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Jellyfish populations in the Mediterranean Sea

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Knowledge of jellyfish populations in the Mediterranean Sea is rather extensive, due to a combination of long-term datasets and interest relating to impacts on human activities. The notorious jellyfish Pelagia noctiluca *appears to be blooming with increased frequency in some areas, and may sting tens of thousands of sea bathers in a single year. In addition, a number of invasive species of jellyfish appear to be thriving in the Mediterranean, some of which have significant impacts on fishing and other industries. In contrast, other groups of jellyfish show variable trends over time, and may be of little interest to the public. Here, we summarize knowledge of jellyfish in the Mediterranean Sea, including temporal trends for a variety of species, and discuss possible anthropogenic causes of increased jellyfish abundance and management interventions in the face of uncertainty.*

Key words: Jellyfishes, gelatinous zooplankton, blooms, pelagic cnidarians, ctenophores, invasive species, management under uncertainty

INTRODUCTION

The Mediterranean Sea is home to numerous species of jellyfish, both native and invasive. Some of these jellyfish, which here include pelagic cnidarians, ctenophores and salps, have been monitored for centuries, while others are rarely sampled or studied. In addition, particular species of jellyfish are of high public interest due to impacts on tourism and other human activities, yet others may be of little concern. While several populations appear to be increasing in recent decades, these increases are not uniform throughout the Mediterranean Sea. Some groups show differing or opposite trends, and these trends may vary widely depending on the region in question.

Despite the variability of jellyfish population dynamics over time, space, and taxa, several conspicuous groups of jellyfish appear to exhibit sustained increases in the Mediterranean Sea. Anthropogenic impacts have been suggested as potential drivers of these increases, including global warming, eutrophication, overfishing, bottom-trawling, mariculture, and increased coastal development. Similar trends in jellyfish populations to those in the Mediterranean Sea have been observed on a global scale. While increases are not ubiquitous, they are both numerous and widespread in coastal ecosystems and seas around the world (BROTZ *et al.*, 2012). The relatively extensive knowledge of jellyfish populations in the Mediterranean Sea provides an ideal opportunity to discuss their abundance trends, along with suggested causes and management practices, in the context of overall ecological changes in that body of water (COLL *et al.*, 2012).

Population dynamics of native jellyfish species

The population dynamics of jellyfishes are generally not studied as is usual with finfishes, *i.e.*, using analytic models with explicit terms representing growth, mortality, and related parameters, although this could be done (PALOMARES & PAULY, 2009). Rather, inferences on the dynamics of jellyfish populations are usually based on the location, relative size, and timing of "blooms" (MILLS, 2001; PURCELL, 2005; BOERO *et al.*, 2008).

By far the most notorious jellyfish in the Mediterranean is the mauve stinger, *Pelagia noctiluca*. This scyphozoan lacks a polyp phase, *i.e.*, it has a holoplanktonic lifestyle that does not restrict it to coastal waters. Nonetheless, blooms of this jellyfish are often found near shorelines, inflicting painful but non-fatal stings to up to tens of thousands of seabathers each year (PURCELL *et al.*, 2007; ANONYMOUS, 2010a). In addition, large blooms of this jellyfish have interfered with coastal dragnet fishing (BERNARD *et al.*, 2011). In the Atlantic Ocean, massive aggregations of *P. noctiluca* have disrupted mariculture operations and caused severe fish kills (DOYLE *et al.*, 2008). While similar events have yet to be reported from the Mediterranean, expanding mariculture production and extensive jellyfish blooms suggest that it may simply be a matter of time.

The population dynamics of *P. noctiluca* can be depicted as "presence-absence" (UNEP, 1984; 1991), whereby blooms occur for several consecutive years followed by periods lacking major outbreak events. A long-term dataset constructed by GOY *et al.* (1989) from various sources contains records of *P. noctiluca* dating back to the 18th century, identifying bloom years and non-bloom years. Although some observations were made from single locations (such as the extensive records of the Station Zoologique de Villefranche-sur-Mer, France), most rigorously described blooms indicate a trend that appears to cover the entire western basin of the Mediterranean (GOY *et al.*, 1989). The analysis from 1875-1986 indicated that episodes of bloom years showed a significant period of about 12 years. However, blooms of *P. noctiluca* began to deviate from this pattern in the late 1990s, and persistent blooms have since occurred in the western Mediterranean quasi-annually (ANONYMOUS, 2008; 2010c; DALY YAHIA *et al.*, 2010). Although the numbers of several species of jellyfish observed along Spain's Catalan coast do not show an obvious trend over the last decade (ATIENZA *et al.*, 2010), there are reportedly increases of *P. noctiluca* in recent years further to the west along Costa Blanca (ANONYMOUS, 2010a). BERNARD *et al.* (2011) report data on *P. noctiluca* from beaches along the French Riviera (from Cannes to Monaco) based on estimates of abundance and the administration of first aid by lifeguards and emergency responders. Between 1981 and 2008, there were large blooms reported from 1981 to 1985, and then again from 1994 to 2008, with the exception of a few years of very low abundance. These reports reflect the presence-absence nature of this species (with a few intermediate years), as well as highlighting the fact that blooms have been persistent in recent years, resulting in a large number of stings.

The recent changes in *P. noctiluca* populations in the western basin are not consistent with the rest of the Mediterranean, where different dynamics have been demonstrated in recent decades. Blooms in the Aegean Sea appear to be maintaining the aforementioned 12-year periodicity (DALY YAHIA *et al.*, 2010). However, blooms of *Chrysaora hysoscella* appear to be much larger in this region in recent years (ÖZTÜRK & İŞINIBILIR, 2010). In the Adriatic Sea, *P. noctiluca* was relatively rare until 1977, when it began blooming frequently (ZAVODNIK, 1987). Blooms continued for about 10 years, until 1987, when they appeared to subside and virtually disappear for more than a decade. However, in 2004, blooms of *P. noctiluca* began in this region again (DALY YAHIA *et al.*, 2010) and continued until 2007 (KOGOVŠEK *et al.*, 2010).

In addition to the periodic appearances of *P. noctiluca*, the northern Adriatic Sea shows other signs of increasing jellyfish populations. KOGOVŠEK *et al.* (2010) performed a wavelet analysis of jellyfish blooms in the northern Adriatic over the last 200 years, and found that blooms have been occurring more frequently in recent decades. Several scyphozoans were included in the analysis, with *Aurelia* spp. being the most frequently reported. Species of this genus showed periodic blooms throughout the timeframe covered by the dataset, but the frequency of these events increased during the 1990s. While increased observations of this species may be partially due to improved sampling techniques, major blooms of *Aurelia* appear to be on the rise in the northern Adriatic, and have occurred annually since 2002 (MALEJ *et al.*, 2012). *Rhizostoma pulmo* also showed similar dynamics, with an increased recurrence of blooms over the last two decades. However, the abundance of this species appears to have decreased since 2006 (KOGOVŠEK *et al.*, 2010).

Information presented by MALEJ (2001) also confirms a possible increase in "irregular events" involving jellyfish in the northern Adriatic. With the exceptions of *P. noctiluca* and *Cotylorhiza tuberculata*, numerous species of jellyfish appeared to show an increase in the frequency of blooms through the 1970s, 1980s, and/or 1990s. These included *Aurelia* spp., *Aequorea forskalea*, *Chrysaora hysoscella*, *Rhizostoma pulmo*, and species of Ctenophora. Interestingly, *C. hysoscella* was documented in the Gulf of Trieste on numerous occasions between 1874 and 1911, but then was not reported again until 1981 (DEL NEGRO *et al.*, 1992), highlighting the fact that jellyfish populations may exhibit different trends over a variety of timescales. Despite the apparent recent increases in large scyphomedusae in the northern Adriatic, BENOVIĆ *et al.* (1987; 2000) document and discuss a decline in the hydrozoan community. The authors point to increased hypoxic and anoxic events due to anthropogenic disturbance in the 1970s and 1980s as a cause for decreased abundance and species diversity, primarily for meroplanktonic species (see below). While it is presumed that the overall biomass of jellyfish in this system has increased due to the increased scyphomedusae and ctenophore blooms, the decline in hydrozoan biodiversity highlights the

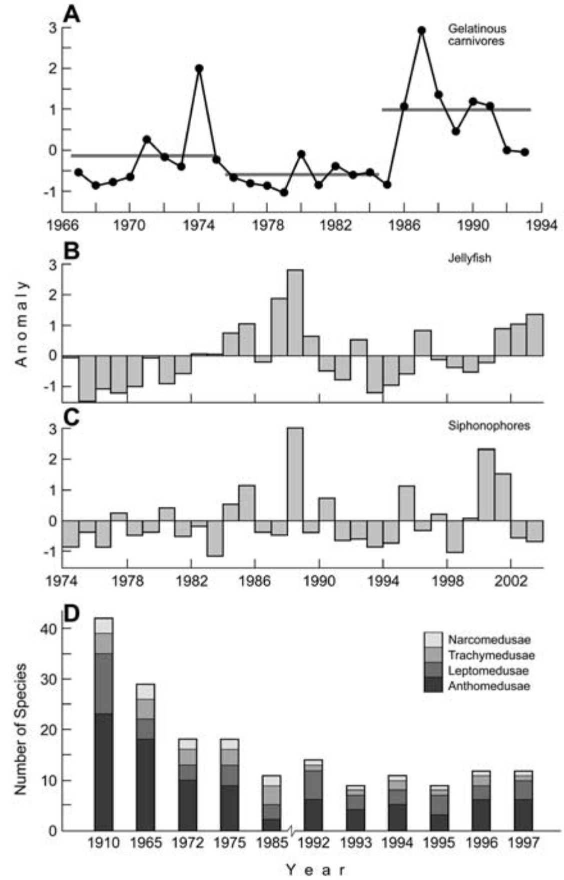

Fig. 1. Examples of time-series data on jellyfish from the Mediterranean Sea. A, B, and C are from data collected at Point B, Villefranche-sur-Mer, France, while D is from the northern Adriatic Sea. Sources: A (MOLINERO et al., 2008a), B and C (GARCÍA-COMAS et al., 2011), D (BENOVIĆ et al., 2000). Note different timescales.

fact that different groups of jellyfish may exhibit dramatically different dynamics over similar temporal and spatial scales.

Increasingly complex patterns of jellyfish abundance are also evident in the western Mediterranean when other gelatinous groups are considered, such as hydromedusae, siphonophores, and ctenophores. Abundance of the small, holoplanktonic hydromedusae *Liriope tetraphylla* showed considerable seasonal, interannual, and decadal variation from 1966-1993 at Villefranche-sur-Mer, but there was no overall increasing or decreasing trend apparent in the dataset (see Fig. 2 in BUECHER *et al.*, 1997). Interestingly, the abundance of *L. tetraphylla*

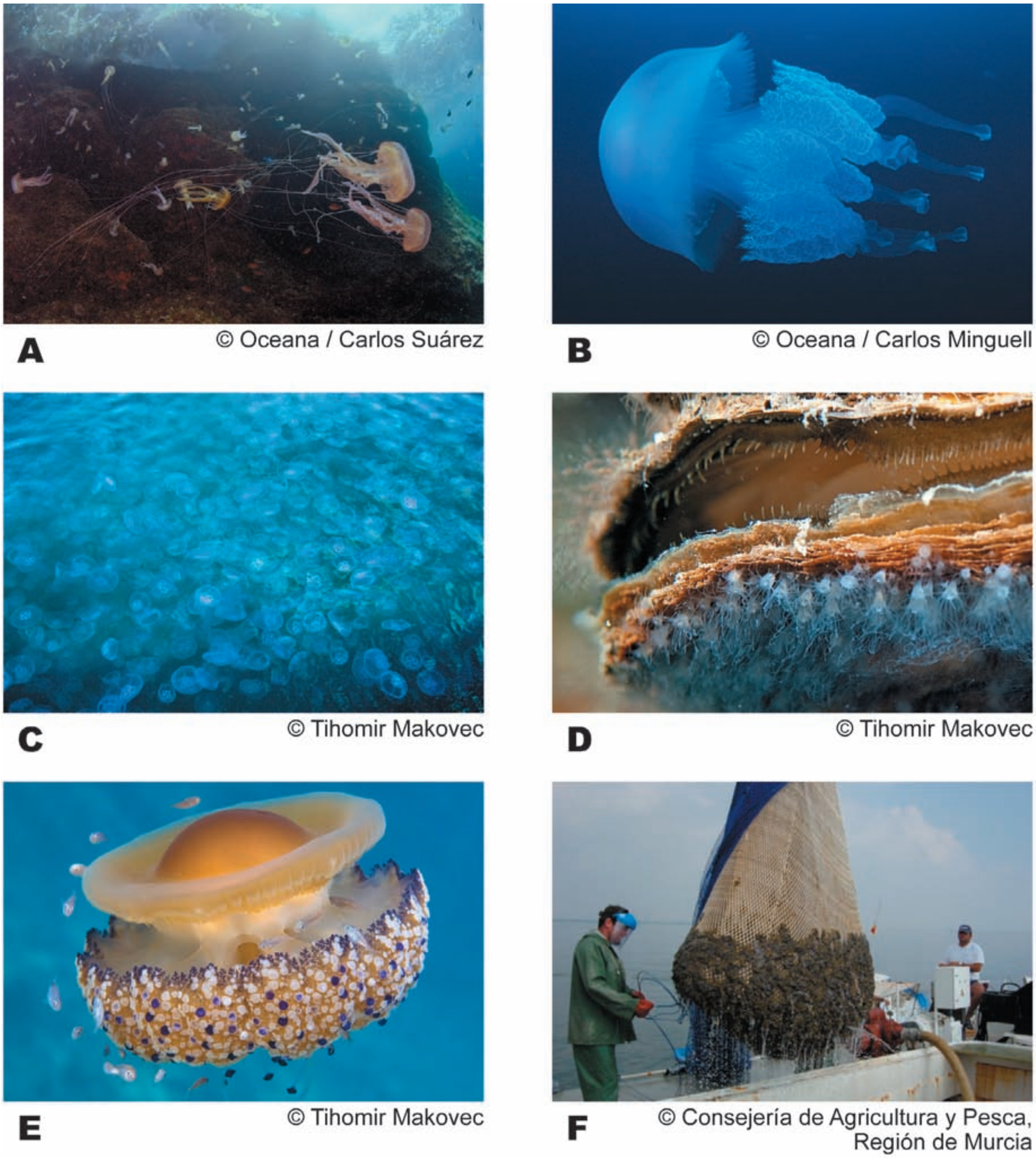

Fig. 2. Photographs of various jellyfish from the Mediterranean Sea. A – Pelagia noctiluca *bloom in Cabrera National Park, Balearic Islands, Spain; B –* Rhizostoma pulmo *in Katakolo, Peloponissos, Greece; C –* Aurelia *bloom in Gulf of Trieste, Slovenia; D –* Aurelia *polyps attached to oyster shell on piling in Gulf of Trieste, Slovenia; E –* Cotylorhiza tuberculata *with juvenile fish near Hvar Island, Croatia; F – Removal of* Cotylorhiza tuberculata *in Mar Menor, Spain*

appeared to correspond negatively to that of *P. noctiluca*, with the strongest years for *L. tetraphylla* occurring during periods when *P. noctiluca* was absent (BUECHER *et al.*, 1997). It remains unclear whether this correlation is due to competition, predation, or environmental conditions (LEGOVIĆ, 1987; BUECHER *et al.*, 1997). GARCÍA-COMAS *et al.* (2011) analyzed the seasonality and abundance of numerous zooplankton groups at Villefranche-sur-Mer using ZooScan

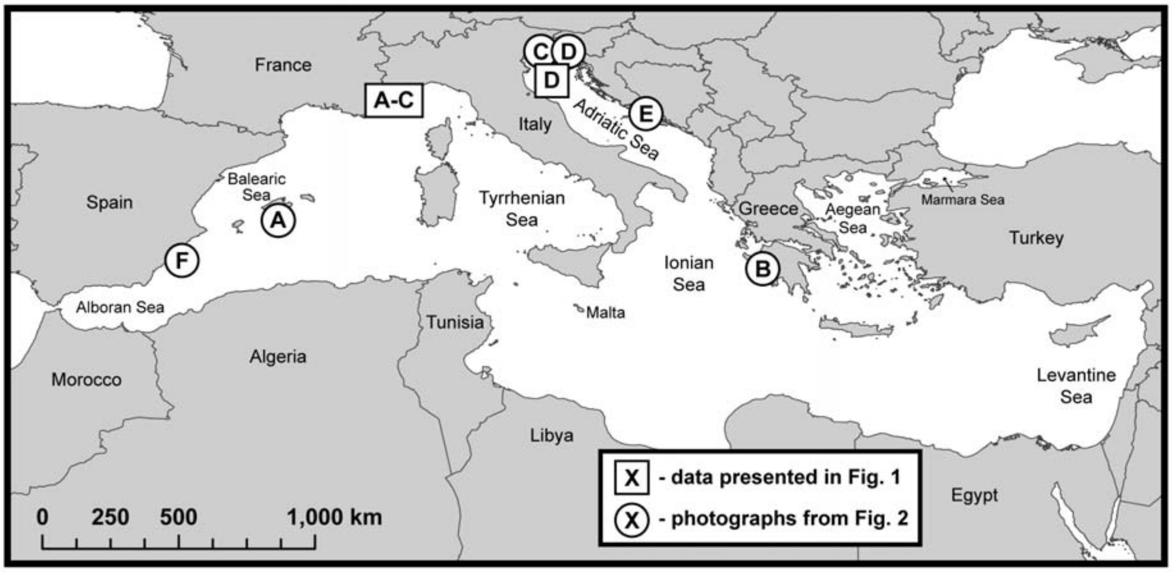

Fig. 3. Map of the Mediterranean Sea showing various locations discussed in the text as well as the locations of data presented in Fig. 1 and the photographs from Fig. 2.

technology, which facilitated the processing of large samples. Data from 1974 to 2003 were included, and gelatinous zooplankton was divided into carnivorous medusae and siphonophores. Both of these groups showed relatively low abundances through the 1970s along with increases through the 1980s (Fig. 1).

These results are consistent with those of MOLINERO *et al.* (2005; 2008a; 2008b), who examined only selected species of jellyfish. However, the increases observed in the early 1990s were not observed in the analysis of the entire jellyfish community. Rather, the medusae and siphonophore populations continued a near-decadal cycle by exhibiting relatively low abundances through the 1990s, followed by returns to higher abundances in the last few years of the dataset (see Fig. 1 and GARCÍA-COMAS *et al.*, 2011). In addition, the ctenophore *Pleurobrachia rhodopis* appeared to decrease in the late 1980s (MOLINERO *et al.*, 2008a), and salps showed periodic blooms, but no consistent trends (LICANDRO *et al.*, 2001). This dataset highlights some of the differences between examining individual species versus considering entire community groups, such as jellyfish and zooplankton. As stated by GARCÍA-COMAS *et al.* (2011), "...the analysis of broad groups […] does not substitute but efficiently complements the species level approach…"

There have been many reports of jellyfish around Malta in recent years, thanks primarily to a recent citizen science campaign entitled "Spot the Jellyfish" (see www.ioikids.net/jellyfish). Not surprisingly, this program has revealed large variations in abundance, with sizeable blooms reported in 2009 and fewer sightings in 2010 (ANONYMOUS, 2010b) and 2011 (ANONYMOUS, 2011c). As problems with jellyfish have been reported from Malta every decade since the 1950s (DEIDUN, 2011), trends in jellyfish populations in Maltese waters remain unclear.

The pleustonic jellyfish commonly known as the Portuguese man o' war (*Physalia physalis*) has also been making headlines in recent years. Human encounters with this siphonophore often result in extremely painful stings (FENNER & WILLIAMSON, 1996). This jellyfish had been absent from the Mediterranean for at least a decade when large blooms were observed along the Spanish coast of the Alboran Sea in 2009 (ANONYMOUS, 2009). However, the distribution of pleustonic jellyfish is especially influenced by wind patters (MACKIE, 1974), and reports of newsworthy blooms often lack a historical context.

Invasive jellyfish species

At least 12 species of jellyfish have invaded the Mediterranean Sea (Table 1), and many appear to be thriving. Notably, the highly invasive ctenophore *Mnemiopsis leidyi* now appears to be successfully established. *M. leidyi* was first recorded in the Mediterranean in the 1990s at several locations including the Aegean Sea near Greece (SHIGANOVA *et al.*, 2001; 2004b) and Turkey (KIDEYS & NIERMANN, 1994), as well as in the eastern Mediterranean near Syria (SHIGANOVA, 1997), and in the Marmara Sea (ISINIBILIR *et al.*, 2004), where a number of jellyfish species appear to have been introduced (ISINIBILIR *et al.*, 2010). *M. leidyi* was subsequently discovered in the northern Adriatic in 2005 (SHIGANOVA & MALEJ, 2009) and in Spain in 2008 (FUENTES *et al.*, 2010). Then, in 2009, large blooms of this invader spanned many disparate locations in the Mediterranean, including Israel (GALIL *et al.*, 2009a), Italy (BOERO *et al.*, 2009), and Spain (FUENTES *et al.*, 2010). The species identity of *M. leidyi* from the Mediterranean has been confirmed using molecular techniques, and given the widespread occurrence of simultaneous blooms, it is likely that this species has been well distributed and established in the Mediterranean for some time (FUENTES *et al.*, 2010). Although the abundances of many other jellyfish were unusually low during the 2009 blooms of *M. leidyi* (FUENTES *et al.*, 2010), the large aggregations of *M. leidyi* suggest that the overall gelatinous biomass in the Mediterranean may be increasing due to this infamous invader.

Interestingly, the reliable predator of *M. leidyi* – *Beroe ovata* – has also been found in the Mediterranean; initially in 2004 in the Aegean Sea (SHIGANOVA *et al.*, 2007), then in 2005 in the Adriatic (SHIGANOVA & MALEJ, 2009), and in 2011 off the coast of Israel (GALIL *et al.*, 2011). Currently, it remains unclear to what extent *B. ovata* is established in the Mediterranean, and whether it has significantly reduced the abundance of *M. leidyi*, as is the case for the Black Sea (SHIGANOVA *et al.*, 2004a).

The conspicuous scyphomedusan *Rhopilema nomadica* first appeared along the coast of Israel in 1977 (GALIL *et al.*, 1990; GALIL, 2000) and blooms have continued to increase there ever since (LOTAN *et al.*, 1992; 1994; MARSHALL, 2010; WALDOKS, 2010). This species appears to have extended its range to Lebanon and Syria (LOTAN *et al.*, 1994), as well as Egypt, Turkey (KIDEYS & GÜCÜ, 1995), Greece (SIOKOU-FRANGOU *et al.*, 2006), and on two occasions, even Malta (ANONYMOUS, 2011b). Massive blooms of *R. nomadica* have occurred annually along the SE Levantine coast since the 1980s, directly interfering with numerous industries and resulting in significant economic losses. Widespread sting events may be severe, with symptoms persisting for months and potentially resulting in hospitalization (ÖZTÜRK & İŞINIBILIR, 2010). Fishers frequently discard entire hauls of their catch due to the medusae, and the operations of ships, power plants, and desalination plants are often affected, requiring the removal of truckloads of jellyfish (SPANIER, 1989; GALIL *et al.*, 2010 and references therein). In Turkey, *R. nomadica* has also interfered with aquaculture operations by preventing fish farmers from lifting their nets to the surface (ÖZTÜRK & İŞINIBILIR, 2010). The continued large blooms of this species suggest it is one of the most successful invasive species of jellyfish in the eastern Mediterranean, and its proliferation may partly be at the expense of the native scyphozoan *Rhizostoma pulmo*, which has exhibited a decline in abundance (GALIL, 2000). However, it is unlikely that the decline of *R. pulmo* is comparable to the dramatic increase in *R. nomadica*, as the former was not frequently reported to form large blooms in the Mediterranean on a historical basis (LILLEY *et al.*, 2009). It should also be noted that blooms of the indigenous *R. pulmo* are still reported from other areas of the Mediterranean, including Mar Menor (see below), as well as near Tuscany and Barcelona (LILLEY *et al.*, 2009).

The invasive *Phyllorhiza punctata* also appears to have established a growing population in the Mediterranean. A solitary specimen was reported from Mediterranean waters in 1965 (GALIL *et al.*, 1990), but there have been reports of individual medusae and large blooms from the coast of Israel since 2005 (GALIL *et al.*, 2009b).

Table 1. Invasive species of jellyfish in the Mediterranean Sea

Genus	Species	Phylum	Class	First detection
Carybdea	*marsupialis*	Cnidaria	Cubozoa	1878*
Cassiopea	*andromeda*	Cnidaria	Scyphozoa	1903*
Clytia	*linearis*	Cnidaria	Hydrozoa	1951
Phyllorhiza	*punctata*	Cnidaria	Scyphozoa	1965
Rhopilema	*nomadica*	Cnidaria	Scyphozoa	1977
Cassiopea	*polypoides*	Cnidaria	Scyphozoa	1987
Mnemiopsis	*leidyi*	Ctenophora	Tentaculata	1990
Clytia	*hummelincki*	Cnidaria	Hydrozoa	1996
Beroe	*ovata*	Ctenophora	Nuda	2004
Marivagia	*stellata*	Cnidaria	Scyphozoa	2006
Catostylus	*tagi*	Cnidaria	Scyphozoa	2010
Aequorea	*globosa*	Cnidaria	Hydrozoa	2011

*original invasion uncertain (see text)

A reproducing population of this invader also exists in a bay on a Greek island in the Ionian Sea, where it has occurred for roughly a decade (ABED-NAVANDI & KIKINGER, 2007). In 2009, a single *P. punctata* specimen was also observed near Sardinia, Italy (BOERO *et al.*, 2009), and in 2010 a bloom of this species forced the closure of six different beaches in Spain's Costa Brava after more than 100 swimmers were stung (ANONYMOUS, 2011d).

Cassiopea andromeda is also suspected to be invasive in the eastern Mediterranean, having been detected in the Aegean Sea and waters near Israel (SPANIER, 1989 and references therein), as well as Lebanon (GALIL *et al.*, 1990 and references therein). There was one observation of this jellyfish from Cyprus at the beginning of the 20th century, but it was not detected again until some 50 years later (see GALIL *et al.*, 1990). It appears the range expansion of *C. andromeda* will continue, with recent sightings from Turkey (ÇEVIK *et al.*, 2006; ÖZGÜR & ÖZTÜRK, 2008) and Malta (SCHEMBRI *et al.*, 2010). Another species in this genus – *C. polypoides* – was reported from the coast of Lebanon in 1987 (LAKKIS, 1991), but it remains unclear to what extent this invader is established.

The only cubomedusan in the Mediterranean, *Carybdea marsupialis*, was initially reported in the Adriatic in 1878 (CLAUS, 1878), but not again until 1985 (BOERO & MINELLI, 1986), after which it became increasingly widespread in the Adriatic (DI CAMILLO *et al.*, 2006). Due to the initial observation of this jellyfish in the late 19th century, the invasiveness of this jellyfish is somewhat unclear. Nonetheless, *C. marsupialis* "is now an obnoxious stinger" in the Mediterranean (CIESM, 2008) and may inflict painful stings (PECA *et al.*, 1997) to thousands of beachgoers in a single season (BORDEHORE *et al.*, 2011). Its range continues to expand beyond the Adriatic, with recent reports of increasing abundance from Italy and Spain (BORDEHORE *et al.*, 2011), as well as France (CUNEO, 2009) and Malta (ANONYMOUS, 2011a).

New invasions of jellyfish continue to be documented in the Mediterranean Sea in recent years. A new genus was described for *Marivagia stellata*, which was first found in Israel in 2006, and several recent detections suggest an established population (GALIL *et al.*, 2010). In 2010, the first sighting of the large scyphomedusan *Catostylus tagi*, which was before restricted to Atlantic waters, was reported from the Sicily Channel in Italy (NASTASI, 2010). In addition, the Indo-Pacific hydromedusan *Aequorea globosa* was observed in Iskenderun Bay, Turkey continuously through 2011, suggesting an established population (TURAN *et al.*, 2011). The growing list of alien jellyfish in the Mediterranean (Table 1) likely represents an underestimate of the actual number of invasive species, as many jellyfish invasions may go unreported due to incomplete treatment, peculiar life histories, and species crypsis (HOLLAND *et al.*, 2004; DAWSON *et al.*, 2005; GRAHAM & BAYHA, 2007). A case in point for the Mediterranean concerns two species of tiny (medusae ~1 mm) hydrozoans in the genus *Clytia*. *C. linearis* was first reported from the Suez Canal in 1938 and then in the Mediterranean in the 1950s (BOERO *et al.*, 2005). The hydroid of this species is now one of the most abundant and widespread in the Mediterranean (BOUILLON *et al.*, 2004). *C. hummelincki* was first reported from the Ionian coast of Italy in 1996 (BOERO *et al.*, 1997), and colonial hydroids of this species have since been widely recorded in the northern Mediterranean, including the Adriatic Sea, Sardinia, and Majorca (GRAVILI *et al.*, 2008). Despite these reports, the spread of these highly successful invaders continues largely unnoticed due a lack of specialists (BOERO *et al.*, 2005; GRAVILI *et al.*, 2008). This problem likely leads to invasions going undetected in other parts of the world as well – in the Baltic Sea, the presence of the highly invasive ctenophore *Mnemiopsis leidyi* was reported only after a female Iranian scientist visited the area and recognized the invader (JAVIDPOUR *et al.*, 2006).

Likely drivers of increasing jellyfish populations

As documented above, although jellyfish populations in the Mediterranean Sea do not exhibit uniform dynamics across time, space, and taxa, it does appear that several populations have increased in numerous areas in recent years and decades. In addition to introduced species, there have been suggestions that increases in jellyfish populations may be due to anthropogenic impacts on the marine environment (MILLS, 1995; 2001; PURCELL *et al.*, 2007; PAULY *et al.*, 2009; RICHARDSON *et al.*, 2009). These suggested drivers include global warming, eutrophication, overfishing, mariculture, and coastal development. With the exception of translocation, none of these factors have been directly demonstrated to cause any increases or blooms (PURCELL *et al.*, 2007). Nonetheless, laboratory experiments and strong correlative data suggest that, in some cases, jellyfish populations may indeed be linked with human activities.

Warmer temperatures due to climate change could benefit some species of jellyfish in the Mediterranean Sea through numerous means, including increased distribution, altered phenology, increased reproductive output, and decreased mortality. Young ephyrae of *Pelagia noctiluca* exhibit reduced survival at temperatures below 8 °C (ROTTINI-SANDRINI, 1982; AVIAN *et al.*, 1991). As such, the increasingly warmer temperatures observed in the Mediterranean Sea may have facilitated the increased populations of this species (MOLINERO *et al.*, 2005; DALY YAHIA *et al.*, 2010). Jellyfish belonging to the genus *Aurelia* have also been shown to benefit from warmer temperatures through increased growth (WIDMER, 2005) and enhanced asexual reproduction (PURCELL, 2007; LIU *et al.*, 2009; PURCELL *et al.*, 2009; HAN & UYE, 2010), which could be involved in the increases observed in some *Aurelia* populations in the Mediterranean. Of course, increased temperatures may be detrimental to other species of jellyfish, as could be the case with the observed decline of the ctenophore *Pleurobrachia rhodopsis* in the northwestern Mediterranean during the late 1980s (MOLINERO *et al.*, 2008b). In addition, the mechanisms involved with changing temperatures and the resulting effects on jellyfish are not always simple. Warmer temperatures can strengthen stratification, which has been shown to decrease the probability of finding large aggregations of salps in the western Mediterranean (MÉNARD *et al.*, 1994).

Jellyfish populations may be influenced by coastal development in a variety of ways. Some mechanisms involve cultural eutrophication, whereby increased nutrient input of anthropogenic origin may create conditions that favor jellyfish over other organisms (PURCELL *et al.*, 1999; ARAI, 2001). Such conditions can include increased food availability, decreased water clarity, and decreased dissolved oxygen (DO) concentrations. Several species of jellyfish that appear to be thriving in the Mediterranean, such as *Aurelia* spp. and *Cassiopea* spp., have been shown to benefit from eutrophication in other systems (*e.g.*, KIDEYS, 1994; NOMURA & ISHIMARU, 1998; KEISTER *et al.*, 2000; SHOJI *et al.*, 2010; STONER *et al.*, 2011), and therefore similar mechanisms may be at work in the Mediterranean. While the increased eutrophication of the Mediterranean Sea may have benefitted some jellyfish populations, the effects may be damaging to others. The benthic stages of many hydrozoans are sensitive to low oxygen concentrations, and hypoxia has been blamed for the reduced diversity of hydromedusae in the Adriatic Sea. BENOVIĆ *et al.* (1987; 2000) document a substantial decline in the total number of meroplanktonic hydrozoan species, especially since the 1960s. The authors point to the increasing frequency and intensity of hypoxic and anoxic events that plagued the bottom waters of the northern Adriatic in the 1970s and 1980s, concomitant with numerous ecological changes including explosions in mucus aggregates (DEGOBBIS *et al.*, 1995). It should be noted that there is also a possibility that increased populations of *P. noctiluca*, which prey on hydromedusae, have also contributed to the observed declines (BENOVIĆ *et al.*, 1987). These important data highlight the fact that different groups of jellyfish will respond differently to anthropogenic impacts, and some groups may be affected negatively (PURCELL *et al.*, 1999). More recently, the northern Adriatic has tended towards more oligotrophic waters (MOZETIČ *et al.*, 2010), and it remains to be seen whether or not this will result in a recovery of hydrozoan diversity in this ecosystem.

Another consequence of coastal development that may benefit jellyfish populations is an increase in marine structures including docks, wharfs, marinas, platforms, breakwaters, and sea walls. Many species of jellyfish have a sessile polyp phase of their life history, which attaches to a hard substrate. Structures of anthropogenic origin may provide increased habitat for polyps, some of which show an affinity for shaded surfaces and synthetic materials (SVANE & DOLMER, 1995; HOLST & JARMS, 2007; HOOVER & PURCELL, 2009). Indeed, jellyfish polyps have been observed on artificial structures in several locations in the Mediterranean Sea. Scyphopolyps were reported in Koper Harbor, Gulf of Trieste, on the undersides of oyster shells attached to piers (DUARTE *et al.*, 2012), and have since been observed in several other eastern Adriatic ports (MALEJ *et al.*, 2012). DI CAMILLO *et al.* (2010) also recorded scyphopolyps on underside portions of an iron shipwreck near Ancona, Italy, but notably did not find polyps in the proximate natural environment, which includes rocky cliffs. Polyps on the wreck were monitored at densities up to 45 polyps$\cdot$cm^{-2} and the authors estimate 780,000 to 2,600,000 ephyrae could be released per m^2. There are also reports of *Rhizostoma pulmo* polyps attached to concrete columns in Badalona, Spain (DUARTE *et al.*, 2012). Although polyps have not been directly observed on anthropogenic structures in Thau lagoon (southwestern Mediterranean), extensive bivalve mariculture operations are suspected to provide suitable substrata for the local population of *Aurelia aurita* (BONNET *et al.*, 2012).

Some combination of these effects is evident in the jellyfish community in coastal Tunisia. TOUZRI *et al.* (2012) examined the composition of gelatinous zooplankton in both the bay and lagoon of Bizerte. A small channel connects the bay and lagoon, with the lagoon receiving the initial flux of anthropogenic inputs as evidenced by increases in nutrient concentrations and primary production. Species diversity of gelatinous zooplankton was significantly lower in the lagoon compared to the bay; however, the hydromedusan *Podocorynoides minima* appears to thrive in the lagoon, presumably benefitting from increased eutrophication and substrate for polyps (TOUZRI *et al.*, 2012).

Perhaps the best example of the correlation between increased jellyfish populations and anthropogenic impacts in the Mediterranean Sea comes from Mar Menor, a Spanish coastal lagoon. This hypersaline lagoon is relatively shallow (~3.5 m average depth) and is separated from the Mediterranean by a sandy barrier with several inlets. Traditionally, this lagoon was a singular ecosystem that supported important artisanal fisheries, as well as a small population of *Aurelia* spp. (PAGÈS, 2001). However, the lagoon has been subject to major environmental changes due to anthropogenic disturbances starting in the 1970s, which have dramatically changed the ecosystem. The disturbances began with the enlargement of several inlets to facilitate the passage of recreational boats, and have continued to include the construction of new harbors, dredging and dumping of sand for artificial beaches, mining operations, changes in runoff, increased eutrophication, and intensive coastal development (PÉREZ-RUZAFA *et al.*, 1991; PAGÈS, 2001). In the mid-1980s, two new scyphozoans (*Cotylorhiza tuberculata* and *Rhizostoma pulmo*) were recorded in the lagoon and began forming large blooms in the mid-1990s (PÉREZ-RUZAFA *et al.*, 2002). These large blooms have been problematic for the tourist industry ever since and there are now efforts to capture and remove thousands of tonnes of jellyfish from this lagoon (PAGÈS, 2001; CONESA & JIMÉNEZ-CÁRCELES, 2007; PRIETO *et al.*, 2010). Nonetheless, it appears that both of these species have completed their life cycle in Mar Menor (FUENTES *et al.*, 2011) and continue to thrive there. Curiously, *R. pulmo* directly consumes diatoms in Mar Menor, and may benefit from increased production due to eutrophication (PÉREZ-RUZAFA *et al.*, 2002; LILLEY *et al.*, 2009). Polyps of *Aurelia* spp. and *C. tuberculata* have been reported from this lagoon attached to artificial dock structures and marine debris (DUARTE *et al.*, 2012). As polyps of *C. tuberculata* appear highly influenced by temperature, it is suspected that blooms of this jellyfish will be increasingly recurrent in Mar Menor under global warming scenarios (PRIETO *et al.*, 2010).

The example of increasing anthropogenic impacts in Mar Menor and the concomitant changes in jellyfish populations illustrate the links and complexities of these relationships in the greater Mediterranean Sea, as well as other parts of the world. Factors and changes rarely occur in isolation, but rather are highly interrelated and may react synergistically (PURCELL *et al.*, 2007). Anthropogenic impacts that stress marine environments may also facilitate species invasions (OCCHIPINTI-AMBROGI & SAVINI, 2003). For example, in harbors, warmer temperatures due to climate change, combined with eutrophication and increased substrate from coastal development, may increase the probability of establishment by non-indigenous jellyfish species introduced by ships (*e.g.*, TURAN *et al.*, 2011). Human stressors may have also facilitated the aforementioned success of invasive hydrozoans in the genus *Clytia* (GRAVILI *et al.*, 2008). Hydroids of these species appear to thrive in urchin barrens, which are likely a result of overfishing and other anthropogenic impacts (FANELLI *et al.*, 1994; MICHELI *et al.*, 2005; GUIDETTI, 2006), although the causal agents are difficult to isolate and identify (SALA *et al.*, 1998; GUIDETTI & DULCIC, 2007).

Overfishing may also result in increased jellyfish populations due to the removal of jellyfish predators and competitors. As the Mediterranean Sea has a long history of overfishing (COLL *et al.*, 2012), the potential effects on jellyfish populations cannot be ignored. Other human industries can also influence jellyfish populations. Similar to the effects of eutrophication and coastal development, increased mariculture operations may ultimately lead to more jellyfish due to increased nutrients, food, and substrate. While the causal factors of increasing jellyfish populations are difficult to ascertain, the correlations are often convincing. In addition to precipitating more investigation, use of the precautionary approach is warranted.

Management under uncertainty

Evidence for a widespread increase in jellyfish has been questioned by CONDON *et al.* (2012), who conjured a “paradigm” (*i.e.*, consensual view) that jellyfish are increasing globally, and which they assert must be refuted. It is clear that there presently could be no such consensus, given the scarcity of jellyfish time-series data and papers analyzing them (but see BROTZ *et al.*, 2012). The contribution by CONDON *et al.* (2012) is no exception: at the time that it was published and discussed in the press, the data gathered in their 'Jellyfish Database Initiative' (JEDI) had not yet been analysed. This point went past dozens of journalists (*e.g.*, ANONYMOUS, 2012; GREENFIELD, 2012; PAGE, 2012) who should have read the paper before reporting that it had "refuted" the notion of widespread jellyfish increases (*i.e.*, shifting a non-existent paradigm). Thus, the article of CONDON *et al.* (2012) and the subsequent media coverage will confuse readers and delay management response to compelling evidence that particular jellyfish species in degraded ecosystems have increased (PURCELL, 2012). For such ecosystems – including the Mediterranean – we need to take management measures despite uncertainty.

As noted by RICHARDSON *et al.* (2012), we need to make the most of the scarce data we have. A case in point is the use by BROTZ *et al.* (2012) of meta-analytic techniques for combining quantitative and anecdotal information in view of assessing trends in jellyfish abundance, especially for blooming species in coastal areas that experience high human impact. Alternatively, we can use reconstructions of historic ecosystems, and compare their jellyfish abundance with the present, a procedure we recommend for the well-studied Mediterranean.

It might take many years for a consensus to emerge about whether jellyfish blooms are increasing globally, and on likely causes if they are. However, in the meantime, we have to deal with the human health impacts and other implications of jellyfish blooms. Harmful algal blooms (HABs), which impact similarly on people, provide a model in this case. Earlier controversies on overall trends in HABs have been overcome through pragmatic discussions of the management of their impact, and more attention is now devoted to the monitoring of HABs (which jellyfish usually lack), reducing eutrophication, and reducing opportunities for invasions. In addition, the examination of long-term datasets have revealed important changes in HABs due to climate change (HINDER *et al.*, 2012). While such time-series are rare for jellyfish, there continues to be historical data which remains unanalysed, as well as a lack of new monitoring programs. It is only by paying more attention to jellyfish that we will be able to reduce uncertainty and gain a better understanding of their dynamics and impacts. Invasive species are often associated with some of the most spectacular jellyfish blooms, and are a continuous problem in the Mediterranean due to its connections to the Red Sea (GALIL, 2007; EL-SEREHY & AL-RASHEID, 2011), as well as intense shipping activities, aquaculture operations, and degraded ecosystems (GRAVILI *et al.*, 2008). Therefore, while there might be no consensus, in the Mediterranean and elsewhere, of the cause(s) of jellyfish blooms, there is enough evidence that they represent a problem which needs to be addressed. That some forms of mitigation are the same as those suggested for HABs even suggests the possibility of synergies, particularly welcome in an age of multiple environmental crises.

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Populacije meduza u Sredozemnom moru

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SAŽETAK

Saznanja o populacijama meduza u Sredozemnom moru su prilično opsežna zahvaljujući dugoročnim setovima podataka i interesa u svezi njihovog utjecaja na ljudske aktivnosti. Zloglasna meduza *Pelagia noctiluca* čija je povećana učestalost u nekim područjima, a mogu opeći nekoliko desetaka tisuća morskih kupača u jednoj godini. Osim toga, broj invazivnih vrsta meduza je u usponu u Sredozemlju, od kojih neke imaju značajan utjecaj na ribarstvo i ostale industrije. Za razliku od drugih grupa meduza pokazuju različite trendove tijekom vremena pa zbog toga nisu od velikog interesa za javnost.

U ovom radu smo prikazali sažeto znanje o meduzama u Sredozemnom moru, uključujući i vremenske trendove za razne vrste, te raspravili moguće antropogene uzroke povećanja brojnost i meduza i upravljanje intervencijama usprkos neizvjesnosti.

Ključne riječi: meduze, želatinasti zooplankton, cvjetanje, pelagički žarnjaci, rebraši, invazivne vrste, upravljanje, neizvjesnost