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Non-indigenous cephalopods in the Mediterranean Sea: a review

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*The present review critically assesses the records of cephalopods that have entered the Mediterranean Sea in the last few decades. It includes 13 species, namely *Sepia dollfusi*, *Stoloteuthis leucoptera*, *Sepioteuthis lessoniana*, *Architeuthis dux*, *Cranchia scabra*, *Taonius pavo*, *Megalocranchia sp.*, *Teuthowenia megalops*, *Cycloteuthis sirventi*, *Taningia danae*, *Octopus cyanea*, *Amphioctopus sp.* and *Tremoctopus gracilis*. The presence of *Sepia pharaonis* needs to be confirmed, whereas that of *Sepia gibba* and *Spirula spirula* is excluded. The arrivals from the Atlantic Ocean through the Strait of Gibraltar are related to the entrance surface current, which either carried passively planktonic paralarvae or favoured in some other way the entrance of subadult and adult stray specimens. As a matter of fact, all Atlantic cephalopods are pelagic oegopsid squids, with the exception of the nekto-benthic sepiolid *S. leucoptera*; all of them have been found only in the western Mediterranean basin. None of them seemingly established a stable population there, apart the latter species. On the contrary, the cephalopods entering the Mediterranean from the Red Sea through the Suez Canal (Lessepsian migrants) lead a benthic mode of life. At least two of them, namely *S. lessoniana* and *Amphioctopus sp.*, set up stable populations in the eastern basin. Lastly the occurrences of the pelagic octopod *T. gracilis* are ascribed, in the literature, to human-mediated transfer.*

Key words: Mollusca, Cephalopoda, exotic species, Lessepsian migrants, cryptic species

INTRODUCTION

In recent years, the invasion of Mediterranean waters by non-indigenous species (NIS) has represented a growing and concerning problem because of their impact on marine ecosystems. The introduction of NIS together with climate

change (THIÉBAULT *et al.*, 2016), resource over-exploitation (e.g. VASILAKOPOULOS *et al.*, 2014; TSIKLIRAS *et al.*, 2015), pollution (e.g. DANOVARO, 2003; FOSSI *et al.*, 2018) and other anthropogenic stressors (e.g. DURRIEU DE MADRON *et al.*, 2011) is threatening the equilibrium of Mediterranean ecosystems and its biodiversity. Recent

reviews have recorded the presence of little less than a thousand NIS in the Mediterranean Sea (BONANNO & ORLANDO-BONACA, 2019; ROTTER *et al.*, 2020). NIS have entered this basin either through one of its two openings, i.e. the Strait of Gibraltar and the Suez Canal, or by other pathways depending on anthropic transport (e.g. shipping, aquaculture, aquarium trade, live food/bait trade, colonized floating man-made objects) or other human-mediated causes (ROTTER *et al.*, 2020). A closer attention has been paid to the entrances from the Red Sea via the Suez Canal, which date since its man-made opening in 1869 (GALIL, 2007). The recent enlargement of this canal has further accelerated and facilitated the introduction of Red Sea species into the Mediterranean Sea (GALIL *et al.*, 2015, 2017; QUEIROZ & POOLEY, 2018).

Only a fraction of these species is capable of spreading, settling and establishing stable populations in the Mediterranean Sea (SERVELLO *et al.*, 2019), whereas other invasions are limited to some areas near their basin of origin, as in the case of molluscan pseudo-populations in the Alboran Sea described by BOUCHET & TAVIANI (1992). Since the '90s the phenomenon of NIS arrivals was seemingly accelerated because of the warming up of the Mediterranean waters, which has favoured the entrance and survival of mainly tropical and sub-tropical fauna and flora elements (ANDALORO & RINALDI, 1998; THIÉBAULT *et al.*, 2016).

As regards Cephalopoda, apparently no NIS had been recorded in the Mediterranean up to the '80s: MANGOLD & BOLETZKY (1988) reported no exotic cephalopod in their review. However, it was afterwards shown that allochthonous cephalopods had been already collected, though misidentified, in the Mediterranean Sea as early as the middle '30s (MIENIS, 2005; ORSI RELINI *et al.*, 2009).

In the last two decades, the occurrence of non-indigenous cephalopods in the Mediterranean has been recognized not to be at all negligible, thanks to the increasing attention on both Atlantic and Lessepsian migrant species, above all by Spanish and Italian scientists as well as Greek, Turkish and Israeli researchers, respec-

tively (see Results). However, the first monitoring experiences on NIS in the Mediterranean Sea paid little attention to the presence of allochthonous cephalopods. For instance, the *CIESM Atlas of Exotic Molluscs in the Mediterranean* (ZENETOS *et al.*, 2004) and its web updates did not mention any species belonging to Cephalopoda. In this respect, the ISPRA project *Identification and distribution of non-indigenous species in Italian Seas* represented the first opportunity to provide an overall revision of allochthonous Mediterranean cephalopods (ANDALORO, 2011; ANDALORO *et al.*, 2012). Today, in light of previous considerations, an update of the current status of non-indigenous cephalopods in the Mediterranean basin is definitely required.

Therefore, the main aim of the present paper is to review and discuss the matter of non-indigenous cephalopods *sensu lato* in the Mediterranean Sea; that is to say all species recorded in the last few decades irrespective of their origin.

HISTORICAL OVERVIEW

As mentioned in the Introduction, allochthonous cephalopods have three ways to enter the Mediterranean basin: i) crossing the only natural passage, the Strait of Gibraltar, from the Atlantic Ocean; ii) passing through the Suez Canal from the Red Sea; iii) being transported by humans in various ways (ROTTER *et al.*, 2020) from anywhere in the world oceans. As the opening of the Suez Canal is dated to comparatively recent times (1869), the first colonization of the Mediterranean by Atlantic cephalopods (as well as all other taxa) through the Gibraltar opening has been dated back to the aftermath of the Messinian salinity crisis, which was not survived by any Mediterranean cephalopods (MANGOLD & BOLETZKY, 1988). The present Mediterranean biodiversity, including its teuthodiversity, originated when the Strait of Gibraltar re-opened to the ocean waters and their load of living organisms during the Zanclean flood (5.3 MYA) (BLANC, 2002). In the following ages, several speciation events occurred within the Mediterranean Sea, through which new cephalopod species were born (BELLO, 2003, 2019). Obviously,

the timing of Mediterranean colonization by individual species is not known. What is known is that this basin was colonized by cephalopods of both Mauretanian (i.e. warm) and Lusitanian (i.e. temperate) affinities, most probably in different periods (BELLO, 2003). The process of the entrance and establishment of Atlantic species in the Mediterranean has seemingly occurred through all the time since the opening of the Gibraltar gate in the post-Messinian period and is still occurring. Hence, it may be rather difficult, in some cases, to decide whether an Atlantic cephalopod, newly discovered in the Mediterranean, is actually a recently arrived species or just one previously overlooked. This is particularly true for those cephalopods that escape most common sampling devices and man's notice, mostly because of their fully pelagic mode of life as well as for other reasons, including their poorly explored habitat, their diminutive size and lack of commercial interest.

To the purpose of assembling a list of the non-indigenous cephalopods *sensu lato* found in the Mediterranean, while taking into account the just mentioned caveats, we set as a baseline the cephalopod catalogue by BELLO (1986), who critically reviewed all previous Mediterranean cephalopod records. Accordingly, SÁNCHEZ (1985) was the first one to document a non-indigenous cephalopod, an early juvenile *Teuthowenia megalops* collected in the Balearic Sea and deemed of Atlantic origin. Few years later, a second purported Atlantic cephalopod species, *Stoloteuthis leucoptera*, was caught in the western basin (ORSI RELINI & MASSI, 1991). As for Lessepsian cephalopod, the first one, "*Octopus aegina*", was reported in the year 1999 (SALMAN *et al.*, 1999).

However, it became evident later that some non-indigenous cephalopods, namely *Amphioctopus "aegina"* and *Tremoctopus gracilis*, had been collected in the Mediterranean Sea as early as in the years 1934 and 1936, respectively, but had been misidentified (MIENIS, 2005; ORSI RELINI *et al.*, 2004).

Afterwards several other exotic cephalopods were recorded in Mediterranean waters, coming from either the Atlantic Ocean or the Red Sea,

so that the checklist includes now 13 documented species. In addition, three more species have been reported whose Mediterranean presence was not sufficiently supported.

MATERIAL AND METHODS

Information on the Mediterranean non-indigenous cephalopods was gathered from the available literature.

In this paper the following terminology was used:

- Geographical distribution outside the Mediterranean: current geographical distribution outside the Mediterranean.
- First Mediterranean documented occurrence: date and place of first occurrence (the first documented occurrence may not coincide with the first literature record).
- First Mediterranean literature record: first piece of literature recording the Mediterranean occurrence of the NIS, whether correctly identified or not, together with the year and place of occurrence.
- Notes on the species: additional available information on the biology and ecology of the NIS, as well as taxonomic comments when pertinent.
- NIS category: whether the entrance into the Mediterranean was due to natural range expansion or was human-mediated.
- Status: whether established or not.

Definitions of the terms used in the present paper:

- NIS a non-indigenous species *sensu* RELINI (2008); it includes cephalopods originating from either the Red Sea through the Suez Canal (Lessepsian species) or anthropic causes (including climate warming) or recent range expansion from the Atlantic Ocean.
- Vagrant: an Atlantic species found only once or very few times in the Mediterranean Sea.
- Lessepsian: Red Sea/Indian Ocean species that entered the Mediterranean Sea through the Suez Canal.
- Human-mediated: directly or indirectly carried by man.

- Cryptogenic: “a species that is not demonstrably native or introduced” (CARLTON, 1996: 1653).
- Established: a NIS that originated a self-sustaining population.
- Questionable NIS: a NIS whose presence in the Mediterranean Sea is not sufficiently warranted.

The supra-systematics adopted in this paper is that proposed in ALLCOCK *et al.* (2014). As for the nomenclature, we followed that of the Italian checklist of marine species (BELLO, 2017a).

RESULTS

Non-indigenous cephalopods

Here below the non-indigenous cephalopods reported in the Mediterranean Sea are listed following a systematic order. The overall systematic list is reported in Table 1.

Sepia dollfusi Adam, 1941 (Decapodiformes: Sepiida: Sepiidae)

- Geographical distribution outside the Mediterranean: Red Sea and southern part of Suez Canal (REID *et al.*, 2005); according to NESIS (1987), it is widely distributed in the Indo-Pacific.
- First Mediterranean documented occurrence and literature record: 2014, at 100 m depth off Alexandria (Egypt), eastern Mediterranean Sea (RIAD, 2015).
- Notes on the species: a small-sized cuttlefish, reaching about 15 cm ML (mantle length) (GABR *et al.*, 1998). It occurs in benthic habitats of the neritic zone (GABR *et al.*, 1998), down to about 100 m (RIAD, 2015).
- NIS category and status: Lessepsian; not established.

The only specimen collected was a female measuring 12.2 cm ML, caught by trawling during commercial fishing operations.

This cephalopod is well known in the Suez Canal where it established a thriving population that represents a main target for the canal fishery (GABR *et al.*, 1998). Therefore, in a sense,

S. dollfusi was expected to enter the Mediterranean basin.

Stoloteuthis leucoptera (Verrill, 1878) (Decapodiformes: Sepiolida: Sepiolidae: Heteroteuthinae)

- Geographical distribution outside the Mediterranean: subtropical and temperate amphiatlantic, from the Gulf of St. Lawrence to the Straits of Florida in the western side of the ocean and from the Bay of Biscay to Namibia in the eastern side, also in the southern Indian Ocean (REID & JEREB, 2005; VECCHIONE & YOUNG, 2013).
- First Mediterranean documented occurrence: 1986, north of Gorgona Island, Ligurian Sea (VOLPI *et al.*, 1995).
- First Mediterranean literature record: 1988, Ligurian Sea (ORSI RELINI & MASSI, 1991).
- Notes on the species: benthic-pelagic small-sized sepiolid, living in the lower sublittoral and upper bathyal, from 160 to 700 m (REID & JEREB, 2005).
- NIS category and status: natural range expansion from the Atlantic Ocean or native; established.

The specimens first reported in the literature were found in the Ligurian Sea: one male, ML = 11.5 mm, collected by IKMT (Isaacs-Kidd Mid-Water Trawl) at 270-400 m of depth off Ventimiglia (Liguria), and two juveniles, ML = 8.5 and 9.5 mm respectively, trawled at 250 m of depth off Sestri Levante (Liguria). However, one specimen of this species had been collected two years earlier, in summer 1986, by trawling at 461 m depth north of Gorgona Island, Ligurian Sea; it was a male, 18 mm ML (VOLPI *et al.*, 1995).

A range extension of this sepiolid was noted shortly after: one specimen netted off the Gulf of Naples (Tyrrhenian Sea) on the sea bottom at 387 m depth, during one of the 1990-92 autumn bottom trawl surveys (WÜRTZ *et al.*, 1995); GIORDANO & CARBONARA (1999) reported the capture of one specimen in the Gulf of Naples during the 1990-95 bottom trawl surveys, which might be the same specimen reported by WÜRTZ *et al.* (1995); 13 additional specimens have been collected on bathyal grounds of the Tyrrhe-

Table 1. Check-list of non-indigenous cephalopods recorded in the Mediterranean Sea. Origin: AO = Atlantic Ocean; RS = Red Sea; HT = human-mediated transport. Status: S = Stray specimen(s); E = Established; C = Cryptogenic

Taxon	Species	Origin	Status	References
DECAPODIFORMES				
Sepiida				
Sepiidae	<i>Sepia dollfusi</i> Adam, 1941	RS	S	RIAD (2015)
Sepiolida				
Sepiolidae	<i>Stoloteuthis leucoptera</i> (Verrill, 1878)	AO	C	ORSI RELINI & MASSI (1991); VOLPI <i>ET AL.</i> (1995); VOLIANI (PERS. COMM.); ORSI RELINI (PERS. COMM.); WÜRTZ <i>ET AL.</i> (1995); SANCHEZ <i>ET AL.</i> (1998); GIORDANO & CARBONARA (1999); BIAGI <i>ET AL.</i> (2002); CORSINI-FOKA <i>ET AL.</i> (2010); CUCCU <i>ET AL.</i> (2010); FANELLI <i>ET AL.</i> (2012); QUETGLAS <i>ET AL.</i> (2013); ZARAGOZA <i>ET AL.</i> (2015); KELLER <i>ET AL.</i> (2017)
Myopsida				
Loliginidae	<i>Sepioteuthis lessoniana</i> Férussac, 1830	RS	C	SALMAN & KATAĞAN (2002); MIENIS (2004); RIAD (2008); LEFKADITOU <i>et al.</i> (2009); TZOMOS <i>et al.</i> (2010); WAHEED & GAREB (2010); HATTOUR (2011); CROCETTA <i>et al.</i> (2014); SHAKMAN <i>et al.</i> (2017); AMMAR & MAAROOF (2019); DRAGIČEVIĆ <i>et al.</i> (2019); KATSANEVAKIS <i>et al.</i> (2020)
Oegopsida				
Architeuthidae	<i>Architeuthis dux</i> Steenstrup, 1857	AO	S	GONZÁLEZ <i>et al.</i> (2000); GUERRA (2006); BUSTAMANTE <i>et al.</i> (2008); ANONYMOUS (2020)
Cranchiidae	<i>Cranchia scabra</i> Leach, 1817	AO	S	QUETGLAS <i>et al.</i> (1999); ZARAGOZA <i>et al.</i> (2015)
	<i>Megalocranchia</i> sp. (<i>cf. maxima</i> Pfeffer, 1884)	AO	S	BELLO & BIAGI (1999)
	<i>Taonius pavo</i> (Lesueur, 1821)	AO	S	QUETGLAS <i>et al.</i> (2013)
	<i>Teuthowenia megalops</i> (Prosch, 1849)	AO	S	SÁNCHEZ (1985)
Cycloteuthidae	<i>Cycloteuthis sirventi</i> Joubin, 1919	AO	C	GUERRA (1992; pers. comm.)
Octopoteuthidae	<i>Taningia danae</i> Joubin, 1931	AO	S	QUETGLAS <i>et al.</i> (2006)
OCTOPODIFORMES				
Octopoda				
Octopodidae	<i>Octopus cyanea</i> Gray, 1849	RS	E?	MIENIS (2003a)
	<i>Amphioctopus</i> sp.	RS	E	SALMAN <i>et al.</i> (1999, 2005); MIENIS (2005)
Tremoctopodidae	<i>Tremoctopus gracilis</i> (Eydoux & Souleyet, 1852)	HT?	E?	KRAMER (1937); BELLUSCIO <i>et al.</i> (2003); ORSI RELINI <i>et al.</i> (2004); RIFI & BEN SOUISSI (2014)

nian Sea, from November 1992 to July 2002 (one reported by SANCHEZ *et al.* (1998); 12 by VOLIANI (pers. comm.)). Several others were netted in the Ligurian Sea in the last twenty years (ORSI RELINI, pers. comm.). The species was also recorded in Sardinian waters by CUCCU *et al.* (2010): one specimen, ML = 10.4 mm, caught on June 2005 in the western Tyrrhenian Sea at 550 m depth; the other, ML = 14.5 mm, caught in February 2007 in the Gulf of Cagliari at the depth of 360 m. Both of them were ripe females, the larger one was mated; they were the first females recorded in the Mediterranean. In addition to the several specimens of *S. leucoptera* collected in Italian seas, i.e. the Ligurian and Tyrrhenian Seas, SANCHEZ *et al.* (1998) reported one individual caught in the Catalan Sea on February 1996, at 357 m depth, and QUETGLAS *et al.* (2013) provided information on the catch of 25 specimens (ML range: 10-25 mm) in the western Mediterranean (Alboran Sea and Balearic Islands) from 1994 to 2010, within the depth range 324-612 m. According to QUETGLAS *et al.* (2013), biological information was available for only 13 individuals: nine immature females and four males (two mature and two maturing individuals) caught during May. Other individuals caught off the Balearic Islands were reported by FANELLI *et al.* (2012), who estimated the species standardised total abundance, 0.25 individuals · ha⁻¹, and biomass, wet weight 0.5 g · ha⁻¹, at the depth of 800 m. In the same location, ZARAGOZA *et al.* (2015) caught one specimen by bongo net at 55 m depth.

In summary, all of the above-mentioned specimens of *S. leucoptera* were caught by bottom trawling, with the exception of two individuals caught by plankton nets in midwater (VOLPI *et al.*, 1995; ZARAGOZA *et al.*, 2015). Therefore, despite the members of the subfamily Heteroteuthinae are generally deemed pelagic, *S. leucoptera* is considered benthopelagic (REID & JEREB, 2005). However, as shown by the rare reported catches in epipelagic (ZARAGOZA *et al.*, 2015) and mesopelagic waters (VOLPI *et al.*, 1995), this species may have a wider bathymetric distribution in the water column, which is possibly underestimated because of the paucity of studies investigating midwaters.

To sum up, the present Mediterranean range of *S. leucoptera* extends in the western basin, from the Alboran and Catalan Seas to the Ligurian and Tyrrhenian Seas.

The hypothesis that *S. leucoptera*, some decades ago, naturally entered the western Mediterranean Sea from the Atlantic Ocean through the Straits of Gibraltar is supported by several elements: many individuals of the species collected in the northwest basin only since the '80s of the last century, its progressive range expansion to the west side of the Tyrrhenian Sea where it had not been found before (CUCCU *et al.*, 2010), and the small size coupled with a benthopelagic mode of life, i.e. the likelihood to be carried by currents over long distances. On this respect it must be pointed out that some areas of the western Mediterranean Sea had been extensively surveyed for cephalopods in the last century (cf. MANGOLD & BOLETZKY, 1988), specifically for Sepiolidae (NAEF, 1923).

Nevertheless, the hypothesis that the Mediterranean *Stoloteuthis* species is a cryptogenic entity cannot be discarded (FERNÁNDEZ-ÁLVAREZ, pers. comm.). The latter hypothesis is supported by both its diminutive size and the fact that deep fishing grounds, where it lives, started to be regularly explored only in the last half of a century. Moreover, the water column, where this heteroteuthine preferentially lives, has been scantily investigated all over the western basin.

The only unquestionable piece of information is that this species has an established self-sustained population in the western Mediterranean Sea, as shown by its many records that include fully mature males and females.

Sepioteuthis lessoniana Férussac, 1830
(Decapodiformes: Myopsida: Loliginidae)

- Geographical distribution outside the Mediterranean: a species-complex inhabiting the tropical Indo-Pacific Ocean, from Hawaii to the Red Sea and the south-eastern African coast (NESIS, 1987; JEREB *et al.*, 2010).
- First Mediterranean documented occurrence and literature record: 2002, Gulf of İskenderun, Turkey (Levant Sea) (SALMAN & KATAĞAN, 2002).

- Notes on the species: medium-sized benthic squid, males larger than females (maximum ML: 42 and 38 cm, respectively); weight to about 2 kg; it occurs in coastal environments, from the surface to about 100 m depth (JEREB *et al.*, 2010). The nominal species *S. lessoniana* – type locality: New Guinea (LESSON, 1830), traditionally reported to live in a wide geographical range in the tropical Indopacific Ocean (NESIS, 1987) – represents indeed a species complex (SEGAWA *et al.*, 1993; NORMAN, 2000; JEREB *et al.*, 2010). Accordingly, the identity of the Mediterranean specimens to *S. lessoniana* should be validated; in fact, theoretically, they might be found to belong to a species other than *S. lessoniana* in the future.
- NIS category and status: Lessepsian; established.

The specimen reported by SALMAN & KATAĞAN (2002), unsexed, 25.2 cm ML and 770 g weight, was found in littoral waters. In the following years, a few more individuals of this loliginid squid were collected in the Levant and Aegean Seas: an individual film-recorded in shallow waters off Achziv (Israel) in spring 2004 (MIENIS, 2004); two males caught in 2009, one 196 mm ML / 356 g by hook-and-line, the other 244 mm ML / 522 g by trammel net respectively, from the waters of Rhodes (Greece) (LEFKADITOU *et al.*, 2009); one or more specimens, ML = 32 cm, fished in Cyprus in 2009 (TZOMOS *et al.*, 2010).

According to the published literature, *S. lessoniana* appears to have initially spread all along the eastern and northern coasts of the Levant Sea, including Cyprus, and to have entered the Aegean Sea from its easternmost access, i.e. the Rhodes Strait. LEFKADITOU *et al.* (2009) drew a map of the possible pathway followed by this squid to reach both the southern side of Rhodes (Levant Sea) and its northern side (Aegean Sea) from its Mediterranean entrance site at Port Said. Later, this species has been recorded along the Mediterranean African coasts, in Egypt (RIAD, 2008; WAHEED & GAREB, 2010), Tunisia (HATTOUR, 2011) and Libya (SHAKMAN *et al.*, 2017). Recently, it also reached the Adriatic Sea: one specimen caught near Ploče beach (Budva,

Montenegro, southern Adriatic Sea) in December 2015; incidentally, this is its northernmost record (DRAGIČEVIĆ *et al.*, 2019).

As for the African specimens, RIAD (2008) described the morphology of the female *S. lessoniana* based on specimens obtained from the artisanal fishery (trammel net) based in Alexandria (Egypt, Levant Sea) and WAHEED & GAREB (2010) studied the morphology, digestive and reproductive systems of an unreported number of male individuals caught off the rocky coast of Abu Qir (Egypt, Levant Sea). The specimen reported by HATTOUR (2011) came from commercial trammel-net catches in central eastern coast of Tunisia, at 8–10 m depth. The one recorded by SHAKMAN *et al.* (2017) off Tripoli (Libya) was caught at about 10 m depth by an angler using jigging technique and measured 170 mm ML.

Several recent additional records of *S. lessoniana* have been reported in the eastern Mediterranean Sea (CORSINI-FOKA *et al.*, 2010; CROCETTA *et al.*, 2014; AMMAR & MAAROOF, 2019; KATSANEVAKIS *et al.*, 2020). AMMAR & MAAROOF (2019) collected two specimens (15.5 and 17.9 cm ML) off the Syrian coasts by bottom trawl fishery, whereas both CROCETTA *et al.* (2014) and KATSANEVAKIS *et al.* (2020) reported several specimens observed underwater, in the upper 6 m depth. CROCETTA *et al.* (2014) referred the observation of nine individuals along the Lebanese coast, and KATSANEVAKIS *et al.* (2020) recorded more than 100 individuals from Lebanon, 15 from Greece and 15 from Cyprus.

This squid has established a stable population in the Levant Sea in less than twenty years since its first record by SALMAN & KATAĞAN (2002), to the extent that it is commercially exploited (CORSINI-FOKA *et al.*, 2010). For instance, in Cyprus the ‘new’ squid is regularly found in fish markets (TZOMOS *et al.*, 2010) and in Rhodes it was even given its own vernacular term, i.e. *soupiocalamaro* (= cuttlefish-squid) by local fishermen (LEFKADITOU *et al.*, 2009). It is evident that *S. lessoniana*, which thrives in shallow warm waters throughout its range, found a suitable environment in the Levant Sea thanks to its comparatively high temperatures, the highest in the Mediterranean. Furthermore,

the hatchling size (mean total length > 5 mm) and robustness, as well as its high grow rate (> 12% body mass/day, in the first 100 days) make *S. lessoniana* early juveniles unique among teuthids, since they are independent from currents, i.e. they leave the planktonic mode of life within two weeks (LEE *et al.*, 1994). Moreover, larger hatchlings benefit of reduced mortality rates. All such features may slow down the population range expansion; on the other hand, though, they favour the establishment of new populations from a few specimens by reducing to a great extent the early juveniles spreading over a too wide area.

This loliginid squid is utilized both in biomedical research (LEE *et al.*, 1994) and for human consumption; the latter use is being practiced in Greek islands (LEFKADITOU *et al.*, 2009; TZOMOS *et al.*, 2010).

Architeuthis dux Steenstrup, 1857 (Decapodiformes: Oegopsida: Architeuthidae)

- Geographical distribution outside the Mediterranean: worldwide oceanic in tropical and temperate waters (ROPER & JEREB, 2010a).
- First Mediterranean documented occurrence and literature record: 1997, Fuengirola, Spain (Alboran Sea) (GONZÁLEZ *et al.*, 2000). These authors recorded the specimen as *Architeuthis* sp.; it was shown afterwards that all architeuthid squids belong to the only species *A. dux*, which is distributed worldwide (WINKELMANN *et al.*, 2013).
- Notes on the species: gigantic oceanic squid, epipelagic to mesopelagic and bathyal (ROPER & JEREB, 2010a).
- NIS category and status: vagrant, sporadically entering from the Atlantic Ocean.

The giant squid recorded by GONZÁLEZ *et al.* (2000) was found stranded on the beach. It was a female approaching sexual maturity, 149.5 cm ML and 104 kg body mass (tentacles missing and body damaged). Subsequently, the occurrence of four additional specimens was documented in the western Mediterranean. Two of them were found in the Alboran Sea: a female trawled at 400 m off Malaga, 2001 (GUERRA *et al.*, 2006) and another female washed ashore near

Algeciras (Andalusia) in 2012 (ANONYMOUS, 2020). The fourth specimen was a male trawled at 450 m off Gandia (Gulf of Valencia) in 2005 (BUSTAMANTE *et al.*, 2008), that is far away from the Strait of Gibraltar. To sum up, four giant squids have been recorded in the Mediterranean Sea.

When the first specimen was found (GONZÁLEZ *et al.*, 2000), it was hypothesized to have entered the Mediterranean Sea through the Gibraltar Strait carried by the surface currents when already moribund (as for the overall Mediterranean current pattern cf. MILLOT & TAUPIER-LETAGE, 2005). Indeed, several *A. dux* specimens have been found in a bad condition, floating on the surface of all oceans (e.g. ANONYMOUS, 2020), which may be linked to its aversion to comparatively warm surface waters because of its respiratory physiology (BRIX, 1983). However, the capture of a healthy male in the Gulf of Valencia compels to reconsider the hypothesis that only dying individuals cross the Strait of Gibraltar coming from the Atlantic Ocean or, else, individuals that enter the Mediterranean become moribund (see also GUERRA & SEGONZAC, 2014). Since no giant squid was ever found elsewhere in the Mediterranean, it may be deemed that this species does not form a stable population in this sea.

Cranchia scabra Leach, 1817 (Decapodiformes: Oegopsida: Cranchiidae: Cranchiinae)

- Geographical distribution outside the Mediterranean: circumglobal in tropical and subtropical open oceanic waters (ROPER & JEREB, 2010c).
- First Mediterranean documented occurrence and literature record: 1998, in Balearic waters, south-west of Mallorca (western Mediterranean Sea) (QUETGLAS *et al.*, 1999).
- Notes on the species: small squid living in the water column, from the epipelagic to the bathypelagic zone (ROPER & JEREB, 2010c).
- NIS category and status: vagrant.

The first specimen recorded was collected by bottom trawling between 506 and 769 m depth. It measured 102 mm ML (sex undetermined because of its bad condition); according to its

size, it was an adult or a subadult. A second record of *C. scabra* was reported by ZARAGOZA *et al.* (2015), a paralarva caught by bongo net in the western Mediterranean Sea at 150 m depth. Both specimens may be considered stray specimens that entered the Mediterranean from the Atlantic Ocean.

Taonius pavo (Lesueur, 1821) (Decapodiformes: Oegopsida: Cranchiidae: Taoniinae)

- Geographical distribution outside the Mediterranean: in the Atlantic Ocean from about 45° N to the Southern Subtropical Convergence and in the SW portion of the Indian Ocean (ROPER & JEREB, 2010c). OKUTANI (2015) reports it also in west Australian waters and in the Pacific Ocean, E to Japan.
- First Mediterranean documented occurrence and literature record: 1998, Gulf of Lion (western Mediterranean Sea) (QUETGLAS *et al.*, 2013).
- Mode of life and habitat: medium-large squid living in the water column, from the epipelagic zone to 2,000 m and deeper (ROPER & JEREB, 2010c).
- NIS category and status: vagrant, sporadically entering from the Atlantic Ocean.

QUETGLAS *et al.* (2013) mention three specimens (ML = 97, 106, 173 mm) netted by a commercial trawler in the Gulf of Lion, in 1998 few days apart in the same place, and a fourth one (ML = 153 mm ML) collected off the Balearic Islands, at 380–609 m depth, in 2010. None of them was sexed.

As all cranchiids, *T. pavo* is also a fully pelagic cephalopod throughout its life, so that its early juvenile and juvenile stages may be easily carried along by currents, which explains its wide distribution. The hypothesis that *T. pavo* entered the Mediterranean Sea through the Gibraltar Strait is well supported. No data are available about the settlement of a stable population in this basin.

Megalocranchia sp. (cf. *maxima* Pfeffer, 1884) (Decapodiformes: Oegopsida: Cranchiidae: Taoniinae)

- Geographical distribution outside the Mediterranean: according to ROPER & JEREB

(2010c), there are at least three species in this genus: *M. maxima* Pfeffer, 1884 in the southern Atlantic and Indian oceans and NW Pacific Ocean, *M. oceanica* (Voss, 1960) in the North Atlantic Ocean, *M. fisheri* (Berry, 1909) in the central North Pacific Ocean.

- First Mediterranean documented occurrence and literature record: 1993, off Gorgona Island, Ligurian Sea (western Mediterranean Sea) (BELLO & BIAGI, 1999).
- Notes on the species: paralarvae and early juveniles are epipelagic; juveniles and subadults progressively descend to more than 2,000 m depth; adults are very large as the generic name suggests.
- NIS category and status: vagrant.

The only specimen of this genus ever collected in the Mediterranean was a large one (weight = 86 kg; conservative estimated ML = 1.70 m), most probably an adult. Only a photograph documented its capture, according to whose examination it was tentatively ascribed to either *Galioteuthis* sp. or, more probably, *Megalocranchia* sp. (BELLO & BIAGI, 1999). Afterwards, the late Kir Nesis assigned this specimen to the latter genus (NESIS, pers. comm. to GB). According to both its size and fin shape, the Mediterranean specimen might belong to *M. maxima* (cf. ROPER & JEREB, 2010c; OKUTANI, 2015); this is the largest *Megalocranchia* species and may reach 1.8 m ML (ROPER & JEREB, 2010c).

Most probably, this individual was a vagrant one that entered the Mediterranean Sea through the Strait of Gibraltar. It is impossible to decide whether it entered as an adult that actively crossed the strait or as a paralarva/juvenile passively carried by the inflow of surface currents from the Atlantic Ocean.

Teuthowenia megalops (Prosch, 1849) (Decapodiformes: Oegopsida: Cranchiidae: Taoniinae)

- Geographical distribution outside the Mediterranean: subarctic and temperate Atlantic Ocean (ROPER & JEREB, 2010c).
- First Mediterranean documented occurrence and literature record: 1983, off Blanes, Catalan Sea (western Mediterranean Sea) (SÁNCHEZ, 1985).

- Notes on the species: medium-sized squid living in the water column, from 40 to 2,700 m depth; early stages inhabit the upper zones and then descend to deeper waters (ROPER & JEREB, 2010c).

- NIS category and status: vagrant.

The only specimen recorded in the Mediterranean was a paralarva, 7.4 mm ML, collected by bongo net in midwater (bottom depth = 190 m).

It was most probably a vagrant specimen that entered this basin from the Atlantic Ocean through the Strait of Gibraltar, passively carried by currents.

Cycloteuthis sirventi Joubin, 1919 (Decapodiformes: Oegopsida: Cycloteuthidae)

- Geographical distribution outside the Mediterranean: tropical to temperate waters of the Atlantic and Indo-West Pacific (JEREB & ROPER, 2010); not reported in the Pacific Ocean by OKUTANI (2015).

- First Mediterranean documented occurrence and literature record: 1969, NW of the Asinara island (Sardinia), Italy (western Mediterranean basin) (GUERRA, 1992).

- Notes on the species: medium-sized squid found from the lower epipelagic to the mesopelagic, rarely in the bathybenthic zone (JEREB & ROPER, 2010).

- NIS category and status: cryptogenic.

The specimen recorded by GUERRA (1992) was collected by IKMT net between 0 and 140 m depth, during the Woods Hole Oceanographic Institution cruise no. 49 (May-June 1969), onboard the R/V "Atlantis II". In addition to the specimen reported by GUERRA (1992) (in this work only specimens pertaining to Iberian waters were described) the same scientist observed three more specimens collected during the same cruise, by IKMT net in the same depth range, in the Tyrrhenian Sea, in the Ionian Sea and in the Levant Sea, respectively (GUERRA, pers. comm.). These specimens were juveniles.

Cycloteuthis sirventi had never been collected before in any of the historical Mediterranean plankton cruises nor from any teuthivorous predator stomach contents. Nonetheless, *C. sir-*

venti, because of its fully oceanic habits, might well be a cryptic inhabitant of the Mediterranean that had been overlooked until GUERRA's (1992, pers. comm.) finding. This hypothesis is supported by the fact that the Mediterranean findings occurred in a quite short lapse of time, widely spread apart in the whole basin (ANDALORO, 2011). On the other hand, the facts that no other specimen has ever been found in this sea, neither before nor after those reported by GUERRA (1992, pers. comm.), and that the only ones found were juveniles evoke another possible scenario. That is, planktonic juveniles recurrently enter the Mediterranean, either passively carried by currents through the Gibraltar Straits or through the Suez Canal, yet they do not succeed in growing to the adult stage, because of environmental constraints; hence their presence in the Mediterranean makes just a pseudo-population (BOUCHET & TAVIANI, 1992). Whichever is the right hypothesis, the safest conduct is to ascribe *C. sirventi* to the cryptogenic species category (CARLTON, 1996).

Taningia danae Joubin, 1931 (Decapodiformes: Oegopsida: Octopoteuthidae)

- Geographical distribution outside the Mediterranean: circumglobal in tropical to temperate waters venturing in the boreal range (ROPER & JEREB, 2010b; OKUTANI, 2015).

- First Mediterranean documented occurrence and literature record: 2003, off the Algerian coast, Alboran Sea (QUETGLAS *et al.*, 2006).

- Notes on the species: large-sized pelagic squid (ML up to 1.6 m) that performs an ontogenetic descent from the epipelagic to deeper waters, down to the bathyal zone (ROPER & VECCHIONE, 1993; ROPER & JEREB, 2010b). Despite its gelatinous body, it is a quite powerful swimmer (KUBODERA *et al.*, 2007).

- NIS category and status: vagrant.

The only collected specimen of *T. danae* was a juvenile (ML = 5.6 cm) netted by bottom trawl at 385-395 m depth (QUETGLAS *et al.*, 2006).

The specimen recorded by QUETGLAS *et al.* (2006) is regarded as a stray individual passively carried into the Mediterranean from the surface inflow of Atlantic waters.

Octopus cyanea Gray, 1849 (Octopodiformes: Octopoda: Octopodidae)

- Geographical distribution outside the Mediterranean: an Indo-Pacific octopod that thrives in the Red Sea as well (NORMAN *et al.*, 2016).
- First Mediterranean documented occurrence and literature record: 1997-98, off the Israel coast (Levant Sea, eastern Mediterranean Sea) (MIENIS, 2003a); GALIL (2007) gives the year 1997 as the collection date for the first recorded specimen).
- Mode of life and habitat: a small octopus, benthic in shallow waters (0 to at least 22 m depth).
- NIS category and status: Lessepsian; established?

MIENIS (2003a) reports the collection of two individuals of this species off the Israeli coast. The first one, from Haifa, is kept in the Biological Collections of the Hebrew University, Jerusalem; the second one, caught off Mikhmoret in May 1998, was kept alive for a while in an aquarium.

Therefore, it may be safely stated that the two individuals recorded by MIENIS (2003a) came into the Mediterranean through the Suez Canal.

Amphioctopus sp. (Octopodiformes: Octopoda: Octopodidae)

- Geographical distribution outside the Mediterranean: the genus *Amphioctopus* has a circumglobal distribution; because of the undefined identity of the Mediterranean individuals, no further information may be given about the distribution of their species.
- First Mediterranean documented occurrence: 1934, off Atlit, Israel, Levant Sea (eastern Mediterranean) (MIENIS, 2005).
- First Mediterranean literature record: 1992, 13 specimens off the Turkish coast (Levant Sea, eastern Mediterranean Sea) (SALMAN *et al.*, 1999).
- Notes on the genus: *Amphioctopus* includes small/medium-sized octopuses, benthic to 40 m depth or more (NORMAN *et al.*, 2016).
- NIS category and status: Lessepsian; established.

The species that we indicate here under the

name *Amphioctopus* sp. is supposedly the first Lessepsian cephalopod. Although its presence in the Mediterranean became officially documented and recorded only towards the end of the past millennium (SALMAN *et al.*, 1999, 2005), MIENIS (2005) based on museum evidences showed that in fact this octopod had entered the Mediterranean as early as December 1934. Many specimens have been collected and recorded since SALMAN *et al.*'s (1999) record, throughout the eastern-most part of the Mediterranean, so that this small octopus can be now considered established in this basin (e.g. ZENETOS *et al.*, 2010).

As regards the nomenclature of this species, it has been variously reported as either *Octopus aegina* Gray, 1849 or *Octopus kagoshimensis* Ortmann, 1888 and generally ascribed to a species complex (e.g. SALMAN *et al.*, 1999, 2005). Lately, it appeared that this species belongs indeed to the genus *Amphioctopus* and has been usually ascribed to *A. aegina* (e.g. ÖZTÜRK *et al.*, 2014). In fact, *Amphioctopus* cf. *aegina* (Gray, 1849) / *kagoshimensis* (Ortmann, 1888) is an unresolved alien species. There is no doubt that this octopus is a member of the genus *Amphioctopus* (cf. the genus description in NORMAN *et al.*, 2016). Anyway, because of both morphological characters and geographical distribution considerations, it does not belong neither to *aegina* (distribution: coastal waters of the Indo-Pacific, from India to northern China, including Indonesia and the Philippines; NORMAN *et al.*, 2016) nor to *kagoshimensis* (distribution: West Pacific Ocean, Taiwan and Japan; NORMAN *et al.*, 2016) (BELLO, 2017b). Hence, we do not assign this alien cephalopod to any *Amphioctopus* species and stress the need to further investigate its taxonomic position.

Tremoctopus gracilis (Eydoux & Souleyet, 1852) (Octopodiformes: Octopoda: Tremoctopodidae)

- Geographical distribution outside the Mediterranean: Indian and Pacific Oceans (FINN, 2016).
- First Mediterranean documented occurrence: 1936, North Adriatic Sea (KRAMER, 1937; misidentified as *Tremoctopus violaceus*).

- First Mediterranean literature record: ORSI RELINI *et al.* (2004).
- Mode of life and habitat: dimorphic pelagic octopodid: females large (ML = 32 cm, total length > 1 m), males dwarfed (ML = 1.5 cm); it lives in the epipelagic zone; females observed in surface waters at night (FINN, 2016).
- NIS category and status: recurring human-mediated transfer?; established?

The story of its occurrence in the Mediterranean Sea is nicely told by ORSI RELINI *et al.* (2004) (see also further iconographic documentation in ORSI RELINI, 2009). After an adult female of this species was photographed in the Tyrrhenian Sea in August 2002 (BELLUSCIO *et al.*, 2003), ORSI RELINI *et al.* (2004) became aware of the 1936 swarm of blanket octopuses in the northern Adriatic Sea reported by KRAMER (1937). The latter author erroneously ascribed them to *Tremoctopus violaceus* Delle Chiaje, 1830, since that was the only member of the genus known to live in the Mediterranean. ORSI RELINI *et al.* (2004) showed that the species described by both KRAMER (1937) and BELLUSCIO *et al.* (2003) belonged indeed to *T. gracilis* and emended KRAMER's (1937) report.

Afterward, this eye-catching octopod has been further recorded in Tunisian waters (RIFI & BEN SOUSSI, 2014).

The Mediterranean records of *T. gracilis* refer to female specimens only.

To explain the occurrence of this pelagic octopod in the northern Adriatic Sea in 1936 (KRAMER, 1937) and in the Tyrrhenian Sea in 2002 (BELLUSCIO *et al.*, 2003), ORSI RELINI *et al.* (2004) suggested transport by ships; given the fragile nature of the individuals of this species some doubts may be cast on this hypothesis.

Questionable record

Sepia pharaonis Ehrenberg, 1831 (Decapodi-formes: Sepiida: Sepiidae)

- Geographical distribution outside the Mediterranean: widely distributed from the western Pacific Ocean to the Red Sea (REID *et al.*, 2005).
- First Mediterranean documented occurrence

and literature record: 2003, Israeli coast (Levant Sea) (MIENIS, 2003b).

- Notes on the species: a benthic, medium-sized cuttlefish that inhabits the bottom of the continental shelf down to 130 m of depth. The nominal species *S. pharaonis* represents a species complex (REID *et al.*, 2005).
- NIS category and status: Lessepsian; presence to be confirmed.

MIENIS (2003b) observed large numbers of washed ashore cuttlebones of this cephalopod, together with cuttlebones of the three autochthonous Mediterranean *Sepia* species – namely *S. officinalis* Linnaeus, 1758, *S. orbignyana* Férussac, 1826 and *S. elegans* Blainville, 1826 – along the Israeli coast, from the 20 to the 24 April 2003. The fact that *S. pharaonis* cuttlebones were spread over long beach stretches (overall extending for some 36 km) and that they seemingly had not floated around for a long time (no epibionts, in particular goose-barnacles, were attached on them) made MIENIS (2003b: 127) state that this cephalopod “has most probably managed to get a foothold in the Eastern Mediterranean. However, this assumption has to be confirmed by the finds of living specimens.” Several cuttlebones were collected and placed in the collections of Tel Aviv University (MIENIS, 2003b).

Sepia pharaonis is known to have gradually moved northwards into the Suez Canal. At first a single cuttlebone was recorded in the Bitter Lakes, along the Suez Canal, by BARASH & DANIN (1972). Afterwards, it colonized the Suez Canal and establish there a stable population that is commercially harvested (GABR *et al.*, 1998). Therefore, notwithstanding the need to confirm its presence in the Mediterranean Sea, it is reasonable that this cuttlefish may have progressed into the Mediterranean basin. To the best of our knowledge, no additional report of its presence in the Mediterranean Sea has been published since. Indeed, in addition to the above MIENIS' (2003b) supposition, another one is conceivable, that is the many washed ashore cuttlebones were discards of products harvested elsewhere (cf, BELLO, 2006); accordingly, *S. pharaonis* may have not entered yet the Mediterranean Sea.

The nominal species *S. pharaonis* represents a species complex. NORMAN (2000) described three different 'forms' of this species; the typical one is found from the Red Sea to at least the western Indian Ocean in accordance with the type locality, viz. the Gulf of Suez (SWEENEY, 2001). Later on, ANDERSON *et al.* (2011), based on genetic analyses, found that the name *pharaonis* encompasses a complex of at least five subclades, one of which was termed 'western Indian subclade' to include specimens from the Red Sea, the Gulf of Aden and the Gulf of Oman. Whatever future research will decide about the taxonomic status of such a species complex, the Red Sea population, hence the individuals that may have entered or will enter the Mediterranean through the Suez Canal, belong to *Sepia pharaonis* Ehrenberg, 1831 *sensu stricto*.

Excluded records

Two more cephalopods have been recorded in recent times in the Mediterranean basin, namely *Spirula spirula* (Linnaeus, 1758) (Decapodiformes: Spirulida: Spirulidae) and *Sepia gibba* Ehrenberg, 1831 (Decapodiformes: Sepiida: Sepiidae). Indeed, no documented Mediterranean record of living individual of either species is available in the literature. All records are in fact based on findings of skeletal remains (see further).

Spirula spirula, a circumtropical micronectonic species provided with a calcareous chambered shell, has been reported in the western Mediterranean since the XIX century thanks to the recurrent occurrence of stranded dead specimens, "not only the plain shell, but also the shell with fleshy remains" (BELLO, 2003: 215) coming from the Atlantic Ocean. Anyway, no truly documented record exists of the entrance of alive specimens into the Mediterranean.

As for *Sepia gibba*, GALIL (2007: 309) reports it in the annex *Aquatic alien species reported from the coastal waters of Israel*, thus: "2001, Ashdod; single record; [native range] Red Sea; [pathway] Suez Canal; Mienis, unpublished." In fact, this record was not substantiated by any documented occurrence of living individuals.

Shortly after, MIENIS (2008) specified that the finding consisted in a partly damaged cuttlebone washed ashore on the beach of Ashdod (Israel). In support of the *S. gibba* presence in the Mediterranean, MIENIS (2008: 6) stated that "No epibionts were found on the cuticle [= cuttlebone], a sign that most probably it did not float for a long time." Indeed, cuttlebones can float for a very long time and over long distances (VOSS, 1974). Moreover, the occurrence of exotic cuttlebones may have an unnatural origin, that is they may be the discard of dressing processes of frozen products coming from all over the world (BELLO, 2006).

In summary, *S. gibba* is to be excluded from the list of Mediterranean allochthonous cephalopods.

DISCUSSION

According to our analyses, the present Mediterranean teuthofauna includes 13 non-indigenous species (NIS) *sensu lato*. Until thirty years ago, it was not believed that there were exotic cephalopods in this basin (MANGOLD & BOLETZKY, 1988), although at least two octopods, namely *Amphioctopus* sp. and *Tremoctopus gracilis*, had been collected half a century earlier but had not been correctly identified (see Results).

The sources for NIS cephalopods are the same as for most other taxa: i) from the Atlantic Ocean via the natural entrance, i.e. the Strait of Gibraltar; ii) from the Red Sea through the artificial Suez Canal; iii) from any ocean by anthropo-phoresy (supposedly in ballast water).

The cephalopod NIS that have crossed the Strait of Gibraltar are mainly vagrant specimens either passively carried or assisted by the entrance current, either during their early stages or as adults/subadults: *Cranchia scabra*, *Taonius pavo*, *Megalocranchia* sp., *Teuthoweina megalops*, *Taningia danae* and, possibly, *Cycloteuthis sirventi*; the latter, a cryptic species, might be a very rarely collected inhabitant of the Mediterranean Sea. All of them are fully oceanic oegopsid squids. In particular, it cannot be excluded that one or more small-sized cranchiid species, all of which we labelled 'vagrant', might indeed

have established stable populations in the West Mediterranean Sea. The remaining Atlantic species, that is *Stoloteuthis leucoptera*, is a benthopelagic heteroteuthine that indeed might be a Mediterranean native; anyway, it would be the only Atlantic cephalopod to have established a stable population in the Mediterranean basin.

As for the Lessepsian migrants, i.e. the cephalopods that crossed the Suez Canal, namely *Sepia dollfusi*, *Sepioteuthis lessoniana*, *Octopus cyanea* and *Amphioctopus* sp., they are benthic animals, partly decabrachians other than oegopsid squids and partly octopods. Lastly, *Tremoctopus gracilis*, an Indo-Pacific pelagic octopod, whose occurrence in the Mediterranean has been recorded a few times, was supposed to have been repeatedly carried in ballast waters (ORSI RELINI *et al.*, 2004); anyway, the option that *T. gracilis* is a Lessepsian migrant cannot be a priori excluded; also the possibility that this species has been misidentified as *Tremoctopus violaceus* some other times in the past (in addition to the misidentification by KRAMER (1937)) cannot be a priori excluded.

To sum up, a quite sharp dichotomy is evident in the mode of life of Mediterranean cephalopod NIS: the Atlantic species are pelagic, the Red Sea ones are benthic. For the first group, a dominant role is played by the inflow of superficial Atlantic waters entering the Mediterranean Sea (anti-estuarine circulation; cf. MILLOT & TAUPIER-LETAGE, 2005) that carries organisms living in the water column. This explains why most of them are stray-animals, somewhat forcedly transported through the Strait of Gibraltar, that are not capable of establishing a stable population in the Mediterranean basin (cf. BOUCHET & TAVIANI, 1992); the only possible exception is *S. leucoptera*. The latter group of NIS includes benthic and nektobenthic species that appear to have crossed the Suez Canal at a comparatively slow pace (e.g. *Sepia dollfusi*; see Results), whose crossing and subsequent establishment in Mediterranean waters have been fostered by favourable environmental conditions, mainly suitable temperatures. In this respect the ‘tropicalization’ of the Mediterranean basin (ANDALORO & RINALDI, 1998; THIÉBAULT *et al.*, 2016) has

played and is still playing a dramatic role as for the Red Sea NIS migration and survival.

In percentual terms, the cephalopod NIS represents the 18.7% of the overall Mediterranean teuthofauna (13 NIS vs. 57 autochthonous species), a percentage surprisingly similar to that of the fish NIS (Osteichthyes + Chondrichthyes + Agnatha), that is 18.8% (update 2010; PSOMADAKIS *et al.*, 2012). The comparison between cephalopods and fishes is pertinent since supported by their many similarities driven by convergent evolution (PACKARD, 1972).

In Results we also disentangled the situation of three species whose occurrence in the Mediterranean is not warranted, namely *Sepia pharaonis*, *Sepia gibba* and *Spirula spirula*. In this respect, the case of *S. gibba* is paradigmatic of how utterly unsupported records of allochthonous species (GALIL, 2007) become afterwards endorsed in a comprehensive list that refers to previous sources (e.g. ZENETOS *et al.*, 2010). Out of those three cephalopods, only *S. pharaonis* might reasonably have crossed or may cross the Suez Canal, since it established a stable population there (GABR *et al.*, 1998); nevertheless, sound records of live or freshly dead specimens in Mediterranean waters are necessary to label it a NIS for this basin.

Lastly, the present paper contributes to fill a gap in the knowledge of the Mediterranean non-indigenous cephalopods. We take advantage of the present paper to suggest the inclusion of these cephalopods in lists of ‘exotic’ molluscs (e.g. the CIESM Atlas of Exotic Molluscs in the Mediterranean by ZENETOS *et al.*, 2004).

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Note: While the present paper was in press, we learned that the Mediterranean population of *Stoloteuthis* belongs indeed to a newly described species, different from *S. leucoptera* (Fernández-Álvarez F.Á., P. Sánchez and R. Villanueva, submitted. Morphological and molecular assessments of bobtail squids (Cephalopoda: Sepiolidae) reveal a hidden history of biodiversity. *Frontiers in Marine Science*)."

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Alohtone vrste glavonožaca u Sredozemnom moru: pregled

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SAŽETAK

U ovom radu autori kritički procjenjuju nalaze glavonožaca koji su ušli u Sredozemno more u posljednjih nekoliko desetljeća, što uključuje 13 vrsta, a to su: *Sepia dollfusi*, *Stoloteuthis leucoptera*, *Sepioteuthis lessoniana*, *Architeuthis dux*, *Cranchia scabra*, *Taonius pavo*, *Megalocranchia sp.*, *Teuthowenia megalops*, *Cycloteuthis sirventi*, *Taningia danae*, *Octopus cyanea*, *Amphioctopus sp.* i *Tremoctopus gracilis*. Prisutnost vrste *Sepia pharaonis* treba biti potvrđena, dok je prisutnost *Sepia gibba* i *Spirula spirula* isključena.

Dolasci vrsta iz Atlantskog oceana kroz Gibraltarski tjesnac povezani su s ulaznom površinskom strujom koja je nosila pasivno planktonske paralarve ili je na neki drugi način favorizirala ulaz subadultnih i odraslih zalutalih primjeraka. Zapravo su svi atlantski glavonošci pelagične lignje, s izuzetkom nekto-bentoskog sepiolida *S. leucoptera*. Čini se da nijedna vrsta od navedenih tamo nije uspostavila stabilnu populaciju, osim potonje navedenih vrsta. Naprotiv, glavonošci koji ulaze u Sredozemno more iz Crvenog mora kroz Sueski kanal (lesepsijski migranti) vode bentoski način života. Ipak, dvije vrste *S. lessoniana* i *Amphioctopus sp.*, uspostavile su stabilne populacije u istočnom dijelu.

Konačno, pojave pelagične hobotnice *T. gracilis* pripisuju se, u literaturi, prijenosu posredovanim antropogenim utjecajem.

Ključne riječi: mekušci, glavonošci, egzotične vrste, lesepsijski migranti, kriptične vrste