at 400 m depth on 1st August 2014; <http://www.observadoresdelmar.cat/>), in Tunisia (34 unpublished records of individuals collected since 2004; Enajjar *et al.* 2015), in Greece (one individual on 5 June 2015; Dailianis *et al.* 2016), in Egypt (3 individuals in May 2012, Farrag *et al.* 2016), in Turkey (1 individual on 13 April 2016, Akyol & Aydin 2017) and in Lebanon (Gerovasileiou *et al.* 2017) (Table III). In their review of non-indigenous species of Calabria, Sperone *et al.* (2015) consider that *S. pachygaster* is now established.

Although the possibility of a Lessepsian migration cannot be excluded, given the circumglobal distribution of the species (Froese & Pauly 2019), this hypothesis should be taken with caution. A Lessepsian migration, if one occurred, was probably unsuccessful, given the wide discrepancy in sightings of the puffer fish between the western and eastern Mediterranean basins (Dulčić 2002, Lipej *et al.* 2013, see also Table III). In addition, no record existed for the eastern Mediterranean until 1991 (Golani 1996), whereas this species has been recorded from 1979 in the Balearic Islands (Oliver 1981). An alternative was proposed by Relini & Orsi-Relini (1995), who speculated on the possibility of a much earlier presence of the species within the Mediterranean on the basis of very old ichthyological illustrations by Salvianus (1558). The depicted fish, from the Nile Delta, might be identified as the blunthead pufferfish. These two hypotheses are no longer considered.

There is a general agreement that *S. pachygaster* entered the Mediterranean through the Gibraltar Strait (e.g. Vacchi & Cau 1986, Quignard & Tomasini 2000, Ben Rais Lasram *et al.* 2008, Psomadakis *et al.* 2008). This Herculean hypothesis is supported by the first record in 1979 of the species in the western Mediterranean (Oliver 1981, see Lipej *et al.* 2013) and the homogeneity of morphometric and meristic data between Atlantic and Mediterranean specimens (Vacchi & Cau 1986). Available information, including the recent work of Lipej *et al.* (2013) using the centroids of spatial distribution and their variance, tends to confirm the general consensus

Table III. – Synthesis of the blunthead pufferfish *Sphoeroides pachygaster* records in the Eastern Atlantic and the Mediterranean.

Locality	Country	Region	Month	Year	n	TL (mm)	W (g)	Z (m)	Source
North-eastern Atlantic									
Estuary of the river Tago	Por	ATL	06	1931	1	225			Gonçalves, 1941
Nazaré	Por	ATL	05	1978	1	125			Calvário et al. 1980
Sintra, 34 Nm NW of Cap Roca	Por	ATL	06	1979	1	218			Calvário et al. 1980
Ribadesella	Esp	ATL	02	1980	1	225			Ortea et al. 1981
Bay de Donegal	Ire	ATL	01	1984	1	157			Wheeler & van Oijen 1985
Plymouth	GB	ATL	02	1987	1	na			Quigley & Flannery 1992
Northern Spain	Esp	ATL	11	1988	1	280			landed
sud Gascogne	Esp	ATL	12	1988	1	340			Quéro et al. 1997
Lorient	Fra	ATL	05	1989	1	340			Quéro et al. 1997
La Rochelle	Fra	ATL	05	1989	1	265			Quéro et al. 1997
S Ireland	Ire	ATL	08	1989	1	300			Quigley 2002
Dingle Bay SW Ireland	Ire	ATL	10	1989	1	345	1015		Quigley 2002
SW Ireland/W Fastnet Rock	Ire	ATL	10	1990	1	370	1425	160	Quigley 2002
SW Ireland	Ire	ATL	01	2002	1	na			Quigley 2002
Mediterranean									
Cala Ratjada, Mallorca	Esp	w	01	1979	1	295			Oliver 1981
Cala Ratjada, Mallorca	Esp	w	04	1983	1	322			Moreno & Roca 1984
Comarca del Garraf, Catalunya	Esp	w		1984	1	140			100-200 Cero & Portas 1984 (in Lipej et al. 2013)
Sicilian Channel, Pantelleria bank	Ita	w		1985	2	137-318			Vacchi & Cau 1985
San Remo	Ita	w		1985	1	302			200 Bartletta & Torchio 1986 (in Lipej et al. 2013)
SW Spain Almeria	Esp	w		1986	2	na			Crespo et al. 1986
Gibraltar, Ceuta	Esp	w		1986	1	na			Crespo et al. 1986
Gulf of Cagliari, Sardinia	Ita	w		1986	5	181-361			40; 70; 170 Vacchi & Cau 1986
Gulf of Tigullio (Portofino)	Ita	w	07	1988	2	115 and 300			60-90 Fiorentino & Zamboni 1990 (in Lipej et al. 2013)
NW Sicilia	Tun	c	01	1990	1	247			160 Arculeo et al. 1994
Gulf of Gabes	Ita	c		1990-1992	many	100-400			Bradaï et al. 2004
Sicilian Channel	Ita	w		1990-1994	403	83-405	26.4-1974.0	50-250	Ragonese et al. 1992
Strait of Sicily	Fra	w		1991	1	115		80-100	Ragonese et al. 1997
off Sète	Isr	e	05	1991	2	140; 183			Quignard & Raibaut 1993
Ashdod									250 Golani 1996
Amendolara, Gulf of Taranto	Ita	c	04	1991	1	135			130 Tursi et al. 1992
Gulf of Gabes	Tun	c	03	1992	3	284			Bradaï et al. 1993
Sušac Island	Cro	a	03-04	1992	5	101; 120			Jardas & Paillarto 1996

Table III.—Continued.

Locality	Country	Region	Month	Year	n	TL (mm)	W (g)	Z (m)	Source
Netanya	Isr	e	06	1992	1	175		360	Golani 1996
Gulf of Gabes	Tun	c	07	1992	1	410	1725	fish auction	Bradaï <i>et al.</i> 1993
Islet Glavat	Cro	a	08	1992	3	147		120	Jardas & Pallaoro 1996
Blitvenica	Cro	a	11	1992	1	213		130-150	Jardas & Pallaoro 1996
Rhodes Islands (Lindos)	Gre	e	11	1992	5	224-345		65	Zachariou-Mamallingga & Corsini 1994
south Adriatic sea	Ita	a		1992	many	na		30-130	Bello 1993
Mola di Bari	Ita	a		1992-1993	5	95-228		80-120	Bello 1993
Albania	Alb	a	03	1993	1	ca. 100		85	Bello 1993
Rhodes Islands (Lindos)	Gre	e	03	1993	10	na			Zachariou-Mamallingga & Corsini 1994
Misrata	Lib	e	06	1993	01	32.5 SL		60-80	Shakman <i>et al.</i> 2017
Ionian Sea	Ita	c		1993-1996	many			130-400	Matarrrese <i>et al.</i> 1996 Sciberras & Schembri 2007 this work
Malta	Mal	c		1994	x	na			
off Saintes-Maries-de-la-Mer	Fra	w	07	1995	1				Bradai <i>et al.</i> 2004
Gulf of Gabes	Tun	c	03	1996	1	na			
Elba	Ita	w	08	1996	1	153		80	Bedini 1998
cape Kamenjak, Istra	Cro	a	11	1998	1	125		45	Dulcic 2002
Saros bay	Tur	e	10	1999	1	167		180	Eryilmaz <i>et al.</i> 2003
Serifos Island	Gre	e		2000	1	164			Zenetas <i>et al.</i> 2007
Ionian Sea (Meganissi Island and Lefkas Island)	Gre	e		2000-2005	16	297-398			Zenetas <i>et al.</i> 2007
Bozcaada Island	Tur	e	05	2001	1	395		125	Eryilmaz <i>et al.</i> 2003
SE Sifnos	Gre	e	08	2003	1		800	103	Peristeraki <i>et al.</i> 2006
South Tunisia	Tun	c	03	2004	3	347-401	997-1624		Enajjar <i>et al.</i> 2015
Anzio	Ita	w	05	2004	1	137	65	360	Psomadakis <i>et al.</i> 2008
South Tunisia	Tun	c	03	2005	1	294	1537		Enajjar <i>et al.</i> 2015
South Tunisia	Tun	c	04	2005	1	473	2276		Enajjar <i>et al.</i> 2015
SE Serifos	Gre	e	06	2005	1		2100	156	Peristeraki <i>et al.</i> 2006
SE Sifnos	Gre	e	06	2005	2		1030	105	Ligas <i>et al.</i> 2006, 2007
Elba	Ita	w	08	2005	1	125	66.4		Zenetas <i>et al.</i> 2007
Serifos	Gre	e	10	2005	2	297 and 436			
Cyprus	Cyp	e		2005	1	na			Katsanevakis <i>et al.</i> 2009
SW Leros	Gre	e	07	2006	1		110	170	Peristeraki <i>et al.</i> 2006
SW Astypalaia	Gre	e	07	2006	1		500	140	Peristeraki <i>et al.</i> 2006
La Ciotat	Fra	w	10	2006	2	ca. 150		100	this work
Tunisia (south and north)	Tun	c	01	2007	6	318-475	815-2205		Enajjar <i>et al.</i> 2015

Table III.—Continued.

Locality	Country	Region	Month	Year	n	TL (mm)	W (g)	Z (m)	Source
South Tunisia off Budva	Tun	c	03	2007	6	295-435	615-2055		Enajjar et al. 2015
South Tunisia	Mtg	a	01	2008	1	450	1460	80	Joksimovic et al. 2009
South Tunisia	Tun	c	02	2008	1	456	1735		Enajjar et al. 2015
South Tunisia	Tun	c	04	2008	1	440	1950		Enajjar et al. 2015
Annaba	Alg	w	11	2008	1	330		150	Hemida et al. 2009
Tyrrhenian sea	Ita	w		2008-2009	1	na			
Gulf of Hammamet	Tun	c	02	2009	2	101 and 95	47.9 and 41.9	360	Guerrero et al. 2010
South Tunisia	Tur	e	10	2010	1	450		50	Chérif et al. 2010
Karatassas coast, Iskenderun Bay	Tur	e	10	2010	1	187		305	Eleftheriou et al. 2011
Samandag, Iskenderun Bay	Ita	w	02	2012	1	na		200	Eleftheriou et al. 2011
Faliconara Albanese, Calabria	Ita	w	03	2012	1	280	461.5		Visentini & Borg 2014
Strait of Messina	Egy	e	05	2012	3	114-169		>150	Giordano et al. 2012
Off Alexandria	Slo	a	11	2012	1	348		22	Farrag et al. 2016
Piran	Mal	c		2012-2014	14	immature			Lipej et al. 2013
Malta	Alg	w	02	2014	1	190	187		Visentini & Borg 2014
Tipasa	Alg	w	02	2014	1	131	80		this work
Bouharoune	Alg	w	02	2014	1	353-540	697-2640		this work
South Tunisia	Tun	c	02	2014	11				Enajjar et al. 2015
Mostaganem	Alg	w	03	2014	1	197	185		this work
Al Aouana	Alg	w	03	2014	1	260	450		this work
Collo	Alg	w	04	2014	1	180	140		this work
Antibes harbor	Fra	w	05	2014	1	ca 300		surface	this work
North Tunisia	Tun	c	05	2014	1	180	146		Enajjar et al. 2015
Alicante	Spa	w	08	2014	1	na		400	http://www.observadorsdelmar.cat/
Latakia	Syr	e	09	2014	4	312-466	1355-1850	250	Rahman et al. 2014
Saronikos Gulf	Gre	e	06	2015	1	509	2523	250	Dailianis et al. 2016
Bay of Izmir	Tur	e	04	2016	1	192	183	80	Akyol & Aydin 2017
Abdeh	Leb	E	4	2017	3	34.4-41.7			Gerovasileiou et al. 2017
La Ciotat	Fra	w	10	2017	1	320	550	100-110	this work

which considers the puffer fish as a recent Herculean species. This fish is undergoing a rapid eastward spread (e.g. Ragonese *et al.* 1992, Lipej *et al.* 2013), as confirmed by the published records of *S. pachygaster* in Greece, Tunisia, Libya, Syria, Egypt and Lebanon since the survey of Lipej *et al.* (2013).

The new records in Algeria (5 at different locations in 2014) and along the French Mediterranean coast (one in 1995, three at the same location in 2006 and 2017, and a third one at another location in 2014) are not consistent with this eastward migration. Today, the Sicily Strait is considered as a central core where the vast majority of all sightings were recorded during the last 20 years (e.g. Ragonese *et al.* 1997, Ragonese & Morara 2012, Schiberras & Schembri 2006, Enajjar *et al.* 2015), and from which the population has spread in different directions, eastward but also towards the northeast of the western basin (Lipej *et al.* 2013). The observations in France of 2006, 2014, and 2017 could be explained by this expansion towards the Ligurian Sea from this core area. On the other hand, the presence of this species on the southwestern coast of the Mediterranean presupposes a different dynamic which consists of an entry via the Strait of Gibraltar of new individuals from the Atlantic.

Most of the Atlantic species that pass through the Strait of Gibraltar are transported by the incoming stream along the North African coast (e.g. Otero *et al.* 2013). The regular warming of the Atlantic Ocean and the influx of Atlantic waters in the Mediterranean would tend to lower the physical and chemical gradient between the eastern region of the Atlantic Ocean and the southern Mediterranean (Ben Rais Lasram *et al.* 2008). The spread of Herculean species can be permanent or recurrent and related to climatic or oceanographic oscillations. Francour & Mouine (2008) showed that the spread of *Kyphosus sectatrix* into the Mediterranean showed two different phases of migration into the Mediterranean: an earlier one (records from 1847 to 1903) and a more recent one (records since 1996), with no mention of captures between 1904 and 1996. Consequently, the recent observations along the western and central Algerian coast could be related to a new phase of the spread of Atlantic individuals of *S. pachygaster* transported by the influx of Atlantic waters. However, a migration from the Sicily Strait hotspot, where the species is well-established (Cherif *et al.* 2010, Enajjar *et al.* 2015), cannot be totally ruled out. The same hypothesis was proposed for the Lessepsian pufferfish *Lagocephalus sceleratus* (Kara *et al.* 2015) and for the individual of *S. pachygaster* trawled along the Eastern coast of Algeria on November 2008 (Hemida *et al.* 2009). Like many tetraodontid fishes, *S. pachygaster* is probably not a powerful swimmer, so, its westward spread against the main current was probably very slow and irregular.

The spread of *S. pachygaster* in the Mediterranean has therefore occurred from the Atlantic through the Strait of Gibraltar over the last 40 years. However, the large

number of *S. pachygaster* trawled between 1990-1994 in the Strait of Sicily (Ragonese *et al.* 1997) suggests that it probably arrived in the Sicilian Strait prior to the date of the first record in the Mediterranean by Oliver (1981) in the Balearic Islands (Ragonese *et al.* 1992, Orsi Relini 2009). Although it cannot be ruled out that this species survived for a while in the Mediterranean (Salvianus, 1558, Relini & Orsi Relini 1995), the absence of sightings from the 16th century until the 1980s makes plausible an Atlantic origin with at least recurrent invasions, related to climatic oscillations (Orsi Relini 2009).

This synopsis of *S. pachygaster* sightings in the Mediterranean gives grounds for the hypothesis of successive entries and a progressive colonization from the core zone. However, only fairly extensive genetic studies would make it possible to clarify the successive routes of entry and spread in the Mediterranean. It is therefore imperative to carry out a study of the genetic structure of this species in the Mediterranean and in the near Atlantic in order to seek a pattern of regional separation, evidence of multiple introductions or traces of founder events (Azzurro *et al.* 2006, Rius *et al.* 2015).

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