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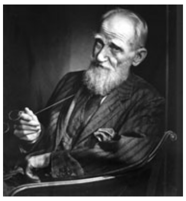

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Etymology of Ghoti

George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

Falling through the cracks: the fading history of a large iconic predator

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Abstract

Human impact on the oceans predates scientific observation, which for many animal populations has captured only recent changes. Such a limited knowledge can hamper finding optimal management and conservation strategies including setting appropriate recovery targets. Sawfishes are among the most endangered marine vertebrates in the ocean. Historical human impacts have resulted in sawfish extinction in many coastal areas around the world; however, in the Mediterranean Sea, their past presence and possible extinction have been debated for decades. Recently, it was concluded that the region never hosted resident populations because of unsuitable environmental conditions. Through an extensive bibliographic and archival search and an extinction analysis, we reconstructed the history of sawfishes in the Mediterranean Sea. Between 1576 and 1959, there were 48 independent accounts of the occurrence of two sawfish species (*Pristis pristis*, Pristidae and *Pristis pectinata*, Pristidae), including 24 documented catches. Sawfishes were mainly recorded in the western Mediterranean, in areas close to large rivers with light human impact. Most of the documented individuals were juveniles, suggesting local parturition. Extinction analyses yielded variable results and were affected by the sparseness of records but suggested that both species went extinct in the

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Mediterranean Sea in the 1960s–1970s. Our results challenge current assumptions on sawfish ecology and biogeography, offer new options for sawfish conservation in the Atlantic and highlight the importance of historical analyses for reconstructing ecosystem baselines and setting recovery targets.

Keywords bibliographic analysis, ecological baselines, extinction analyses, historical ecology, museum records, sawfish

Introduction

There is growing evidence that human impact on marine ecosystems largely predates scientific observation (Pauly 1995, Jackson *et al.* 2001). Many shallow nearshore ecosystems were depleted before written records, in some regions starting as far back as the last glacial period (Rick and Erlandson 2008; Holm *et al.* 2010). Conversely, only in the last few hundred years have changes in the composition, structure and functioning of marine communities been described scientifically (Jackson *et al.* 2001). For most of human history, the states of nature and their changes were only qualitatively described in early naturalistic accounts and in archaeological artefacts (Bekker-Nielsen and Bernal Casasola 2007; Guidetti and Micheli 2011).

Integration of pre-scientific information with modern accounts has demonstrated that hundreds to thousands of years ago a suite of predators was extremely abundant in the ocean (McClenachan *et al.* 2012). Marine predators were larger, distributed over much broader geographic ranges and were prone to rapid depletion by human activities (Jackson *et al.* 2001; Lotze and Worm 2009; Guidetti and Micheli 2011). These results were confirmed along present-day spatial gradients of human impact (Sandin *et al.* 2008; Nadon *et al.* 2012) and used to question crucial tenets of community ecology dealing with the structure and functioning of natural marine communities (Jackson 2006; Sandin *et al.* 2008).

A biased perspective of what constitutes natural marine ecosystems has profound implications for management and conservation. In particular, it hampers finding optimal management and conservation strategies for depleted populations and ecosystems, including setting appropriate recovery targets (McClenachan *et al.* 2012).

Sawfishes are among the most vulnerable predators in the ocean. Reaching 5-7 m in total length, they occur in tropical and subtropical coastal regions, have small home ranges (Thorson 1982a), are constrained to inshore marine (0–122 m depth) and freshwater habitats and are thus exposed to high levels and long histories of human impact (Lotze *et al.* 2006; Halpern *et al.* 2008). With their large body and peculiar toothed rostrum, sawfishes are easy and lucrative to catch (Thorson 1982b Simpfendorfer 2000; McDavitt and Charvet-Almeida 2004; Seitz and Poulakis 2006; Wueringer *et al.* 2009), but grow slowly (few centimetres per year), mature late (no earlier than 10 years of age) and give birth from one to 20 pups each litter (Simpfendorfer 2000; Wueringer *et al.* 2009). Hence, they cannot sustain even minimal levels of fishing (Simpfendorfer 2000).

In the last century, directed fisheries, incidental by-catch and habitat depletion caused the decline in abundance and geographic distribution of all six sawfish species (Harrison and Dulvy 2014). In the Atlantic, the two endemic species, the largetooth sawfish (*Pristis pristis*) and the smalltooth sawfish (*Pristis pectinata*) formerly ranged from Uruguay to USA in the west, and from Angola to Mauritania in the east (Fernandez-Carvalho *et al.* 2014; Harrison and Dulvy 2014). Currently, the smalltooth sawfish remains in suitable habitats around the Bahamas, the south-eastern United States (mainly in Florida) and in small areas of Cuba, Belize and Honduras. The largetooth sawfish persists in the Amazon river basin, and riverine Nicaragua. In the eastern Atlantic, it is unconfirmed whether any sawfishes remain in Guinea-Bissau (Leeney and Poncelet 2013, Fernandez-Carvalho *et al.* 2014; Tamburello *et al.* 2014).

The Mediterranean is one of the most densely populated and impacted regions on the planet (Coll *et al.* 2010). Ancient civilizations developed along its shores millennia ago, depleting resources, eradicating predators and reducing the extent and quality of marine and coastal habitats (Hughes 1994; Bekker-Nielsem 2005; Lotze *et al.* 2006;

Airoldi and Beck 2007; Bekker-Nielsen and Bernal Casasola 2007). Describing here what is natural is more difficult than elsewhere. Largetooth and smalltooth sawfishes were often included in historical and recent regional faunal lists (Tortonese 1956; Whitehead *et al.* 1984). However, whether they had local stable populations has been debated for decades (Tortonese 1956; Whitehead *et al.* 1984; Bilecenoglu *et al.* 2002). In a recent review of sawfish global population structure, Faria *et al.* (2013) suggested that sawfishes had never formed resident, breeding or core populations in the Mediterranean. This view was shared in the latest IUCN global sawfish conservation strategy workshop (London, May 2012), where it was concluded that the Mediterranean Sea was not part of the sawfish's historical distribution range (Harrison and Dulvy 2014). Such a conclusion was based on the perception that reliable evidence of sawfish historical occurrences in the basin is lacking, as well as information derived from three additional lines of reasoning: (i) a large portion of Mediterranean coastal waters are seasonally too cold to host stable sawfish populations; (ii) no sawfish records are available from Mediterranean sectors with the most suitable environmental conditions for sawfish (e.g. the Nile delta); (iii) the Mediterranean has been a global-trade crossroad for millennia, and thus, museums or personal exhibits of sawfish from the region are possibly non-Mediterranean specimens acquired from curio markets. Therefore, the few sawfish occurrences reported in the literature were viewed as cases of vagrant or stray specimens originating from areas outside the Mediterranean, such as the Atlantic Ocean and/or Red Sea.

Here, we present a thorough review and synthesis of previously published and new information on the presence of sawfish in the Mediterranean Sea. We addressed the question of whether sawfishes once occupied this region, and if so, whether and when they went extinct. We thoroughly examined each record in the context of the ecology of the species and the historical and current environmental features of the Mediterranean Sea to evaluate the plausibility of the hypotheses developed excluding the region from the historical distribution range of the sawfish. We present evidence supporting the view that the Mediterranean Sea was formerly part of the sawfish's distribution range, and argue that the alternative case is based on hypotheses having scarce empirical support and on an incomplete understanding of sawfish ecology and historical distribution. We show how our results might have notable implications for sawfish conservation in the eastern Atlantic, for motivating further research on sawfish historical ecology, and in general for reconstructing baselines of historically depleted ecosystems.

Material and methods

We constructed a database of all sawfish records we could find in the Mediterranean using different sources and multiple strategies (Appendix S1). First, we searched and reviewed historical bibliographic references. Bibliographic items were searched in electronic archives (Google Scholar, ISI web of knowledge) and on the Internet (including online biodiversity databases such as the Ocean Biodiversity Information System (OBIS 2014), the Global Biodiversity Information Facility (GBIF 2014), FishBase (Froese and Pauly 2014), and their linked database networks) using a combination of scientific, common and vernacular names (see Appendix S1). Following the latest sawfish reclassification (Faria *et al.* 2013), all occurrences of *Pristis microdon* and *Pristis perotteti* were treated as largetooth sawfish. We looked for all references reporting the capture, sighting or any other documented proof of sawfish occurrence in the Mediterranean such as for example, its presence in local fish markets. Starting from an initial publication pool identified through these searches, we followed through citations in the listed references to investigate data sources and retrieve further historical literature unaccounted for in conventional search engines. Through this approach, we delineated the history of each account and determined whether a record was original or redundant meaning that it was not reporting first-hand observational data but existing bibliographic references. The historical period covered by the publications we reviewed went from pre-dynastic Egypt (~4,400 BC) to the present day but excluding publications of fossil records.

Second, we compiled an inventory of museum collections holding sawfish exhibits labelled as having a Mediterranean origin (Table S1), and we contacted their curators requesting additional information to characterize the identity, origin and age of the specimen through evidence such as photographs, morphometric data or documents recording the acquisition. From the acquired photographic material, we verified the classification of the species (where possible) and checked their correspondence with the museum labels. Exhibits reidentified as non-Mediterranean species (e.g. of green sawfish [*Pristis zijsron*, Pristidae], dwarf sawfish [*Pristis clavata,* Pristidae], or narrow sawfish [*Anoxypristis cuspidata,* Pristidae]) were not considered for further investigations.

To test whether the specimens were vagrants from the Atlantic or the Red Sea, we collected the morphometric measurements reported or retrievable from all bibliographic, archival or museum records detailing actual sightings, catches or preserved specimens. Sawfishes are site-specific fishes, especially in the juvenile stages. Newborns spend their early life stages, up to several years, in estuaries or rivers. Adults can occasionally roam for hundreds of kilometres (Thorson 1982a), but juveniles never range too far from the place they were born (In Florida, smalltooth sawfishes <2 m show home ranges ≤1.2 km^2; Simpfendorfer 2003; Whitty *et al.* 2009; Simpfendorfer *et al.* 2010; Carlson *et al.* 2014). It is thus expected that vagrant sawfishes are adult individuals able to undertake long distance movements. When total length (TL) was not available, we estimated it by multiplying rostral length by 4.28 for the largetooth sawfish and 3.91 for the smalltooth sawfish (Faria *et al.* 2013). When only body weight was available, we converted it to TL using length–weight relationships reported in Simpfendorfer (2000).

Sightings and catches with information on location were georeferenced and mapped to explore their spatial distribution. We also produced maps of sea surface temperature (SST, Appendix S1) to compare the locations where sawfish had been recorded with the seasonal distribution of temperatures in the Mediterranean. Available data on sawfish temperature tolerance are scant and indirect but suggest that sawfishes prefer temperatures between 18 and 30 °C with a lower letal range between 8 and 12 °C (Poulakis *et al.* 2011, 2013; Simpfendorfer *et al.* 2011).

For each species, records including capture or sighting year were used to construct a time series of presence-absence (henceforth called sighting record, SR). When year was not available, we used the publication year if the account was deemed contemporary, or inferred it from the information contained in the publication. This SR was used to test the hypothesis (H_O) that the species still persists in the Mediterranean Sea, and to estimate the likely year of extinction from the region. Given the sparseness of the SR, we did not have enough statistical power to estimate whether the population was stable or changing during our observation period (Appendix S1). Therefore, we tested H_O under three scenarios:

1. We assumed that the sightings followed a stationary Poisson process implying that the species was rare but stable over time. Accordingly, if T is the length of the time period and t_n is the ordinal year of the last sighting record, Solow (2005) demonstrates that the p-value of H_O is $(t_n/T)^n$.
2. We assumed that the sightings followed a non-stationary Poisson process from which we assumed that sawfishes were exponentially declining during our observation window. In this case, P-value of H_O is given by $F(t_n)/F(T)$, where

$$F(x) = 1 - \Sigma_{i=1}^{\frac{s}{x}} (-1)^{i-1} \binom{n}{i} \left(1 - \frac{ix}{s}\right)^{n-1} \quad (1)$$

   and $s = \Sigma_{i=1}^{n} t_i$ (Solow 2005).
3. We made no assumptions on the sighting record process and used a method based on the distributional properties of the last entries (k) of a sighting record. Given a long time series of sightings, if we keep only the k most recent sightings, their joint distribution follows a Weibull extreme value distribution regardless of the parent probability distribution characterizing the entire time series (Solow 2005). As our sightings were few and relatively recent compared to the whole exploitation history of the Mediterranean Sea, we assumed that these more recent records represented the most recent of a large number of unobserved historical sightings. We will illustrate that especially between the end of the Roman Empire and the dawn of ichthyological research (16th century), the probability of finding explicit and direct mentions to sawfish from the literature was much lower than in later periods (Appendix S1). According to this method, the P-values of H_O is $e^{[-k(t_n/t_k)]}$, where t_k is the least recent sighting and t_n the most recent sighting (Solow 2005).

We used these scenarios of population status also to estimate the extinction year ($\widehat{T}_E$), and its 95% confidence upper bound ($\widehat{T}_E^u$) following the methods in Solow (2005). Furthermore, many bibliographic records did not report tangible sightings but suggested nonetheless that sawfishes were seen in other locations and/or periods. We treated these accounts (B) as additional sightings and added them to the above SR. We reran the extinction probability analyses for this extended time series (SR + B) to account for both detailed and more generic occurrence records.

Finally, during our investigations, we encountered three unpublished communications of sawfish occurrence. These anecdotes were retrieved without any targeted search effort and were uncertain taxonomically, spatially and temporally. However, we decided to report their details in the Appendix for completeness, and explore their effect on the extinction analyses both with a hypothesis testing and Bayesian approach (Appendix S1).

Results

We retrieved 82 bibliographic references, 21 museum specimens (Table 1) and three unpublished anecdotal records documenting the possible occurrence of sawfish in the Mediterranean. Publications were ancient and modern naturalistic treatises, bestiaries, geographic dissertations, taxonomic descriptions, species checklists, species and museum catalogues, fish dictionaries, statistical reports and fisheries surveys. (Table S2), not uniformly covering a time span of $\sim$2400 years. 41% of this literature was redundant (for either or both sawfish species), repeating facts already reported elsewhere. The remaining 48 publications held new information we could not link to a previous bibliographic source. Of these original accounts, 55% documented the presence of the largetooth sawfish, 29% recorded the presence of the smalltooth sawfish and 16% were generic records of sawfishes (*Pristis* spp., Fig. S1).

None of the 21 museum exhibits had complete or detailed information on their acquisition; 11 were labelled simply as 'Mediterranean', while the others had a more precise location but no details on their capture (Table 1). For 15, we had photographs which helped us reidentify nine exhibits as narrow sawfish or green sawfish, and thus dismiss them as non-Mediterranean. This analysis left 12 museum specimens of probable Mediterranean origin, which together with the bibliographic accounts, documented evidence of 24 sawfish catches, 11 of smalltooth sawfish and 13 of largetooth sawfish (Fig. 1, Table 2).

Although we found mentions of sawfish as classical antiquity and throughout the Middle Ages and the Renaissance (Fig. 2a and Appendix S1), most of the useful and unequivocal records demonstrating the historical presence of sawfish in the region were from the 18th and the 19th centuries (Fig. 2b, Appendix S1). During this period, the first scientific species catalogues from multiple Mediterranean sectors were published, and many included sawfishes, sometimes with explicit details of catches or landings (Table 2 and S3–S5, Appendix S1). Both species were generally perceived as rare, though such a perception, differed from region-to-region and changed over time, sometimes being contradictory within the same location. In southern France, catches were referred to as infrequent but systematic since the end of the 18th century (Table 2 and Appendix S1). Conversely in Malta, the largetooth sawfish was considered a non-rare landing by some authors, but a rare occurrence by others (Appendix S1). Catches and sightings recorded in the 18th and 19th centuries were mainly reported first-hand by ichthyologists, while most of the 20th century accounts were second-hand reports from fishers or other researchers. In the 20th century, sawfishes became to be considered extremely rare, to the point that doubts on their actual Mediterranean occurrence began to grow (Appendix S1).

Modern records from the 18th century onwards were documented from nine Mediterranean countries (Fig. S1b), with 45 common names in nine languages (Appendix S1). Most accounts came from Spain, France, Italy and Malta. Catches were reported from southern France, the southern Tyrrhenian Sea, the Adriatic Sea, the Balearic Islands and the Levantine Sea (Table 2 and Fig. 1). The largetooth sawfish was exclusively recorded in the western Mediterranean, while the smalltooth sawfish had a more localized distribution off Provence, the southern Adriatic Sea, the strait of Messina and the Levantine Sea (Fig. 1). From the latter, we found only two explicit accounts, and an ambiguous pre-historical record from the Nile valley (Appendix S1 and Fig. S2).

Of the 21 sawfishes with morphometric data, 15 were young of the year or slightly older (median length: 127.7 cm, range: 70–537.5 cm, Fig. 3). Six of these came from southern France, three from the Gulf of Naples, two from the Adriatic, one from Messina and the remaining three from unspecified locations (Table 2).

Table 1 List of museum exhibits tagged as coming from the Mediterranean Sea.

	Museum[1]	Catno[2]	Species[3]	Tagged[4]	Location	References
1	Museo Civico di Rovereto	inv.no42	*Anoxypristis cuspidata*	*Pristis* spp.	Genova (Italy)	I. Ribaga, personal communication
2	–	inv.no41	*Anoxypristis cuspidata*	*Pristis pectinata*	–	I. Ribaga, personal communication
3	–	inv.no40	*Pristis zijsron*	*Pristis pectinata*	Venezia (Italy)	I. Ribaga, personal communication
4	Museo di Storia Naturale di Firenze sezione di Zoologia La Specola	6112	*Pristis pectinata*		Messina (Italy)	Vanni (1992)
5	Museo di Storia Naturale e del Territorio dell Universita di Pisa	Pe 0116	*Anoxypristis cuspidata*	*Pristis pectinata*	Mediterranean Sea	Carnevale *et al.* (2007)
6	Museo di Zoologia della Regia Universita di Roma	MZRUR1gen	*Pristis pectinata*		–	Vinciguerra (1889)
7	Museo di Zoologia di Napoli	MZSN1gen	*Pristis pristis*	*Pristis microdon*	Gulf of Naples (Italy)	Costa (1857)
8	Museo di Zoologia e Anatomia Comparata dellUniversita di Torino	MZACUT1gen	*Pristis pectinata*		Mediterranean Sea	Tortonese (1956)
9	Museu de Ciences Naturals de Barcelona	MZB 82-5329	*Anoxypristis cuspidata*	*Pristis pectinata*	–	E. Garcia, personal communication
10	–	MZB 82-5327	*Pristis pristis*		–	E. Garcia, personal communication
11	–	MZB 82-5331	*Pristis pristis*	*Pristis pectinata*	–	E. Garcia, personal communication
12	Museum of Natural History of Dubrovnik	PMD 20	*Pristis pectinata*		Dubrovnik (Croatia)	J. Sulić Šprem, personal observation
13	Museum of Natural History of Rijeka	PMR VP37	*Pristis zijsron*	*Pristis pectinata*	Mediterranean?	M. Kovacic, personal communication
14	Museum of Zoology University of Navarra (MZNA)	107129	*Anoxypristis cuspidata*	*Pristis pristis*	Mediterranean Sea	A.H. Ariño, personal communication
15	–	107128	*Pristis pectinata*		–	A.H. Ariño, personal communication
16	–	107145	*Pristis zijsron*	*Pristis pristis*	–	A.H. Ariño, personal communication
17	–	107127	*Pristis zijsron*	*Pristis pectinata*	–	A.H. Ariño, personal communication
18	Natural History Museum of Nimes		*Pristis pectinata*		Gulf of Lion	B. Seret, personal observation
19	–	NHMN2gen	*Pristis pristis*		–	B. Seret, personal observation
20	Natural History Museum of Split	inv. br. 10	*Pristis pectinata*		Southern Adriatic Sea	J. Sulić Šprem, personal observation
21	Observatoire de la Mer du Brusc	OMB1gen	*Pristis pristis*		Embiez (France)	Capapé (1977)

[1]Dashes are used for cell values equal to the above. It also applies to Location.
[2]Original or generated (indicated by the suffix 'gen') catalogue number.
[3]Correct nomenclature or our re-identification based on photographic evidence.
[4]Species names as previously reported in the original museum tag. When *Tagged* is missing, the reported name coincides with the name in Species.

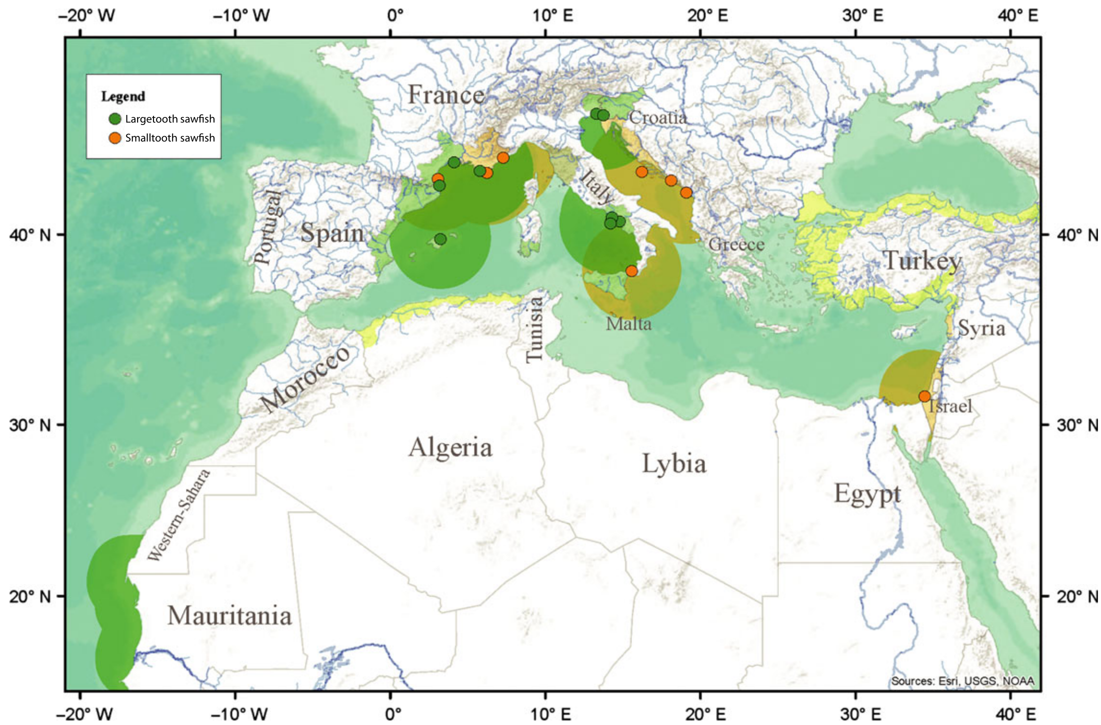

Figure 1 Map of records. Mediterranean map indicating regions and point locations from where smalltooth sawfish (orange), largetooth sawfish (green) and *Pristis* spp. (grey area) have been observed since the 18th century. Coloured regions are coastal areas where sawfishes were reported to occur but specific catches or sightings were not detailed. In yellow are sectors where the historical occurrence of sawfish is doubtful. Dots indicate locations of actual sightings or catches. Permanent primary, secondary and tertiary rivers flowing into the Mediterranean Sea are indicated in blue. Transparent orange and green buffers around the records indicate hypothetical home ranges of the sighted sawfishes. We fixed the buffer distance at 280 km, which is the ceiling of the greatest observed distance travelled by tagged sawfishes (279.1 km, Carlson *et al.* 2014). These buffers are included to contextualize the distance between the records in the Mediterranean and the upper limit of the historical sawfish distribution in the eastern Atlantic.

The last sawfish catch of the Mediterranean was recorded by a tuna fishing boat operating off Grau-du-Roi (Languedoc-Roussillon) in 1959 (Table 2). Together with other contemporary records, this catch record suggested that sawfishes occurred in southern France until the second half of the 20th century. Regional persistence, however, was variable across the Mediterranean. In the Adriatic Sea, the last record was dated 1902, and in the Gulf of Naples, there were no records after 1867 (Table 2). Records from Sicily, Malta and Spain were from the 19th century and were almost exclusively indirect observations or undated museum exhibits.

Extinction results for the time series of sightings (SR) were not significant (*P*-value of $H_0 > 0.05$, Table 3, Fig. 2c). However, by adding the less-detailed bibliographic accounts to this time series (SR + B), results became significant suggesting that the largetooth sawfish went extinct between 1975 and 1979 (depending on the population change assumption used), and the smalltooth sawfish between 1966 and 1970.

Discussion

Evidence for competing hypotheses

Our literature analysis and investigations of museum materials provided support for the hypothesis that the Mediterranean once hosted local sawfish populations. Since the 18th century, 48 original and independent accounts documented the historical occurrence of two species. Twenty-four were reports of catches, the majority of which related to juveniles or young of the year, indicative of local parturition. Conversely, we found scarce empirical evidence for excluding the

Table 2 List of sawfish records reporting information on species catches or sightings.

	Species	Year	Length (cm)[1]	Locality	Evidence	References
1	Smalltooth sawfish		100.1	Mediterranean Sea	Museum (individual)	A.H. Arino, personal communication
2	–		537.5	Dubrovnik, Croatia	Museum (rostrum)	J. Sulić Šprem, personal observation
3	–	<1777	*70*	Provence, France	Catch (individual)	Duhamel Du Monceau (1777)
4	–	<1810	*150*	Nice, France	Catch (individual)	Risso (1810)
5	–	1837	135	Messina, Sicily, Italy	Museum (individual)	Vanni (1992)
6	–	<1863	*82*	Pyrenees-Orientales, France	Museum (individual)	B. Seret, personal observation
7	–	<1889	*115*	Mediterranean Sea	Museum (individual)	Vinciguerra (1889)
8	–	1901	285.2	Southern Adriatic Sea	Museum (rostrum)	J. Sulić Šprem, personal observation
9	–	1902		Vis, Croatia	Catch (rostrum)	Milišic (1994)
10	–	<1953		Israel	Catch (individual)	Ben-Tuvia (1953)
11	–	<1956		Mediterranean Sea	Museum (individual)	Tortonese (1956)
12	Largetooth sawfish		515.8	Mediterranean Sea	Museum (rostrum)	E. Garcia, personal communication
13	–		127.7	Mediterranean Sea	Museum (rostrum)	E. Garcia, personal communication
14	–	1573	*316.8*	Southern Tyrrhenian Sea, Italy	Catch (rostrum)	de Robertis (1853)
15	–	1833	247	Napoli, Italy	Catch (individual)	de Robertis (1853)
16	–	1833	247	Napoli, Italy	Catch (individual)	de Robertis (1853)
17	–	1853	*79.2*	Trieste, Italy	Catch (individual)	de Robertis (1853)
18	–	1853	*79.2*	Trieste, Italy	Catch (individual)	de Robertis (1853)
19	–	<1857	*73.7*	Gulf of Naples, Italy	Museum (individual)	Costa (1857)
20	–	<1863	*93*	Pyrenees-Orientales, France	Museum (individual)	B. Seret, personal observation
21	–	<1868		Mallorca, Spain	Sighting (individual)	Barcelo (1868)
22	–	<1880	105	Mediterranean Sea	Museum (rostrum)	Doderlein (1979–1880)
23	–	1959	*130*	Grau-du-Roi, France	Catch (individual)	Granier (1964)
24	–	<1966	*100*	Embiez, France	Museum (individual)	Capapé (1977)

[1]Length values (TL) taken from the original publication or museum tag are in italic, otherwise are estimated values.

Mediterranean Sea from the historical sawfish distribution.

The spatiotemporal distribution of our records was consistent with the known ecology and vulnerability of the species (Wueringer *et al.* 2009). Sawfishes were mainly recorded in the western Mediterranean in areas close to riverine systems (e.g. Ebro, Rhone, Fig. 1) characterized by a lighter human footprint. South-eastern France, for example, was the Mediterranean sector with the longest time series of records and the most recent confirmed occurrences. Here, the Camargue National Park, the oldest (est. in 1929) and largest coastal natural reserve in the Mediterranean which extends for 1450 km^2 around the Rhone delta, might have played a crucial role in ensuring the persistence of the species in the surrounding areas. Similar suitable habitats for sawfishes (Simpfendorfer and Wiley 2005; Simpfendorfer *et al.* 2010; Moore 2014) existed in many other Mediterranean sectors (Airoldi and Beck 2007) but began to be impacted already during Ancient Egypt, Rome and in Medieval times (Hughes 1994; Lotze *et al.* 2006; Airoldi and Beck 2007). The pace and timing of this habitat loss differed geographically throughout history (Airoldi and Beck 2007) and likely dictated the pattern of sawfish persistence across regions.

The Nile Delta might have provided one of the most suitable sawfish habitats, but it is also the Mediterranean sector with the longest history of human impact (Hughes 1994), and could be one of the first places where sawfish became extinct. The pre-historical sawfish artefacts found in the upper Nile (Fig. S2) require further investigation, but suggest that the dearth of sawfish records from the region might relate more to the difficulty of retrieving early archaeological evidence from ancient Egypt than to the local absence of sawfish historically (see the Appendix S1 for a more detailed account on Egypt).

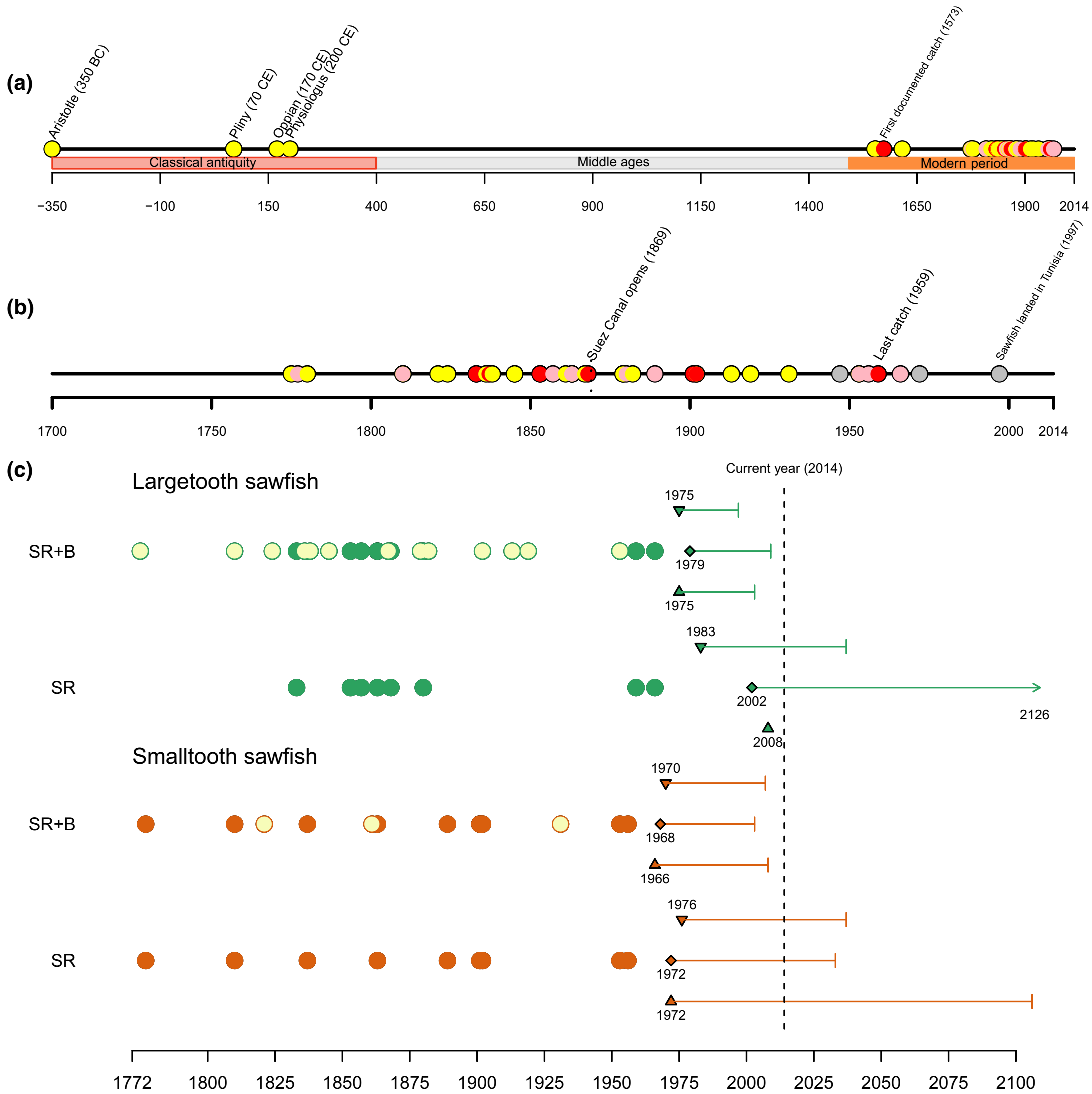

Figure 2 Time lines of records and extinction analyses. (a) Time line of catch records (red) and original bibliographic accounts (yellow) in the Mediterranean Sea. Dots in light red are records without a precise date of capture and thus associated with their publication year. Panel (b) zooms in the period when scientific species catalogues began to be produced. Panel (c) shows the sighting records by species (green dots are for the largetooth sawfish, and orange dots for the smalltooth sawfish), together with the associated estimates of extinction years ($\widehat{T}_E$) and upper bounds of their 95% confidence interval ($\widehat{T}_E^u$). Diamonds are $\widehat{T}_E$ estimates making no assumption on the sighting record process, straight triangles are estimates under the assumption of a declining population, and upside-down triangles are those under the stationary assumptions. SR is the original sighting record. SR + B is the sighting record plus bibliographic accounts (yellow dots).

In general, for the eastern Mediterranean, it is unclear whether the records we found referred to endemic or recently established populations, and/or to individuals occasionally reaching this region from the Red Sea. The two explicit records we found in Syria and Israel were from decades after the opening of the Suez Canal in 1869 and far away from the closest western records. They referred to the smalltooth sawfish (Appendix S1), a species that does not occur in the Red Sea, but, on other occasions, has been confused with the Red Sea's green sawfish and narrow sawfish (e.g. Table 1).

Vagrant or seasonal immigrants might have entered the Mediterranean from the Atlantic

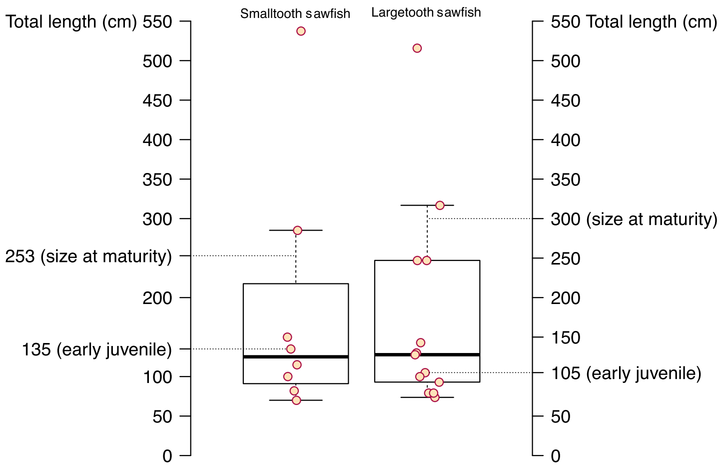

Figure 3 Size distribution of records. Box plots of length distributions of smalltooth and largetooth sawfish catches recorded in the Mediterranean. Size at maturity for both species was taken from Simpfendorfer (2000).

Table 3 *P*-values of the hypothesis that largetooth sawfish and smalltooth sawfish still persist in the Mediterranean Sea, evaluated for different statistical scenario and sighting records.

Species	Data[1]	statistical assumption	*P*-value
Smalltooth sawfish	SR	Stationary	0.11
		Non-stationary	0.12
		Non-parametric	0.08
	SR + B	Stationary	0.04
		Non-stationary	0.04
		Non-parametric	0.03
Largetooth sawfish	SR	Stationary	0.12
		Non-stationary	0.56
		Non-parametric	0.40
	SR + B	Stationary	0.01
		Non-stationary	0.03
		Non-parametric	0.04

[1]SR is the conventional sighting record. SR + B is the sighting record plus bibliographic accounts (details are in methods).

Ocean. Such incursions were historically postulated in some of the literature we reviewed (Adanson 1845; de Robertis 1853) and repeatedly suggested for historical records of sawfish in temperate latitudes of the United States such as off New Jersey and New York (Bigelow and Schroeder 1953; Simpfendorfer 2005; Wiley and Simpfendorfer 2010; Carlson *et al.* 2014). However, based on available sawfish's telemetry data (Thorson 1982a; Simpfendorfer 2003; Whitty *et al.* 2009; Simpfendorfer *et al.* 2010; Carlson *et al.* 2014), these large-scale movements seem unsupported, and particularly unlikely for the multiple records of juveniles we found in areas thousands of kilometres from the uppermost limit of the historical Atlantic sawfish distribution (there are ~3300 km from Mauritania to Provence, and ~3800 km to the Gulf of Naples). Sawfishes are large animals that can be hypothesized to travel these long distances, but such a behaviour has never been demonstrated empirically. The greatest distance ever observed for the largetooth sawfish is 250 km (Thorson 1982a), and 279.1 km for the smalltooth sawfish (Carlson *et al.* 2014).

We contend that information on the physiology, historical population structure and ecology of sawfish is too limited to consider the Mediterranean unsuitable to host residential populations. Occurrence records from the end of the 18th century demonstrated that global sawfish populations contracted in distribution and nearly disappeared from entire coastal continental stretches in less than three centuries (Faria *et al.* 2013; Fernandez-Carvalho *et al.* 2014; Harrison and Dulvy 2014). This period is a small fraction of the whole history of human impact on coastal ecosystems (Rick and Erlandson 2008; Holm *et al.* 2010) and is thus unlikely to represent the full range contraction of baseline sawfish populations. Similarly, available information on sawfish habitat preferences and physiological requirements (including temperature tolerance) is mainly based on a few sawfish populations of Florida and northern Australia (Whitty *et al.* 2009; Poulakis *et al.* 2011, 2013; Simpfendorfer *et al.* 2011), and thus might not be representative of the ecological adaptations of extinct populations.

Is the Mediterranean too cold?

Mediterranean coastal waters encompass the full extent of the thermal range recorded for sawfish (8–30 °C), though in winter, and for northern regions, SST remain below suitable levels (<16 °C, Fig. S4). Also, in some northernmost sectors such as the Gulf of Lions and the northern Adriatic Sea, SST can reach winter minima within the sawfish lethal range (Appendix S1). Thus, the question of how juveniles (<1–2 years) could endure the cold winter waters in rivers, estuaries and coastal waters of these regions remains. A possibility is that these juveniles were unviable offspring of stray pregnant females. Yet, among our records, six juveniles were subadults and thus had sustained at least a winter in the Mediterranean before being captured. Also, this hypothesis entails that multiple gravid females embarked in a multi-thousand kilometre trip from at least Mauritania and were able to arrive in France, Italy or Croatia within a gestation period [5 month for the largetooth sawfish (Thorson 1976), and unknown for the smalltooth sawfish]. Smalltooth sawfishes have been shown to move with an average speed of 1.4 km per day (range: 0.1–9.2 km day^{-1}; Carlson *et al.* 2014). Even if all gravid females travelled at the highest speed recorded, they would have taken 11–13 months to reach these coasts assuming they travelled in a straight line and at a steady rate. Whereas to conclude the trip in 5 months, they would have needed to travel at a speed of 25 km day^{-1}. No sawfish has shown to move with this combination of speed and distance.

Alternatively, we propose two non-mutually exclusive explanations: (i) Mediterranean sawfishes had a greater tolerance to colder temperatures than current remnant populations. A complex stock composition with varying affinities to different temperature regimes is frequent for fishes distributed across wide latitudinal stretches (Brander 1995). Genetic analyses demonstrated that sawfishes have fine-scale geographic population structures (Phillips *et al.* 2011; Faria *et al.* 2013). This is expected for species whose early life stages develop in distinct and geographically complex areas (Sinclair and Iles 1989), have limited mobility and demonstrate high philopatry (Phillips *et al.* 2011; Faria *et al.* 2013). (ii) Mediterranean sawfishes undertook seasonal latitudinal and bathymetric migrations within the basin. Mediterranean water masses below the seasonal surface mixed layer are always warmer than 12 °C (Fig. S5; Millot 1999). Hence, while adults might have moved to southern regions in colder seasons, the less mobile juveniles could have taken refuge in deeper waters.

Sawfish regional extinction

It is unlikely that sawfishes still persist in the Mediterranean 55 years after the last documented catch. The extinction analyses results were variable, influenced by the data used and in a lesser degree by the statistical assumptions adopted; however, but were likely conservative suggesting that sawfish disappeared from the Mediterranean between the 1960s and the 1970s. Our sighting records were sparse and covered only the last 250 years, a period which produced useful scientific publications. These publications differed in the detail they reported and their degree of scientific rigour, and many of them omitted useful information which would have made possible the identification of specific sightings. In fact, only when we combined sightings and less-detailed bibliographic records, did extinctions become significant. Furthermore, not all Mediterranean sectors were equally monitored. The south-eastern Mediterranean is an area generally less researched and was less efficiently covered by our literature search. Finally, we assumed that the conditions influencing the species' abundance and the probability of detection and reporting remained constant through time. In reality, human impact and observation effort have increased rapidly in the last centuries in the Mediterranean (Airoldi and Beck 2007; Coll *et al.* 2010), making omissions of more recent catches or sightings of this peculiar fish highly unlikely. We trust that in the light of the rapid expansion of Mediterranean archaeofaunal records due to improved archaeological methods (Bekker-Nielsen and Bernal Casasola 2007), more findings may become available in the future to help increase the spatial and temporal precision of sawfish extinction history in the region.

Ecological and conservation implications

Evidence supporting the historical occurrence of sawfish in the Mediterranean has notable implications for the biogeography, taxonomy, ecology and conservation of the genus. The historical presence of resident populations would enlarge the historical range of the genus moving it into temperate latitudes, so challenge our current understanding of sawfish temperature tolerance, population structure, migration patterns and from a conservation standpoint, increase the magnitude of global sawfish population decline. Contemporarily, there would be more options to avoid the complete extinction of sawfish from the eastern Atlantic. While some of the recommendations proposed within the Global Sawfish Conservation Strategy (Harrison and Dulvy 2014) may no longer apply in the Mediterranean, reintroduction programmes in some historical habitats of the species might be opportunities worth exploring. Due to challenging socio-economic and marine governance conditions, reintroductions have been considered difficult to implement in Guinea-Bissau where the last eastern Atlantic sawfishes possibly occur (Leeney and Poncelet 2013; Tamburello *et al.* 2014). These actions, however, might be considered in southern France where we identified the last sawfish stronghold of the Mediterranean. The littoral waters of the Camargue National Park still conserve suitable sawfish habitats. France benefits from multiple legal frameworks of management and conservation at the international (such as the Convention on International Trade in Endangered Species), Mediterranean (e.g. the Barcelona Convention) and European Community level (Community actional plan for the conservation of cartilaginous fishes [COM(2009) 40 final], and a stringent ban on fining [Regulation (EU) No 605/2013]), and a well-developed system of monitoring and enforcement. Hence, our results expand the range of possible sites for sawfish reintroductions. Nonetheless, we recognize these programmes can be difficult to implement (Sherkow and Greely 2013) and a careful consideration of potential opportunities and local circumstances at candidate sites would be a first critical step.

If it happened for sawfish, it can happen for all

The history of sawfish in the Mediterranean is an exceptional example of an acute shifting baseline syndrome (Pauly 1995) where the possible occurrence and eventual extinction of large and charismatic marine predators gradually faded from scientific record. A similar process has been described for ecological data sets which show temporal degradation and loss of information when data are not properly organized, described and maintained over time (Michener 2006). For sawfish, we had scant records, published in fugitive and hardly accessible literature, in most cases outliving their original investigator, with a variable level of scientific rigour, and in many cases hidden by linguistic barriers. These factors are compounded by an incomplete understanding of sawfish ecology and of their past distribution which have contributed to a change of perception of sawfish in the Mediterranean. Early on, sawfishes were viewed as natural components of Mediterranean marine communities (late 18th, early 19th century). Subsequently, understanding their abundance and distribution became contradictory and variable (late 19th century, early 20th century). This period was followed by an increasing concern to protect the last individuals left in the area (Cavanagh and Gibson 2007). Finally, the possibility that residential populations have ever existed in the area are now often doubted (Harrison and Dulvy 2014, Faria *et al.* 2013).

We have restored this fading history with a bibliographic and archival approach. We were aided by an increasing availability of digitized historical literature, the millenarian cultural history of the region and by the iconic nature of these fishes. Sawfish peculiar features and cultural importance (Harrison and Dulvy 2014) make them more likely than other species to be found in the literature, artefacts, museums and archives. For many other vulnerable and less peculiar animals, genetic and chemical analyses on museum remains may be the only options to reconstruct their baselines in the Mediterranean and other marine regions. These analyses now provide exciting opportunities to address the uncertainty that still remains with the museum material we inventoried and also makes it possible to test the hypotheses proposed to explain the occurrence of the species in the basin. Nevertheless, fully utilizing historical information from multiple sources can provide important cues for reconstructing structure and function of the ocean, and provide alternative views of the extent of decline of many marine predators, and of overall change of marine ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Summary of the original sawfish accounts found in the Mediterranean Sea: (a) proportions of accounts for smalltooth, largetooth and unidentified sawfishes. Number of accounts is indicated in parentheses; (b) barplot of accounts by nation (most of the *Pristis* spp. accounts had no information on location). Colorcoding of the bar portions is the same as the pie plot's.

Figure S2. Prehistoric remains of sawfish in Egypt.

Figure S3. Possible view point of Mr. Hammontree sighting (a); picture depicting Mr. Hammontree standing in his bunk in front of a map where the air carrier's route had been drawn (b).

Figure S4. Sea Surface Temperature (SST) of the Mediterranean Sea in the coldest and warmest day of 2007.

Figure S5. Profile temperature a northwestern Mediterranean sector in the coldest moth of the year.

Figure S6. Selection of bibliografic and museum finds of sawfish.

Figure S7. Red Sea distribution of *A. cuspidata* (a), according to D'Anastasi *et al.* (2013), and *P. zijsron* (b), according to Simpfendorfer (2013).

Figure S8. Estimates of extinction years ($\hat{T}_E$) and upper bounds of their 95% confidence interval ($\hat{T}_E^u$) when each combination of anecdotal records (*y*-axis) is added to the smalltooth sawfish's SR + B time series.

Figure S9. Estimates of extinction years ($\hat{T}_E$) and upper bounds of their 95% confidence interval ($\hat{T}_E^u$) when each combination of anecdotal records (*y*-axis) is added to the largetooth sawfish's SR + B time series.

Figure S10. Kernel density plots of the posterior distributions of extinction year T_e.

Appendix S1. Supplementary information and results.

Table S1. Sawfish exhibits available in Mediterranean museum of natural history.

Table S2. Structure of the medsharks database.

Table S3. Original quotes extracted from bibliographic accounts about *Pristis pristis*.

Table S4. Original quotes extracted from bibliographic accounts about *Pristis pectinata*.

Table S5. Original quotes extracted from bibliographic accounts about *Pristis* spp.