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Spatial distribution and life history traits of two sympatric, cryptic species of sole in the Adriatic Sea basin

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Abstract

The common sole, *Solea solea* (Linnaeus, 1758), one of the main fishery demersal resources in the Mediterranean, coexists in the Adriatic Sea with the Egyptian sole, *Solea aegyptiaca* (Chabanaud, 1927), which is a congeneric and cryptic species. This study, for the first time in this basin, investigated the spatial distribution of the Egyptian sole by combining all data available from fishery-dependent and independent sampling activities and comparing certain life history traits of the two sole species. The Egyptian sole was common in the north-western coastal waters, with a concentration area of juveniles around the Po River mouth and larger individuals on medium sandy sediments associated with ancient delta systems in the central part of the Gulf of Venice. The hypothesis posits that these areas serve as essential habitats for the Egyptian sole. The two sole species exhibited similar characteristics, with positive allometric growth and sexual dimorphism. An analogous growth trend was observed during ontogeny, characterized by fast growth until the second year of life, with maximum size achievement starting from the third year of life. Both species have the potential to attain lifespans exceeding 10 years. All these analogies confirmed their classification as cryptic species. The hypothesis posits that the two species rely on olfactory sense rather than visual signals for intraspecific recognition. This study represents an initial endeavor to elucidate the characterizing traits and habits that enable these two sibling soles to coexist as distinct species, thereby providing useful information to support resource assessment and management in the Adriatic Sea.

Keywords: common sole; cryptic species; Egyptian sole; life history traits; Mediterranean.

Introduction

The identification and description of cryptic species (classified as a single nominal species due to their ostensibly superficially indistinguishable morphology) are crucial, as they have significant implications for the conservation, protection, and management of biodiversity and natural resources (Bickford *et al.*, 2007). It is necessary to study the main biological and ecological traits to characterize populations and identify their boundaries, even more so in the case of exploited stocks, for which it is essential to develop the most adequate management solutions (Froese & Binohlan, 2000). Life history traits, such as age and growth, constitute the basis for estimating the main parameters (growth rate, mortality rate, and productivity) used in stock assessment analyses (Campana, 2001) and for subsequent management (Hilborn & Walters, 1992).

The common sole, *Solea solea* (Linnaeus, 1758), has

a wide spatial distribution and is considered one of the main demersal resources in the Mediterranean, particularly in the Adriatic Sea, where it accounts for about 37% of the Mediterranean and Black Sea sole landings (GFCM, 2023). Most of the catches are provided by the northern and central areas of the basin (FAO-GFCM GSA17), where the species is mainly exploited by the Italian *rapi-do* trawlers and the Italian, Slovenian, and Croatian set netters (Grati *et al.*, 2013). Common sole coexists with a congeneric species, the Egyptian sole, *Solea aegyptiaca* Chabanaud, 1927. The latter is common in the coastal areas of the south-eastern Mediterranean, extending from Tunisia to Lebanon (Fisher *et al.*, 1987), and is also found in the Adriatic Sea (Tortonese, 1946; Pagotto, 1971; Sabatini *et al.*, 2018), the Gulf of Lion (Borsa & Quignard, 2001), Greece (Boukouvala *et al.*, 2012; Karachle *et al.*, 2016), and the Red Sea, probably having migrated through the Suez Canal (She *et al.*, 1987a; Chanet *et al.*, 2012). Its presence in the Adriatic has been reported since

the 1940s in the south-eastern coastal waters of Albania (Tortonese, 1946), and later, in the late 1960s, the species was also documented in the north-western waters (Pagotto, 1971; Sabatini *et al.*, 2018). These species share the same habitats, consisting of sandy-muddy bottoms in marine and brackish waters. The Egyptian sole exhibits preferences for coastal waters, while the common sole has a wider distribution from the shore to deeper waters (Quéro *et al.*, 1986; Fisher *et al.*, 1987).

These species can be defined as cryptic (Bickford *et al.*, 2007), as they appear to be very similar morphologically: in the past, they were classified as two subspecies or forms of the same species *Solea vulgaris* (Tortonese, 1946; Pagotto, 1971) or, in some cases, as a single species (Ben-Tuvia, 1990; Tinti & Piccinetti, 2000). They are currently recognized as two valid species (Espiñeira *et al.*, 2008; Vachon *et al.*, 2008), and several studies have demonstrated that they are reproductively isolated wherever they have been observed in sympatry (Quignard *et al.*, 1984; She *et al.*, 1987b; Borsa & Quignard, 2001). *Solea aegyptiaca* is an important fishery resource in the eastern Mediterranean, particularly in Egypt, where it is the most common species among soles (Mehanna, 2007; Gabr, 2015). Several authors have defined the resource as being under high fishing pressure (Mehanna, 2007; Gabr, 2015; Desouky, 2016). In other Mediterranean areas, including the Adriatic Sea, the species is absent from fishery statistics due to misidentification by fishermen, with its commercial catches recorded under the landings of common sole (Boukouvala *et al.*, 2012).

The common sole, a species of high commercial value in the Adriatic Sea, is the focus of annual biological and ecological studies to assess stock status for fishery management purposes (Masnadi *et al.*, 2020; FAO-GF-CM SAC, 2022; STECF, 2022; Carbonara *et al.*, 2023). Conversely, we still lack knowledge about the Egyptian sole. Studies on the latter species mainly refer to the south-eastern areas of the Mediterranean Sea, where it is more frequent. Several authors have investigated the reproductive aspects (Ahmed *et al.*, 2010; Khalifa *et al.*, 2019), age and growth, and stock parameters (Mehanna, 2007; Gabr, 2015; Desouky, 2016).

For the first time in the Adriatic Sea, this study aims to: 1) investigate the spatial distribution of the Egyptian sole by combining all data available from fishery-dependent and independent sampling activities; and 2) compare the age and growth of the Egyptian and common sole. The ultimate objective is to shed light on their life history traits to understand the coexistence of two cryptic but distinct species and provide updated basic information to support resource assessment and management in the Adriatic Sea.

Material and Methods

Study area and sampling methods

Fishery-dependent and independent samplings were conducted in the northern and central Adriatic Sea (Fig.

1). Monthly samples of both species were collected in 2021 from commercial fishing activities utilizing different fishing gears (otter trawl, *rapido* trawl, and gillnet) in the Gulf of Venice. The sampling area was chosen based on evidence of the persistence of Egyptian sole through SoleMon (Solea Monitoring Project) surveys and personal field observations. The use of various gear types ensured the collection of specimens across the most comprehensive length range and facilitated sampling during the summer trawl fishing ban. Given the COVID-19 pandemic, onboard activities were avoided, and sampling was carried out at the landing site of the Chioggia fishing fleet, the largest of the Adriatic basin. Fishermen provided geographic information on fishing spots. Further specimens were caught during the SoleMon *rapido* trawl surveys, which are conducted annually in the fall according to a depth-stratified sampling scheme with random allocation of stations across the central and northern Adriatic Sea (Grati *et al.*, 2013; Anonymous, 2019). Moreover, additional information on the presence of Egyptian sole in the north-western Adriatic Sea was obtained from past fishery sampling activities conducted in the same area between 2011 and 2016 under the framework of European Data Collection (EU, 2017).

Sample processing

All the analyzed specimens were obtained from fishery landings and survey activities, without manipulating live animals. The two species were identified by evaluating the external characteristics of the caudal peduncle and, being fresh samples, the color pattern on the right side (Sabatini *et al.*, 2018). All ambiguous specimens were excluded from the analyses. Approximately 60 individuals per species, representing the entire size range, were selected monthly. For each specimen, total length (TL, to the nearest millimeter below), total weight (TW, 0.1 g), sex (female, male, undetermined), and macroscopic maturity stage were recorded. The sagittal otoliths were removed from the inner ear, cleaned, and stored dry in tubes. Both whole otoliths were immersed in ethanol with the distal surface facing upwards (*sulcus acusticus* facing downwards) and read under a stereomicroscope using reflected light against a black background (5x and 10x magnification). When the age estimation was doubtful (in larger/older specimens), the right otolith was transversely sectioned down to the core. The otolith was burned at 350°C for 10 minutes in a muffle furnace. The burned otolith was then embedded in resin (Crystalbond 509 Amber), ground on abrasive paper, and polished with alumina powder. Otolith sections were immersed in fresh water and read under a stereomicroscope with reflected light against a black background (10x magnification). Burning and sectioning techniques were used to improve the quality of observations, enhancing the growth ring contrast (Panfili *et al.*, 2002). This approach is useful with older specimens' otoliths, which increase their thickness and change their growth axis (the "cliff-edge effect") after they reach sexual maturity (Fig. 2). Soles

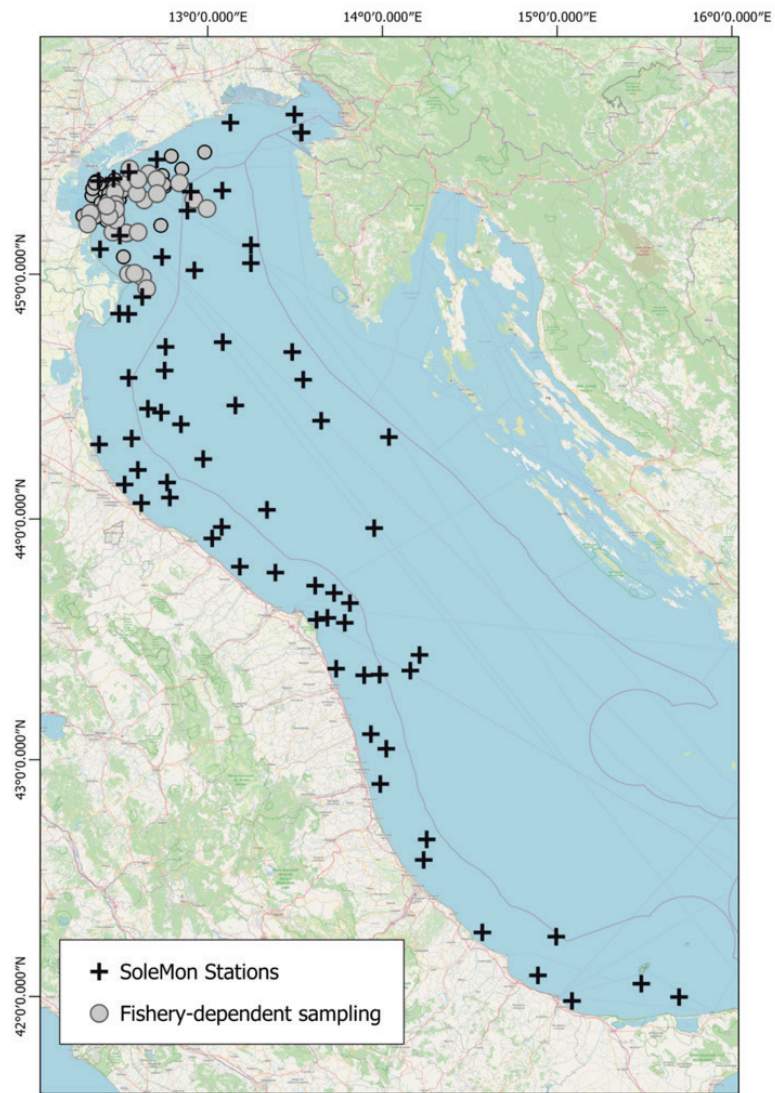


Fig. 1: Map of the study area (north and central Adriatic Sea) with SoleMon survey stations (black crosses) and fishery-dependent sampling spots (gray circles). Background layer from OpenStreetMap (openstreetmap.org/copyright).

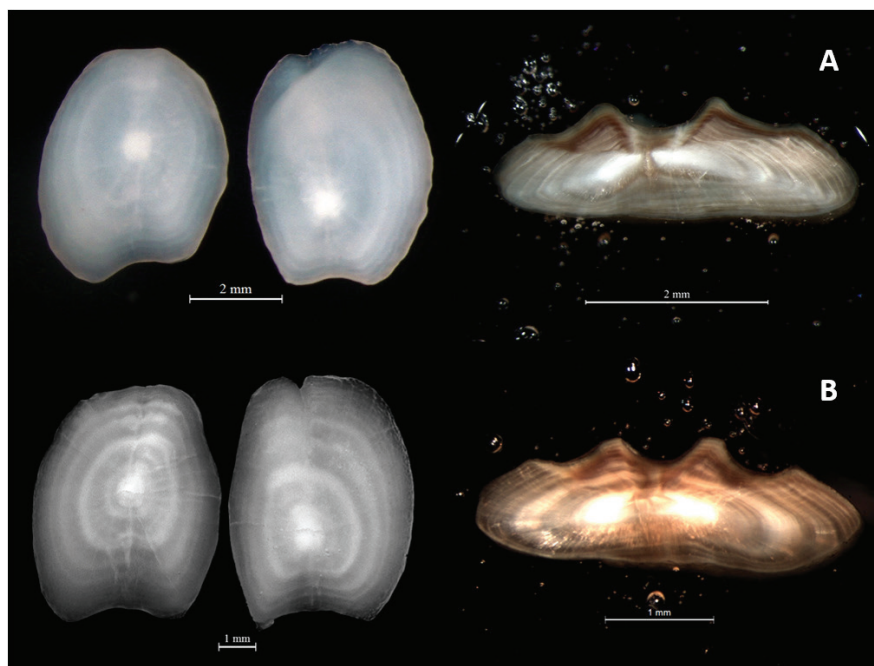


Fig. 2: Whole and sectioned otoliths of Egyptian (A) and common soles (B). It is possible to note the “cliff-edge effect” (the change of the otolith growth axis in older fishes) in both sections.

and other flatfish in the Adriatic Sea are characterized by an opposite pattern of deposition compared to that of other fishes of temperate and cold waters, as the opaque ring is laid down in winter/spring and the translucent ring in summer/autumn (Froglia & Giannetti, 1985, 1986). One opaque and one translucent ring were considered an annual growth (*annulus*) (Carbonara & Follesa, 2019). Two readers independently read the otoliths by counting the opaque rings from the core to the outer edge (Carbonara & Follesa, 2019). The age estimates were compared, and in instances of disagreement, a third evaluation was conducted. The samples were discarded if consensus was not reached. The final age classification considered the edge type (opaque or translucent), the date of capture, and the date of birth. Both species are classified as winter spawners (Vallisneri *et al.*, 2000, 2001; Ahmed *et al.*, 2010; Khalifa *et al.*, 2019); thus, the theoretical date of birth was established as January 1st, a conventionally adopted standard for species with reproductive periods spanning late autumn to early spring (Carbonara & Follesa, 2019).

Data analysis

Maps depicting the spatial distribution of Egyptian sole were generated by comparing the catches from SoleMon surveys and fishery sampling activities. The individuals were arbitrarily grouped into four length classes (< 21 cm; 21-25 cm; 26-29 cm; > 29 cm) to represent the size composition of the catches. These classes were defined on the basis of preliminary available biological information on both species' age, growth, and maturity, as well as the commercial landing size classes (small, medium, large, and extra-large). Abundance and biomass indexes (N km⁻² and kg km⁻², respectively) were calculated for the catches recorded during each annual SoleMon trawl survey (2011-2022). The indices were compared using the Kruskal-Wallis test. When the main test was significant, a post hoc analysis was performed to determine which years differed (Bonferroni's correction was used to adjust the p-values for multiple comparisons). The percentage contribution of the Egyptian sole to the total sole catches was estimated for both fishery-dependent and fishery-independent activities.

The sex ratio (the percentage of females to males) was calculated for each species, and a Chi-squared test (χ^2) was applied to investigate the deviation from the 1:1 ratio. The length frequency distributions (LFD) of females and males were compared using the Kolmogorov-Smirnov two-sample test.

The length-weight relationship was analyzed to describe the growth characteristics of the whole sample and each sex according to the exponential equation: $TW = a TL^b$ (Le Cren, 1951; Froese, 2006). Before fitting the linear regression to \log_{10} -transformed data, the outliers were corrected, when possible, or removed from the sample (Froese *et al.*, 2011). The test for allometry was applied to the b value to assess whether the species exhibited isometric or allometric growth. The F-test was then applied to compare the parameters of the W-L relationship be-

tween females and males and between the two species (Sokal & Rohlf, 1995).

The accuracy of age readings between the two readers was evaluated by calculating the average percentage error (APE) and the mean coefficient of variation (CV) indices (Campana, 2001). Additionally, otolith edge-zone analysis (the monthly percentage of otoliths with an opaque edge) was performed to evaluate the pattern of ring formation and confirm the seasonal deposition of different rings.

The von Bertalanffy growth function (VBGF) was fitted to the length and age data (estimated from the sections) of each species in the form $L_t = L_\infty (1 - e^{-k(t-t_0)})$ (von Bertalanffy, 1938). The function parameters were estimated separately for each sex and the total sample using the R package FSA (Ogle *et al.*, 2023). The Kimura likelihood ratio test was performed to detect differences in growth parameters between sexes and species (Kimura, 1980). The growth performance index was computed according to the formula: $\phi' = \text{Log}_{10} k + 2 \text{Log}_{10} L_\infty$ (Pauly & Munro, 1984) to compare the growth between the two species and with other studies. The significance level was set at $p < 0.05$ for all tests used in the analysis.

Results

Sample size and spatial distribution

A total of 852 Egyptian soles (417 females, 428 males, and 7 undetermined) and 659 common soles (378 females, 280 males, and 1 undetermined) were analyzed. The sex ratio between males and females was 1:0.97 in Egyptian sole and 1:1.35 in common sole. The ratio significantly differed from unity only in common sole (Egyptian sole: Chi-square test, $\chi^2 = 0.14$, $P = 0.71$; common sole: Chi-square test, $\chi^2 = 14.60$, $P < 0.001$).

Table 1 depicts the total length and weight ranges of specimens. Length frequency distributions of sexes were roughly bimodal in both species (Fig. 3). The modal classes for Egyptian sole were 17 cm and 25 cm for males, and 21 cm and 28 cm for females, whereas the modal classes for common sole were 20 cm and 25 cm for males, and 20 cm and 26-27 cm for females. Females attained a larger size than males in both species, and the two-sample Kolmogorov-Smirnov test revealed a significant difference between the two length frequency distributions (Egyptian sole: $D = 0.255$, $P < 0.001$; common sole: $D = 0.281$, $P < 0.001$).

The SoleMon surveys (data from 2011 to 2022) mainly recorded smaller and medium-sized Egyptian soles (length classes < 21 cm and 21-25 cm) in the north-western coastal waters (Fig. 4A, Table S1). The catches of the largest individuals (length categories 26-29 cm and > 29 cm) were more frequent from commercial fishery activities, particularly from otter trawlers and gillnetters. Fishing provided additional information on the spatial distribution of this species, as the largest individuals were mainly caught in the central area of the Gulf of Venice (Fig. 4B). Several fishermen confirmed the presence of

Table 1. Results of the length-weight relationship analysis for Egyptian (SA) and common sole (SS): *a* and *b* parameters (95% confidence limits); coefficient of determination (R^2); number of specimens without outliers (N); total length (TL) and weight ranges referring to the total sample and each sex; t test for allometry (t-test) and associated probability (P). Significant test results are shown in bold.

		a (95% CL)	b (95% CL)	R²	N	TL (cm)	Weight (g)	t-test	P
SA	Total	0.0038 (0.0034-0.0042)	3.29 (3.26-3.32)	0.98	841	14.3-37.0	24-632	17.09	< 0.0005
	Females	0.0031 (0.0027-0.0036)	3.36 (3.31-3.40)	0.98	410	15.1-37.0	28-632	15.32	< 0.0005
	Males	0.0055 (0.0048-0.0064)	3.16 (3.12-3.21)	0.98	424	14.3-33.7	25-389	6.74	< 0.0005
SS	Total	0.0032 (0.0028-0.0037)	3.30 (3.26-3.34)	0.98	655	13.0-37.5	15-712	14.66	< 0.0005
	Females	0.0031 (0.0026-0.0036)	3.32 (3.27-3.37)	0.98	378	13.0-37.5	15-712	12.26	< 0.0005
	Males	0.0044 (0.0036-0.0054)	3.19 (3.13-3.26)	0.97	276	13.3-29.8	18-230	5.70	< 0.0005

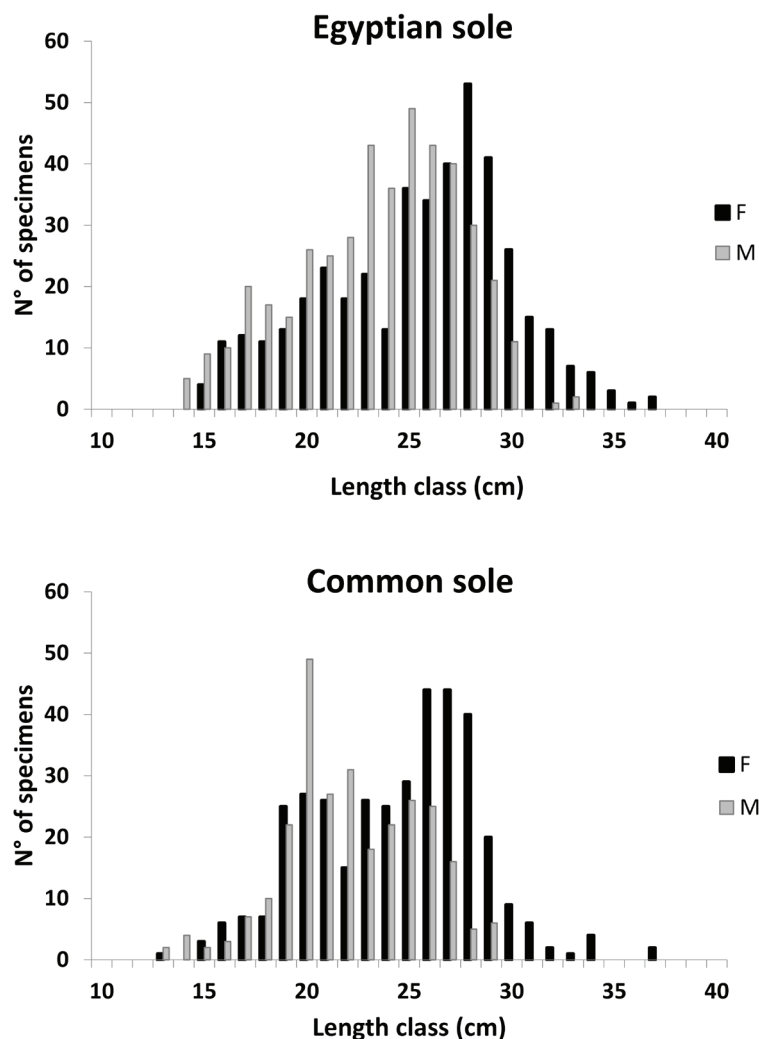


Fig. 3: Length-frequency distributions (1-cm length classes) of females (black bars) and males (gray bars) of Egyptian (A) and common soles (B) from the Adriatic Sea basin.

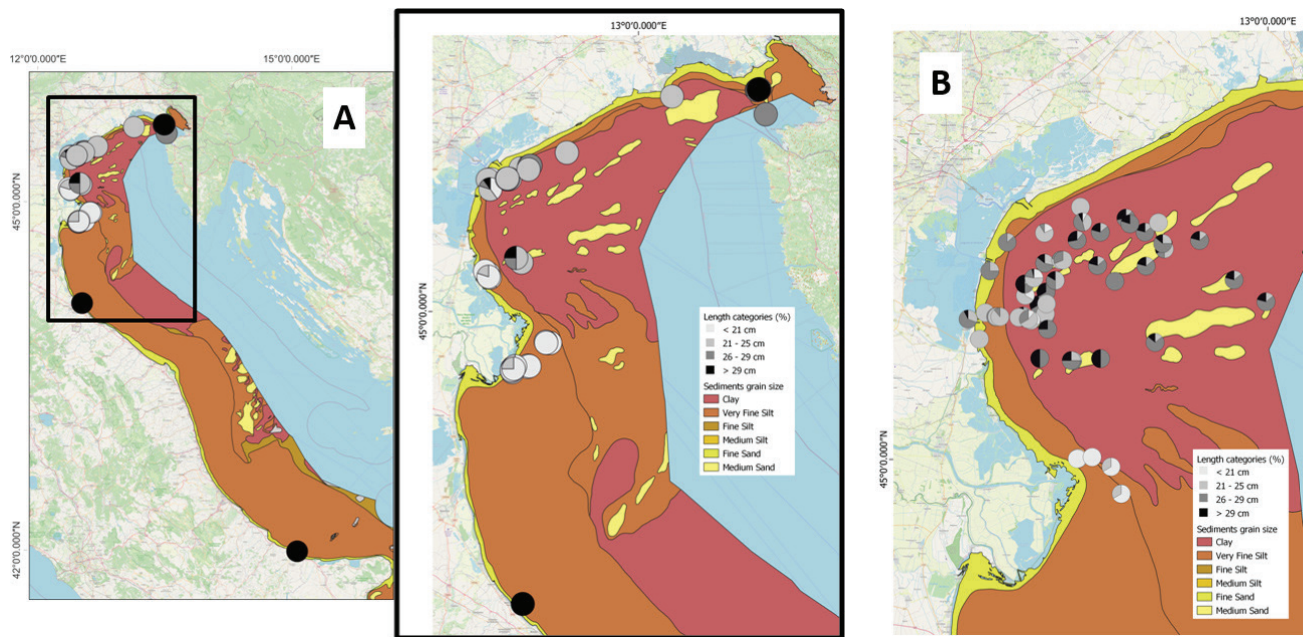


Fig. 4: Maps of the spatial distribution of Egyptian sole catches in the north and central Adriatic Sea: A) data from SoleMon surveys (from 2011 to 2022) and B) data from fishery-dependent sampling activities (2011-2016 and 2021). Pie charts show the percentage of the four length classes (< 21 cm, 21-25 cm, 26-29 cm, and > 29 cm). Sediment distribution layer modified from CARG (Cartografia geologica e geomatica. Carte geologiche dei mari italiani [foglio NL-33-7 Venezia]). Produced by CNR ISMAR and digitalized by ISPRA. Background layer from OpenStreetMap (openstreetmap.org/copyright).

large soles on medium sand sediments that extend parallel to the Venetian coasts between 8 and 10 nautical miles. The coordinates provided by fishers were superimposed on the sediment map (Fig. S1). The presence of Egyptian sole in the SoleMon surveys reached approximately 0.5-1% of the total soles caught (Table S1), whereas the species amount in commercial landings ranged from 0.1% to over 80% (Table S2). The abundance and biomass indices fluctuated over time, reaching the lowest values during the SoleMon survey in 2017 and the highest values in 2020 (Fig. S2). Nevertheless, the Kruskal-Wallis test did not reveal any significant differences between the years for both indices (abundance index: $H_{11} = 7.46$, $P = 0.76$; biomass index: $H_{11} = 7.60$, $P = 0.75$).

Life history traits

A length-weight relationship analysis was performed for the whole sample (including the unsexed individuals) and each sex (Table 1). Both species showed positive allometric growth, with parameter b significantly higher than 3. The comparisons of the W-L relationships showed a significant difference between the sexes (Egyptian sole: Fisher test, $F = 32.88$, $P < 0.0001$; common sole: Fisher test, $F = 8.87$, $P = 0.003$). No evidence of a significant difference in slopes was detected in the length-weight relationship between the two species (all samples: $F = 0.204$, $P = 0.65$; females: $F = 1.154$, $P = 0.28$; males: $F = 0.518$, $P = 0.47$); however, there was a significant difference in the intercept parameter (in all the comparisons, $p < 0.00001$). Therefore, regardless of the log-transformed lengths of the fish, there was a consistent difference between the log-transformed weights of the two species.

The comparison of age precision between the two readers showed good concordance for both species (Table S3). Interestingly, the precision increased when the age was estimated from sectioned otoliths, as sectioning possibly reveals less unambiguous ring patterns.

The otolith edge-zone analysis confirmed the alternation of one opaque and one translucent ring laid down annually for both species. The opaque ring was laid between late winter and spring until June for the Egyptian sole and May for the common sole (Fig. 5).

The age was estimated for 695 Egyptian soles and 948 common soles (estimations of all otoliths collected during the SoleMon survey 2021 were added to better cover all the age classes). The maximum age classes recorded were 7⁺ and 9⁺ years through the analysis of whole otoliths in Egyptian and common soles, respectively, while 16⁺ and 15⁺ years were determined through the reading of otolith sections. More than 80% of the individuals ranged between 0⁺ and 2⁺ years. The analysis of sectioned otoliths revealed that some individuals were over 10 years old, and the oldest specimens were not only those with the greatest length.

The von Bertalanffy growth curves showed a similar trend between species, with fast growth in the first two years of life and asymptotic-length achievement starting in the third year (Fig. 6). The trend was similar between sexes, but females tended to be bigger and reached a higher asymptotic length than males (Table 2). The likelihood ratio test revealed a difference between the overall growth curves of the two species, even when the same sex was compared. Still, no single parameter was significantly different from the other. Evident differences between the sexes were detected in both species. The asymptotic length of females was significantly greater than that of

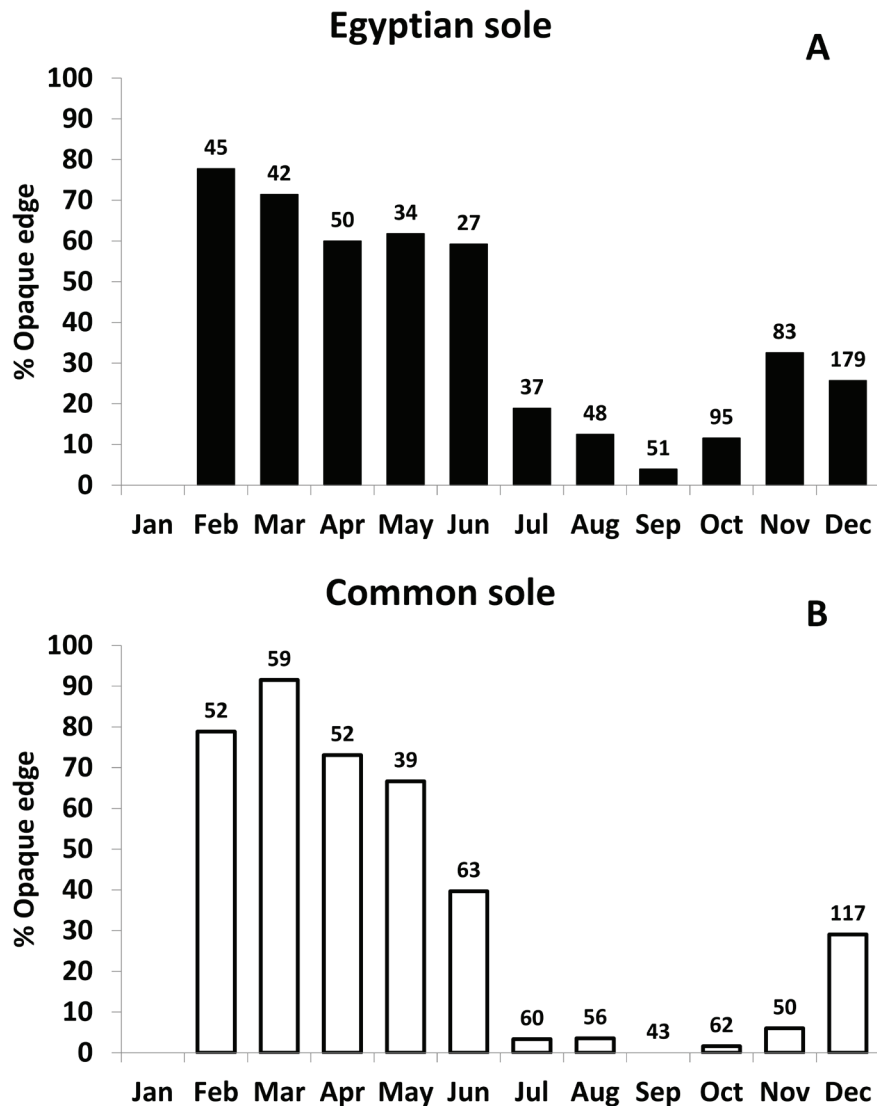


Fig. 5: Otolith edge analysis showing the monthly percentage of otoliths with an opaque edge for Egyptian sole (A) and common sole (B). Values on the bars indicate the number of specimens analyzed.

males. The k value was higher in males, but the difference was only significant in the common sole (Table 3).

Discussion

Spatial distribution of Solea aegyptiaca in the Adriatic Sea

To date, published information on Egyptian sole in the Adriatic Sea is limited to some records from different basin areas. Tortonese (1946) recorded the species' presence in the Albanian coastal waters, while Pagotto (1971) reported the species from the sole landings at the Chioggia market in the north-western Adriatic. More recently, a study conducted by Sabatini *et al.* (2018) focused on the genetic and morphological differentiation between the common and Egyptian sole. The study collected specimens from different Adriatic areas, including the Venice lagoon, the coastal area adjacent to the Po Delta, the Gulf of Trieste, Slovenia, and Termoli. One of the objectives

of this study was to combine recent field data with existing information to shed light on the presence of this cryptic species in the Adriatic. The SoleMon surveys, established in 2005 to monitor demersal and benthic fishery resources, particularly the common sole in the north and central Adriatic Sea (Anonymous, 2019), provided valuable information on the persistence of the Egyptian sole. Scientific personnel began to record its presence in 2011. Since then, some specimens have been caught every year, especially in the northwestern coastal area. Furthermore, scientific fishing mainly captured small and medium-sized individuals, corroborating the hypothesis that the mouth of the Po River and the littoral zone are essential habitats for the juveniles of several marine species, including the Egyptian sole (Franzoi *et al.*, 2010; Colloca *et al.*, 2015). The southernmost record (Termoli's seashore) occurred in proximity to the Lesina and Varano Lagoons, which potentially serve as other essential habitats for this species that need to be investigated in the future (Sabatini *et al.*, 2018). The fishing fleet data consolidated the information, indicating the presence of

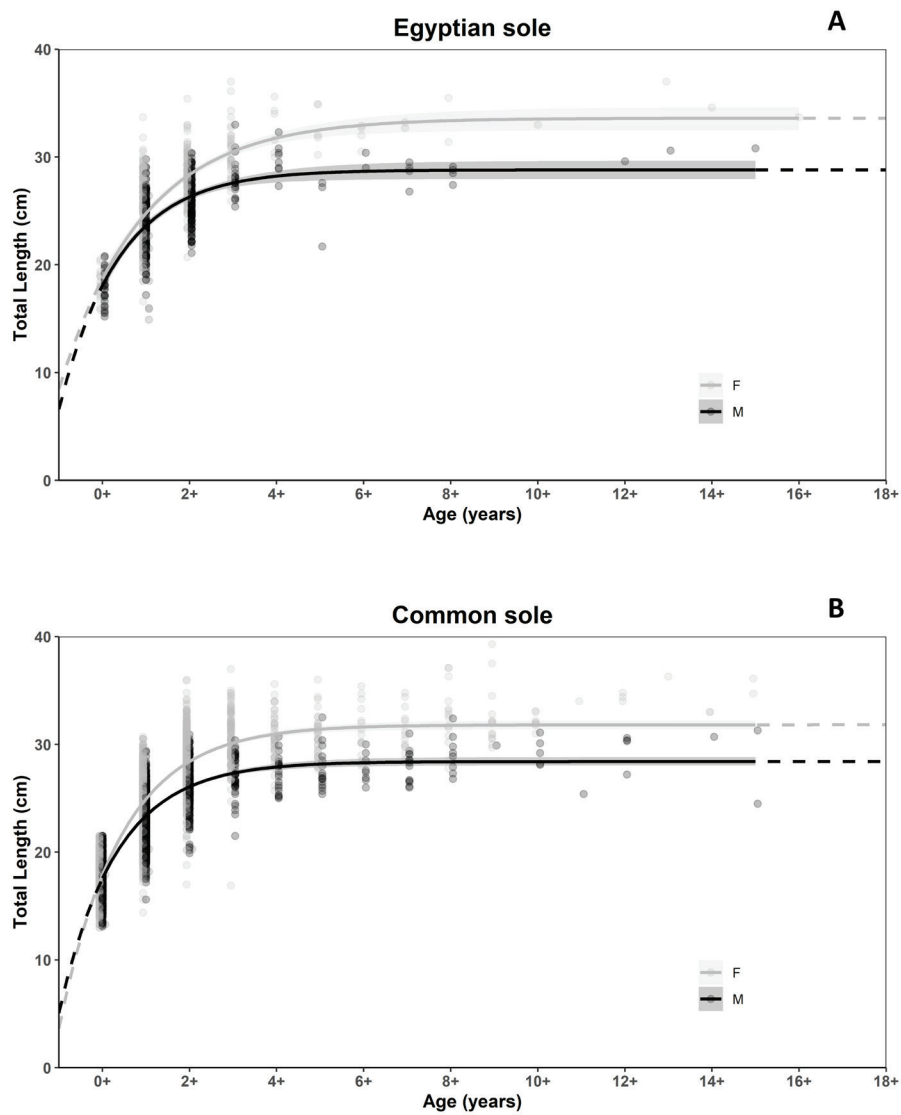


Fig. 6: Von Bertalanffy growth functions fitted on age-length data pairs of females and males estimated for Egyptian sole (A) and common sole (B).

Table 2. Von Bertalanffy growth curve parameters (L_{∞} = asymptotic length, k = growth rate coefficient, t_0 = theoretical age at length zero) and growth performance index (ϕ').

		L_{∞}	k	t_0	ϕ'
Egyptian sole	Total sample	31.3	0.60	-1.5	2.77
	Females	33.6	0.52	-1.6	2.77
	Males	28.8	0.73	-1.4	2.78
Common sole	Total sample	31.8	0.53	-1.4	2.73
	Females	33.7	0.48	-1.5	2.74
	Males	29.0	0.61	-1.4	2.71

the largest individuals in the central area of the Gulf of Venice. This observation was corroborated by several fishermen, who shared their knowledge on the existence of concentration areas of large soles in correspondence to medium sandy sediments extending between 8 and 10

nautical miles from the Italian coast (shown in Fig. S1). These sediments are classified as Aeolian sand accumulations (dunes) associated with ancient delta systems at different depths: 20-30 m, around 40 m, and between 70 and 100 m (Fig. S3) (Brambati & Venzo, 1967). The Hol-

Table 3. Kimura likelihood ratio test comparing von Bertalanffy parameters between sexes and the two species (SA = *Solea aegyptiaca*, SS = *Solea solea*, F = females, M = males, χ^2 = test value, P = associated probability). Significant test results are shown in bold.

	L_{∞}		k		t_0		all	
	χ^2	P	χ^2	P	χ^2	P	χ^2	P
SA F vs SA M	28.18	< 0.001	3.75	0.053	0.55	0.460	98.97	< 0.001
SS F vs SS M	44.50	< 0.001	5.20	0.023	0.74	0.390	146.97	< 0.001
SA F vs SS F	0.004	0.953	0.35	0.554	0.04	0.840	32.53	< 0.001
SA M vs SS M	0.15	0.704	1.97	0.161	0.008	0.927	61.75	< 0.001
SA vs SS	0.78	0.376	1.29	0.256	0.15	0.703	53.01	< 0.001

ocene transgression, characterized by the alternation of expansion and regression stages, modeled the shorelines with typical continental or shallow water morphologies, such as beaches, deltas, dunes, channels, riverbeds, etc., at different depths. Some of these dunes reach 3 m in height and create complex dune-beach systems that extend for kilometers along different bathymetric contours (Brambati, 1992). Concentration areas can explain the high amount of Egyptian sole recorded in certain commercial landings, mainly from otter trawlers (Table S2). This ontogenetic spatial separation may be affected by several biological factors, such as prey availability or predation risk, which are, in turn, influenced by hydrological and geomorphological conditions (Able *et al.*, 2005), as hypothesized for the common sole distribution in the Adriatic (Grati *et al.*, 2013). Indeed, common sole is characterized by ontogenetic migration, with juveniles concentrated along the Italian side, mostly around the mouth of the Po River and in lagoons. During their growth, these juveniles progressively move along the entire coast from Trieste to Ancona and south-east toward deeper waters (Grati *et al.*, 2013; Scarcella *et al.*, 2014). The central-eastern offshore waters (south-west from the Istrian peninsula) were described as an area where adults congregate. This area has been defined as a “sole sanctuary” (Scarcella *et al.*, 2014) due to the presence of a unique benthic community, dominated by holothurians and bryozoans (Santelli *et al.*, 2017), which provides protection to large spawners from trawl fishing activities. The examination of sediment distribution over the entire basin (Fig. S4) indicates that the “common sole sanctuary” is associated with sand sediments. It is plausible to assume that the adults of both species concentrate on substrates with this granulometry as they can find suitable prey. Additional research on feeding habits in relation to food availability will elucidate the factors underlying these ontogenetic spatial distributions.

This study demonstrated the usefulness of involving sea users in scientific research. Local fishermen’s knowledge can be a powerful tool to enhance and complement scientific observations (Huntington, 2000), supporting the ecosystem approach to fishery resource management (Berkes, 2009; Bastari *et al.*, 2022), particularly for rare and lesser-known species. The integration of fishery-independent and dependent sampling provided a clearer picture of the spatial range of a less-frequent species, namely the Egyptian sole. In contrast to the common sole, which occupies a wider depth range (Piccinetti & Giovanardi, 1984; Scarcella *et al.*, 2014), its preference for shallow and brackish waters (depth less than 40 meters, Table S1) was confirmed (Chabanaud, 1927; Quéro *et al.*, 1986). In-depth investigations into the ecological roles and connections between the described aggregation areas may prove to be useful for management purposes. Area-based fisheries management measures are widely developed and implemented to protect key elements and promote the sustainable use of resources by the fisheries (Petza *et al.*, 2021; Ortega *et al.*, 2023). The evidence of their function as essential habitats could lead to the implementation of spatial management tools, i.e., permanent or temporal fishing restrictions, to strengthen the network of key areas for the different life stages. Finally, to better understand the actual spatial distribution of Egyptian sole in the entire Adriatic basin, it is essential to integrate the information with data collected from other harbors along both coastal sides and from the lagoons.

Comparison of life history traits

The specimens of both species examined in this study exhibited positive allometric growth, with individuals having a higher rate of increase in weight or width than in length (Froese *et al.*, 2011). It was observed that, at

equal sizes, Egyptian soles tended to be more massive than common soles. The comparison with the length-weight relationships available for each species confirmed the positive allometric growth observed in this study area (Fig. S5). Data regarding the Egyptian sole is limited and pertains almost exclusively to the Eastern Mediterranean region (Egypt). Researchers documented isometric growth in the city of Port Said and Quarun Lake ($b = 3$ and 2.9 , respectively) (Mehanna, 2007; Desouky, 2016), while positive allometric parameters ($b = 3.179$ and 3.146) were observed in the Bardawil Lagoon and in samples collected from Egyptian waters (Gabr, 2015; Mehanna & Farouk, 2021). Information available for the common sole covers the entire distribution range of the species. Even in this case, the parameter b varied from isometry to positive allometry without a discernible geographical pattern (Table S4). Within-species variations in length-weight relationships are common, influenced by population characteristics, seasonal factors, and changes in environmental conditions (Froese, 2006). Both species exhibited sex-related dimorphism. Larger females may have an advantage in sustaining larger eggs and higher offspring production. Indeed, fish fecundity may increase disproportionately with body mass, and energy investment into offspring may heighten with the increment in parental size (Hixon *et al.*, 2014; Barneche *et al.*, 2018).

The otolith edge-zone analysis showed a similar ring deposition pattern between species, consisting of winter-spring deposition of opaque rings and summer-autumn deposition of translucent rings. The annual periodicity of ring deposition was thus confirmed and corresponded to the pattern reported for flatfish in the Adriatic Sea (Frogliola & Giannetti, 1985, 1986). The authors noted an opposite deposition pattern to most cold and temperate water species. Environmental conditions (temperature and food availability) and biological and physiological cycles, such as reproduction and settlement, which can change over time and space, influence the process of otolith growth and ring deposition (Campana, 1999; Panfili *et al.*, 2002).

Both species demonstrated an analogous growth trend during ontogeny, marked by rapid growth until the second year of life and the attainment of asymptotic length beginning in the third year of life. A wide length range at each age was also observed, signifying considerable heterogeneity in individual growth. Based on tagging data, Piccinetti & Giovanardi (1984) reported very different growth rates among specimens of the same age, such as 2 cm per month versus 2 cm per year. The growth process depends on an array of intrinsic and extrinsic factors such as temperature, food supply, oxygen, etc. (Weatherley, 1990). Therefore, the high variation observed can be influenced by the birth month and ecological conditions that can change temporally or spatially, depending on environmental variability (Fanelli *et al.*, 2022).

The common sole values of asymptotic size obtained in this study were lower than those documented in research undertaken in other geographical areas, particularly the northeastern Atlantic. Conversely, the Adriatic Sea sole population exhibited higher values of the Brody growth rate coefficient k (Fig. S6, Table S5). It is plausi-

ble to hypothesize that the northern Adriatic area, characterized by eutrophic waters and lagoon systems, provides favorable environmental conditions that promote body growth before sexual maturity (Taylor *et al.*, 2007; Brehmer *et al.*, 2013). Indeed, favorable environmental conditions support metabolism, functional abilities, and lifespan (Lloret *et al.*, 2014). It should also be noted that the application of different methods may yield discrepancies in age and growth parameter estimations. The growth parameters and performance index of the Egyptian sole estimated in this study were similar to those reported in the Eastern Mediterranean by Mehanna (2007) (Fig. S6, Table S5).

The analysis of sectioned otoliths revealed the actual longevity of these species in the study area, indicating the possibility of a lifespan exceeding ten years of age. The presence of very old (and large-sized) individuals is remarkable since they bolster population resilience against natural and anthropic perturbations, significantly influencing long-term population dynamics (Froese, 2004; and references therein; Hixon *et al.*, 2014). In fact, long-lived individuals are usually reservoirs of a better genetic inheritance, and their prolonged reproductive phase can promote recruitment success (Froese, 2004). As previously mentioned, larger and older females contribute more significantly to population replenishment, being much more prolific and producing larger and more resistant offspring over a longer lifespan. Hixon *et al.* (2014) highlighted the essential role of the big-old-fat-fecund-female fishes (BOFFFFs) in fostering stock productivity and stability and the importance of implementing management actions focused on conserving the old-growth age structure in fished stocks. Considering all these observations, the sectioning method is necessary to obtain the most reliable population age estimate, avoiding an underestimation of longevity. This approach is applied to common sole (Carbonara & Follesa, 2019; Vitale *et al.*, 2019), and the studies conducted in Mediterranean waters reported a maximum age of 8-9 years (Ramos, 1982; Türkmen, 2003; Cerim & Ateş, 2020). In this study, the older individuals reached 15 years of age, which is more comparable to the values reported for the Atlantic area (Table S5), where the species can exceed 20 years of age (Deniel, 1990). Previous research on Egyptian sole reported a maximum age of 3 to 4 years based solely on whole otolith readings, potentially underestimating its longevity (Mehanna, 2007; Gabr, 2015). However, even when comparing the age estimates derived from the same reading approach (whole otoliths), the values obtained for the Egyptian sole in the Adriatic Sea basin were higher than those in Egyptian waters, 7+ years versus 4 years, respectively. These differences could be the effect of sampling activities (areas, intensity, harvest methods, etc.) and the different size ranges investigated (14.3-37 cm in the Adriatic versus 9.5-31 cm in the eastern Mediterranean), although old individuals of 27-30 cm were also observed in the Adriatic Sea. The presence of very old individuals among the Adriatic common soles was explained by the existence of the "sole sanctuary", the offshore area southwest of the Istrian peninsula where elder specimens

can survive due to the absence of trawl fishing (Scarcella *et al.*, 2014). No Egyptian soles have ever been harvested in that “sanctuary” area, and all the oldest Egyptian sole specimens were derived from the fishery-dependent sampling. It is plausible to also hypothesize the presence of refuge areas for this species. The complex system of Aeolian dunes (Fig. S3), characterized by variable morphologies and structures that can rise up to 3 meters from the seabed (Brambati, 1992), may provide refuge that reduces the probability of capture by trawling. Furthermore, the Egyptian sole prefers shallow and brackish waters; therefore, coastal lagoons may represent another safer area for the species. As previously stated, these hypotheses indicate the need for further investigation into the functions of these habitats for the species and, if necessary, the implementation of protection measures. Spatial management measures may enhance the survival prospects of the largest and oldest specimens, thereby supporting population maintenance and proliferation.

In conclusion, this study presents a first comparison of specific life history traits between the Egyptian and common soles in the northern and central Adriatic Sea basin. The species exhibited similar growth characteristics, confirming their classification as cryptic species and clarifying the challenges faced by fishermen in identifying them. There are several reasons why morphology is not used to differentiate between the species. According to Bickford *et al.* (2007), cryptic species typically rely on pheromones or mating calls, rather than visual signals, to recognize a conspecific. Additionally, they may be exposed to certain conditions, such as extreme environments, that promote their morphological stasis. Sibling species are common among species with more highly developed chemical senses than visual ones (Mayr, 1963). Studies investigating the feeding behavior of flatfish concluded that soles have more well-developed olfactory sensors than sight, which they use to detect prey in the sediments (de Groot, 1969; 1971). It may be hypothesized that the olfactory sense plays a role in intraspecific recognition, negating the primary importance of the external aspect in this circumstance. Moreover, other traits, such as different reproductive cycles and/or trophic niches, may play a role in species separation. Intrinsic and extrinsic factors can influence these characteristics, causing them to change spatially and temporally (Rijnsdorp *et al.*, 1991; Gibson, 1997; Able *et al.*, 2005; Vinagre *et al.*, 2008; Tsikliras *et al.*, 2010). Studies on the reproductive period classified both species as winter spawners; however, information for the Adriatic Sea is available only for the common sole (Piccinetti & Giovanardi, 1984; Vallisneri *et al.*, 2000, 2001), whereas information on Egyptian sole refers to the south-eastern Mediterranean (Ahmed *et al.*, 2010; Khalifa *et al.*, 2019). Although there are no comparative studies on feeding habits, the diet of both species was separately investigated at Port Said (Egypt). What emerged was that both species are opportunistic feeders, relying on a wide range of benthic invertebrates, mainly polychaetes (Sharaf *et al.*, 2007; El-mor & Ahamed, 2008). The prey spectrum was described at a high taxonomic level, so no thorough discussion on trophic overlapping was report-

ed. Given these considerations, additional comparative investigations between the two soles in the Adriatic Sea are needed to unveil which habits and traits, such as reproductive cycle and feeding activities, enable them to coexist as similar yet distinct species.

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Supplementary Material

The following supplementary material is available for this article:

Fig. S1: Spatial distribution of medium sand sediments indicated by fishermen (light blue diamond) superimposed on the map of sediments (layer modified from CARG (Cartografia geologica e geomatica). Carte geologiche dei mari italiani (foglio NL-33-7 Venezia). Produced by CNR ISMAR and digitalized by ISPRA). Background layer from OpenStreetMap (openstreetmap.org/copyright).

Fig. S2: Egyptian sole A) abundance index (N km⁻²) and B) biomass index (kg km⁻²) from SoleMon surveys 2011-2022.

Fig. S3: Reconstruction of the submarine morphology of the northern Adriatic continental shelf (modified from Brambati & Venzo 1967, in Brambati 1992).

Fig. S4: Sediment distribution across the Adriatic Sea (modified from Pigorini 1968, in Brambati 1992).

Fig. S5: Scatterplots of log *a* vs *b* from available WLRs studies (modified from FishBase <https://fishbase.se>. Accessed on 03 October 2023). Dots represent the samples from this study (black), other estimates of the same species (red - 2 studies for Egyptian sole (A) and 27 studies for the common sole (B)), other soleids (green), and other bony fishes (yellow).

Fig. S6: Scatterplots of *k* parameter vs asymptotic length from available studies (modified from FishBase <https://fishbase.se>. Accessed on 03 October 2023). Dots refer to the samples from this study (black), other estimates of the same species (red - 2 studies for Egyptian sole (A) and 32 studies for the common sole (B)), other soleids (green), and other bony fishes (yellow).

Table S1. *Solea aegyptiaca* and *Solea solea* indices of abundance (N km⁻²) and biomass (kg km⁻²) by depth strata (0-30 m, 30-50 m, 50-120 m) recorded within SoleMon trawl-surveys (2011-2022), S.D. = standard deviation.

Table S2. Total catches (kg) of both sole species and percentage of Egyptian soles in some daily commercial fishing landings monitored during the study (GNS = gillnetters; OTB = otter trawlers; TBB = *rapido* trawlers; SA = *S. aegyptiaca*; SS = *S. solea*).

Table S3. Mean coefficient of variation (CV) and index of average percentage error (APE) as measures of age reading precision between the two readers.

Table S4. Growth parameters (a and b) of *S. solea* from different localities and sampling years; coefficient of determination (R^2); number of specimens (n); total length (TL).

Table S5. von Bertalanffy growth curve parameters and growth performance index of common and Egyptian sole from different localities and sampling years (modified from FishBase <https://fishbase.se>. Accessed on 03 October 2023); Max age = maximum age estimated (s = sectioned otoliths, w = whole otoliths, na = information not available).