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Hydrozoan species richness in the Mediterranean Sea: past and present

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Abstract

The Mediterranean hydrozoan fauna (Siphonophora excluded) comprises 400 species; most (68%) occur in the Atlantic Ocean, 20% are endemic to the Mediterranean, 8% are of Indo-Pacific origin, and 4% are non-classifiable. There are 69 nonindigenous (NIS) species in the basin: 44% of these are casual (recorded just one or very few times), 28% established (widely recorded in the basin), 6% invasive (established NIS that are able rapidly or largely to disseminate away from the area of initial introduction, having a noticeable impact on the recipient community), and 22% questionable (of doubtful taxonomic status). Entry through the Suez Canal and range expansion through the Gibraltar Strait, often enhanced by ship traffic, appear to be the main processes for recent species introductions, but uncertainties remain for many NIS. Species additions immediately result in larger local or regional species pools, but the newcomers might impact on populations of native species, altering extinction probabilities. A more reliable evaluation of the species pool can be accomplished by adding new species when they enter the taxonomic record (*i.e.* the records of any taxon in all types of literature), and by removing species that have not been found for a 'reasonable' time (*e.g.* several decades). Of the 400 non-siphonophoran hydrozoan species known to occur in the Mediterranean Sea, positive records in the last 10 years are available for 156 species (39%), whereas records of the remaining 244 species are older than a decade: 67 species have not been recorded for 41 years, 13 for 31–40 years, 79 for 21–30 years, and 85 for 11–20 years.

Introduction

Species lists and distribution records are fundamental to biodiversity research (Costello *et al.* 2001; Mora *et al.* 2011). Biodiversity research has a long history in the Mediterranean Sea, which is one of the best known seas globally. Yet, reliable fauna inventories and easily accessible regional species lists are only available for a few taxonomic groups. Lists of nominal species, such as the ERMS (European Register of Marine Species; Costello *et al.* 2001), do not provide resolution of records at the regional scale (Boero 2002; Occhipinti-Ambrogi *et al.* 2011). Both historical and ecological factors contribute to high biodiversity in the Mediterranean (Bianchi & Morri 2000; Bianchi 2007). In particular, pronounced seasonality is thought to facilitate the spatial coexistence of species by creating niche differentiation in time, and by allowing the occurrence of species with temperate and tropical affinities in the same basin (Coma *et al.* 2000).

The biodiversity of the Mediterranean Sea is changing dramatically, partly linked to global warming, which is thought to contribute to the establishment of tropical nonindigenous species in the basin (Coll *et al.* 2010;

Lejeusne *et al.* 2010). The arrival of new species of tropical provenance increases the regional species pool, being possibly counterbalanced by regressions of resident species that are adapted to colder water (Boero *et al.* 2008). The diversity of the Hydrozoa in the Mediterranean Sea is well known (Bouillon *et al.* 2004, 2006; Schuchert 2006, 2007, 2008a,b, 2009, 2010), and Hydrozoa can be considered a good proxy for marine biodiversity, being widely represented both in the plankton and in the benthos. Here we limit our treatment to non-siphonophoran Hydrozoa (NSH); they are not a formally recognized taxon, but the Siphonophora have, traditionally, been studied separately. NSH, both as polyps and/or medusa stages, are common in all oceans and seas, and syntheses of their global distribution are available for the medusa stage (Kramp 1959, 1961, 1968).

The aim of this paper is to review the knowledge about the diversity of Mediterranean NSH. We assess current estimates of the size of the species pool, and examine whether species might have become locally or regionally extinct.

Material and Methods

Our list of NSH species of the Mediterranean Sea is based on the monograph by Bouillon *et al.* (2004), on other taxonomic revisions (*e.g.* Schuchert 2001, 2006, 2007, 2008a,b, 2009, 2010), and on a revison of the Mediterranean NSH that is currently in preparation (Gravili C. & Boero F., unpublished data). We identified nonindigenous species (NIS), examining records from the 19th century to 2010, to trace the origin, date, method of introduction, current distribution and establishment status, and global distribution of NIS. With few exceptions, we named taxa according to Bouillon *et al.* (2006).

NIS have been classified into five categories according to their establishment status, following Zenetos *et al.* (2010): *casual* (found just a few times), *established* (widely recorded in the basin), *invasive* (established NIS that are able to rapidly or largely disperse away from the area of initial introduction, having a noticeable impact on the recipient community), and *questionable* (of doubtful taxonomic status). We decided to discard the category *cryptogenic* (species whose probable introduction occurred in 'early times' and has not been witnessed, *e.g.* prior to the XIX century) because no species was ascribed to it in this analysis.

The date and location of the first observation of each NIS in the Mediterranean Sea were extracted from the literature. Whenever possible, the actual date of first collection has been reported, along with the publication date of the paper first recording a NIS, since the two dates only rarely coincide.

The vectors of NIS introduction are the most probable mechanism by which a NIS reached the Mediterranean Sea; however, they are often just presumed and are factually demonstrated in only a very few cases. Mediterranean records of Indo-Pacific species, for instance, are often labelled as the result of Lessepsian immigration through the Suez Canal (Por 1978). In this article, however, *Lessepsian immigrants* (LI) are only the species with established populations in the Red Sea that have expanded their distribution to the Mediterranean Sea by using the new connection, whereas the species that are recorded from the Indo-Pacific but not from the Red Sea, are labelled as *Possible Lessepsian immigrants* (PLI). The difference implies that LI crossed the Suez Canal using natural means (*i.e.* own mobility, drifting, rafting, etc.), whereas PLI entered the Mediterranean via human vectors. The route of entrance of PLI, in fact, might have been the Suez Canal, but an Indo-Pacific species transported by a ship, for instance, would reach the Mediterranean even if the ship were to circumnavigate Africa, and hence the passage through the Canal would be only circumstantial. Our knowledge of the hydrozoan fauna of the Red Sea is unfortunately not as detailed as that of the Mediterranean Sea (see Table 1, for a list of Red Sea NSH). The Indo-Pacific species recorded from the Mediterranean Sea, but not yet from the Red Sea, are therefore just considered as PLI. The type locality, broad geographic distribution (comprising all historical records) and native range are given for each NIS.

To identify species that have not been positively recorded for some time, records of all Mediterranean NSH were entered into a relational database whose entries can be arranged to list the collection localities of each taxon in chronological order. Taxonomic records (*i.e.* records of each taxon, in any kind of report) are reported on a time scale from the original description to the last citation in the literature. Mediterranean species were ranked according to the date of their last record in the basin: species not recorded for 41 years or more, species not recorded for 31–40 years, species not recorded for 21–30 years, species not recorded for 11–20 years, and species recorded in the last 10 years.

Results

How many species?

Picard's (1958) list of Mediterranean Antho- and Leptomedusae includes 191 species, Boero & Bouillon (1993) report 346 NSH species, and Bouillon *et al.* (2004) list 396 NSH taxa of 457 hydrozoan species (*i.e.* including the Siphonophora); this represents about 11% of the

Table 1. Summary table of non-siphonophoran hydrozoan species of the Red Sea and neighbouring areas.

Taxa	Citations	Locality	Remarks	Mediterranean
Class Hydroidomedusae				
Subclass Anthomedusae				
Bougainvillia fulva	Hartlaub (1909), Kramp (1968), Schmidt (1973)	Eilat Bay, Red Sea, Gulf of Aqaba, Gulf of Aden		
Bougainvillia muscoides	Schmidt (1973)	Red Sea	Misidentifications of closely related species (see Schuchert 2007)	
*Bougainvillia muscus**	Billard (1904) as *Bougainvillia muscus*, Billard (1926) as *Bougainvillia ramosa muscus,* Schmidt (1973)	Suez Canal, Red Sea, Gulf of Aden		X
Bougainvillia platygaster	Schmidt (1973)	Red Sea		X
*Köllikerina fasciculata**	Schmidt (1973)	Red Sea, Gulf of Aden		X
Köllikerina multicirrata	Schmidt (1973)	Red Sea		
Köllikerina octonemalis	Schmidt (1973)	Red Sea		
Thamnostoma eilatensis	Schmidt (1972a, 1973)	Eilat Bay, Red Sea		
Pachycordyle conica	Schmidt (1973)	Eilat Bay, Red Sea, Gulf of Aden		
*Corydendrium parasiticum**	Billard (1926, 1933)	Suez Canal		X
*Turritopsis dohrnii**	Billard (1926) as *Dendroclava dohrni,* Schmidt (1973) as *Turritopsis nutricula*	Suez Canal, Gulf of Aqaba, Red Sea		X
Cytaeis nassa	Vervoort (1967), Hirohito (1977)	Abiad Bay, Entedebir, Dahlak Archipelago, southern Red Sea, Eilat, Gulf of Aqaba		
*Cytaeis tetrastyla**	Schmidt (1973)	Eilat Bay, Red Sea, Gulf of Aden		X
*Hydractinia echinata**	Mergner & Wedler (1977)	Alexandria		X
Hydractinia kaffaria	Schmidt (1972b)	Gulf of Aqaba, Red Sea		
Hydractinia meteoris	Schmidt (1973) as *Podocoryne meteoris*	Eilat Bay, Red Sea, Gulf of Aden		
Podocoryne denhami?	Stechow (1912)	Gulf of Aden	Doubtful status	
*Podocorynoides minima**	Schmidt (1973) as *Podocoryne minima*	Red Sea, Gulf of Aden		X
Allorathkea ankeli	Schmidt (1972a)	Eilat Bay, Red Sea		
Distichopora violacea	De Blainville (1834), Klunzinger (1879), Boschma (1959, 1968)	Red Sea		
Calycopsis bigelowi	Vanhöffen (1911)	Gulf of Aden		
Calycopsis chuni	Vanhöffen (1911)	Gulf of Aden		
Heterotiara anonyma	Schmidt (1973)	Eilat Bay, Gulf of Aqaba, Red Sea, Gulf of Aden		
*Eudendrium capillare**	Hirohito (1977) as *Eudendrium tenellum*	Gulf of Aqaba		X
Eudendrium deciduum	Mergner & Wedler (1977)	Around Perim, Gulf of Aden		
Eudendrium mucronatum	Billard (1926) as *Eudendrium racemosum mucronatum*	Suez Canal		
Eudendrium ramosum	Thornely (1908), Mergner & Wedler (1977), Mergner (1987)	Khor Dongola, Suez Canal, Red Sea, around Perim, Gulf of Aden		X

Table 1. (Continued).

Taxa	Citations	Locality	Remarks	Mediterranean
*Amphinema rugosum**	Schmidt (1973)	Eilat Bay, Red Sea		X
Leuckartiara gardineri	Schmidt (1973)	Red Sea		
*Leuckartiara octona**	Schmidt (1973)	Red Sea		X
Merga violacea	Schmidt (1973)	Eilat Bay, Red Sea, Gulf of Aden		X
Pandeopsis ikarii?	Schmidt (1973) as *Pandeopsis scutigera*	Gulf of Aqaba, Red Sea		
*Proboscydactyla ornata**	Schmidt (1973)	Red Sea, Gulf of Aqaba, Gulf of Aden		X
Protiara tropica	Schmidt (1973)	Gulf of Aqaba, Red Sea		
Sphaerocoryne bedoti	Mergner & Wedler (1977)	Around Perim		X
Zancleopsis gotoi	Schmidt (1973)	Gulf of Aqaba, Red Sea		
Corymorpha annulata	Schmidt (1973) *as Euphysora annulata*	Red Sea		X
Corymorpha bigelowi	Schmidt (1973) as *Euphysora bigelowi*	Red Sea		X
*Corymorpha forbesii**	Schmidt (1973) as *Vannuccia forbesii*	Eilat Bay, Red Sea, Gulf of Aden		X
*Corymorpha nutans**	Schmidt (1973) as *Steenstrupia nutans*	Gulf of Aden		X
Dicodonium cornutum	Haeckel (1879), Kramp (1968), Halim (1969)	Gulf of Suez, Red Sea	Unrecognizable species (see Schuchert 2001)	
Euphysilla piramidata	Schmidt (1973)	Eilat Bay, Gulf of Aqaba, Red Sea		
*Euphysa aurata**	Schmidt (1973)	Eilat Bay, Red Sea, Gulf of Aden		X
Pennaria disticha	Thornely (1908) as *Pennaria symmetrica*, Billard (1926, 1933) as *Pennaria disticha* var. *australis*, Vervoort (1967) as *Halocordyle disticha* var. *australis*, Schmidt (1972b, 1973) as *Halocordyle disticha* var. *australis*, Hirohito (1977) as *Halocordyle disticha,* Mergner & Wedler (1977) as *Halocordyle disticha* var. *australis*, Mergner (1987) *as Halocordyle disticha* var. *australis,* Vervoort (1993)	Gulf of Suez, Shab al Shubuk, Suakim, Umm Aabak, Dahlak Archipelago, southern Red Sea, Eilat, Gulf of Aqaba		X
Pennaria grandis	Schmidt (1973)	Gulf of Aden		
Solanderia secunda	Thornely (1908) as *Ceratella crosslandi*, Vervoort (1967) as *Solanderia crosslandi* and *S. minima,* Schmidt (1972b), Mergner & Wedler (1977) as as *S. minima* and *S. secunda*, Mergner (1987) as *S. minima* and *S. secunda*, Vervoort (1993)	Port Sudan, Umm Aabak, Dahlak Archipelago, Djidda, Red Sea, Eilat, Gulf of Aqaba		
*Ectopleura crocea**	Schmidt (1972b) as *Tubularia mesembryanthemum,* Vervoort (1993) as *Tubularia crocea*	Eilat, Gulf of Aqaba, Red Sea		X
*Ectopleura larynx**	Billard (1926) as *Tubularia larynx*, Schmidt (1972b) as *Tubularia larynx*	Suez Canal, Gulf of Aqaba, Red Sea		X
Millepora dichotoma	Klunzinger (1879), Crossland (1941), Boschma (1968), Mergner (1987)	Eilat, Gulf of Aqaba, Red Sea		
Millepora exaesa	Klunzinger (1879), Crossland (1941), Mergner (1987)	Red Sea		
Millepora platyphylla	Klunzinger (1879), Crossland (1941), Boschma (1968), Mergner (1987)	Red Sea, Eilat, Gulf of Aqaba		
Millepora tenella	Boschma (1968) as *Millepora tenera*	Cundabilu, Dahlak Archipelago, southern Red Sea		

Table 1. (Continued).

Taxa	Citations	Locality	Remarks	Mediterranean
Porpita porpita	Vervoort (1967)	Landing Bay, Entedebir, Red Sea, Gulf of Aden		X
Velella velella	Halim (1969)	Red Sea		X
*Zanclea costata**	Vanhöffen (1911), Schmidt (1973)	Red Sea	Misidentifications based on polyp records only (see Schuchert 2010)	X
Zanclea dubia	Schmidt (1973)	Eilat Bay, Red Sea		
Halocoryne orientalis	Hartlaub (1909) as *Zanclea* sp., Schmidt (1973) as *Z. orientalis*	Eilat Bay, Red Sea, Gulf of Aden		
Subclass Leptomedusae				
*Aequorea forskalea**	Haeckel (1879) as *Octocanna octonema*, Schmidt (1973) as *Aequorea aequorea*	Red Sea		X
Aequorea australis	Schmidt (1973)	Red Sea		
Aequorea coerulescens	Schmidt (1973)	Eilat Bay, Red Sea, Gulf of Aqaba, Gulf of Aden		
Aequorea macrodactyla	Schmidt (1973)	Eilat Bay, Red Sea, Gulf of Aden		
Aequorea parva	Hartlaub (1909), Schmidt (1973)	Red Sea, Gulf of Aden		
*Aequorea pensilis**	Halim (1969)	Red Sea		X
*Aglaophenia latecarinata**	Mergner & Wedler (1977)	Aroun Perim		X
Cladocarpus alatus	Rees & Vervoort (1987)	Gulf of Aden		
Cladocarpus dofleini	Rees & Vervoort (1987)	Gulf of Aden		
Cladocarpus sewelli	Rees & Vervoort (1987)	Gulf of Aden		
Gymnangium eximium	Marktanner-Turneretscher (1890) as *Halicornaria flabellata*, Schmidt (1972b), Mergner & Wedler (1977), Mergner (1987), Rees & Vervoort (1987), Vervoort (1993), El Beshbeeshy (1995)	Gulf of Suez, Red Sea, Gulf of Aqaba, around Perim, Gulf of Aden		
Gymnangium eximium millardae n.var.	El Beshbeeshy (1995)	Southern Red Sea		
Gymnangium gracilicaule	Stechow (1912) as *Halicornaria gracilicaulis*, Jäderholm (1920) as *Halicornaria gracilicaulis*, Billard (1933) as *Halicornaria gracilicaulis*, as Vervoort (1967) as *Halicornaria gracilicaulis*, Mergner & Wedler (1977) as *Gymnangium gracilicaulis*	Gulf of Suez, Nocra, Cundabilu, Dahlak Archipelago, around Perim, Red Sea, Gulf of Aden		
Gymnangium hians var. *balei*	Marktanner-Turneretscher (1890) as *Aglaophenia balei*, Mergner & Wedler (1977), Mergner (1987)	Djidda, Red Sea, around Perim		
Lytocarpia flexuosus	Mergner & Wedler (1977) as *Thecocarpus flexuosus* var. *flexuosus*, El Beshbeeshy (1995) as *Lytocarpia flexuosa flexuosa*	Southern Red Sea, Gulf of Aden		
Lytocarpus (?) hornelli	Thornely (1908)	Suez Bay	Doubtful status	
Macrorhynchia balei	Mergner & Wedler (1977) as *Lytocarpus balei*	Around Perim		
Macrorhynchia meteor	El Beshbeeshy (1995)	Southern Red Sea		

Table 1. (Continued).

Taxa	Citations	Locality	Remarks	Mediterranean
Macrorhynchia philippina	Marktanner-Turneretscher (1890) as *Lytocarpus philippinus*, Thornely (1908) as *Lytocarpus philippinus*, Stechow (1919) as *Lytocarpia philippina*, Billard (1926, 1933) as *Lytocarpus philippinus*, Schmidt (1972b) as *Lytocarpus philippinus*, Mergner & Wedler (1977) as *Lytocarpus philippinus*, Mergner (1987) as *Lytocarpus philippinus*, Rees & Vervoort (1987) as *Lytocarpus philippinus,* Vervoort (1993)	Suez Canal, Suakim Harbour, Gulf of Aqaba, Red Sea, around Perim, Gulf of Aden		X
*Cuspidella humilis**	Mergner & Wedler (1977), Mergner (1987)	Gulf of Aqaba, Eilat		X
Eirene kambara	Schmidt (1973)	Eilat Bay, Red Sea		
Eirene tenuis	Schmidt (1973)	Red Sea		X
*Eirene viridula**	Hartlaub (1909) as *Irene pellucida*, Kramp (1968), Schmidt (1973)	Red Sea, Gulf of Aden		X
Eutima commensalis	Schmidt (1973)	Red Sea		
Eutima curva	Schmidt (1973)	Red Sea		
Eutima hartlaubi	Hartlaub (1909) as *Octorchandra orientalis*, Kramp (1968), Schmidt (1973)	Red Sea, Gulf of Aden		
Eutima levuka	Schmidt (1973)	Red Sea		
Eutima modesta	Hartlaub (1909) as *Eutimalphes modesta*, Kramp (1968), Schmidt (1973)	Red Sea, Gulf of Aden		
*Eutonina scintillans**	Hartlaub (1909) as *Phialidium* sp., Kramp (1968)	Gulf of Aden		X
*Helgicirrha schulzei**	Schmidt (1973)	Red Sea		X
*Halecium beanii**	Billard (1933), Mergner & Wedler (1977)	Gulf of Suez, Southern Red Sea, around Perim, Gulf of Aden		X
Halecium labiatum	Billard (1933), Vervoort (1967)	Gulf of Suez, Umm Aabak, Dahlak Archipelago, southern Red Sea		
*Halecium sessile**	Billard (1933)	Gulf of Suez, Red Sea		X
Antennella secundaria	Vervoort (1967), Mergner & Wedler (1977), El Beshbeeshy (1995)	Landing Baym Entedebir, Dahlak Archipelago, southern Red Sea, around Perim, Gulf of Aden		X
Halopteris alternata	Thornely (1908) as *Plumularia alternata*	Khor Dongola		
Halopteris campanula	Billard (1933) as *Theocaulus campanula*	Gulf of Suez		
Halopteris catharina	Billard (1904) as *Plumularia catharina* var. *articulata*, Stechow (1925) as *Plumularia catharina*	Red Sea, Gulf of Aden		X
*Halopteris diaphana**	Billard (1904) as P*lumularia alternata*, Thornely (1908) as *Plumularia alternata*	Gulf of Aden, Khor Dongola, Red Sea		X
Halopteris platygonotheca	Schmidt (1972b), Mergner & Wedler (1977) as *H. glutinosa*	Gulf of Aqaba, Red Sea, around Perim		
*Anthohebella parasitica**	Mergner & Wedler (1977) as *Hebella parasitica,* Mergner (1987) as *Hebella parasitica*	Around Perim, Djidda, Red Sea		X

Table 1. (Continued).

Taxa	Citations	Locality	Remarks	Mediterranean
Hebella dyssymmetra	Billard (1933), Vervoort (1967)	Gulf of Suez, Nocra, Cundabilu, Dahlak Archipelago, southern Red Sea		
Hebella scandens	Billard (1904) as *Lafoea calcarata*, Billard (1933) as *Hebella calcarata*, Vervoort (1967, 1993)	Gulf of Suez, Cundabilu, Dahlak Archipelago, Red Sea, Gulf of Aden		X
Hebella venusta	Mergner & Wedler (1977), Mergner (1987)	Djidda, Red Sea, around Perim, Gulf of Aden	Doubtful status	
*Kirchenpaueria pinnata**	Schmidt (1972b)	Gulf of Aqaba, Red Sea		X
Pycnotheca mirabilis	Mergner & Wedler (1977)	Around Perim		
*Ventromma halecioides**	Thornely (1908) as *Plumularia halecioides*, Billard (1926) as *Kirchenpaueria halecioides*, Vervoort (1967) as *P. halecioides*, Vervoort (1993)	Suez Canal, Gulf of Aqaba, Nocra, Dahlak Archipelago, southern Red Sea, Eilat, Gulf of Aqaba, Gulf of Aden		X
*Acryptolaria conferta**	El Beshbeeshy (1995)	Southern Red Sea		X
*Filellum serratum**	Billard (1933), Rees & Vervoort (1987)	Gulf of Suez, Gulf of Aden		X
Zygophylax armata	Mergner & Wedler (1977)	Around Perim, Hodeida (Red Sea)		
Zygophylax millardae	El Beshbeeshy (1995)	Southern Red Sea, Gulf of Aden		
Laodicea fertilis	Schmidt (1973)	Red Sea		
Laodicea indica	Vanhöffen (1911) as *Laodice maasi*, Kramp (1968), Schmidt (1973)	Red Sea, Gulf of Aden		
*Eucheilota maculata**	Billard (1933) as (?) *Campanulina hincksii*	Gulf of Suez		X
Eucheilota menoni	Schmidt (1973)	Red Sea		
Eucheilota tropica	Kramp (1968)	Red Sea		
Eucheilota ventricularis	Vanhöffen (1911) as *Euchilota ventricularis*	Red Sea		X
Lovenella assimilis	Schmidt (1973)	Red Sea		
Octophialucium indicum	Schmidt (1973)	Eilat Bay, Red Sea, Gulf of Aqaba		
Mitrocomella polydiademata	Billard (1926) as *Cuspidella grandis*	Gulf of Suez		
*Nemertesia ramosa**	Mergner & Wedler (1977) as *Nemertesia ramosa* var. *plumularioides*	Around Perim		X
*Plumularia setacea**	Thornely (1908), Billard (1933), Mergner & Wedler (1977), Mergner (1987)	Gulf of Suez, Khor Dongola, Djidda, Red Sea, around Perim		X
Plumularia strobilophora	Billard (1933) as *Plumularia strobilifera*	Gulf of Suez		
Plumularia wasini	Mergner & Wedler (1977)	Around Perim		
Abietinaria filicula	El Beshbeeshy (1995)	Gulf of Aden		
Amphisbetia minima	Thornely (1908)	Gulf of Suez		
Diphasia digitalis	Mergner & Wedler (1977)	Around Perim		
Diphasia heurteli	Billard (1933) as *Diphasia heurteli* var. *simplex*	Gulf of Suez		

Table 1. (Continued).

Taxa	Citations	Locality	Remarks	Mediterranean
Diphasia mutulata	Thornely (1908), Billard (1933), Mergner & Wedler (1977)	Suez docks and Suez Bay, Djidda, Red Sea, around Perim		
Dynamena cornicina	Billard (1926, 1933), Vervoort (1967), Schmidt (1972b), Mergner & Wedler (1977), Mergner (1987)	Suez Canal, Nocra, Dahlak Archipelago, Red Sea, Eilat, Gulf of Aqaba, around Perim		
Dynamena crisioides	Marktanner-Turneretscher (1890) as *Dynamena tubuliformis*, Billard (1904) as *Thuiaria tubuliformis*, Thornely (1908) as *Thuiaria tubuliformis,* and as *Synthecium maldivense,* Billard (1926, 1933), Vervoort (1967) as *Dynamena crisioides crisioides*, Schmidt (1972b) as *Dynamena crisioides crisioides,* Hirohito (1977)	Gulf of Suez, Gulf of Aqaba, Landing Bay, Entedebir, Dahlak Archipelago, southern Red Sea, Gulf of Aden		
Dynamena quadridentata	Mergner & Wedler (1977), Mergner (1987)	Djidda, Red Sea		
Calamphora campanulata	Mergner & Wedler (1977), El Beshbeeshy (1995) as *Sertularella campanulata*	Southern Red Sea, around Perim, Gulf of Aden		
Sertularella diaphana	Billard (1933), Vervoort (1993), El Beshbeeshy (1995)	Gulf of Suez, Red Sea, Gulf of Aden		
*Sertularella mediterranea**	Schmidt (1972b), Mergner & Wedler (1977), Mergner (1987), El Beshbeeshy (1995)	Gulf of Aqaba, Eilat, Red Sea, around Perim, Gulf of Aden		X
Sertularella natalensis	Mergner & Wedler (1977)	Nile Delta		
*Sertularella polyzonias**	Mergner & Wedler (1977), El Beshbeeshy (1995)	Southern Red Sea, around Perim, Gulf of Aden		X
*Sertularia distans**	Billard (1933) as *Sertularia distans* var. *gracilis*	Gulf of Suez		X
Sertularia ligulata	Mergner & Wedler (1977)	Around Perim		
Sertularia trigonostoma	Mergner & Wedler (1977)	Around Perim		
Synthecium elegans	Mergner & Wedler (1977), Mergner (1987), El Beshbeeshy (1995)	Djidda, Red Sea, around Perim, Gulf of Aden		
Thyroscyphus fruticosus	Thornely (1908) as *Campanularia juncea*, Billard (1926) as *Thyroscyphus vitiensis*, Billard (1933), Vervoort (1967), Schmidt (1972b), Mergner & Wedler (1977), Mergner (1987), Vervoort (1993), El Beshbeeshy (1995)	Suez Canal, Gulf of Aqaba, Eilat, Khor Dongola, Umm Aabak, Nocra, Cundabilu, Dahlak Archipelago, Jebel Attair, Red Sea, around Perim		X
Campanularia denticulata	Thornely (1908)	Khor Shinab		
Clytia ambigua	Schmidt (1973) as *Phialidium ambiguum*	Red Sea		
Clytia arborescens	Billard (1933)	Suez Canal		
Clytia hemisphaerica	Schmidt (1972b, 1973) as *Phialidium hemisphaericum,* Mergner & Wedler (1977) as *Campanularia (Clytia) hemisphaerica*	Gulf of Aqaba, Eilat Bay, Red Sea, around Perim		X

Table 1. (Continued).

Taxa	Citations	Locality	Remarks	Mediterranean
Clytia latitheca	Thornely (1908) as *Campanularia denticulata*, Mergner & Wedler (1977) as *Campanularia (Clytia) latitheca*, El Beshbeeshy (1995)	Suez Canal, around Perim, Southern Red Sea		
Clytia linearis	Billard (1904) as *Campanularia gravieri*, Billard (1926) as *Clytia (?) foxi*, Billard (1933) as *Laomedea gravieri*, Vervoort (1967) as *Campanularia (Clytia) gravieri*, Schmidt (1972b) as *Campanularia gravieri*, Hirohito (1977), Mergner & Wedler (1977) as *Campanularia (Clytia) gravieri*, Mergner (1987) as *Campanularia (Clytia) gravieri*	Gulf of Suez, Gulf of Tadjoura, Landing Bay, Entedebir, Nocra, Cundabilu, Dahlak Archipelago, Gulf of Aqaba, southern Red Sea, around Perim, Gulf of Aden		X
Clytia lomae	Kramp (1968) as *Phialidium lomae*	Red Sea		
Clytia malayense	Schmidt (1973) as *Phialidium malayense*	Red Sea		
Clytia paulensis	Mergner & Wedler (1977) as *Campanularia (Clytia) paulensis*	Around Perim		X
Gastroblasta timida	Keller (1883), Halim (1969)	Red Sea		
Obelia bidentata	Thornely (1908) as *Obelia bifurcata*	Khor Shinab		X
Obelia dichotoma	Thornely (1908) as *Campanularia cheloniae,* Billard (1926), Schmidt (1972b) as *Laomedea (Obelia) dichotoma*, Mergner & Wedler (1977) as *Laomedea (Obelia) dichotoma,* Mergner (1987) as *Laomedea (Obelia) dichotoma*	Khor Dongola, Red Sea, Suez Canal, Gulf of Aden, Gulf of Aqaba, Eilat		X
Obelia geniculata	Billard (1926)	Suez Canal		X
Obelia longissima ?	Billard (1904)	Gulf of Aden		X
Orthopyxis crenata	Billard (1926) as *Orthopyxis lennoxensis*	Suez Canal		X
Malagazzia carolinae	Schmidt (1973) as *Phialucium carolinae*	Eilat Bay, Red Sea, Gulf of Aqaba		
Class Automedusa				
Narcomedusae				
Solmundella bitentaculata	Schmidt (1973)	Red Sea, Gulf of Aden		X
Cunina frugifera	Schmidt (1973)	Red Sea, Gulf of Aden		
Cunina mucilaginosa	Vanhöffen (1908) as *Solmaris mucilaginosa*	Gulf of Aden	Doubtful status	
Cunina octonaria	Schmidt (1973)	Red Sea, Gulf of Aden		X
Cunina peregrina	Schmidt (1973)	Red Sea		
Cunina tenella	Schmidt (1973)	Red Sea, Gulf of Aden		
Pegantha aureola	Haeckel (1879) as *Solmoneta aureola*, Halim (1969)	Red Sea	Doubtful status	
Pegantha clara	Schmidt (1973)	Gulf of Aden		
Pegantha forskalii	Haeckel (1879) as *Polycolpa forskalii*, Halim (1969)	Red Sea	Doubtful status	
Pegantha laevis	Schmidt (1973)	Red Sea, Gulf of Aden		
Pegantha martagon	Schmidt (1973)	Eilat Bay, Red Sea, Gulf of Aden		
Pegantha triloba	Schmidt (1973)	Red Sea, Gulf of Aden		X
Solmaris flavescens	Vanhöffen (1908)	Gulf of Aden		X
Trachymedusae				
Geryonia proboscidalis	Schmidt (1973)	Gulf of Aqaba, Red Sea		X
Liriope tetraphylla	Vanhöffen (1902), Hartlaub (1909) as *Liriope rosacea*, Halim (1969), Schmidt(1973)	Eilat Bay, Red Sea, Gulf of Aqaba, Gulf of Aden		X

Table 1. (Continued).

Taxa	Citations	Locality	Remarks	Mediterranean
Petasus eucope	Haeckel (1879) as *Petasata eucope*	Red Sea	Doubtful status	
Aglaura hemistoma	Vanhöffen (1902), Furnestin (1958), Halim (1969), Schmidt (1973), Khalil & El-Rakman (1997)	Eilat Bay, Red Sea, Gulf of Aqaba, Gulf of Aden		X
Amphogona pusilla	Hartlaub (1909)	Gulf of Aden		X
Colobonema sericeum	Schmidt (1973)	Red Sea, Gulf of Aden		
Pantachogon haeckeli	Vanhöffen (1902) as *Pantachogon rubrum*	Red Sea, Gulf of Aden		X
Rhopalonema funerarium	Halim (1969), Schmidt (1973)	Red Sea, Gulf of Aden		X
Rhopalonema velatum	Halim (1969), Schmidt (1973)	Red Sea, Gulf of Aden		X
Sminthea eurygaster	Schmidt (1973)	Red Sea		X

Sources for distribution: Billard (1904, 1926, 1933); Boschma (1959, 1968); Crossland (1941); De Blainville (1834); El Beshbeeshy (1995); Furnestin (1958); Haeckel (1879); Halim (1969); Hartlaub (1909); Hirohito (1977); Jäderholm (1920); Keller (1883); Khalil & El-Rakman (1997); Klunzinger (1879); Kramp (1968); Marktanner-Turneretscher (1890); Mergner (1977, 1987); Mergner & Wedler (1977); Rees & Vervoort (1987); Schmidt (1972a,b, 1973); Stechow (1912, 1919, 1925); Thornely (1908); Vanhöffen (1902, 1908, 1911); Vervoort (1967, 1993).
X, presence in Mediterranean.
*species first recorded from the Mediterranean Sea, and even from boreal seas, and only later recorded in the Red Sea.

3702 nominal known species of the superclass Hydrozoa globally (Bouillon *et al.* 2006). New records of Mediterranean hydrozoans are continually improving our knowledge of the fauna (Schuchert 2001, 2006, 2007, 2008a,b, 2009, 2010; Galea 2007; Gravili *et al.* 2007, 2008; Morri *et al.* 2009), resulting in the most current estimate of 400 NSH species (Fig. 1). Most of these (68%) occur in the Atlantic Ocean and are subdivided into Mediterranean Atlantic (14%), tropical Atlantic (10%), boreal (12%), and circumtropical (21%), cosmopolitan (11%); 20% are endemic to the Mediterranean, 8% are of Indo-Pacific origin, and 4% are non-classifiable.

How many nonindigenous species?

Recent additions to regional faunal lists (*e.g. Diphasia digitalis*, *Dynamena quadridentata*, *Sertularia thecocarpa*, *Campanularia morgansi*) are almost invariably represented by nonindigenous species (NIS), whereas description of new species is rarer. Sixty-nine nonindigenous species (NIS) of NSH have been recorded in the Mediterranean (Fig. 2; Table 2; Appendix 1): 30 are casual, 20 established, four invasive, and 15 questionable. No cryptogenic species are recognized. Nonindigenous taxa include Hydroidomedusae (Anthomedusae: 24 species; Leptomedusae: 34 species; Laingiomedusae: two species; Limnomedusae: three species), and Automedusae (Trachymedusae: six species) (Table 2).

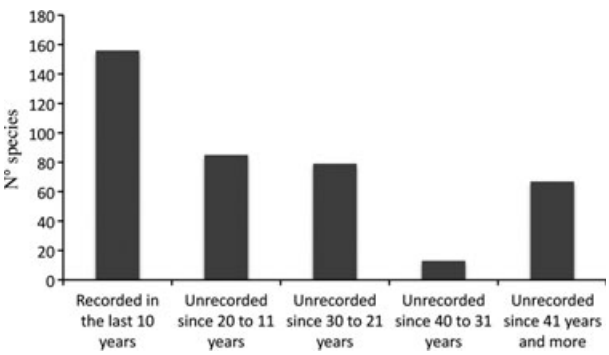

Fig. 1. Periods of last records in the taxonomic literature of all the non-siphonophoran hydrozoan Mediterranean species.

NIS were grouped into three main categories according to their distribution: recorded throughout the basin (27), recorded in the Levantine basin (27), recorded in the Strait of Gibraltar and/or Alboran Sea (15) (Table 2, Fig. 2). At the sub-regional scale, more NIS are found in the eastern basin (42 species), with a peak of 38 in the Levant Sea, followed by the Gulf of Lions and the Ligurian Sea (21 species), the Ionian and Adriatic Seas (19 species), the Strait of Gibraltar and nearby areas (22 species), the Tyrrhenian Sea (nine species), Algeria and North Tunisia (three species). Some NIS have been recorded in more than one of these areas.

Fifteen NIS listed in Table 2 are considered as 'questionable', mainly due to uncertainties about their taxonomic status and distributional patterns. Twenty NIS are established, with self-maintaining and self-perpetuating populations unsupported by and independent of humans in at least one sector of the Mediterranean Sea (See Appendix 1), four (6%) are invasive species having overcome biotic and abiotic barriers to develop large populations in the Mediterranean waters, and for 30 species (43%) casual records have been reported from one or a few locations only. Modes of introduction are unknown for many NIS (36%). Nine per cent have been introduced by ships. Other probable ways of introduction are the

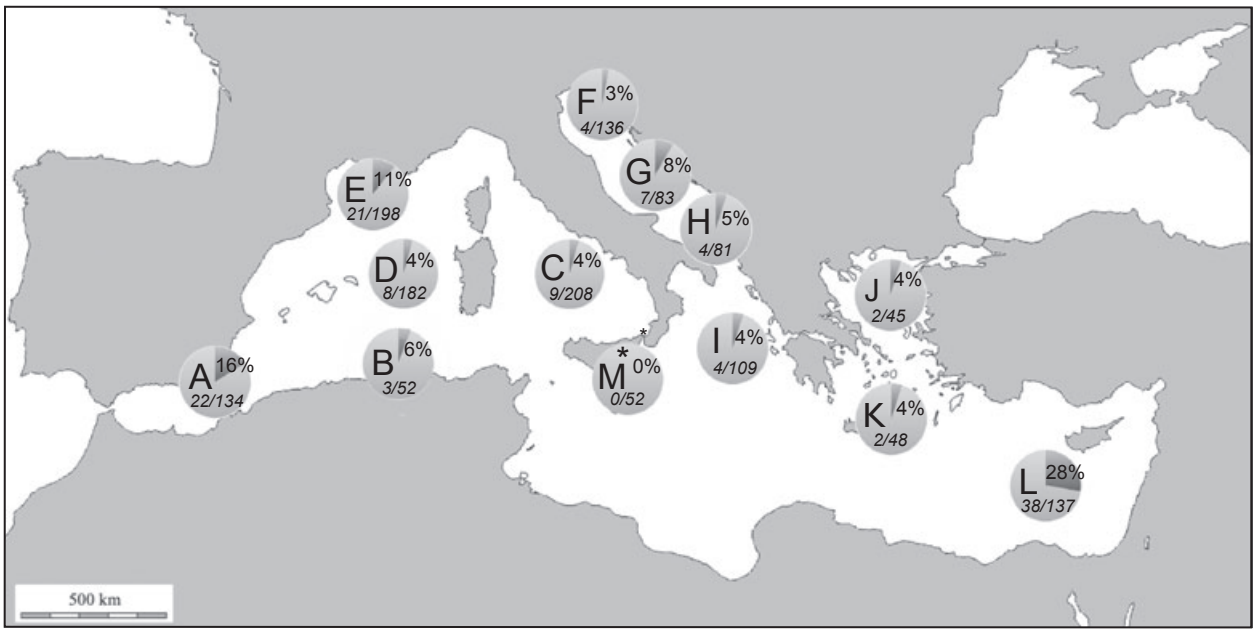

Fig. 2. Distribution of nonindigenous species of Hydrozoans (excluding Siphonophora) in each biogeographic sector within the Mediterranean Sea. (A) Alborán Sea; (B) Algeria and North Tunisia coasts; (C) Southern Tyrrhenian Sea; (D) Balearic Sea to Sardinia Sea; (E) Gulf of Lions and Ligurian Sea; (F) Northern Adriatic Sea; (G) Central Adriatic Sea; (H) Southern Adriatic Sea; (I) Ionian Sea; (J) Northern Aegean Sea; (K) Southern Aegean Sea; (L) Levant Sea; (M) Strait of Messina (marked by asterisk). Biogeographic sectors according to Bianchi (2007). For each sector, nonindigenous species (NIS) percentage and NIS number/non-syphonophoran Hydrozoa (NSH) total number are shown.

expansion of natural ranges through the Strait of Gibraltar (22%) and the Suez Canal (19% of Mediterranean NIS as Possible Lessepsian immigrants, and about 14% as Lessepsian immigrants).

As an example of the expansion of a NSH-NIS in the Mediterranean we chose *Clytia linearis* (Thornely, 1900), a successful Lessepsian immigrant that, in the last decades, has been recorded to be abundant at almost every Mediterranean location surveyed, occurring from shallow waters to shaded rocky bottoms (Fig. 3). This species probably colonised the Mediterranean from the Suez Canal (the first Mediterranean record is by Billard in 1926), and then, from Gibraltar, it expanded its distribution to the Atlantic coast of Spain (Altuna Prados 1995; Boero *et al.* 2005).

The Mediterranean–Red Sea relationship

Red Sea species that have also been found in the Mediterranean are listed in Table 1. Many of them are Lessepsian immigrants to the Mediterranean, but many others (marked by an asterisk in Table 1) were first recorded from the Mediterranean Sea, and even from boreal seas, and were only later recorded in the Red Sea. Thirty species are casual, having seldom been recorded, possibly because they are not established in the basin, but their inconspicuousness might have prevented proper records of their presence.

How many species could we possibly have lost?

Fewer than 160 species of NSH have been positively recorded in the last 10 years. Conversely, there are no positive records of 67 species in the last 40 years or longer. Four decades of absence might be long enough to suggest the possibility that regional extinction (or at least range contraction) may be considered. This period precedes the first signs of the impact of global warming on Mediterranean biota. However, species might have remained unrecorded simply because their descriptions were not sufficient to allow subsequent positive identification, or due to scant expertise on the taxon, with little sampling efforts. As an example, *Tricyclusa singularis* Schulze 1876, is case of a species that has been 'absent' for a very long time. It is a species of boreal affinity, after its original description from Trieste (the northernmost part of the Northern Adriatic and the coldest part of the Mediterranean); it has never been recorded again from the Mediterranean Sea (Fig. 4). Instead, it was recorded several times from Roscoff (Atlantic coast of France) (*e.g.* Bedot 1911; Teissier 1965), resulting in a disjunct distribution. The disappearance of *T. singularis* represents not

Table 2. List of non-siphonophoran Hydrozoa NIS.

Subclass	NIS in the Mediterranean Sea, not restricted to Levantine or Alboran Seas	NIS present only in the Levantine waters	NIS present in the Strait of Gibraltar, in the Alborán Sea or near areas (absent in the rest of the Mediterranean Sea)
Anthomedusae	*Garveia franciscana* (I), *Trichydra pudica* (Q), *Calycopsis simplex* (C), *Eudendrium carneum* (E), *Eudendrium merulum* (E), *Amphinema rubrum* (C), *Octotiara russelli* (Q), *Moerisia inkermanica* (C), *Corymorpha annulata* (Q), *Coryne eximia* (E)	*Bougainvillia aurantiaca* (Q), *Bougainvillia niobe* (Q), *Nubiella mitra* (Q), *Cytaeis vulgaris* (Q), *Paracytaeis octona* (C), *Halitiara inflexa* (C), *Moerisia carine* (E), *Sphaerocoryne bedoti* (C), *Euphysa flammea* (Q), *Corymorpha bigelowi* (Q), *Ectopleura minerva* (Q), *Plotocnide borealis* (Q)	*Russellia mirabilis* (C), *Tubularia ceratogyne* (Q)
Leptomedusae	*Gymnangium montagui* (E), *Cirrholovenia tetranema* (E), *Eutima mira* (E), *Filellum serratum* (E), *Eucheilota paradoxica* (E), *Campalecium medusiferum* (E), *Monotheca pulchella* (E), *Diphasia rosacea* (C), *Clytia hummelincki* (I), *Clytia linearis* (I), *Clytia mccrady* (E)	*Aequorea conica* (C), *Macrorhynchia philippina* (I), *Laodicea fijiana* (Q), *Eucheilota ventricularis* (E), *Diphasia digitalis* (C), *Dynamena quadridentata* (E), *Sertularia thecocarpa* (E), *Sertularia marginata* (E), *Campanularia morgansi* (C), *Obelia fimbriata* (C)	*Aglaophenia parvula* (C), *Cladocarpus multiseptatus* (C), *Cladocarpus pectiniferus* (C), *Cladocarpus sinuosus* (C), *Halecium sibogae* (C), *Pseudoplumaria marocana* (C), *Kirchenpaueria bonnevieae* (C), *Cryptolaria pectinata* (C), *Diphasia attenuata* (C), *Diphasia delagei* (C), *Diphasia margareta* (C), *Hydrallmania falcata* (C), *Sertularella robusta* (Q)
Laingiomedusae		*Fabienna oligonema* (C), *Kantiella enigmatica* (C)	
Limnomedusae	*Gonionemus vertens* (E), *Scolionema suvaense* (Q)	*Olindias singularis* (E)	
Trachymedusae	*Haliscera bigelowi* (E), *Haliscera racovitzae* (C), *Amphogona pusilla* (C), *Arctapodema australis* (C)	*Halitrephes maasi* (C), *Tetrorchis erythrogaster* (E)	

Establishment success (C = Casual; E = Established; I = Invasive; Q = Questionable).

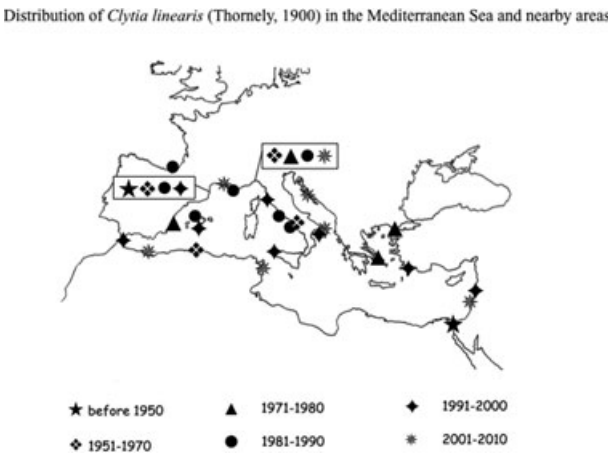

Fig. 3. The distribution map of the species *Clytia linearis*.

only the putative local extinction of a species but also the disappearance from the Mediterranean of the family Tricyclusidae that comprises just this single species and genus (Boero & Bonsdorff 2007).

Discussion

Changes in the size and composition of regional species pools can provide important insights about environmental change. In general, species lists for an area are updated by adding new species as soon as they enter the taxonomic record (*i.e.* records of taxa from any source). These updates disregard the species that were in the previous lists and that have not been recorded anymore from the area for a reasonably long period, for instance more than 40 years, before the appreciation of the impacts of global change, as proposed here. An alternative approach, including putative loss of species, may indicate endangered or even extinct species, but these are usually charismatic and popular species, whereas inconspicuous taxa (the bulk of biodiversity) are usually disregarded. The Mediterranean Sea today represents a model basin for all oceans, being subjected to a period of temperature increase that is radically changing its biota (Bianchi 2007; Boero & Bonsdorff 2007; Lejeusne *et al.* 2010). Our analysis of records over time can provide 'early warning

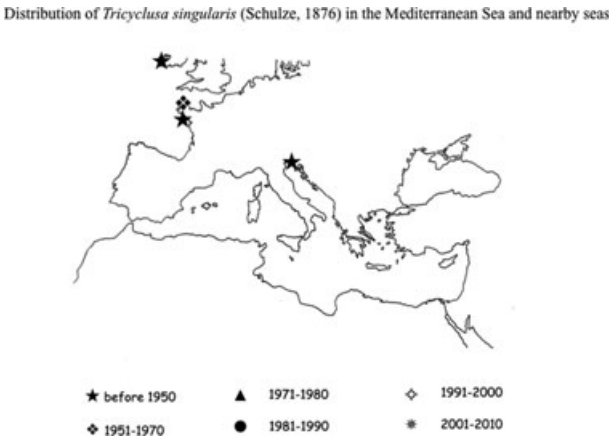

Fig. 4. The distribution map of the species *Tricyclusa singularis*.

signals' of species that may face higher probabilities of local or regional extinction.

The increased number of tropical species recently recorded from the Mediterranean Sea has been called *tropicalisation* and also occurs in other taxa (Bianchi 2007). Twenty-eight of the 45 species with tropical affinity have been cited first from the Levant basin and most of them are of Indo-Pacific biogeographic affinity. The rest (17) are tropical Atlantic species. All the Indo-Pacific species have been usually labelled as Lessepsian immigrants and, thus, as having entered through the Suez Canal by the expansion of their natural range. This assumption, however, is correct only if the species in question have been recorded from the vicinities of the Suez Canal or, at least, from the Red Sea. Only 11 of 34 NIS species of Indo-Pacific origin have been recorded from the Red Sea and only these, thus, can be considered Lessepsian immigrants with some confidence. Thirty-eight species recorded from the Red Sea are typically Mediterranean (Table 1). They might represent misidentifications, but might also be anti-Lessepsian migrants or cryptogenic hydrozoan NIS for the Mediterranean Sea.

Twenty-four of 69 NSH-NIS are of Atlantic affinity; eight are of these are restricted to the Gibraltar region or, at least, to the Alboran Sea and 16 expanded further into the Western Mediterranean Basin (see Appendix 1). These species might not even be NIS, having been present, albeit unnoticed, at these locations for a long time. These species might be removed from the list but, as literature reports are very scant for this part of the Mediterranean Sea, their status remains a matter of pure speculation.

The number of NIS (69) matches closely the number of species that have not been recorded for more than 40 years (67). If the latter are removed from the species pool, introduction of new species would not result in a net increase. This is also suggested by data about a hydroid fauna that has been studied over the long term by Puce *et al.* (2009): the number of species tends to remain stable but the composition of the species assemblage changes. In spite of wide speculation about the impact of global warming on marine biodiversity, the work by Puce *et al.* (2009) is cited as the only report on the effects of global warming on populations of marine invertebrates in a recent review on this topic (Burrows *et al.* 2011). The cumulative species list thus shows an increase in biodiversity but this may not correspond to the number of species actually present at any given time. Our data suggest that the regional species pools tend to remain stable, and that the tropical NIS colonising the Mediterranean Sea are probably filling the gaps of species that are becoming rarer than before (thus not being recorded) or are even locally extinct. It is debatable whether lack of records is due to scant sampling effort (which, however, has led to recording of the NIS), or to impact of either abiotic (*i.e.* rising temperatures) or biotic (*i.e.* competition or predation) factors, or of a blend of the three possible causes. The processes of species extinction operate at different paces and involve different mechanisms at different spatial scales (Carlton *et al.* 1999). Red lists of endangered species almost invariably deal with charismatic species (a negligible minority) and disregard the bulk of marine biodiversity, *i.e.* inconspicuous species. We propose here the lack of records of a species for several decades as an operational tool to recognize putative extinctions. Obviously, the fact that a species is unrecorded from a given area does not mean that it is extinct in that area. Decades of absence of records, however, might allow one to raise hypotheses of putative extinctions that need to be tested with focussed samplings, increasing the bearing of biodiversity estimates in terms of species pools.

The Hydrozoa are well studied along the northern coast of the Western Mediterranean Sea and the Adriatic Sea, but records are scant for the rest of the basin. Hence, the present figures might not accurately reflect biodiversity for the entire Mediterranean. It is probable that more hydrozoan invaders will arrive from tropical regions, as the Mediterranean basin is going through a period of tropicalisation (Bianchi 2007). Moreover, the species with the ability to become dormant under adverse conditions will be favoured (Boero 2002), as well as those with the ability to reverse their life cycle, surviving long journeys in ballast water (Miglietta & Lessios 2009); such ontogeny reversal is more widespread across cnidarians than previously thought (Piraino *et al.* 2004).

The origins of Mediterranean hydrozoan NIS have not been investigated with molecular tools so far. Molecular approaches will, hopefully, improve our understanding of

the origin of NIS and their modes of dispersal (*e.g.* Miglietta & Lessios 2009). The number of NIS in the Mediterranean Sea is probably underestimated. Especially for the Hydrozoa, the key areas for species introductions (*i.e.* the eastern basin and the Gibraltar Strait) are still understudied. It is probable that, at least for shallow waters, the additions to the Mediterranean hydrozoan fauna will mostly consist of NIS, as demonstrated for fish assemblages of the Levantine shallow marine ecosystems (Goren & Galil 2005). The results shown here suggest that species lists are dynamic, requiring continual updating that considers both additions of introduced species and putative subtractions of species with historical but not contemporary records. Without these subtractions, the species lists will never show possible biodiversity crises at the level of species pools, as biodiversity is always on the rise due to the arrival of NIS.

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Conflicts of Interest

None of the authors have any potential conflicts of interest.

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Appendix 1

Non-siphonophoran hydrozoan NIS in the Mediterranean Sea.

Taxa	Type locality and original description	Extra-Mediterranean distribution	1st Mediterranean record	Distribution in Mediterranean	Way of introduction	Patterns of frequency in main Mediterranean sectors (*sensu* Zenetos *et al.* 2010)				
						Western Mediterranean	Central Mediterranean including Ionian Sea	Adriatic Sea	Eastern Mediterranean	Red Sea and neighbouring areas
Class Hydroidomedusae										
Subclass Anthomedusae										
Bougainvillia aurantiaca Bouillon, 1980	Papua New Guinea	Indo-Pacific	Lebanon: survey from 1969 to 1989 (Goy *et al.* 1991)	Leb	PLI				Questionable (see Schuchert 2007)	–
Bougainvillia niobe Mayer, 1894	Bahamas, Atlantic Ocean	Atlantic	Lebanon (Goy *et al.* 1988) as *Bougainvillia platygaster*	Leb	U				Questionable (see Schuchert 2007)	–
Garveia franciscana (Torrey, 1902)	San Francisco Bay, NE Pacific	Circumtropical	Venice lagoon (Italy): 1978 (Morri 1979)	Adr, Medl	S	Invasive		Invasive		–
Nubiella mitra Bouillon, 1980	Papua New Guinea	Indo-Pacific	Lebanon (Goy *et al.* 1990)	Leb	PLI				Questionable (see Schuchert 2007)	–
Cytaeis vulgaris Agassiz & Mayer, 1899	Fiji Islands, South Pacific Ocean	Indo-Pacific	Lebanon (Goy *et al.* 1990)	Leb	U				Questionable	–
Paracytaeis octona Bouillon, 1978	Seychelles, Indian Ocean	Indo-Pacific	Lebanon: survey from 1970 to 1982 (Lakkis & Zeidane 1985)	Leb	PLI				Casual	–
Trichydra pudica Wright, 1857	Scotland, NE Atlantic	Atlantic, Indo-Pacific	Croatia (Adriatic Sea): collected in 1973–1974 (Schmidt & Benovic 1979)	Cro, Leb	U			Questionable	Questionable (see Schuchert 2009)	–
Calycopsis simplex Kramp & Damas, 1925	Norway	Atlantic	Villefranche-sur-Mer: 1966 (Goy 1973)	Fr	ENR	Casual				–
Eudendrium carneum Clarke, 1882	Virginia, USA (Atlantic Ocean)	Circumtropical	Medes Isles: 1983 (Gili 1986)	Medl, Tyrr, Lig, Fr, Cro, Lev, Leb	LI	Established		Established	Established	+
Eudendrium merulum Watson, 1985	SW Pacific (Australia)	Circumtropical	Portofino (Ligurian Sea, Italy): 1984 (Bavestrello & Piraino 1991)	Lig, Tyrr, Cro, Chaf, Fr, Ion, Lev	S	Established	Established	Established	Established	–
Amphinema rubrum (Kramp, 1957)	Antarctic (South Orkney Islands)	Antarctic (Atlantic section)	Villefranche-sur-Mer: 1963 (Goy 1973)	Fr, Blls	ENR	Casual				–
Octotiara russelli Kramp, 1953	SW Pacific (Australia)	Indo-Pacific	Bay of Villefranche-sur-Mer: 1954 (Goy 1973) as *Octotiara violacea*	Fr	U	Questionable (see Schuchert 2007)				–
Halitiara inflexa Bouillon, 1980	Papua New Guinea	Indo-Pacific	Lebanon: survey from 1969 to 1989 (Goy *et al.* 1991)	Leb	PLI				Casual	–
Heterotentacula mirabilis (Kramp, 1957)	Antarctic	Antarctic, Atlantic (West Indies)	Alborán Sea: 1997 (Pagès *et al.* 1999)	Alb	S	Casual				–
Moerisia carine Bouillon, 1978	Papua New Guinea	Indo-Pacific	Lebanon: survey from 1970 to 1982 (Lakkis & Zeidane1985)	Leb	PLI				Established	–

Appendix 1 (Continued).

Taxa	Type locality and original description	Extra-Mediterranean distribution	1st Mediterranean record	Distribution in Mediterranean	Way of introduction	Patterns of frequency in main Mediterranean sectors (*sensu* Zenetos *et al.* 2010)				
						Western Mediterranean	Central Mediterranean including Ionian Sea	Adriatic Sea	Eastern Mediterranean	Red Sea and neighbouring areas
Moerisia inkermanica Paltschikowa-Ostroumova, 1925	Black Sea	Atlantic, Indo-Pacific	Gulf of Pozzuoli: Brinckmann-Voss (1987) as *Ostroumovia inkermanica*	Tyrr, Lev	U	Casual			Casual	–
Sphaerocoryne bedoti Pictet, 1893	Malay Archipelago	Atlantic, Indo-Pacific	Lebanon: survey from 1969 to 1989 (Goy *et al.* 1991)	Leb	LI				Casual	+
Coryne eximia Allman, 1859	British Isles	Atlantic and Pacific Oceans	Ligurian Sea (polyp): Puce *et al.* 2003; medusa: doubtful records in the Mediterranean Sea (see Schuchert 2001)	Fr?, Lig, Leb?	U	Established			Questionable (see Schuchert 2001)	–
Corymorpha annulata (Kramp, 1928)	Sunda Strait, Indo-Pacific	Indo-Pacific	Adriatic Sea, Croatia: 1973–1974 (Schmidt & Benovic 1977)	Cro, Adr	LI			Questionable (see Schuchert 2010)		+
Corymorpha bigelowi (Maas, 1905)	Malay Archipelago and Australia, W Pacific	Indo-Pacific	Lebanon (Goy *et al.* 1988)	Leb	LI				Questionable (see Schuchert 2010)	+
Euphysa flammea (Hartlaub, 1902)	Bear Island (Norway)	Arctic circumpolar, Atlantic, Indo-Pacific	Lebanon: survey from 1969 to 1989 (Goy *et al.* 1991)	Leb	ENR				Questionable (see Schuchert 2010)	–
Ectopleura minerva Mayer, 1900	Tortugas, Florida (Atlantic Ocean)	Indo-Pacific	Lebanon: collected between 1969 and 1989 (Goy *et al.* 1990)	Leb, Lig	U	Questionable (see Schuchert 2010)			Questionable (see Schuchert 2010)	–
Plotocnide borealis Wagner, 1885	White Sea	Arctic and Subarctic, circumpolar, Atlantic, Indo-Pacific	Lebanon (Goy *et al.* 1988)	Leb	U				Questionable (see Bouillon *et al.* 2004; Schuchert 2010)	–
Tubularia ceratogyne Pérez, 1920 ? (probably conspecific with *Tubularia indivisa*, see Schuchert 2010)	Pas-de-Calais (Boulonnais), Atlantic Ocean	Northeastern Atlantic	Strait of Gibraltar and nearby areas of Gulf of Cádiz (Medel & López-González 1996)	SG	ENR	Questionable (see Schuchert 2010)				–
Subclass Leptomedusae										
Aequorea conica Browne, 1905	Ceylon, Indian Ocean	Indo-Pacific	Lebanon (Goy *et al.* 1988)	Leb	PLI				Casual	–
Aglaophenia parvula Bale, 1882	SW Pacific (Australia)	Eastern Atlantic, S Australia	Caños de Meca (near Strait of Gibraltar): 1991 (Medel & Vervoort 1995)	SG	U	Casual				–
Cladocarpus multiseptatus (Bale, 1915)	Great Australian Bight, Australia	N Spain, Australia	Alboràn Sea, off the coast of Morocco: 1984 (Ramil & Vervoort 1992)	Alb	U	Casual				–
Cladocarpus pectiniferus Allman, 1883	Porto Praya, St. Iago (Cape Verde Islands, Atlantic Ocean)	Northeastern Atlantic, from Iceland to Morocco	Straits of Gibraltar, Alboràn Sea, near the coast of Morocco (BALGIM): 1984 (Ramil & Vervoort 1992)	SG, Alb	ENR	Casual				–
Cladocarpus sinuosus Vervoort, 1966	Off Durban, South Africa	Eastern Atlantic (coasts of Africa), Indian Ocean (south Africa)	Alboràn Sea near the coast of Morocco: 1984 (Ramil & Vervoort 1992)	Alb	U	Casual				–
Gymnangium montagui (Billard, 1912)	Roscoff, eastern Atlantic Ocean	Eastern Atlantic	Banyuls-sur-Mer (Redier 1962)	Fr, SG	ENR	Established				–

Appendix 1 (Continued).

Taxa	Type locality and original description	Extra-Mediterranean distribution	1st Mediterranean record	Distribution in Mediterranean	Way of introduction	Patterns of frequency in main Mediterranean sectors (*sensu* Zenetos *et al.* 2010)				
						Western Mediterranean	Central Mediterranean including Ionian Sea	Adriatic Sea	Eastern Mediterranean	Red Sea and neighbouring areas
Macrorhynchia philippina (Kirchenpauer, 1872)	Manila, Philippines, W Pacific	Tropical Atlantic, Pacific and Indian Oceans	Suez (Stechow 1919) as *Lytocarpia philippina*	SC, Leb, Trk, Lev	LI				Invasive	+
Cirrholovenia tetranema Kramp 1959	Indo-Pacific	Atlantic, Indo-Pacific	Gulf of Naples (Italy): 1963 (Brinckmann 1965)	Tyrr, Fr, Leb	PLI	Established			Casual	–
Eutima mira Mc Crady, 1859 (= *E. orientalis*)	South Carolina, USA	Atlantic, Indo-Pacific	Haifa Bay, coast of Israel: 1956 (Schmidt 1973)	Isr, Leb, Egy, Tn	U	Casual			Established	–
Halecium sibogae Billard, 1929	Indonesia	Indo-Pacific, Eastern Atlantic warm waters	Straits of Gibraltar, Alboràn Sea, off the coast of Morocco: 1984 (Ramil & Vervoort 1992)	SG, Chaf	U	Casual				–
Pseudoplumaria marocana (Billard, 1930)	Off the coast of Morocco (east Atlantic)	Tropical temperate Eastern Atlantic	San García, Algeciras Bay, Strait of Gibraltar: 1991 (Medel & Vervoort 1995)	SG	ENR	Casual				–
Kirchenpaueria bonnevieae (Billard, 1906)	Trondhjem Fiord, Norway and two localities between the Faroes and Shetland Islands, North Atlantic	North Atlantic, Indo-Pacific, Indian Ocean	Alborán Sea, close to the coast of Morocco (BALGIM): 1984 (Ramil & Vervoort 1992)	Alb	ENR	Casual				–
Cryptolaria pectinata (Allman, 1888)	Off New Zealand	Deep waters of the Atlantic and Pacific Oceans	Strait of Gibraltar: 1984 (Ramil & Vervoort 1992)	SG	U	Casual				–
Filellum serratum (Clarke, 1879)	Near Havana, Cuba	Circum(sub)tropical	Naples, Secca della Gajola; Ischia, Nisida (Stechow 1923)	Tyrr, Egy, Trk, Sp, Fr, Blls, SG, Alb, Chaf, Lev, Lig	S	Established			Established	+
Laodicea fijiana Agassiz & Mayer, 1899	Fiji Islands (S Pacific Ocean)	Indo-Pacific	Lebanon: Goy *et al.* (1988)	Leb	U				Questionable	–
Campalecium medusiferum Torrey, 1902	Long Beach (California), Pacific coast of North America	Atlantic, Eastern Pacific	Port-Vendres, Cap Abeille (Western Mediterranean Sea): Motz-Kossowska (1911)	Lig, Tyrr, Adr, Ion, Fr, Sp	U	Established	Established	Established		–
Eucheilota paradoxica Mayer, 1900	Tortugas, Florida	Atlantic, Indo-Pacific	Near Dubrovnik (S Adriatic Sea): 1967 (Schmidt & Benovic 1977)	Adr, Alb, Leb, Fr, Tn	U	Casual	Casual	Casual	Established	–
Eucheilota ventricularis McCrady, 1959	South Carolina, USA	Circumtropical	Lebanon: between 1970 and 1982 (Lakkis & Zeidane 1985)	Leb	LI				Established	+
Monotheca pulchella (Bale, 1882)	Indo-Pacific	Atlantic coasts of the Strait of Gibraltar, Indo-Pacific, Atlantic coast of Argentine	Murcia (Spain): 1968 (García Corrales *et al.* 1978 as *Plumularia femina*)	Sp, Blls	U	Established				–

Appendix 1 (Continued).

Taxa	Type locality and original description	Extra-Mediterranean distribution	1st Mediterranean record	Distribution in Mediterranean	Way of introduction	Patterns of frequency in main Mediterranean sectors (*sensu* Zenetos *et al.* 2010)				
						Western Mediterranean	Central Mediterranean including Ionian Sea	Adriatic Sea	Eastern Mediterranean	Red Sea and neighbouring areas
Diphasia attenuata (Hincks, 1866)	British Isles, E Atlantic Ocean	Mainly records from temperate and tropical eastern Atlantic, but also several records from the Pacific	Strait of Gibraltar (Isla de Tarifa, Punta Saudiño, Benzù, Punta Almina): 1984 (Medel Soteras *et al.* 1991)	SG	ENR	Casual				–
Diphasia delagei Billard, 1912	E Atlantic Ocean	Temperate and tropical eastern Atlantic	Only found at the Strait of Gibraltar (Tarifa, Spain): 1984 (Ramil & Vervoort 1992)	SG	ENR	Casual				–
Diphasia digitalis (Busk, 1852)	Prince of Wales Channel, Torres Strait, Australia	Circumtropical	Levant Sea, Hadera: 2004 (Morri *et al.* 2009)	Lev	LI				Casual	+
Diphasia margareta (Hassall, 1841)	N Atlantic Ocean	Temperate and sub-tropical northeastern Atlantic	Levante, Spain (García Corrales *et al.* 1980)	Sp, SG	ENR	Casual				–
Diphasia rosacea (Linnaeus, 1758)	Brighton, Sussex (English Channel)	Eastern and Western Atlantic	1929 (collections of the RBINS – Leloup's specimen; see Bouillon *et al.* 1995)	Lig, SG	ENR	Casual				–
Dynamena quadridentata (Ellis & Solander, 1786)	African coast (more likely Atlantic Ocean) near Ascension Island	Circumtropical	Levant Sea, around Selaata: 1999 (Morri *et al.* 2009)	Lev	LI				Established	+
Hydrallmania falcata (Linnaeus, 1758)	Kent, English Channel	Mainly North Atlantic (western and eastern), but also records from South Africa (probably doubtful) and from North Pacific Ocean, Arctic Seas (White, Kara and Barents Sea)	Strait of Gibraltar (the west side): 1984 (Ramil & Vervoort 1992)	SG	ENR	Casual				–
Sertularella robusta Coughtrey, 1876	New Zealand	Indo-Pacific, S Atlantic	Levante, Spain: collected between 1968 and 1971 (García Corrales *et al.* 1980)	Sp	U	Questionable				–
Sertularia marginata (Kirchenpauer, 1864)	Pacific Ocean	Circumtropical	Syria Coast: collected between 1929 and 1930 (Billard 1931)	Syr, Isr, Trk, Lev, Sp	PLI	Established			Established	–
Sertularia thecocarpa (Jarvis, 1922)	Madagascar	Indo-West Pacific	Levant Sea, Jbail northward: 1999 (Morri *et al.* 2009)	Lev	PLI				Established	–
Campanularia morgansi Millard, 1957	False Bay, South Africa	South Africa, Madagascar	Israel coast: 2009 (De Vito *et al.* 2010)	Isr	PLI				Casual	–
Clytia hummelincki (Leloup, 1935)	West Indies, Caribbean Sea (Atlantic Ocean)	Circumtropical	Copanello (Calabria, Italy): 1996 (Boero *et al.* 1997)	Ion, Adr, Balls, Tyrr, Lig	S	Invasive	Invasive	Invasive		–

Appendix 1 (Continued).

Taxa	Type locality and original description	Extra-Mediterranean distribution	1st Mediterranean record	Distribution in Mediterranean	Way of introduction	Patterns of frequency in main Mediterranean sectors (*sensu* Zenetos *et al.* 2010)				
						Western Mediterranean	Central Mediterranean including Ionian Sea	Adriatic Sea	Eastern Mediterranean	Red Sea and neighbouring areas
Clytia linearis (Thornely, 1900)	New Britain (Papua New Guinea), Indo-Pacific	Circumtropical	Suez Canal (Billard 1926) as *Clytia foxi*	SC, Egy, Fr, Lig, Tyrr, Sp, Trk, Alb, MedI, Balls, Gr, Ion, Chaf, Tn, Adr, Ion, Lev	LI	Invasive	Invasive	Invasive	Invasive	+
Clytia mccrady (Brooks, 1888)	Bahama Islands, Atlantic Ocean	Circumtropical	Villefranche-sur-mer (Bougis 1963)	Fr, Lig, Tyrr, Leb	ENR	Established			Established	–
Obelia fimbriata (Dalyell, 1848)	Scotland	Atlantic and Pacific Oceans	Lebanon: collected between 1969 and 1989 (Goy *et al.* 1991)	Leb	ENR				Casual	–
Subclass Laingiomedusae										
Fabienna oligonema (Kramp, 1955)	Gulf of Guinea (W Africa)	Atlantic	Lebanon (Goy *et al.*1988 as *Pochella oligonema*)	Leb	U				Casual	–
Kantiella enigmatica Bouillon, 1978	Seychelles Islands, Indian Ocean	Indo-Pacific	Lebanon (Goy *et al.* 1988)	Leb	PLI				Casual	–
Subclass Limnomedusae										
Olindias singularis Browne, 1905	Maldives, Indian Ocean	Indo-Pacific	Egyptian Mediterranean Sea: 1984 (Zakaria 2004)	Egy	PLI				Established	–
Gonionemus vertens A. Agassiz, 1862	Puget Sound, Pacific coast of North America	Circumboreal	Trieste (Joseph 1918) as *Gonionemus vindobonensis*	Adr, Lig, Fr, Tyrr	S	Established		Established		–
Scolionema suvaense A. Agassiz & Mayer, 1899	Fiji Islands, S Pacific	Indo-Pacific	Villefranche-sur-Mer: 1950 (Picard 1951)	Fr, Lig, Tyrr	U	Established				–
Class Automedusa										
Subclass Trachymedusae										
Haliscera bigelowi Kramp, 1947	E tropical Pacific	Atlantic, Indo-Pacific, Arctic	Dubrovnik (S Adriatic Sea): 1965 (Schmidt & Benovic 1977)	Adr, Sp, Blls	U	Established		Established		–
Haliscera racovitzae (Maas, 1906)	Bellingshausen Sea, Antarctic	Atlantic, Indo-Pacific, and in the Antarctic and Sub-Antarctic	Planier canyon (NW Mediterranean): 1994 (Gili *et al.* 1998)	Fr	U	Casual				–
Halitrephes maasi Bigelow, 1909	Off coast of Peru	Atlantic, Indo-Pacific, Antarctic	Lebanon (Goy *et al.* 1988)	Leb	PLI				Casual	–
Amphogona pusilla Hartlaub 1909	Gulf of Aden, Arabian Sea	Indo-Pacific	Villefranche-sur-Mer (Ligurian Sea): 1964 (Goy 1973)	Lig, Fr	LI	Casual				+
Arctapodema australis (Vanhöffen, 1912)	Antarctic	Antarctic, Indo-Pacific	Dubrovnik (S Adriatic Sea) (Schmidt & Benovic 1977)	Adr, SG, Fr	U	Casual		Established		–
Tetrorchis erythrogaster Bigelow, 1909	E tropical Pacific	Indo-Pacific, Atlantic	Lebanon: survey from 1970 to 1982 (Lakkis & Zeidane 1985)	Leb	U				Established	–

Taxa: Class, subclass, species. Distribution in the Mediterranean Sea: Adr = Adriatic Sea; Alb = Alborán Sea; Blls = Balearic Islands; Chaf = Chafarinas Islands; Cro = Croatia; Egy = Egypt; Fr = Corsica and France; Gr = Greece; Medl = Medes Isles; Ion = Ionian Sea; Isr = Israel; Leb = Lebanon; Lev = Levant Sea; Lig = Ligurian Sea; SC = Suez Canal; Sp = Spain; SG = Strait of Gibraltar; Syr = Syria coast; Tn = Tunisia; Trk = Turkey; Tyrr = Tyrrhenian Sea. Way of introduction: ENR - Expansion Natural Range; LI = Lessepsian Immigrant; PLI = Possible Lessepsian Immigrant; S = Shipping; U = unknown. Red Sea and neighbouring areas: + (present), – (absent).
See text for the sources for the Mediterranean distribution, and Table 1 for the sources for the Red Sea and neighbouring areas.