Toxic marine microalgae and noxious blooms in the Mediterranean Sea: a contribution to the global HAB status report

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ABSTRACT

We review the spatial distribution of toxic marine microalgal species and the impacts of all types of harmful algal events (Harmful Algal Blooms, HABs) in the Mediterranean Sea (MS), including the Black Sea, the Sea of Marmara, coastal lagoons and transitional waters, based on two databases compiled in the Ocean Biogeographic Information System (OBIS). Eighty-four potentially toxic species have been detected in the MS (2,350 records), of which 16 described from these waters between 1860 and 2014 and a few suspected to have been introduced. More than half of these species (46) produce toxins that may affect human health, the remainders ichthyotoxic substances (28) or other types of toxins (10). Nevertheless, toxicity-related events are not frequent in the MS (308 records in 31 years), and mainly consist of impacts on aquaculture, caused by the dinoflagellates *Dinophysis* and *Alexandrium*, along with a few actual shellfish poisoning cases. *Pseudo-nitzschia* blooms are widespread, but domoic acid in shellfish rarely exceeds regulatory levels. Fish kills are probably less sporadic than reported, representing a problem at a few places along the southern MS coasts and in the Ebro River Delta. Since the last decade of the 20th century, blooms of the benthic dinoflagellates *Ostreopsis* cf. *ovata* have regularly occurred all along rocky shores of the MS, at times with human health problems caused by toxic aerosol. New records of *Gambierdiscus* and *Fukuyoa*, until now reported for the westernmost and easternmost MS coasts, raise concerns about the risk of ciguatera, a syndrome so far known only for subtropical and tropical areas. Recent discoveries are the dinoflagellates *Vulcanodinium rugosum*, responsible for the presence of pinnatoxins in French lagoons' shellfish, and the azaspiracid-producers *Azadinium* spp. Mucilages and discolorations have a major impact on tourism in summer. Reports of toxic species and HABs have apparently increased in the MS over the last half century, which is likely related to the increased awareness and monitoring operations rather than to an actual increase of these phenomena. Indeed, while the case of *Ostreopsis* appears as a sudden upsurge rather than a trend, no actual increase of toxic or noxious events has so far emerged in intensively studied areas, such as the French and Spanish coasts or the Adriatic Sea. Moreover, some cases of decrease are reported, e.g., for *Alexandrium minutum* blooms disappearing from the Harbour of Alexandria. Overall, main HAB risks derive from cases of massive development of microalgal biomass and consequent impacts of reduced coastal water quality on tourism, which represents the largest part of the marine economy along the MS coasts.

Keywords: HABs; Mediterranean Sea; microalgae; toxicity; OBIS

1. Introduction

The Mediterranean Sea (MS, from the Latin *mare Mediterraneum* = the sea surrounded by land) is an enclosed basin surrounded on the north by southern Europe and Anatolia, on the south by North Africa and on the east by the Levant. It occupies an area of approximately 2,510,000 km^2 lying between latitudes 30° and 46° N. The narrow and shallow Strait of Gibraltar to the West connects it with the Atlantic Ocean, the Dardanelles to the East with the Black Sea through the Sea of Marmara and the Bosporus, while to the south-east the Suez Canal, opened in 1869 and recently expanded, allows the exchange with the Red Sea. In spite of its geographic position within the northern temperate latitudes, the quite shallow sill (170 m) at the Atlantic boundary blocks the entrance of deep, cold oceanic waters and determines temperate-subtropical conditions in the whole area, with minimum temperatures rarely and only at certain locations going below 12 °C.

The size, location, and morphology of the MS are at the base of its complex physical dynamics with a distinctive thermohaline circulation and permanent or semi-permanent sub-basin gyres. A marked oligotrophy, increasing along both the west-east and the north-south directions, characterizes the MS (Siokou-Frangou et al., 2010). However, along the Mediterranean coasts there are densely populated areas while a number of large rivers with extended catchment basins flow in the MS (e.g., the Po in the northern Adriatic, the Nile in Egypt, the Ebro in Spain, and the Rhone in France). This implies that meso- and eutrophic conditions, and at times pollution, can affect various coastal areas (UNEP/MAP, 2012).

The MS has been the crossroad of various cultures since the very beginning of the human colonization and the development of ancient civilizations. Trading routes, migrations, invasions and the struggle for power have shaped the dynamic history of populations around the basin for millennia. The population grew from 281 million in 1970 to 419 million in 2000 and 472 million in 2010, and is predicted to reach 572 million by 2030. Coastal administrative entities make less than 12% of the surface area of the Mediterranean countries, but host more than a third of the population of the whole region. Coastal population grew from about 100 million in 1980 to 150 million in 2005 and could reach 200 million by 2030 (UNEP/MAP, 2017).

The MS also represents a unique geographic landscape that generates wealth but requires cooperation among the different countries to preserve the environment and the biological resources. The conservative value of the economic assets of the MS has been estimated to be in the order of US$ 5.6 trillion, generating an annual economic value of US$ 450 billion (Randone et al., 2017). A large fraction of the economic value is represented by tourism and related activities; fisheries come as second but >80% of the fish stock is presently threatened. Aquaculture in the MS has considerably expanded over the last decades reaching about 1.3 million tons in 2009 with an estimated value of US$ 3,700 million (Rosa et al., 2012). Most of the marine aquaculture production comes from the north Mediterranean countries, which are also the most intensively monitored, but it is rapidly expanding also in Turkey and Egypt.

In spite of the dramatic alteration of habitats, depletion of natural resources and increased number of alien species, the MS is still characterized by high biodiversity in most animal and algal groups and a considerable number of endemic species (Coll et al., 2010).

The rate at which climatic conditions (e.g., surface temperature, heat waves and sea level) have changed in the MS over the last decades is higher than the global average (Cramer et al., 2018). These changes, coupled with increased population size, urbanization and changes in land use at many coastal places, may pose at serious risk the quality of the environment, the quality and quantity of food and consequently the health and safety of the local populations (Cramer et al., 2018). Especially in view of the growing need to exploit marine resources, HABs and toxic species may represent an increasing risk for human health and economic activities.

Few are the papers reviewing the occurrence of harmful species and/or events at the scale of the whole Mediterranean basin. Fifty years ago Jacques and Sournia (1978-1979) published a first account of the cases of water discoloration (‘eaux rouges’) and the species involved. The overview included mainly dinoflagellate blooms, along with a few cases of anoxia but with no evidence of toxic effects in humans or marine fauna in those years when microalgal toxins were still almost unknown. In an overview of nearly twenty years later, cases of PSP and DSP – mainly attributable to *Alexandrium minutum* and *Dinophysis* spp., respectively – were reported from the northern coasts of the basin, along with the records of various potentially toxic or ichthyotoxic dinoflagellates at different sites (Honsell et al., 1995). A subsequent overview of toxic and harmful microalgae covering up to 2009 pointed at the sudden spreading of *Ostreopsis* cf. *ovata* blooms along the rocky Mediterranean shores (Zingone, 2010).

The present overview covers the MS distribution of marine, toxin-producing microalgae, as included in the IOC-UNESCO Taxonomic Reference List of Harmful Micro Algae (Moestrup et al., 2009) and the cases of toxin-related harmful events (Sections 2.1 and 2.2), including direct impact on human health or natural resources or indirect impact to aquaculture industry. In addition, we review non-toxic events that include high biomass harmful algal blooms (HB-HABs) causing seawater discolorations, anoxia or any other damages to the environment or human activities (Section 2.3). Finally, we discuss the trends of HABs in the MS in general and particularly in the Adriatic Sea, which is considered a HAB hotspot (Section 3). The overview is based on information from more than 600 scientific publications and technical reports collected in two curated databases in the Ocean Biogeographic Information System OBIS (Zingone et al., submitted): the MS-HABMAP-OBIS (https://obis.org/), gathering records of toxic species occurrence, and the Harmful Events Database (HAEDAT, http://haedat.iode.org/), collecting information of either toxic or non-toxic events, i.e., cases of intoxications, closures of aquaculture plants, seawater discolorations and mucilages. The present review is a contribution to a first appraisal of the current knowledge of HAB occurrences across the world seas, namely, the Global HAB Status Report, (Hallegraeff et al., 2017; Zingone et al., 2017). The requirement for such an assessment has emerged from the apparent worldwide increase and spreading of HABs and their negative impacts contrasted by the lack of an overview founded on a robust basis of data.

2. HABs in the Mediterranean Sea: toxic species and harmful event distribution

2.1 Toxic species

Of the more than 140 potentially toxic species listed in the IOC-UNESCO taxonomic reference list (Moestrup et al., 2009), 84 have been found in the MS so far: 17 diatoms, 54 dinoflagellates, 3 dictyochophytes, 6 haptophytes, and 4 raphidophytes (Table 1, and some examples in Fig. 1). These records cover both species actually found to produce toxins in the MS and species known to be toxic from other areas. Given the known variability in toxin production among strains of the same species, non-tested local populations are only ‘potentially toxic’ in most cases, but for brevity they will be referred to as ‘toxic’ in the context of this paper. Sixteen of the toxic species have actually been discovered and described from the MS (Table 2), the first ones (*Prorocentrum lima*, *Dinophysis caudata*, *D. sacculus* and *D. tripos*) in the second half of the 19th century and the most recent ones (*Vulcanodinium rugosum*, *Azadinium dexteroporum*, *Nitzschia bizertensis* and *Ostreopsis fattorussoi*) in the current decade. Some of the HAB species of the MS, such as *D. caudata* and *Chattonella subsalsa*, are widely distributed worldwide while others, including the recently described *N. bizertensis* and *O. fattorussoi*, so far seem to be restricted to specific areas of the MS.

The discovery of potentially toxic species in the MS has undergone an evident escalation over the years (Fig. 2), from the first descriptions of more than a century before the discovery of their toxicity to the rapid increase after the 1960s and the most recent findings. Information on their distribution has also markedly increased along with the intensification of monitoring operations and studies on planktonic and benthic microalgae (e.g., Zingone et al., 2006; Aligizaki et al., 2009; Pistocchi et al., 2012; Balkis and Taş, 2016; Fernández et al., 2019) and of their resting stages in the sediments (Bravo et al., 2006; Satta et al., 2013) or sediment traps (Montresor et al., 1998). Yet the actual range of most toxic species in the MS is far from being known. Indeed, the identification of some of the most represented genera in the MS, such as *Alexandrium*, *Karenia*, *Karlodinium* and *Pseudo-nitzschia*, as well as of many other flagellates, is quite problematic. In many cases the observation of live material or methods more complex than light microscopy are needed. Cryptic diversity discovered in many microalgal taxa over the last decades also concerns several harmful genera and species, which have undergone careful taxonomic investigations more than other non-toxic taxa. This trend has led to the discovery of non-toxic taxa morphologically similar to toxic ones, such as several species in the *P. delicatissima* and *P. pseudodelicatissima* species-complexes (Bates et al., 2018), the non-toxic *A. tamutum* hardly distinguishable from *A. minutum* (Fig. 1A, Montresor et al., 2004),

and the non-toxic chain-forming *Gymnodinium impudicum* (as *Gyrodinium impudicum*, Fraga et al., 1991) which was misidentified as *Gymnodinium catenatum* in studies predating its discovery (e.g., Carrada et al., 1991). Recent studies coupling detailed morphological investigations with the analysis of different molecular markers and toxin production have attempted to clarify species identity within the *Alexandrium tamarense*-species complex (John et al., 2014; Litaker et al., 2018). The case of *Chattonella subsalsa* is interesting because, based on several molecular markers, two different genotypes with different geographic distributions exist for the species (Klöpper et al., 2013). All these taxonomic insights have invalidated many previous identifications of presumed toxic taxa, as detailed in the following sections.
In recent years, information on the presence of toxic species is also gathered through molecular identification of environmental DNA samples (e-DNA metabarcoding), which may give relevant information on the presence and seasonality of cryptic or rare species (Ruggiero et al., 2015; Dzhembekova et al., 2017; Grzebyk et al., 2017). Nonetheless, new findings of species through molecular methods should always be confirmed by morphological studies.
Some of the toxic species of the MS have been suspected to be non-indigenous species (NIS), i.e., introduced outside their natural past or present distribution. The main possible NIS in the MS are *Pseudo-nitzschia multistriata*, *Alexandrium pacificum* and *Ostreopsis* cf. *ovata*. The first MS record of *Pseudo-nitzschia multistriata,* a chain-forming diatom having a distinctive sigmoid shape (Fig. 1G), was in 1992 in the Gulf of Naples, where phytoplankton have been intensively studied since the beginning of the 1980s. The species has shown an increasing trend afterwards in the same area (D'Alelio et al., 2010) and has subsequently been found in Spanish (Quijano-Scheggia et al., 2008), Greek (Moschandreu and Nikolaidis, 2010),

Tunisian (Sahraoui et al., 2011) and Moroccan waters (Rijat Leblad et al., 2013) and in the Adriatic Sea (Pistocchi et al., 2012; Turk Dermastia et al., 2020). The chain-forming dinoflagellate *Alexandrium pacificum* (as *A. catenella*) was found for the first time in low density in 1983 along the Spanish coast (Margalef and Estrada, 1987). In the following years, *A. pacificum* formed blooms on the Spanish coast (Gomis et al., 1996; Vila et al., 2001) and in the Thau Lagoon (as *A. tamarense*/*catenella*, Abadie et al., 1999; Lilly et al., 2002). Subsequently it was progressively found eastward along the Italian (Lugliè et al., 2003, 2017; Satta et al., 2013), Algerian (Frehi et al., 2007) and Tunisian coasts (Turki and Balti, 2007; Fertouna-Bellakhal et al., 2015), whereas it is still unrecorded in the rest of the MS. The benthic dinoflagellate *Ostreopsis* cf. *ovata* showed a sudden emergence in the MS at the end of the last century (see section 2.2.4). A much higher genetic variability and several cryptic species characterize this taxon along the Japanese coasts compared to the Mediterranean-Atlantic area (Sato et al., 2011; Penna et al., 2012) where genetic differences are seen only at the population level with AFLP markers (Italiano et al., 2014). This situation suggests a relatively recent radiation of the species in the latter area and, given the lack of hydrographic links between the two regions, a possible man-mediated transport, although it is impossible to establish when this occurred (Sato et al., 2011). In lack of type material, or material from the type locality, it has not been established which of the numerous morphologically similar taxa corresponds to *Ostreopsis ovata*. Therefore these taxa should be referred to as *O.* cf. *ovata* (Penna et al., 2010; Sato et al., 2011). Benthic *Gambierdiscus* and *Fukuyoa* species are also a novelty in the MS, and their distribution, presently limited at the two ends of the basin, hints at a possible recent introduction from both the Atlantic and the Red Sea.

2.2 Toxic events

2.2.1 Diarrhetic Shellfish Poisoning (DSP)

DSP toxins in mollusks represent the most frequently reported cases of seafood contamination in the MS. Eight toxic species of the genus *Dinophysis*, plus *Phalacroma rotundatum* (Table 1), have been observed along the Mediterranean coasts (Fig. 3A). *Dinophysis caudata* and *D. sacculus* (Fig. 1C), the most frequently reported species, were both described from the MS more than one century ago (Kent 1881; Stein 1883), but risks for human health have first been recognised only in the 1980s in the Gulf of Lion (Belin et al., 1995). In the northern Adriatic Sea, DSP toxicity events have occurred on both the western and eastern side, often causing the closure of shellfish farms (Sedmak and Fanuko, 1991; Boni et al., 1992, 1993; Della Loggia et al., 1993; Orhanović et al., 1996; Bernardi Aubry et al., 2000; Francé and Mozetič, 2006; Marasović et al., 2007; Ninčević-Gladan et al., 2008). In the period 1989-2018, such closures occurred regularly along the Slovenian coast (northern Adriatic) with an exceptionally long period from May 2010 to March 2011 in which relatively high *Dinophysis* abundances were recorded (around 2,000 cells·L^{-1} of *D. fortii*, Francé et al., 2018). These high abundances, never recorded again, were related to long-lasting low salinity and extremely high temperatures in June – July surface waters (<30 °C) causing a marked water column stratification (Francé et al., 2018). High levels of okadaic acid (OA) and/or dinophysistoxin (DTX) in several instances also led to halt shellfish harvesting along the French (Belin et al., 2020) and Spanish coasts of the MS (García-Altares et al., 2016; Fernández et al., 2019). Recurrent toxic *Dinophysis* blooms have been recorded in the Thermaikos Gulf (Greece, North Aegean Sea) since 2000, when they caused great economic losses (EU 5 million) to aquaculture (Koukaras and Nikolaidis, 2004). More occasionally, high levels of DSP toxins have been reported from the eastern Mediterranean (Orhanović et al., 1996; Bazzoni et al., 2018) and Tunisian waters (Armi et al., 2012).

Nonetheless, there have been just a few cases of DSP diagnoses in humans, in the Adriatic (Boni et al., 1992) and Tyrrhenian Seas (Lugliè et al., 2011), and two major accidents. One occurred in 2000, when 200 people were hospitalized following the above-mentioned *Dinophysis* bloom in the Thermaikos Gulf (Koukaras and Nikolaidis, 2004). The other happened in 2010 in Piemonte (north-western Italy), with more than 150 people harmed by the consumption of toxic mussels from the northern Adriatic Sea (Pistocchi et al., 2012).

Other DSP producers widely distributed in the MS are two benthic species of the genus *Prorocentrum* (Fig 3A), *P. lima* (Fig. 1F) and *P. rhathymum*, but no toxicity events have been related with their presence.

2.2.2. Paralytic Shellfish Poisoning (PSP)

PSP events in the MS are related to toxins produced by species of the genus *Alexandrium* and by *Gymnodinium catenatum.* Of the six *Alexandrium* species known to produce PSP toxins found in the MS, *A. minutum,* the type species of the genus (Fig. 1A), and *A. pacificum* (as *A. catenella* in records before 2014) are the most commonly reported ones (Table 1, Fig. 3B). In some cases these species have reached high densities (up to 10^7 cells·L^{-1}) causing seawater discolorations. *Alexandrium taylorii* has also caused discolorations at several Spanish and Italian touristic places (section 2.3.1, table S1) but no toxicity has ever been found in MS populations of this species.

Reports of PSP events initially associated with *A. tamarense* (Boni et al., 1983; Honsell et al., 1992; Abadie et al., 1999), a species that should not produce saxitoxins

(John et al., 2014), were later reinterpreted and attributed to *A. minutum* (Pistocchi et al., 2012) or *A. pacificum* (Lilly et al., 2002). However, one strain of *A. tamarense* from Sardinian coasts has recently been found to be toxic (Lugliè et al., 2017). Since the first observations of massive natural fish mortalities in Egypt (Zaghloul and Halim, 1992), *A. minutum* produced toxic blooms with consequent ban of both fishing and shellfish harvesting in Morocco (Labib and Halim, 1995), Spain (Delgado et al., 1990; Forteza et al., 1998), France (Belin et al., 2020) and Italy (Honsell et al., 1996). After 2000, only a few cases of shellfish farm closures attributed to *A. minutum* have been reported in northern Sardinia (Italy; Lugliè et al., 2011), Catalonia (Spain; Vila et al., 2005; Bravo et al., 2008; Sampedro, 2018) and southern France coasts (Belin et al., 2020). Because of a very similar non-toxic species discovered in the MS, *A. tamutum*, the identification of *A. minutum* can be problematic and should be confirmed by molecular or toxin analyses. *Alexandrium pacificum* was responsible for toxic blooms along the Catalan coast (Bravo et al., 2008), in the Thau Lagoon (Abadie et al., 1999), in Sardinia (Lugliè et al., 2011) and Sicily (Dell'Aversano et al., 2019), at times causing shellfish harvesting closures (Vila et al., 2001; Bravo et al., 2008).

Alexandrium andersonii and *A. ostenfeldii* are much less frequently recorded and possibly overlooked or misidentified in plankton studies. At times their presence has been traced as resting stages (e.g., Montresor et al., 1998; Bravo et al., 2006; Satta et al., 2013). Two other *Alexandrium* species recorded in the MS, *A. balechii* and *A. pseudogonyaulax*, do not produce PSP toxins but are considered potentially ichthyotoxic.

Gymnodinium catenatum was first reported in southern Spain in 1987 (Bravo et al., 1989). The worst, and apparently unique, fatal case of human intoxication in the whole Mediterranean was due to a bloom of this species that caused 4 deaths and the hospitalization of 23 people in Morocco in 1994 (Tagmouti-Talha et al., 1996). Shellfish harvesting ban due to high concentrations of *G. catenatum* have however been frequent in Andalusia (Spain) during the last 3 decades (HAEDAT). Records of this species in the central and eastern MS should be considered with caution because of possible misidentification of *G. impudicum* (Gómez, 2003).

2.2.3 Amnesic Shellfish Poisoning (ASP)

Sixteen of the 26 *Pseudo-nitzschia* species known to produce domoic acid (DA) have been found so far in the MS. Species-level identification is problematic in light microscopy and often requires the use of electron microscopy and/or molecular markers. It follows that in most publications only the genus is reported, or taxa are clustered into two 'groups', only distinguishing the thin (*P. delicatissima*-group) and the thicker morphotypes (*P. seriata*-group). In the last decades, potentially toxic *Pseudo-nitzschia* species have been identified properly from several locations of the MS (Fig. 3C) where the presence of the cold-water species *Pseudo-nitzschia seriata*, often reported in old studies, has never been confirmed.

Seasonal blooms of *Pseudo-nitzschia* spp., at times including toxic ones, occur all along Mediterranean coasts (Fig. S1), with abundances up to several million cells·L^{-1} (e.g., Caroppo et al., 2005; Cerino et al., 2005; Quiroga et al., 2006; Quijano-Scheggia et al., 2008; Ljubešić et al., 2011; Marić et al., 2011; Cabrini et al., 2012; Ruggiero et al., 2015; Taş and Lundholm, 2017; Totti et al., 2019a). Nevertheless, the detection of DA has caused the closure of aquaculture plants only in a limited number of cases (4% of toxicity events in HAEDAT) in southern Spain (HAEDAT) and France (Amzil et al., 2001), whereas DA values below the regulatory limit have occasionally been found in shellfish from the Adriatic Sea (Ciminiello et al., 2005; Ujević et al., 2010; Arapov et al., 2016), Greece (Kaniou-Grigoriadou et al., 2005), and in 65% of 180 mussel samples from mid-Tyrrhenian waters (Rossi et al., 2016). In a few cases, the presence of DA in bivalves was related to a specific taxon, i.e., *P. calliantha* along the Croatian coast (Marić et al., 2011) and in the Gulf of Trieste (Honsell et al., 2008) and *P. brasiliana* in the Bizerte Lagoon in Tunisia (Sahraoui et al., 2011).

Nitzschia bizertensis, described from the Bizerte Lagoon (Tunisia), is one of the two *Nitzschia* species known to produce domoic acid. At least in one case, the presence of this species was related to the detection of domoic acid in mussels (Bouchouicha-Smida et al., 2014). Less clear is the toxicity and the distribution of the other benthic species *Halamphora coffeaeformis*.

2.2.4. Ostreopsis *and species responsible of Ciguatera Fish Poisoning (CFP)*

The benthic dinoflagellate *Ostreopsis* cf. *ovata* produces ovatoxins, which are palytoxins-like molecules that can intoxicate humans by inhalation or ingestion of contaminated seafood. The species was first detected in the MS in the plankton of Villefranche-sur-Mer (France) after a strong *mistral* wind event in 1972 (Max Taylor, pers. comm.), when it was identified with the name of the only species known at that time, *O. siamensis*. The presence of the species was then documented from the coasts of Lebanon in 1980 (Abboud-Abi Saab, 1989) and central Italy in 1986 (Zingone in Tognetto et al., 1995). Around the 2000s, monitoring programs implemented following a series of harmful events (see below) made it evident that *Ostreopsis* species were growing all along the rocky shores of the northern MS (Fig. 4A) in summer/autumn, thriving as epiphyte on macroalgae or epibionthic on a number of benthic substrata, with concentrations up to 10^6 cells·g^{-1} fresh weight of macroalgal thalli (Mangialajo et al., 2011). At lower concentrations *Ostreopsis* spp. were also found along the northern African coasts (Illoul et al., 2012; Ben Gharbia et al., 2019). Of the three species so far identified in the MS, the most common and widespread is *O.* cf. *ovata,* whereas *O.* cf. *siamensis* and *O. fattorussoi* have a much more restricted distribution (Fig. 1E). An interesting aspect of the annual dynamics of *Ostreopsis* species is the rather repetitive patterns of summer and/or autumn peaks, with timing that vary from place to place and is scarcely related to temperature or to other obvious environmental parameters (Zingone, 2010; Accoroni and Totti, 2016).

First problems caused by *Ostreopsis* in the MS were fish and invertebrate kills in 1998 along the coasts of Tuscany (northern Tyrrhenian Sea) (Sansoni et al., 2003; Simoni et al., 2003). Some years later (2002) more than 200 people coming from the beach of the city of Genoa (Ligurian Sea) were hospitalized with fever, red eyes and wheeze (Ciminiello et al., 2006). The only known problems caused by benthic microalgae at that time were those related to ciguatera fish poisoning (CFP) in subtropical areas, whereas cases of toxic aerosol were only known for planktonic *Karenia brevis* blooms in the Gulf of Mexico. In those years, similar human health problems and dermatitis cases were reported from the Catalonia and Balearic Islands (Vila et al., 2008), French (Cohu et al., 2013) and Algerian coasts (Illoul et al., 2012), and are still reported nowadays at several MS places (e.g., Croatian coast, Ninčević Gladan et al., 2019). Both the presence of toxins in the aerosol (Ciminiello et al., 2014) and toxicological data on the effects of inhalation exposure in mice (Poli et al., 2018) support a link between *Ostreopsis* toxins and the respiratory symptoms reported during blooms. However, those health problems do not occur during all phases of a bloom (Vila et al., 2016) and are quite sporadic compared to the widespread and often massive presence of the suspected causative species.

The presence of *Ostreopsis* toxins in marine animals used as food and their impacts on the animal health are relevant for their sanitary implications, which are still controversial (Tubaro et al., 2011). Apparently healthy organisms (e.g., mussels and sea urchins) during *Ostreopsis* blooms can accumulate fairly large amount of toxins (Aligizaki et al., 2008; E. Fattorusso & V. Soprano, pers. comm.), but macroscopic damages have been reported for various benthic organisms in the MS (Sansoni et al., 2003, Simoni et al., 2003; Accoroni and Totti, 2016) and elsewhere (Shears and Ross, 2009). In mussels, *Ostreopsis* can induce important and not completely reversible ultrastructural damages (Carella et al., 2015) and immunological, histological and oxidative responses (Gorbi et al., 2013) while in sea urchins *Ostreopsis* blooms affect reproduction and offspring health (Migliaccio et al., 2016).

Four species of the dinoflagellate genus *Gambierdiscus*, which can produce CFP toxins, have recently been found in the MS. *Gambierdiscus australes*, *G*. cf. *belizeanus*, *G*. *carolinianus, G*. *silvae* and some unidentified *Gambierdiscus* spp., have been reported from the Balearic Islands (Tudó et al., 2018), Greece and Cyprus (Aligizaki and Nikolaidis, 2008; Holland et al., 2013; Aligizaki et al., 2018; Tudó et al., 2018), with the highest diversity in Crete. *Fukuyoa paulensis* also has been found in the Balearic Islands (Laza-Martínez et al., 2016) and Cyprus (Tudó et al., 2018). Yet CFP cases are not known in the MS countries with the exception of a suspected case of ciguatoxins in rabbitfish (*Siganus rivolutus*) reported from Israeli coasts (Bentur and Spanier, 2007).

2.2.5. Azaspiracid Shellfish Poisoning (AZP)

The toxins azaspiracids (AZAs), produced by a number of dinoflagellate species of the genera *Azadinium* and *Amphidoma*, and the human syndrome they can cause, AZP, have been discovered at the beginning of this century (James et al., 2002). Subsequently AZAs have been reported in shellfish from numerous sites, including the MS (Bacchiocchi et al., 2015). A new species described from the MS, *A. dexteroporum* (Percopo et al., 2013, Fig. 1 B), produces a whole suite of AZAs that can cause direct harm to molluscs (Rossi et al., 2017; Giuliani et al., 2019). Another toxic *Azadinium*, *A. poporum*, has been found in Greek waters (Luo et al., 2018) but no impacts related to AZAs have been reported so far.

2.2.6 Ichthyotoxicity

About half of the potentially toxic MS species produce a variety of toxins that differ from those related to the syndromes mentioned in the previous sections. Of these, the majority (28 species, Table 1) produce substances that have been associated with fish and/or shellfish kills. With a few exceptions, species in this list are unarmoured dinoflagellates, e.g., *Karenia* and *Karlodinium*, and other flagellates belonging to the prymnesiophytes, raphidophytes and dictyochophytes, which are all hardly identifiable in fixed material under the light microscope, and hence are overlooked in most monitoring and ecological investigations. The large majority of the information on the presence of these ichthyotoxic species (Fig. 4B) comes from fish mortality events, mainly located near fish-farming plants, in which the identification of the culprit became necessary.

The few fish mortality events in the MS known before 1975 were related to HB-HABs of non-ichthyotoxic species causing anoxia in bottom waters (see section 2.3.1) rather than to ichthyotoxic species (Jacques and Sournia, 1978-79). In the subsequent years, fish kills by ichthyotoxic species were reported sporadically from Catalan coasts, Spain (Garcés et al., 1999), caused by *Karlodinium* spp., and Sardinia (Italy), caused by *Chattonella subsalsa* (Stacca et al., 2016). Occasional fish mortality events were related to *Prymnesium* spp., in the Ebro Delta (Spain, Comín and Ferrer, 1978) and in a Tuscany lagoon (Italy, Mattioli and Simoni, 1999), *Karenia selliformis* in the Gulf of Gabes (Tunisia, Romdhane et al., 1998; Feki et al., 2013) and *Karenia brevis* and *Pseudochattonella* cf. *verruculosa* in Greece (Ignatiades and Gotsis-Skretas, 2010). In other cases, fish kills occurred during blooms of species toxic to humans, like in Egypt in 1987 (Zaghloul and Halim, 1992; Labid and Halim, 1995) where *Alexandrium minutum* was the culprit. No fish or shellfish kill accidents in the MS have ever been associated with blooms of two potentially ichthyotoxic *Alexandrium* species, *A. balechii* and *A. pseudogonyaulax*.

Benthic cyanobacteria are poorly investigated in Mediterranean waters, but blooms of filamentous cyanobacteria have been the cause of massive fish mortalities in Alexandria waters (Egypt) during spring 2005 (Ismael, 2012).

2.2.7 Other toxins

The dinoflagellates *Gonyaulax spinifera*, *Lingulodinium polyedra* and *Protoceratium reticulatum*, which are quite widespread in the MS (Fig. 4 B), produce yessotoxins (YTX). These substances were initially associated to DSP because their presence gives similar positive results in mouse bioassay, but they are not considered toxic to humans (Tubaro et al., 2010). However, YTXs caused economic impacts in 2002, 2004 and 2007, when mussel harvesting was halted for a long time (average closure 153 days) in the north-western Adriatic Sea (Poletti et al., 2008).

Vulcanodinium rugosum produces pinnatoxins (Rhodes et al., 2010; Nézan and Chomérat, 2011) a neurotoxin that has lethal effects on sea urchin larvae, oysters and

Artemia. Currently there are no problems related to this species, while toxic effects on humans are not known.

2.3. Non-toxic events

Independent from toxin production, all microalgae may exert a negative impact when they reach a high biomass producing seawater discolouration, mucilages or anoxia in bottom waters (Zingone and Enevoldsen, 2000). Although several microalgal species are frequently associated with these HB-HABs, as detailed in the next sections, the number of species that may cause harm with no specific toxin production is in theory unlimited, and can vary from place to place. For this reason it is not possible to define a global or regional list of non-toxic harmful microalgae. In addition to HB-HAB-formers, some non-toxic species, mainly diatoms, may cause mechanical harm to invertebrates' gills (Bell, 1961), but no information on such events is available for the MS. In case of fish or invertebrate kills, at time it is hard to discern whether the cause has been anoxia, toxic substances or mechanical damages. In many cases, species known to produce toxins may produce non-toxic HB-HABs, which have no impact on human or marine fauna health but important consequences for tourism. For all these reasons, the boundaries between events described in the previous and next sections cannot always be well defined.

2.3.1 Discolorations

In the MS, discolouration or anoxia have frequently been caused by unarmoured dinoflagellates either toxic (e.g., *Margalefidinium polykrikoides*) or non-toxic (e.g., *Noctiluca scintillans*), but also by numerous armored dinoflagellates, diatoms, prasinophytes, prymnesiophytes and raphidophytes (Table S1). Change of seawater color caused by HB-HABs (Fig. 5) have been noticed since the first half of the XX century in both lagoons and coastal sites, where they were given several names (*purga de mar*, *punti verdi*) before the one of *red tides* gained popularity. The oldest records include discolorations caused by *Chattonella subsalsa* in 1956 in the Algiers harbor (Hollande and Enjumet, 1957), *Alexandrium minutum* in 1957 in the Alexandria harbor (Halim, 1960) and *Prorocentrum cordatum* in the Gulf of Naples in September 1962 (Yamazi, 1964).

Different dinoflagellates (e.g., *Alexandrium* spp., *Noctiluca scintillans, Karlodinium* spp.), raphidophytes (*Chattonella subsalsa* and *Fibrocapsa japonica*, Fig. 1D) and chlorophytes (*Tetraselmis wettsteinii* and *Pyramimonas* spp.) occasionally produced discoloration (Table S1, Fig. 5), which in some cases were also associated with fish kills and/or massive death of marine invertebrates caused by anoxic conditions (e.g., Arzul, 1994; Halim and Labib, 1996; Garcés et al., 1999). A couple of such cases of fish mortality events attributed to anoxia were already reported in the review by Jacques and Sournia (1978-79): in Ismir Bay (Nümann, 1955, in Jacques and Sournia, 1978-79) and in the Adriatic Sea (Piccinetti and Manfrin, 1969; Froglia, 1970), during blooms of *Gymnodinium* sp. and *Protoperidinium depressum*, respectively.

Discolorations were particularly frequent in the northern Adriatic Sea in summer in the 1970–'80s, when dinoflagellate blooms (e.g., *Lingulodinium polyedra, Alexandrium mediterraneum* and *Lepidodinium chlorophorum*) turned the sea into various colours (Boni, 1983, Table S1), at times extending offshore as in the case of *N. scintillans* in 1980 (Fonda Umani et al., 2004) and *L. chlorophorum* in 1984 (Artegiani et al., 1985). Some summer blooms were caused by diatoms (e.g., *Skeletonema marinoi* and *Chaetoceros* spp.), particularly after intense freshwater inputs (Boni, 1983; Regione Emilia Romagna, 1982-2018). Over the last decades blooms of *F. japonica* (Fig 1D) became common in late summer (Cucchiari et al., 2008) in shallow coastal waters where they lasted up to 20–40 days. Along the eastern Adriatic coast, ‘red tides’ were limited to eutrophicated semi-enclosed bays (Marasović et al., 1991) or to unusual phenomena such as bloom of the silicoflagellate *Octactis* (formerly *Distephanus*) *speculum* in summer 1983 in bottom waters in the Gulf of Trieste, causing anoxia (Fanuko, 1989). An increasing number of discolorations have been observed over two decades in the Golden Horn Estuary of the Sea of Marmara (Taş et al., 2016). An unusual bloom of the coccolithophore *Holococcolithophora sphaeroidea* (as *Calyptrosphaera sphaeroidea*) caused a white-green-turquoise discoloration in a vast area off the Tarragona harbor (Spain, Cros et al., 2002). The most recent event has been a long-lasting bloom of *Margalefidinium* cf. *polykrikoides* that produced a yellow brownish discoloration in a touristic area of the Ionian Sea (Italy) in July-August 2018, recurring in the same place in summer 2019 (Roselli et al., 2020).

In summer, discolorations can be a serious problem along Mediterranean beaches where they have an impact on tourism and recreational use of the sea. This is the case of the recurrent *Alexandrium taylorii* blooms along the Sicilian and Sardinian coasts (Italy) and in the Balearic Islands (Spain) (e.g., Basterretxea et al., 2005; Giacobbe et al., 2007; Satta et al., 2010; Sampedro, 2018).

2.3.2 Mucilages

In the MS, a number of cases of mucilaginous aggregate formation related to microalgal growth have been described, the most conspicuous of which occurred in the northern Adriatic Sea in the 1990s. Mucilaginous macroaggregates represent the last stage of aggregation of organic matter, mainly refractory polysaccharides derived from phytoplankton exudates (Myklestad, 1995) and/or from bacterial capsular material (Stoderegger and Herndl, 1998) whose hydrolysis cannot be sustained by phosphorous-limited bacteria (Danovaro et al., 2005). Whereas marine snow (aggregates of 0.5-1 cm diameter) is common in all the oceans (Simon et al., 2002), the mucilage event in the northern Adriatic Sea was unique in that those aggregates covered hundred square kilometres of both coastal and offshore areas. The formation of larger aggregates was favored by the strong stratification of the water column and reduced circulation that retained freshwater in the northern Adriatic basin (Russo et al., 2005). The direct responsible of the phenomenon were often thought to be the most abundant phytoplankton species in the aggregates, such as *Cylindrotheca closterium* (Revelante and Gilmartin, 1991) and *Gonyaulax fragilis* (Pompei et al., 2003), both capable to produce large amounts of refractory polysaccharides (Pistocchi et al., 2005; Urbani et al., 2005). In fact, phytoplankton communities associated with mucilage aggregates largely vary, depending on sampling area and period (Totti et al., 2005, and references therein), while the aggregates represent a self-sustained microcosm hosting a rich microorganism community (Simon et al., 2002).

Pelagic mucilages have been reported at several other Mediterranean sites, such as the Greek (Gotsis-Skretas, 1995; Nikolaidis et al., 2008) and Catalan coasts (Sampedro et al., 2007) where *Gonyaulax fragilis* was thought to be involved in their production, and the Sea of Marmara (Turkey) where *Cylindrotheca closterium*, *Skeletonema costatum* and *Gonyaulax fragilis* were indicated as the most abundant species (Tüfekçi et al., 2010). In the Tyrrhenian Sea, extensive pelagic aggregates were observed in 1991, 2000 and 2012 (Fig. 5 A, Calvo et al., 1991; Innamorati et al., 1993; Escalera et al., 2018). Foam accumulated massively along the Catalan coast in

March 2006 during a *Phaeocystis* sp. bloom, an event that was related to anomalous hydrographic winter conditions (Arin et al., 2014).

Massive mucilage events have also concerned the benthic environment. *Ostreopsis* cf. *ovata* during intense blooms forms a network-shaped mucilaginous biofilm that can harm benthic invertebrates (Schiaparelli et al., 2007). In the Tyrrhenian and Ligurian Seas (western MS), benthic mucilages have occurred since 1991 (Sartoni and Sonni, 1991), and have been attributed to the massive growth of several macro- and microalgae such as the filamentous brown alga *Acinetospora crinita* and the colonial pelagophytes *Nematochrysopsis marina* and *Chrysonephos lewisii* (Giuliani et al., 2005; Schiaparelli et al., 2007). The allochthonous pelagophyte *Chrysophaeum taylorii*, recorded in the western MS since 2005, in recent years was involved in the formation of dense layers of mucous covering macroalgae, gorgonians and the surrounding rocks (Lugliè et al., 2008; Caronni et al., 2015).

3. Trends in the Mediterranean HABs

3.1 General trends

The MS has undergone profound changes over the last centuries. Human action has mainly been visible along the coasts of the basin, which have become increasingly populated and deeply modified by coastal and riverine engineering and deforestation which, along with cultural eutrophication, are all potential drivers of deep changes in phytoplankton communities (Garcés and Camp, 2012). Natural and/or man-induced meteorological and climatic variations superimpose to these changes often with an amplifying effect. The most striking characteristic of the MS HABs over the last 50 yrs, which approximately correspond to the time since when they have been studied more intensively, is the remarkable increase of the toxic species list, from a few taxa to the more than 80 of the present review (Fig. 2). Over the same period, the records of these species across the MS have also remarkably increased (Fig. 6). This trend is parallel to that of the increased list of toxic species and of their records worldwide, which is an obvious result of the intensification of the taxonomic and toxin studies on marine microalgae (Zingone et al., 2017). The increase of the records of actual HAB events from the less than 30 cases listed by Jacques and Sournia (1978-1979) and Honsell et al. (1995) to the several hundred cases of halted aquaculture operations, seawater discoloration and minor human health accidents presently recorded in HAEDAT is also impressive (Fig. 7). Damages to aquaculture caused by ASP and PSP toxins in mussels have been limited over the last 30 years while DSP cases have represented about 75% of the harmful events, with an increase between the decade 1987-1997 and the two following ones (Fig. 7). This trend should however be interpreted with caution because it has been paralleled by a remarkable growth of the coastal MS population (section 1), much more intensive use of marine resources, and consequent raise of the level of attention to the integrity and safety of marine resources.

In fact, toxic blooms as well as mucilage events and discolorations in the MS have generally shown an unpredictable interannual periodicity, like in the case of the conspicuous blooms of *Noctiluca scintillans* in the Adriatic Sea (Fonda Umani et al., 2004), Moroccan (Tahri Joutei et al., 2003), Catalan (Lopez and Arte, 1971) and French coasts (M.-O. Soyer in Jacques and Sournia, 1978-1979). There are cases of decreases, e.g., the blooms of *Alexandrium pacificum* occurring on the Catalan coast from 1996 to 1998 (Vila et al., 2001) but rarely recorded afterwards (Sampedro, 2018). Blooms of *A. minutum* were recurrent in Egyptian waters but not recorded any longer after 1994 (Ismael and Halim, 2001), while their frequency doubled from 2000 to 2012 along the Catalan coast (Sampedro, 2018). Blooms of the ciliate *Mesodinium rubrum* hosting cryptophyte chloroplasts were not recorded in the MS (Jacques and Sournia, 1978-1979) until their occurrence in both the Adriatic (Sorokin and Ravagnan, 1999) and Tyrrhenian Seas (Siano et al., 2006), and afterwards have only been observed in 2017 in the North Aegean Sea (Genitsaris et al., 2019).

In the case of *Ostreopsis* cf. *ovata*, rather than an increase the phenomenon in the MS has shown a sudden upsurge around the 2000, followed by an expansion of the known range for the species in the next years and a relative stability in the following decade. Indeed *Ostreopsis* cf. *ovata* provides the most evident case of range expansion and increased impact over time in the MS. Although benthic microalgae have received scarce attention until the late 20^{th} century, it is unlikely that the species might have been abundant but undetected before. The apparent sudden range expansion and impact of *Ostreopsis* cf. *ovata* is in line with an increasing trend of species of the same genus in New Zealand and some other temperate areas around the world (Parsons et al., 2012). On the other hand, no clear increase of the impact or of species abundance has been reported since the 2000 outburst, while the above-mentioned range expansion has coincided with a dramatic increase in monitoring programs and research projects focused on benthic microalgae. Initially, the sudden relevance of the phenomenon was associated with an increase of temperature in the MS, based on the belief that all *Ostreopsis* species were of tropical origin. In fact, *Ostreopsis* cf. *ovata* and its close relatives are widely distributed in temperate areas, also matching the apparent preference of the species for moderately high rather than very high temperature (Mangialajo et al., 2011; Scalco et al., 2012). Overall, the trend observed for this species in the MS, with an outburst followed by a stabilizing trend, recalls that of an invasive species rather than that of a species favored by a temperature increase.

3.2 HAB trends in the Adriatic Sea, a case study

The Adriatic Sea (AS) represents a unique system for its semi-enclosed morphology, shallow depth and oligotrophic nature in most parts but with eutrophic characteristics along the north-western coasts driven by inputs from the Po River and other rivers (Mozetič et al., 2010; Cozzi and Giani, 2011). The AS is considered one of the hotspots of MS HABs (Garcés and Camp, 2012), in terms of both occurrence and impacts. However, compared to the great variety of potentially toxic species (Mozetič et al., 2019), toxicity cases are limited, and the most common toxins found above the regulatory limits in the Adriatic shellfish to date are DSP toxins (okadaic acid group) and other lipophilic toxins (yessotoxins and pectenotoxins).

Because of the early development of marine-related activities, there is a wealth of information from the area dating back to the last century, which allows some insights on possible HAB trends. Phytoplankton in certain areas of the AS (e.g., Gulf of Trieste, Gulf of Venice, Senigallia-Susak transect, Kaštela Bay) have been extensively studied for decades (Ninčević-Gladan et al., 2010; Bernardi Aubry et al., 2012; Marić et al., 2012; Mozetič et al., 2012; Cerino et al., 2019; Totti et al., 2019a), highlighting a number of changes, such as trends or regime shifts in main phytoplankton groups (Mozetič et al., 2010; Totti et al., 2019a) and in bloom forming species (Cabrini et al., 2012). However, no trends specifically related to toxic species is evident from these long-term studies, neither in terms of increased frequency nor of abundance. In fact, most studies on HAB species are snapshots of isolated toxic episodes (Pistocchi et al., 2012, and references therein). Similar conclusions can be drawn also from toxicity events: aquaculture operations have been halted frequently over the last 20 years (section 2.2.1), but without any significant trend for DSP events.

Nevertheless, some changes in phytoplankton community structure of the AS have involved a number of HAB species, such as *Pseudo-nitzschia multistriata,* an allochthonous species (section 2.1) that became a regular component of the autumn phytoplankton communities of the NW AS (Totti et al., 2019a). In the Gulf of Trieste, previously rare *Dinophysis tripos* have become a regular member of the autumn phytoplankton assemblages since 2010, along with higher temperatures recorded in this decade (Francé et al., 2018), whereas further south *D. sacculus* has replaced *D. caudata* as one of the indicator species of spring phytoplankton communities (Totti et al., 2019a).

HB-HABs caused by dinoflagellates, occurring in summer and often associated with water discoloration and bottom anoxia, were a major problem in the AS until the end of the 1980s (see section 2.3.1). At the time, because of the heavy impact on the local economy, the Italian government adopted countermeasures to reduce P content in detergents and improve the urban wastewater treatment plants, leading to a strong reduction of P load in coastal waters. Since the end of the 1980s, summer dinoflagellate blooms became a rarer phenomenon, their decline coinciding with the years of large mucilaginous macroaggregate appearance.

Mucilages in the AS (see section 2.3.2) were known since the beginning of 1700, when they were named ‘mare sporco’. In more recent years, massive episodes have occurred in the years 1988 to 1991 and 1997 to 2004, typically in summer (Giani et al., 2005), while a spatial and temporal reduction occurred in subsequent years. An anomalous occurrence in autumn-winter was reported in 2006-2007, probably in relation to a water temperature increase (Danovaro et al., 2009). The mucilage appearance, and the concurrent disappearance of summer water discolorations have both been associated with the decrease of inorganic and organic P (Degobbis et al., 2005), but also to hydrographic changes related to large-scale climatic changes around the end of the ‘80s, which could have driven a regime-shift affecting not only the AS but also other European Seas (Conversi et al., 2010).

In the last decade (2008-2018), HB-HABs of both diatoms and dinoflagellates occurred without a regular temporal pattern, reflecting the meteorological events that nowadays tend to be more intense and unhampered by a regular seasonal rhythm (Totti et al., 2019a, b). Blooms of *Fibrocapsa japonica* that were common at the end of the 1990s seem to be rarer since 2012 (Regione Emilia-Romagna, 1982-2018), and mucilage events occurred shortly in 2014 and in 2018 (Regione Emilia-Romagna, 1982-2018).

As a whole, HABs in the AS show unpredictable time variability that is partly related to the irregularity and intensity of meteorological events in the last decades. Prolonged periods of drought (Cozzi et al., 2019) with oligotrophic conditions (Mozetič et al., 2010) alternate with nutrient pulses from continental water runoff that can drive the occurrence of anomalous intense blooms at any time of the year (Totti et al., 2019a).

4. Conclusions

A deep knowledge on the spatial and temporal distribution of harmful species and the blooms that they produce is an indispensable goal towards a safe use of marine resources and an informed management and planning of the coastal zone. In the MS this goal is even more crucial considering the importance of the economy deriving from the use of the sea for tourism and recreational use, fishery and aquaculture. The information about HABs has grown remarkably over the last 50 years since the first review (Jacques and Sournia, 1978-1979) all over the MS areas. However, the marked west-east and north-south gradients in the knowledge of HABs and HAB species distribution persist, with long traits of coast with scarce or no information available. Overall, the MS hosts a high number of potentially toxic species, many of which have a wide distribution across its coastal waters. Yet the cases of intoxication are extremely rare, while the impact on aquaculture appears to be limited to a few hot spots in the northern Adriatic, Spain and France coasts. A variety of toxins have actually been detected in several instances in microalgae strains from the MS, while seafood toxicity, when detected, has commonly remained below the safety limits. The typical oligotrophic offshore Mediterranean waters that influence most coastal areas and the enhanced alongshore circulation in many places may play a role in keeping toxic algae at levels rarely exceeding critical density thresholds, thus preventing their excessive accumulation in seafood. On the other hand, quite effective monitoring operations have accompanied the development of aquaculture over the last decades, thus reducing the possibility of accidents to a minimum level.

In terms of microalgal toxins, the only major concern seems to reside in the large amount of palytoxin-like substances that every summer accumulate along the rocky Mediterranean shores because of *Ostreopsis* blooms. Although sea urchins and wild mussels inhabiting those environments at time accumulate those toxins to considerable levels, no cases of seafood intoxication have occurred so far.

Contaminated herbivorous fishes represent a problem in areas where they ingest macroalgal substrates colonized by toxic microalgae, i.e. in the ciguatera areas, but species capable of this transfer link may be missing in the MS trophic webs, or toxins are neutralized in the transfer. Nonetheless, the guard level must be kept high because sudden changes might occur, e.g., due to penetration of benthic herbivorous fish in the MS and consequent novelties in the local food webs.

Overall, the present overview demonstrates a relatively low risk deriving from toxic blooms and a higher risk from high biomass blooms affecting the aesthetic qualities of coastal areas devoted to tourism in the MS. No clear trends in occurrence nor expansions emerge for either toxic or HB-HABs. While EU regulation and national initiatives have promoted actions addressing seawater quality and aiming at a good environmental status (GES), human densities along the coasts is predicted to keep on increasing in the next decades. Therefore, a larger use of marine resources in the future, in the MS like in other coastal areas of the world, will probably lead to an increased impact of the risks posed by HABs even in absence of any trends in their abundance and frequency (Zingone and Wyatt, 2005). In addition, predicted changes in climate and consequent modifications in hydrographical features may drive local variations in microbial populations both in the plankton and in the benthos. Continued monitoring and further studies on HAB patterns and trends are therefore mandatory goals to be able to predict their evolution and protect human health and wellbeing in the MS.

Acknowledgements

We are grateful to Pieter Provoost (IOC-OBIS) for providing the maps of the toxic species, and to Henrik Enevoldsen (IOC) and Laura Schweibold for assistance with HAEDAT. LE was partially supported by the project Ostreopsis-Regione Campania.

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Figure captions

Figure 1: Examples of toxic species from the Mediterranean Sea. A) *Alexandrium minutum* stained with calcofluor. B) *Azadinium dexteroporum*. C) *Dinophysis sacculus*. D) *Fibrocapsa japonica*. E) *Ostreopsis fattorussoi* stained with Calcofluor (courtesy of S. Accoroni). F) *Prorocentrum lima*. G) *Pseudo-nitzschia multistriata*. Scale bars in A and B: 5 µm; in C, D, E, F and G: 20 µm.

Figure 2: Cumulative numbers of known toxic species in the Mediterranean Sea in different years**.**

Figure 3: Geographic range of potentially toxic species in the Mediterranean Sea. Distribution of species known to produce toxins related to: A) Diarrhetic Shellfish Poisoning (DSP), *Dinophysis* spp. and the benthic species *Prorocentrum lima* and P.

rhathymum. B) Paralytic Shellfish Poisoning (PSP), *Alexandrium* spp. and *Gymnodinium catenatum*. C) Amnesic Shellfish Poisoning (ASP), *Pseudo-nitzschia* spp. and *Nitzschia bizertensis*. For the genera *Dinophysis*, *Pseudo-nitzschia* and *Alexandrium*, which include both toxic and non-toxic species, the maps represent only toxic species and, in case of cryptic or problematic species, only the records validated by electron microscopy, molecular methods and/or toxin production.

Figure 4: Geographic range of potentially toxic species in the Mediterranean Sea. A) *Ostreopsis* spp. (mostly *O.* cf. *ovata*) and species related to the Ciguatera Fish Poisoning (CFP). B) Species producing ichthyotoxins (*Alexandrium pseudogonyaulax*, *Karenia* spp., *Karlodinium* spp., *Chattonella* spp., *Vicicitus globosus*, *Prymnesium* spp., etc.) and other toxins. The latter include mainly a few widespread dinoflagellate species that produce yessotoxins (*Lingulodinium polyedra*, *Gonyaulax spinifera* and *Protoceratium reticulatum*), but also other dinoflagellates producing azaspiracids (*Azadinum* spp.), pinnatoxins (*Vulcanodinium rugosum*) and other toxins with poorly known effects (e.g., *Prorocentrum* spp., *Margalefidinium polykrikoides*). See Table 1 for a complete list.

Figure 5: A) Mat of *Oscillatoria acutissima* in the Eastern Harbour of Alexandria (Egypt). B) Bloom of *Noctiluca scintillans* in Thermaikos Gulf (Thessaloniki, Greece). C) Discoloration caused by *Euglena viridis* in the Golden Horn Estuary (Sea of Marmara, Turkey). D) Shellfish mortality in Ras El-Bar (Egypt) in 2011 due to the proliferation of *N. scintillans* and consequent oxygen depletion. E) Pelagic mucilages in the Gulf of Naples (Italy).

Figure 6: Distribution of potentially toxic species, mucilages and discolorations in the Mediterranean Sea. A) Distribution of species known to be toxic and harmful events

until 1995 as reported in Jacques and Sournia (1978-1979) and Honsell et al. (1995). B) Distribution of potentially toxic species (excluding *Ostreopsis* and CFP species) and harmful events updated to the present status of knowledge. The position of the circles in several cases has been slightly modified to reduce overlapping.

Figure 7. Harmful events related to microalgae in the Mediterranean Sea (n=501) based on records in the Harmful Algae Event Database HAEDAT (http://haedat.iode.org/). High density phytoplankton blooms with no impacts were not considered. A) Relative abundance of different types of nuisance with details of seafood toxicity. B) Interannual variations of ASP, DSP and PSP toxicity events.

Figure 1

Click here to access/download;Figure;Fig.1.tif

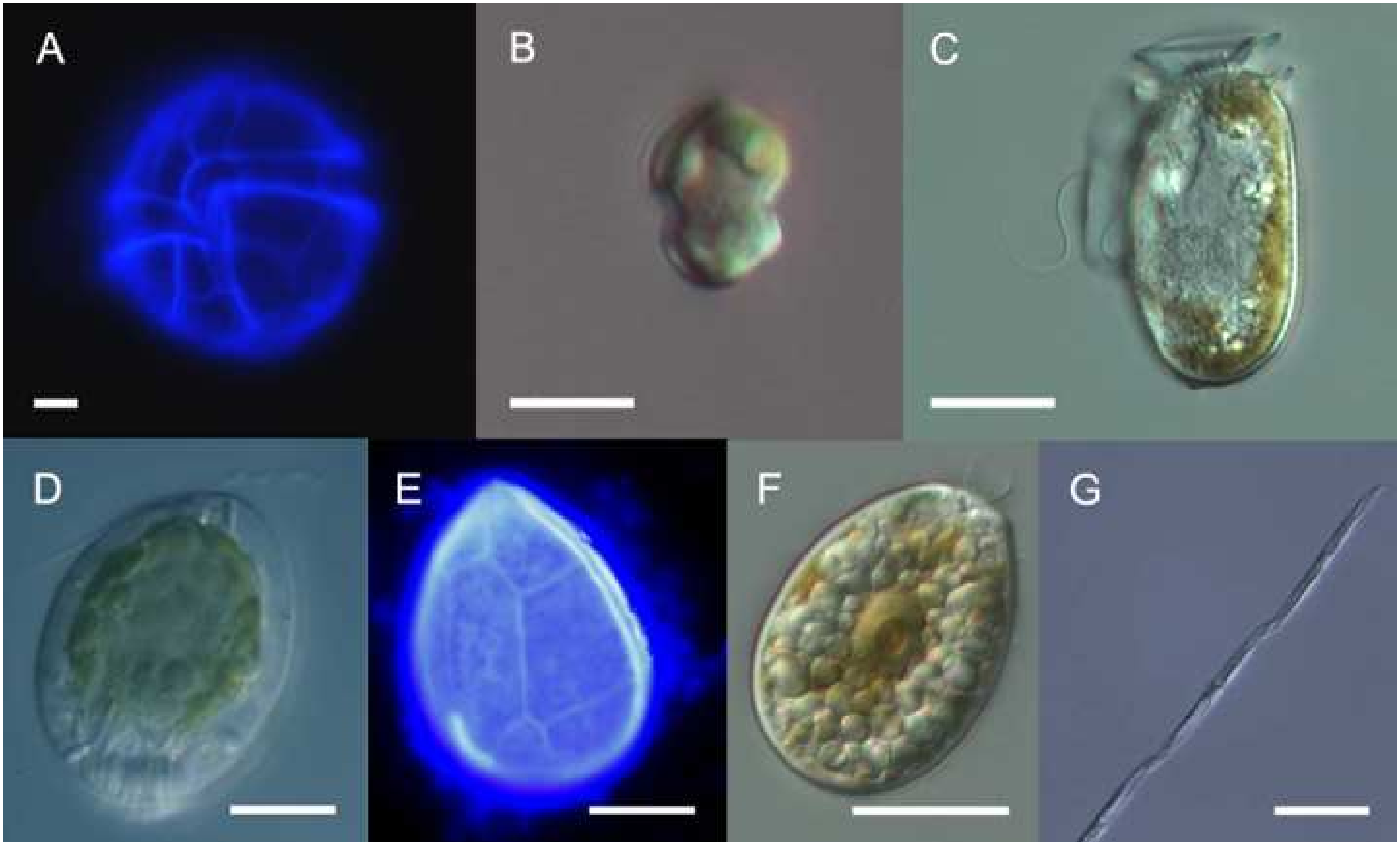
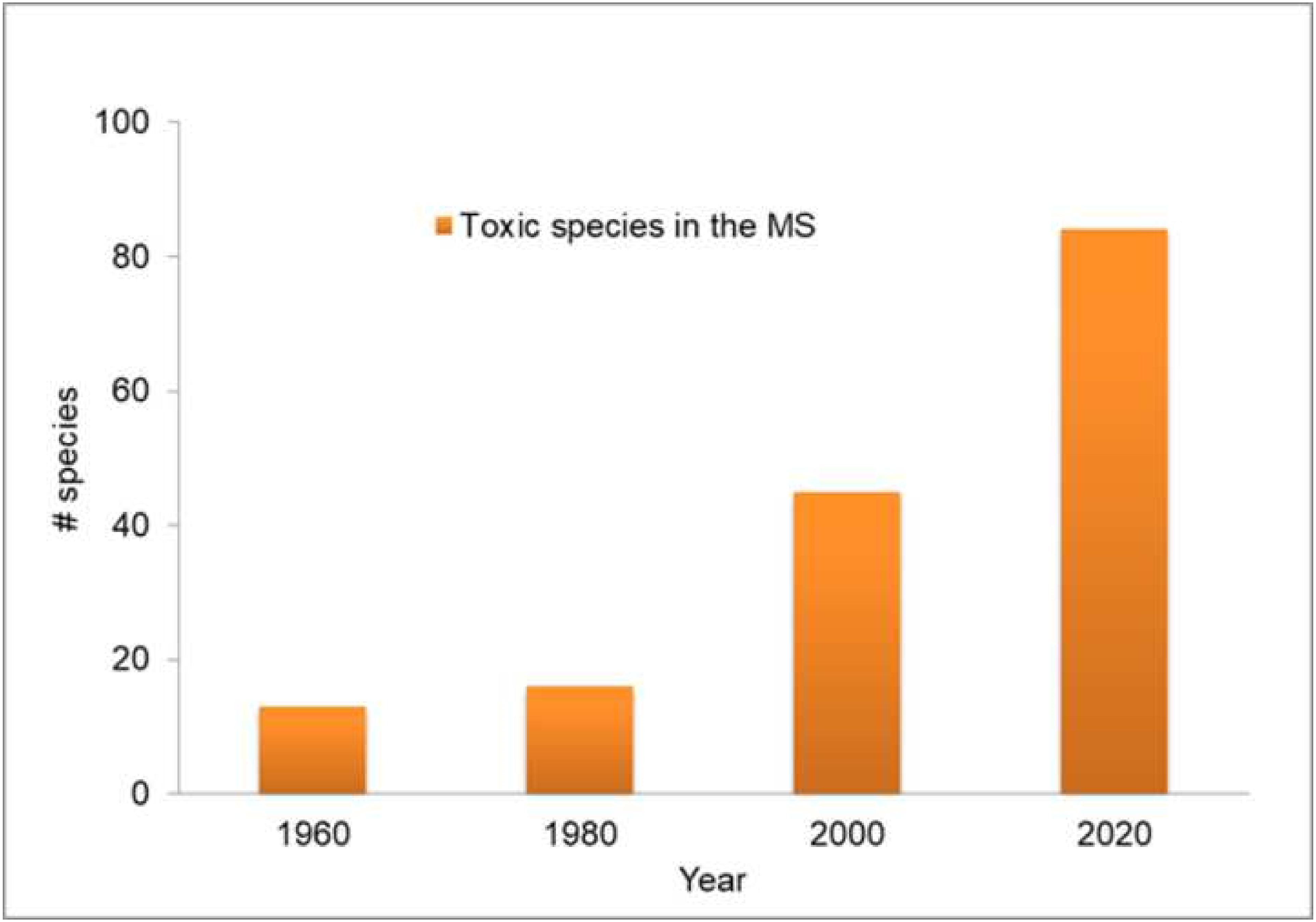


Figure 2



Toxic species in the MS
100
80
60
40
20
0
species
1960
1980
2000
2020
Year

Figure 3 Click here to access/download;Figure;Fig.3.tif

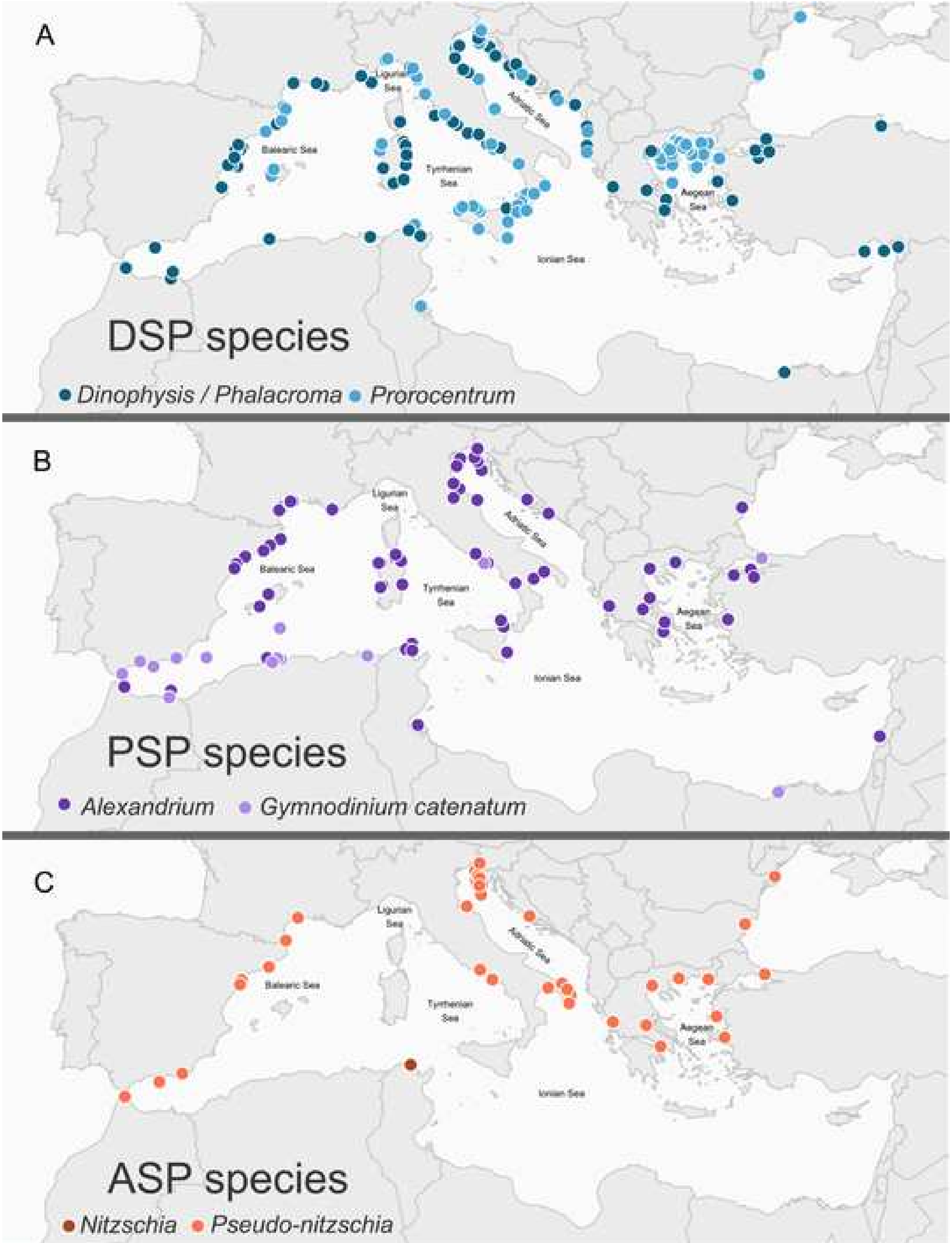


Figure 4

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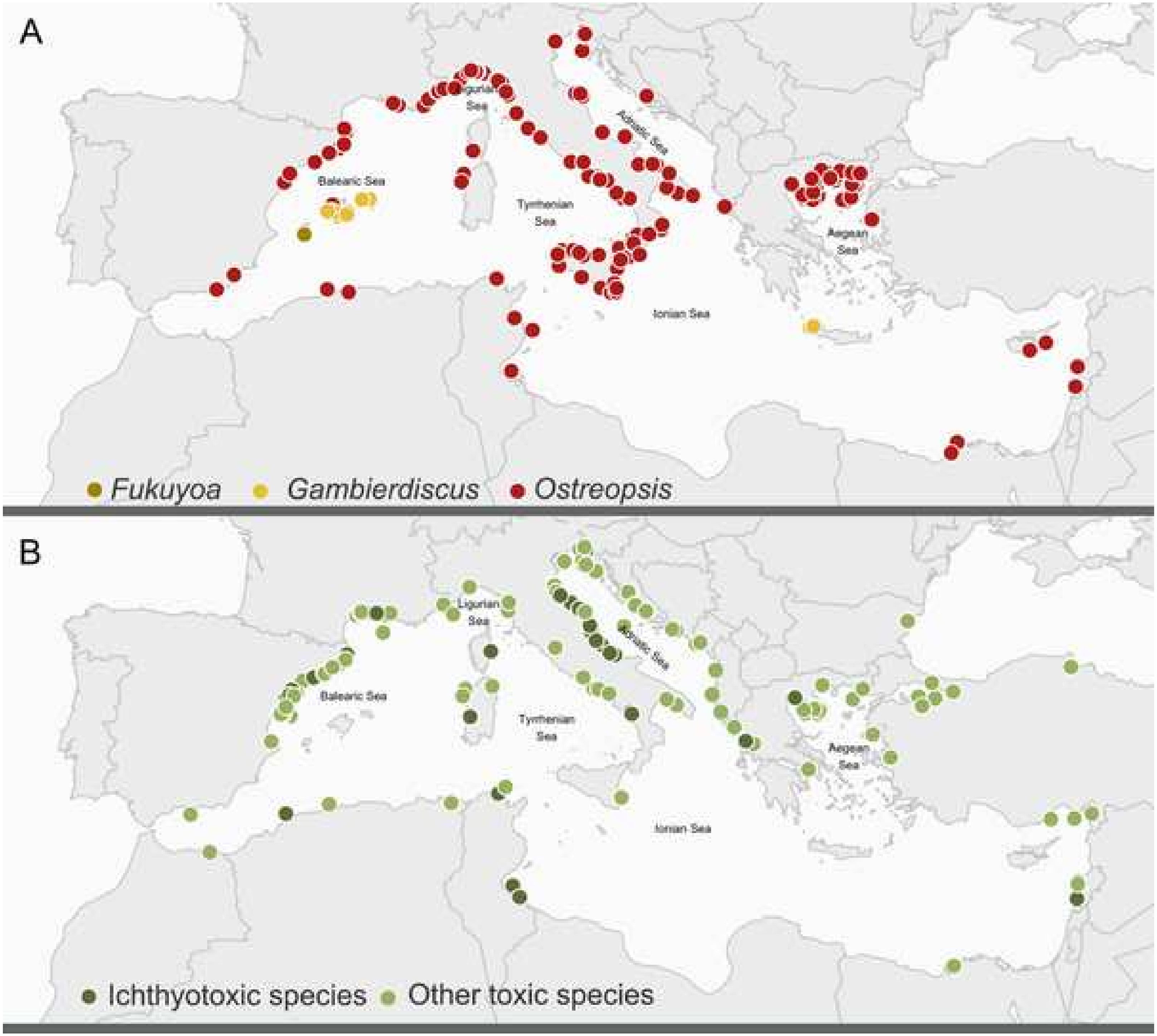

Figure 5

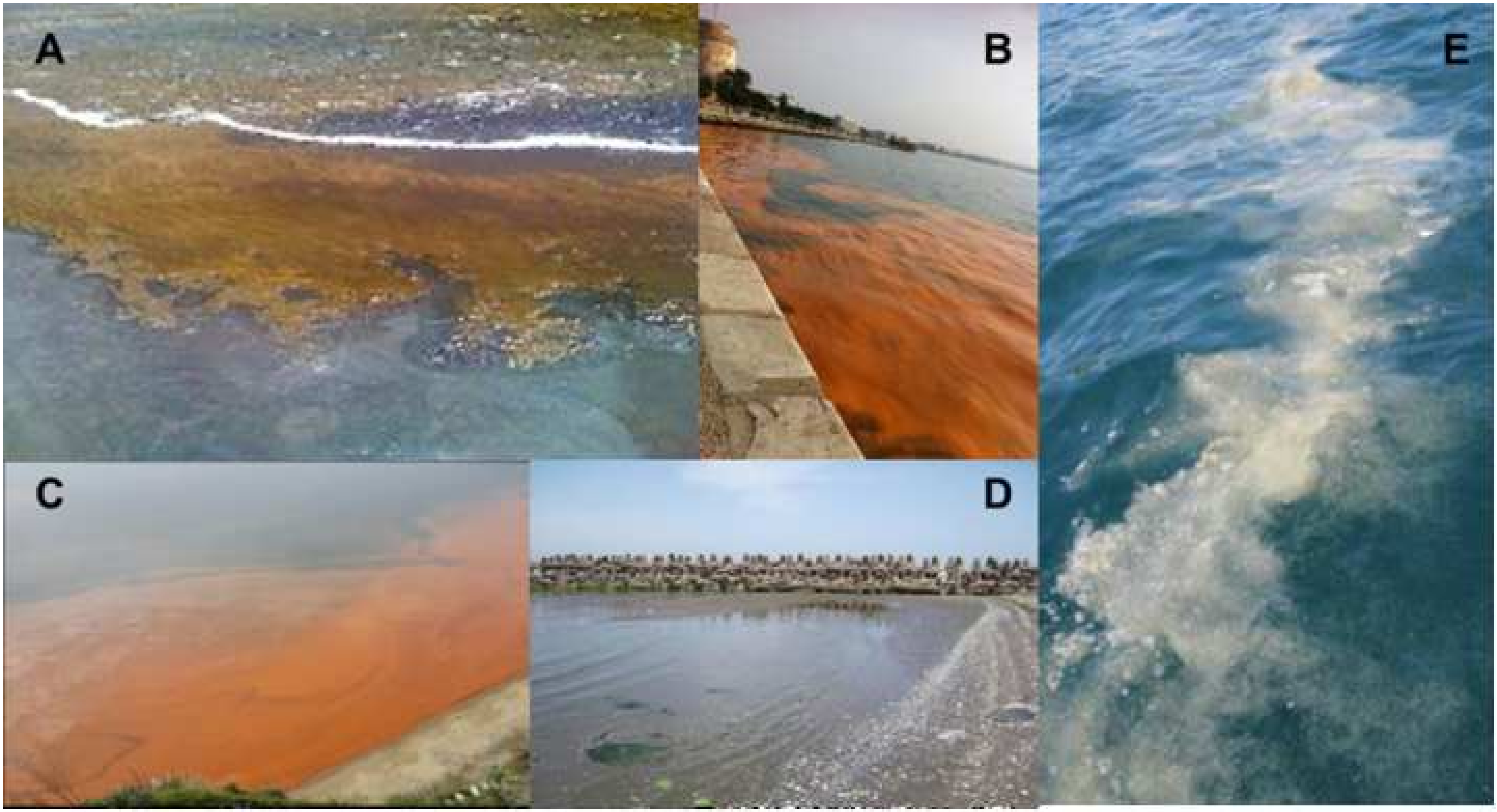

Figure 6

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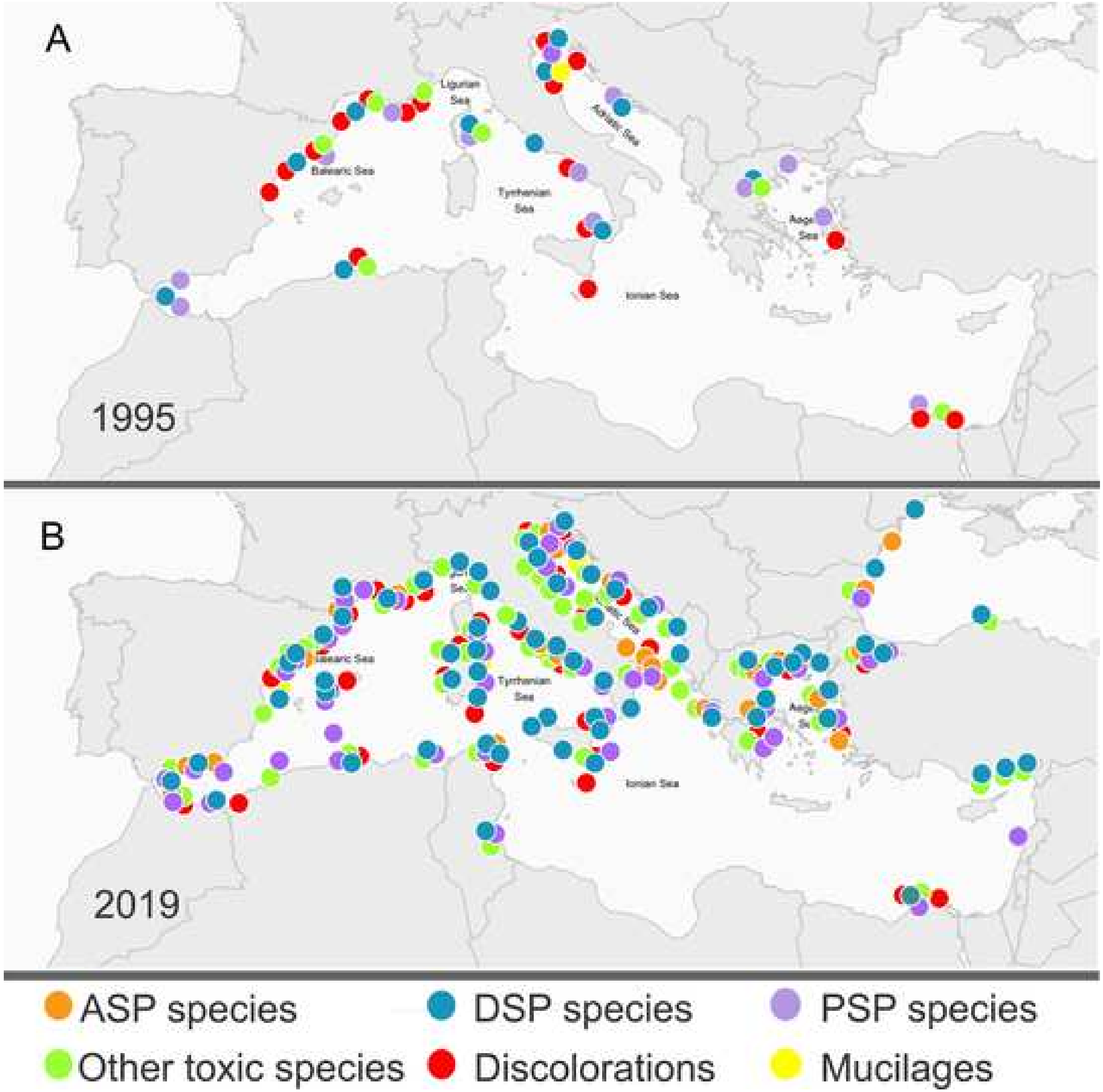

Figure 7

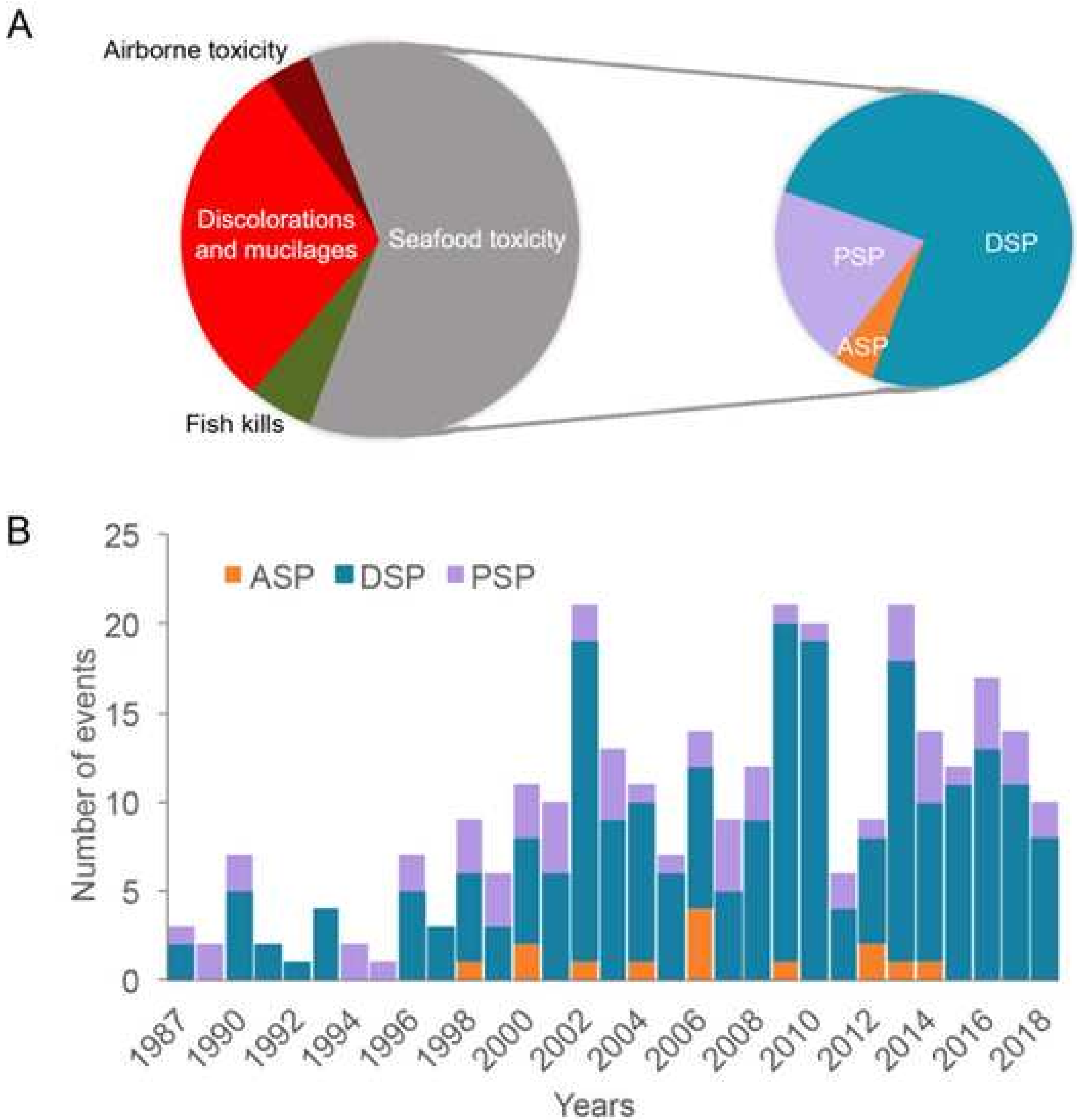
A
Airborne toxicity
Discolorations and mucilages
Seafood toxicity
Fish kills
PSP
DSP
ASP
B
ASP
DSP
PSP
Number of events
0
5
10
15
20
25
1987
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018
Years

Table 1: Potentially toxic species in the Mediterranean Sea and associated types of syndromes or impacts (see Moestrup et al., 2009 and Lassus et al., 2016 for details). ASP, Amnesic Shellfish Poisoning; AZP, Azaspiracid Shellfish Poisoning; DSP, Diarrhetic Shellfish Poisoning; PSP, Paralytic Shellfish Poisoning; CFP, Ciguatera Fish Poisoning. 'Other toxins' include unknown toxins or toxins with poorly known effects.

Bacillariophyceae	
Halamphora coffeaeformis	ASP
Nitzschia bizertensis	ASP
Pseudo-nitzschia australis	ASP
Pseudo-nitzschia brasiliana	ASP
Pseudo-nitzschia caciantha	ASP
Pseudo-nitzschia calliantha	ASP
Pseudo-nitzschia cuspidata	ASP
Pseudo-nitzschia delicatissima	ASP
Pseudo-nitzschia fraudulenta	ASP
Pseudo-nitzschia galaxiae	ASP
Pseudo-nitzschia hasleana	ASP
Pseudo-nitzschia multiseries	ASP
Pseudo-nitzschia multistriata	ASP
Pseudo-nitzschia pseudodelicatissima	ASP
Pseudo-nitzschia pungens (1)	ASP
Pseudo-nitzschia subfraudulenta	ASP
Pseudo-nitzschia subpacifica	ASP
Dictyochophyceae	
Pseudochattonella farcimen	Ichthyotoxicity
Pseudochattonella verruculosa	Ichthyotoxicity
Vicicitus globosus	Ichthyotoxicity
Dinophyceae	
Alexandrium andersonii	PSP
Alexandrium balechii	Ichthyotoxicity
Alexandrium minutum	PSP
Alexandrium ostenfeldii	PSP
Alexandrium pacificum (2)	PSP
Alexandrium pseudogonyaulax	Ichthyotoxicity
Alexandrium tamarense (2)	PSP
Alexandrium taylorii	PSP
Amphidinium carterae	Ichthyotoxicity
Amphidinium klebsii	Ichthyotoxicity
Azadinium dexteroporum	AZP
Azadinium poporum	AZP
Dinophysis acuminata	DSP
Dinophysis acuta	DSP
Dinophysis caudata	DSP
Dinophysis fortii	DSP
Dinophysis infundibulum	DSP
Dinophysis ovum	DSP
Dinophysis sacculus	DSP
Dinophysis tripos	DSP

Fukuyoa paulensis	CFP
Gambierdiscus australes	CFP
Gambierdiscus belizeanus	CFP
Gambierdiscus carolinianus	CFP
Gambierdiscus silvae	CFP
Gonyaulax spinifera	Other toxins
Gymnodinium catenatum	PSP
Karenia bicuneiformis	Ichthyotoxicity
Karenia brevis	Ichthyotoxicity
Karenia cristata	Ichthyotoxicity
Karenia longicanalis	Ichthyotoxicity
Karenia papilionacea	Ichthyotoxicity
Karenia selliformis	Ichthyotoxicity
Karlodinium armiger	Ichthyotoxicity
Karlodinium corsicum	Ichthyotoxicity
Karlodinium veneficum	Ichthyotoxicity
Lingulodinium polyedra	Other toxins
Margalefidinium polykrikoides	Ichthyotoxicity
Ostreopsis fattorussoi	Airborne disease
Ostreopsis cf. *ovata*	Airborne disease
Ostreopsis cf. *siamensis*	Airborne disease
Pfiesteria piscicida	Ichthyotoxicity
Phalacroma mitra	DSP
Phalacroma rotundatum	DSP
Polykrikos hartmannii	Other toxins
Prorocentrum borbonicum	Other toxins
Prorocentrum cordatum	Other toxins
Prorocentrum emarginatum	Other toxins
Prorocentrum lima	DSP
Prorocentrum mexicanum	Other toxins?
Prorocentrum rhathymum	DSP
Protoceratium reticulatum	Other toxins
Vulcanodinium rugosum	Other toxins
Haptophyceae	
Chrysochromulina leadbeateri	Ichthyotoxicity
Phaeocystis globosa	Other toxins
Prymnesium calathiferum	Ichthyotoxicity
Prymnesium faveolatum	Ichthyotoxicity
Prymnesium parvum	Ichthyotoxicity
Prymnesium polylepis	Ichthyotoxicity
Raphidophyceae	
Chattonella marina (3)	Ichthyotoxicity
Chattonella subsalsa	Ichthyotoxicity
Heterosigma akashiwo	Ichthyotoxicity
Fibrocapsa japonica	Ichthyotoxicity

(1) Including *P. pungens* var. *aveirensis*
(2) *A. pacificum* (group IV) and *A. tamarense* (group III), following the ribotype group designation in John et al. (2014) and Litaker et al. (2018)

(3) Including *Chattonella marina* var. *antiqua*

Table 2: Potentially toxic species described from the Mediterranean Sea

Species name	Described in	Described as	Type locality
Alexandrium minutum Halim	Halim (1960)		Harbour of Alexandria, Egypt
Alexandrium pseudogonyaulax (Biecheler) Horiguchi ex K.Yuki & Y.Fukuyo	Biecheler (1952)	*Goniodoma pseudogonyaulax*	Thau Lagoon, Gulf of Lion, France
Azadinium dexteroporum Percopo & Zingone	Percopo et al. (2013)		Gulf of Naples, Italy
Chattonella subsalsa Biecheler*	Biecheler (1936)		Saltern of Villeroy, Sète, France
Dinophysis caudata Kent	Kent (1881)		Nearby Fano, Marche Region, Italy
Dinophysis fortii Pavill.	Pavillard (1923)		Thau Lagoon and/or Sète harbour, France
Dinophysis infundibulum J.Schiller	Schiller (1928)		Southern Adriatic Sea
Dinophysis sacculus F.Stein	Stein (1883)		Kvarner Gulf, Croatia
Dinophysis tripos Gourret	Gourret (1883)		South of Ratonneau, Gulf of Marseille, France
Karlodinium armiger Bergholtz, Daugbjerg & Moestrup	Bergholtz et al. (2006)		Alfacs Bay, Catalonia, Spain
Karlodinium corsicum (Paulmier, Berland, Billard & Nézan) Siano & Zingone	Paulmier et al. (1995)	*Gymnodinium corsicum*	Diana Lagoon, Corse, France
Nitzschia bizertensis Bouchouicha-Smida, Lundholm, Hlaili & Mabrouk	Bouchouicha-Smida et al. (2014)		Bizerte Lagoon, Tunisia
Ostreopsis fattorussoi Accoroni, Romagnoli & Totti	Accoroni et al. (2016)		Batroun, Lebanon
Prorocentrum lima (Ehrenb.) F.Stein	Ehrenberg (1860)	*Crytoptomonas lima*	Sorrento, Gulf of Naples, Italy
Prymnesium faveolatum Fresnel	Fresnel et al. (2001)		Beach of Roquebrun, Cap Martin, France
Vulcanodinium rugosum Nézan & Chomérat**	Nézan and Chomérat (2011)		Ingril Lagoon, France

*A second, distinct genotype also discovered in Mediterranean waters (Klöpper et al., 2013).

** First report in Rhodes et al. (2010) from New Zealand.