Harmful algae and pressure-impact relationship: Noxious blooms and toxic microalgae occurrence from coastal waters of the Apulia region (Adriatic and Ionian Seas, Mediterranean)

Leonilde Roselli[a,*], Carmela Caroppo[b], Stanislao Bevilacqua[c,d], Pierangelo Cosimo Ciciriello[e], Nicola Ungaro[e], Maria Rosaria Vadrucci[e]

[a] *Stazione Zoologica Anton Dohrn, Department of Research Infrastructure for Marine Biological Resources, Villa Comunale, 1, 80121, Naples, Italy*
[b] *Water Research Institute, National Research Council, Unit of Taranto, Via Roma, 3, 74121, Taranto, Italy*
[c] *Department of Life Sciences, University of Trieste, Via Licio Giorgieri, 10, 34127, Trieste, Italy*
[d] *CoNiSMa, Piazzale Flaminio 9, 00196, Roma, Italy*
[e] *Agency for the Environmental Prevention and Protection (ARPA Puglia), Corso Trieste 27, 70126, Bari, Italy*

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ABSTRACT

The spatial distribution of harmful microalgal taxa along the coasts of the Apulia region (Mediterranean Sea) based on results of eight years (2012–2019) of routine monitoring program and a series of sporadic observations is presented. A total number of 69 potentially harmful taxa were found during the study period. Occurrence, abundance and richness of harmful taxa (toxic, potentially toxic and high biomass producers) varied along the Apulian coasts. The occurrence of harmful species was significantly higher where most of anthropogenic pressures overlap than only a few or no pressures existed. The physical alteration of coast is the most important pressure determining this pattern. Despite the variety and the abundances of the harmful microalgae, to our knowledge, no human health problems or risks have been ever recorded, nor were full-blown consequences on marine organisms such as fish kills during algal blooms. However, blooms coupled with water discoloration phenomena could become a big issue to tourism and recreational activities that have locally important socio-economic value.

1. Introduction

The occurrence of harmful algal blooms (HABs) seems to suggest an increase in their intensity and frequency at a global scale, leading to the spreading of potentially toxic and non-indigenous species (Hallegraeff, 1993; McGeoch et al., 2010; Pyšek et al., 2012; Simberloff et al., 2013). Although forecasting the possible trends is still speculative and requires intensive multidisciplinary research (Wells et al., 2015), HABs are observed globally and, whether actually increasing or not, they undoubtedly constitute a growing threat to maritime human activities, including fishery, aquaculture, recreational activities and tourism (Berdalet et al., 2016; Zingone et al., 2017). HABs expansion is closely linked with an enhanced scientific awareness of harmful species and the increase of monitoring programs (Hallegraeff et al., 2021), it can also be favored by anthropogenic pressure and its consequences. It is generally accepted that the availability of dissolved inorganic nutrients likely mediates phytoplankton growth in most coastal and sheltered areas such as harbours, small bays and coastal lagoons (Howarth and Marino, 2006). As increases in human coastal populations, industrialization, and the intensification of agriculture have elevated the supply of nitrogen and phosphorus to coastal waters (Ferreira et al., 2011), the role of anthropogenic nutrient enrichment and associated changes in nutrient ratios are among the most frequently proposed and debated hypotheses relating to increased HABs in coastal waters (Smayda, 1990; Harrison et al., 2012; Heisler et al., 2008). However, other factors acting at different spatial and temporal scales, such as expanded utilization of coastal waters for aquaculture, habitat modification, and human-mediated introduction of non-indigenous species (Heisler et al., 2008; Su-Myat and Koike, 2013; Kudela and Gobler, 2012; Sarkar, 2018; Hallegraeff et al., 2021), but also the complexity of the algal life cycle

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* Corresponding author.
E-mail addresses: leonilde.roselli@szn.it (L. Roselli), carmela.caroppo@irsa.cnr.it (C. Caroppo), sbevilacqua@units.it (S. Bevilacqua), p.ciciriello@arpa.puglia.it (P.C. Ciciriello), n.ungaro@arpa.puglia.it (N. Ungaro), m.vadrucci@arpa.puglia.it (M.R. Vadrucci).

(Wells et al., 2015; Figueroa et al., 2018; Glibert et al., 2018; Roselli et al., 2020) could influence the dynamics of HABs. Hence, a careful consideration of trends in HABs requires species-level assessments carried out at a local or regional scale (Hallegraeff et al., 2021).

In this work we provided an overview of the harmful and potentially harmful species, toxic and non-toxic, recorded so far along the coasts of the Apulia region that is quite scarce, to our knowledge, with respect to other Mediterranean regions (i.e. Zingone et al., 2006; Ignatiades and Gotsis-Skretas, 2010; Zingone et al., 2021 and references herein). This region is subjected to agriculture, industrial and touristic activities taking place mainly along the coastal zone. Previous studies on HABs dynamics along the Apulian coasts and transitional waters showed the presence of toxins producers as well as high-biomass producers (Caroppo et al., 1999a, 1999b, 2005, 2006, 2016; Cerino et al., 2012; Roselli et al., 2019, 2020), even if full-blown consequences on marine organisms or risk for human health were not registered. However, in the recent years, water discoloration and mucilage presence has begun to influence the tourist activity of particular coastal areas (Roselli et al., 2019).

Routine monitoring programs (WFD 2000/60/EC, MSFD 2008/56/EC, BWD 2006/7/EC), pilot projects and scattered and sporadic observations over eight years are included to investigate variations in bloom-forming and potentially toxic taxa along the Apulian coast. We also assess the contribution of some anthropogenic pressures insisting on the area (wastewater, urban runoff, agriculture and physical alteration of the coast) in explaining patterns of occurrence, species richness and average abundance of HABs species over the whole coast.

2. Methods

2.1. Study area

The coastline of the Apulia region extends for 985 km (Regional coastal plan, 2011), both on the Adriatic and Ionian seas. The region is populated by about 4 million inhabitants distributed over 19,345 km^2, with high densities along the coasts where summer-bathing tourism is much developed. Although characterized by the presence of high-value naturalistic landscapes as well as protected areas, intense agriculture and industrial activities take place all along the coastal zone and further enhance the anthropogenic impact on transitional and marine waters. The main coastal towns with commercial or industrial ports are Manfredonia, Bari, Monopoli and Brindisi on the Adriatic Sea, and Taranto on the Ionian Sea. According to the geomorphological and hydrological features as well as the relevant anthropogenic pressures, the entire regional coast was subdivided in water bodies (WBs) according to Water Framework Directive (WFD, 2000/60/CE).

Marine coastal waters are characterized by six coastline geomorphological types (terrace coast, articulate coast, river plain, shore platform, cliffs, dune plain) described by Brondi et al. (2003) and two hydrological types defined by low and medium water column stability (Giovanardi et al., 2018). Transitional waters are characterized by two typologies: non-tidal polyhaline coastal lagoons (Lesina and Varano lagoons located in the northern part of Gargano peninsula on the Adriatic Sea) and non-tidal euhaline lagoons (Porto Cesareo bay and the Mar Piccolo semi-enclosed system on the Ionian Sea). For details on hydro-geomorphology of WBs see the supplementary material (Table S1).

2.2. Phytoplankton data sources

The data reported in this work, over the period from 2012 to 2019, came from i) water monitoring programs (according to WFD 2000/60/EC, MSFD 2008/56/EC, BWD 2006/7/EC) routinely carried out by the Regional Agency for the Environmental Prevention and Protection (ARPA Puglia); ii) pilot monitoring projects carried out by the Environmental Agency and research institutes (e.g. Flagship RITMARE project, http://www.ritmare.it/) and iii) sporadic observations of environmental criticalities highlighted by Authorities or citizen's reporting and registered by the Environmental Agency. The WFD monitoring plan consists of 84 sampling stations located on 42 transects. For each transect, two sampling sites are located at 0.1 and 1 nautical mile from the coastline and they are monitored every two months, however, phytoplankton analysis is performed only the most coastal stations. Transitional waters are monitored seasonally, we included in this study 9 stations (Fig. 1). The MSFD monitoring plan includes both stations offshore (3, 6 and 12 nautical miles) and inshore (Brindisi and Taranto harbours) (Fig. 1) monitored every two months. The BWD monitoring plan includes 21 stations (Fig. 1) in which the presence and abundance of *Ostreopsis* spp. and *Ostreopsis* cf. *ovata* were estimated every two weeks from April to September. Data from three pilot projects are also included. For Flagship Project RITMARE, plankton samplings were carried out seasonally from February 2013 to June 2014 at six stations of the Mar Piccolo in Taranto (Caroppo et al., 2016).

For pre-survey project Marine Strategy offshore one sampling was performed in 2015. For Nearshore Project 16 sampling sites very close to the coast were seasonally sampling from 2017 to 2018 (Fig. 1). The methods for sampling and quantitative analysis are consistent across all the projects as reported below.

2.2.1. Phytoplankton sampling and analysis

During sampling seawater was collected with a 5 L Niskin bottle and fixed with Lugol's iodine solution, some of them were kept *in vivo* in order to help the identification process (Tomas, 1997). In case of environmental criticality, a telescopic rod was used to collect surface water; one sample was kept *in vivo* while the other one was immediately fixed in Lugol's solution. Light microscopy (LM) equipped with phase contrast at a magnification of 200 ×, 400 × and 600 × was mainly used for species identification. However, in some cases transmission electron microscopy (TEM) and scanning electron microscopy (SEM) were used for the identification at species level. The quantitative analysis was performed on the fixed samples following the Utermöhl sedimentation method (Edler and Elbrächter, 2010). We used the IOC-UNESCO taxonomic lists (included the "grey list" of the species of uncertain harmfulness) (Moestrup et al., 2009, onwards) for reference of the harmful taxa and high biomass producers. In this work, we arbitrarily choose 0.5×10^6 cell L^{-1} value as threshold limit for considering bloom concentration. First, it is the typical value of the seasonal peaks in the Southern Adriatic Sea (Caroppo et al., 1999a; Cerino et al., 2012) and Northern Ionian Sea

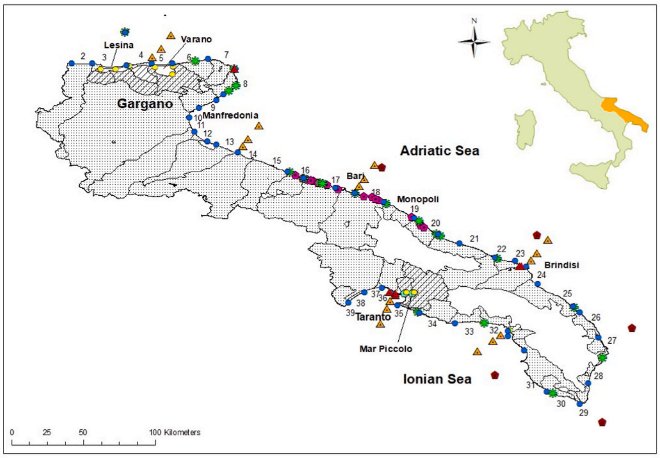


Fig. 1. Map of Apulia region with subdivision in marine-coastal (dotted area) and transitional water (dashed area) bodies (WBs, numbers in the figure). The map includes the monitoring station for WFD (blue circles for CWs and yellow circles for TWs), MSFD (orange triangles for pelagic environment and red triangles for harbours), BWD (green stars), monitoring pilot projects (light blue, violet and red pentagons).

(Caroppo et al., 2006, 2016). And, second, the above-mentioned threshold limit for algal bloom was the half of that defined by Kim et al. (1993) for species larger than 30 μm that is retained suitable to reveal pressure –impact relationships linked to noxious blooms.

2.3. *Assessment of anthropogenic pressures-impacts relationship*

The assessment of anthropogenic pressures and expected impacts on marine-coastal waters was carried out according the Italian SNPA-Guide Lines (Fiorenza et al., 2018). This method with pressures, expected impacts, their relative indicators and thresholds on water bodies (WBs) was summarized in Table 1.

The anthropogenic pressure types are those identified, classified and codified according to the WISE-WFD database (https://www.eea.europa.eu/data-and-maps/data/wise-wfd-3). In general, the method identifies 26 types of relevant anthropogenic pressures in coastal marine areas divided in seven categories: point sources, diffuse sources, physical alteration of coastal areas, presence of invasive species and pathogens unknown pressures, long-time pressures and, other pressures. We focused on the type of pressures that might cause nutrient enrichment, eutrophication risk and bloom outbreak. The *point source* pressure as wastewater treatment plants and their discharges (WISE 1.1) has been identified using the Water Protection Plan of Apulia Region (PTA, 2015–2021); the *diffuse source* pressure due to the “urban run-off” and “agriculture” (WISE 2.1 and 2.2, respectively) has been identified using the CORINE Land Cover maps (EEA, 2018); *physical alteration* pressure (WISE code 4.1) has been identified using the Apulian Regional Technical Chart Italy (2011). ArcGIS ver 10.2 software was utilized to manage and display pressure data. The reference zones for the assessment of the pressures are: i) the afferent basin catchment area of the WB and, ii) its relative buffer zone defined as a 500 m wide area from the shoreline, and iii) the WB.

According to this method, for the types of pressures reported in Table 1, the expected impact is *nutrient pollution*. Impact indicators used in this study are those reported in Fiorenza et al. (2018) that are considered more relevant for marine environments. They are: i) total phosphorus concentration (annual average value of P_{tot}) because it is considering a limiting nutrient in the Mediterranean Sea (Tanaka et al., 2011), ii) biomass concentration (annual average values of chlorophyll *a*), and iii) number of microalgal blooms/peaks in one year (Table 1). The full dataset collected in this study was used for impact indicators (Table 1).

According to the WFD (2000/60/EC; CI S-WFD, 2003) a pressure was estimated as significant when “*on its own, or in combination with other pressures, would be liable to cause a failure to achieve the environmental objectives set out under Article 4 (good quality status)*”. In this context, the impact was estimated as “significant” when the relative indicator values exceed the threshold limits as reported in the mentioned SNPA-Guide Lines (Fiorenza et al., 2018). Hereafter, we refer to a “significant pressure or impact” according to WFD.

2.4. *Statistical analysis*

A linear regression of the total number of events exceeding the threshold limits recorded along the whole coast for P_{tot} and chlorophyll *a* concentration, and algal blooms, against time (years) was fitted to check for temporal trends in these variables. For algal blooms, in order to explore also the temporal trend in the total number of blooms, an exponential regression was fitted to the total number of blooms along the whole coast vs. time (years).

For HABs, we checked for temporal trends in their occurrence, species richness and average abundance along the whole coast through regression analysis. WBs was divided in three groups according to the presence of 0–1, 2, or 3–4 pressures and a one-way ANOVA was also performed to test for differences in these variables among groups of WBs subjected to different cumulative pressure. Cochran’s *C*-test (Underwood, 1996) was used to test the assumption of homogeneity of variances prior to analysis and data were transformed to reduce variance heterogeneity if required. A non-parametric multivariate regression (DISTLM, distance-based multivariate multiple regression based on a linear model; McArdle and Anderson, 2001) was used to explore the relationships between biological variables for which ANOVA detected a significant effect of impact level and the full set of anthropogenic pressures. Prior to analysis, all explanatory variables (i.e., the variables measuring anthropogenic pressures) were normalized. Analyses were based on Euclidean distance and tests done using 999 permutations. All statistical analyses were carried out using R.

Table 1

- Italian tool for the assessment of pressure-impact relationships (Fiorenza et al., 2018). In the table are reported only pressures consider relevant for the study area. CW = marine water body, TW = transitional water body, EI = equivalent inhabitants, P_{tot} = Total phosphorus. * see the text for definition. ** see the text for details.

PRESSURES					**IMPACTS**			
Pressure type (WISE code)		**Pressure indicators**	**Threshold limits and reference area**	**Data sources**	**Impact type**	**Impact indicator**	**Threshold limits and reference area**	**Data sources ****
Point source	**Presence of wastewater and their discharges (1.1)**	CW = Unitary EI= Sum of EI in the catchment area /km of shoreline TW = Unitary EI= Sum of EI in the catchment area /km^2 of catchment area	CW ≥ 2000 EI/kml TW ≥ 60 EI/Km^2 Catchment area*	Water protection plan of Apulia Region (update 2015-2021)	**Nutrient pollution**	a) Annual average value of P_{tot} b) Annual geometrical average values of chlorophyll *a* c) Number of microalgal blooms in one year	a) CW low stability > 0.3 μM/L medium stability > 0.4 μM/L TW > 50 μg/L b) CW low stability > 0.6 μg/L medium stability >1.0 μg/L TW > 10% of typical average concentration (value obtained by historical data) of the water body c) CW no bloom TW > 1 bloom Water body*	Monitoring programs: WFD 2000/60/EC MSFD 2008/56/EC BWD 2006/7/EC Projects: Flagship RITMARE Metropolitan city Bari Sporadic observations: Environmental criticality or citizen’s reporting
Diffuse source	**Urban run-off (2.1)**	Percentage of land coverage related to urban run-off in the buffer area	≥ 15% Buffer area*	CORINE Land Cover maps (EEA, 2018)				
	Agriculture (2.2)	Percentage of land coverage related to agriculture in the catchment area	≥ 50% Catchment area*	CORINE Land Cover maps (EEA, 2018)				
	Physical alteration (4.1)	Percentage of the coast with alongshore and cross shore defence works and docks (only in TWB)	≥ 50% Buffer area*	Apulian Regional Technical Chart Italy 2011				

3. Results

3.1. Harmful taxa recorded

Overall 69 harmful taxa (HABs, high biomass producers and potentially toxic microalgae) were found during the sampling period (2012–2019): 27 belonged to diatoms, 29 to dinoflagellates and 13 to other groups ("others"). Among the overall 69 taxa, 44 taxa caused 234 blooms with concentrations higher than 0.5 × 10^6 cells L^{-1}. Among the 32 taxa reported as potentially toxic (according IOC lists), 7 also caused blooms. Some of them occasionally produced change of seawater color ("discoloration") (Fig. 2). See the supplementary material for the list and the details on abundance, occurrence, spatio-temporal distribution (Tables S2, S3, S4) and the geographical distribution (Figs. S1 and S2) of harmful microalgae recorded along the coasts of Apulia.

Most of the blooms occurred in transitional waters (47%), in marine waters within 1 nautical mile from the coast (24%), and, in the harbours (21%). Only 8% of the blooms occurred offshore. 79% of the events was registered during routine monitoring, 12% as environmental criticality and 9% were highlighted during the pilot projects. Of the 234 blooms, 67% of the events were caused by diatoms, 10% by dinoflagellates and 23% by the others group. As concerning the species composition, among the 44 taxa causing blooms, 55% were diatoms, 20% dinoflagellates and 25% belonging to others. Moreover, 56% of the blooms occurred during the warm period, in the Mediterranean Sea considered from May to October, while 44% during the cold period from November to April.

As concerning the species, *Skeletonema costatum* complex occurred with the largest number of the events (22), followed by *Chaetoceros throndsenii* and *Tenuicylindrus belgicus* (20 events), *Plagioselmis* cf. *prolonga* (16), *Chaetoceros* spp. (15), *Skeletonema marinoi* (13) and *Fibrocapsa japonica* (11). All the other taxa occurred less than 10 times over the study period (Table S3). Among diatoms, the most representative genus were *Chaetoceros* (22.7%). This genus produced blooms occurring in each system, from the harbors and transitional waters (e.g. *C. throndsenii* reached 5.32 × 10^5 cells L^{-1} in Varano lagoon) to offshore. The second most important genus was *Pseudo-nitzschia* (11.4%) with blooms occurred mainly in transitional waters (e.g. *P. delicatissima* group in the Mar Piccolo of Taranto with 1.03 × 10^7 cells L^{-1}) and harbours (*P. frau-subfraudulenta* in the Brindisi harbour 5.71 × 10^5 cells L^{-1}). Several dinoflagellates causing discoloration were identified: *Noctiluca scintillans* with maximum concentration along the Adriatic Sea (5.10 × 10^6 cells L^{-1}); *Gymnodinium impudicum* with maximum concentration along the northern coast (4.35 × 10^6 cells L^{-1}); summer blooms of *Margalefidinium* cf. *polykrikoides* with the highest concentration in a semi-closed bay (5.70 × 10^7 cells L^{-1}); *Prorocentrum shikokuense* in the Brindisi harbour with 2.30 × 10^7 cells L^{-1}. Among others, *Dunaliella salina* registered the highest concentration recorded during the period of this study (7.9 × 10^7 cells L^{-1}) along the northern Adriatic coast near by the inlets of Margherita di Savoia salt plant.

Apart the 7 of the 32 potentially toxic taxa causing blooms as above-described, the remaining 25 taxa occurred in low abundances with values ranging from 1.9 × 10 cells L^{-1} to 2.73 × 10^5 cells L^{-1}. Details on cell abundance and geographical distribution and cell abundance of potentially toxic taxa grouped per type of impact are available in supplementary material (Fig. S2). Five *Pseudo-nitzschia* taxa, that are potentially domoic acid (DA) producers, represented the most abundant potentially toxic species in the marine and transitional waters of Apulia region. Among the potential DSP-toxin producers, *Dinophysis* species were found with low abundances ranged between 1.90 × 10^1 cells L^{-1} and 1.40 × 10^4 cells L^{-1}. In general, *Dinophysis* species were present during all seasons and in every system. The genus *Alexandrium* potentially producers of the paralytic shellfish poisoning (PSP), was also found during all seasons and systems, although with low occurrence (less than 2%) and low abundances found in general in all months and systems. *Ostreopsis* cf. *ovata*, a palitoxins-like producer, was recorded with both low occurrence and abundance considering deep column water samples according WFD and MSFD monitoring. Nevertheless, this species is an important component of the epibenthic communities of the Apulian coasts. In fact, considering the *ad hoc* monitoring program BWD, *O.* cf. *ovata* reached cell abundance with highest values along the northern Adriatic coast (Fig. S3). Species potentially producing ichthyotoxins were also recorded along Apulian coasts. *Karenia* cf. *mikimotoi* and *Karenia* cf. *papilionacea* were observed with low occurrences and low abundances. Others, such as *Karlodinium veneficum* and *Polykrikos hartmannii* were rarely reported. *Margalefidinium* cf. *polykrikoides* and *F. japonica* caused bloom events. *C.* cf. *subsalsa* and *H. akashiwo* were

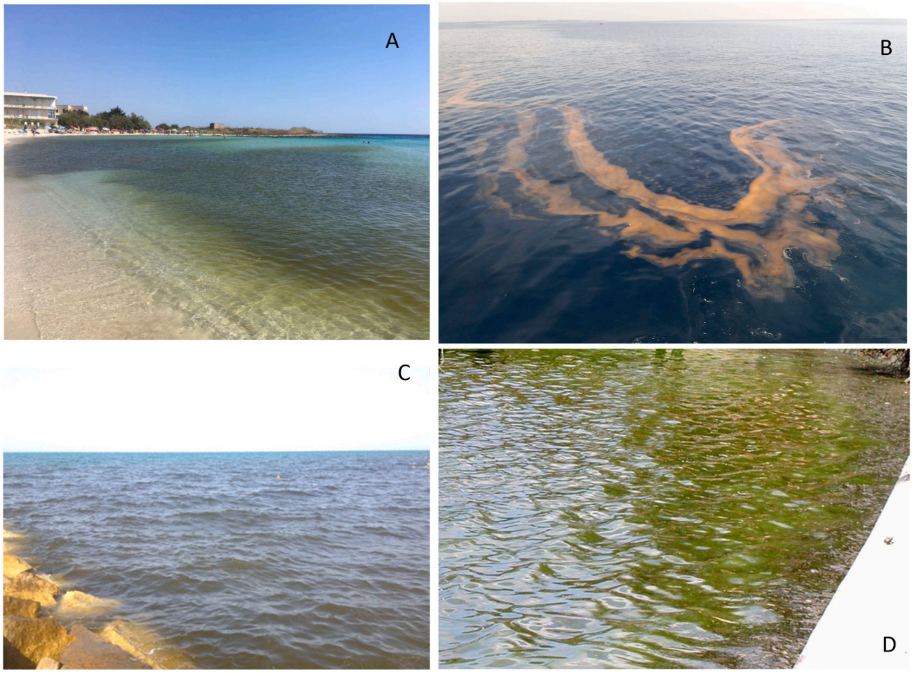


Fig. 2. Discoloration caused by a) *Margalefidinium* cf. *polykrikoides* in the Porto Cesareo bay (2019); b) *Noctiluca scintillans* offshore Punta Rondinella along Taranto coast (2019); c) *Fibrocapsa japonica* in Aloisa mouth along Margherita di Savoia coast (2017); d) *Tenuicylindrus belgicus* along Molfetta-Bari coast (2017).

sporadically observed with low abundances. Among potentially yessotoxin (YTX) producers, apart from *P. cordatum* with a peak of 7.02×10^5 cells L^{-1}, they were found with occurrences less than 2% and low abundances.

3.2. *Pressure-impact assessment on the HABs features*

Along the coasts of the Apulia region, the overall occurrence of episodes of P_{tot} exceeding the threshold limit showed an increasing trend from 2013 to 2019 (Adj. $R^2 = 0.78$, $P < 0.01$; Fig. 3; Table 2). The same trend seems to characterize the chlorophyll *a* concentration, although the linear regression was not significant (Adj. $R^2 = 0.08$, $P = 0.27$; Fig. 3). The chlorophyll *a* indicator exceeded the threshold limit, along northern coasts of the Apulia region, in the area of the Gulf of Taranto on the Ionian Sea and in transitional waters (Table 2). The number of blooms indicator exceeded the threshold limit along the northern coasts of the Apulia region in the recent years. This also occurred in the Brindisi – Cerano water body, in which the Brindisi harbour is included, in the area of the Gulf of Taranto on the Ionian Sea, and in the transitional waters of Varano and Lesina lagoons (Table 2). However, there was no evidence of an increase in the number of blooms exceeding the threshold with time (Adj. $R^2 = 0.39$, $P = 0.08$; Fig. 3). In contrast, the total number of blooms along the whole coast exponentially increased (Adj. $R^2 = 0.73$, $P < 0.01$) since 2012 (Fig. 4). The occurrence of HABs along the whole coast increased linearly over time (Adj. $R^2 = 0.73$, $P < 0.05$), but it dropped in 2019 (Fig. 5a). HABs richness also seemed to increase in the investigated period (Fig. 5b) although the linear regression was not significant (Adj. $R^2 = 0.11$, $P < 0.22$). This was probably due to the decrease in HABs richness in 2019, mirroring the drop in their overall occurrence. Indeed, after removing data of 2019, linear correlation was very high and significant (Adj. $R^2 = 0.88$, $P < 0.01$). Average abundance of HABs across the whole coast, instead, strongly decreased in time following a power law (Adj. $R^2 = 0.58$, $P < 0.05$; Fig. 5c).

ANOVA detected a significantly higher occurrence of HABs species during the investigated period in WBs characterized by 3–4 pressures exceeding thresholds values with respect to WBs having 2 or less pressures above limits (Table 3). The set of anthropogenic pressures explained the 22% of such variations, with 'Physical alteration' resulting as the most influencing pressure (Table 4). No difference between WBs at different level of impact were detected for HABs richness and average abundance (Table 3).

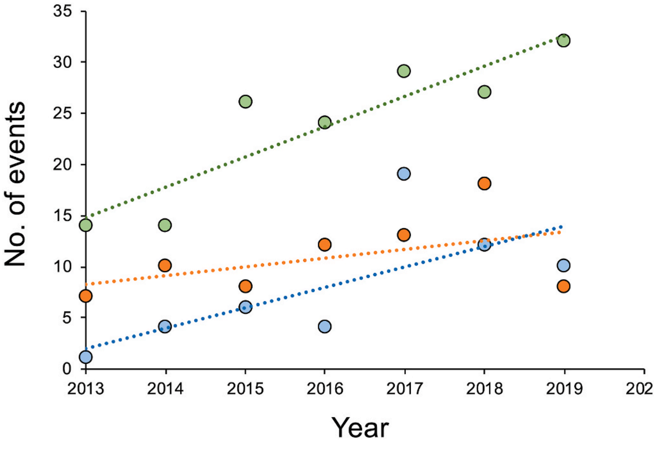


Fig. 3. Temporal trend of the total number of events exceeding the threshold limits for total phosphorous (light green circles), chlorophyll 'a' (orange circles) and the algal blooms (light blue circles), recorded along the whole investigated coast. Linear models fitted to data are also showed (dotted lines). Total phosphorous: Adj. $R^2 = 0.78$, $P < 0.01$; chlorophyll 'a': Adj. $R^2 = 0.08$, $P = 0.27$; algal blooms: Adj. $R^2 = 0.39$, $P = 0.08$.

4. Discussion

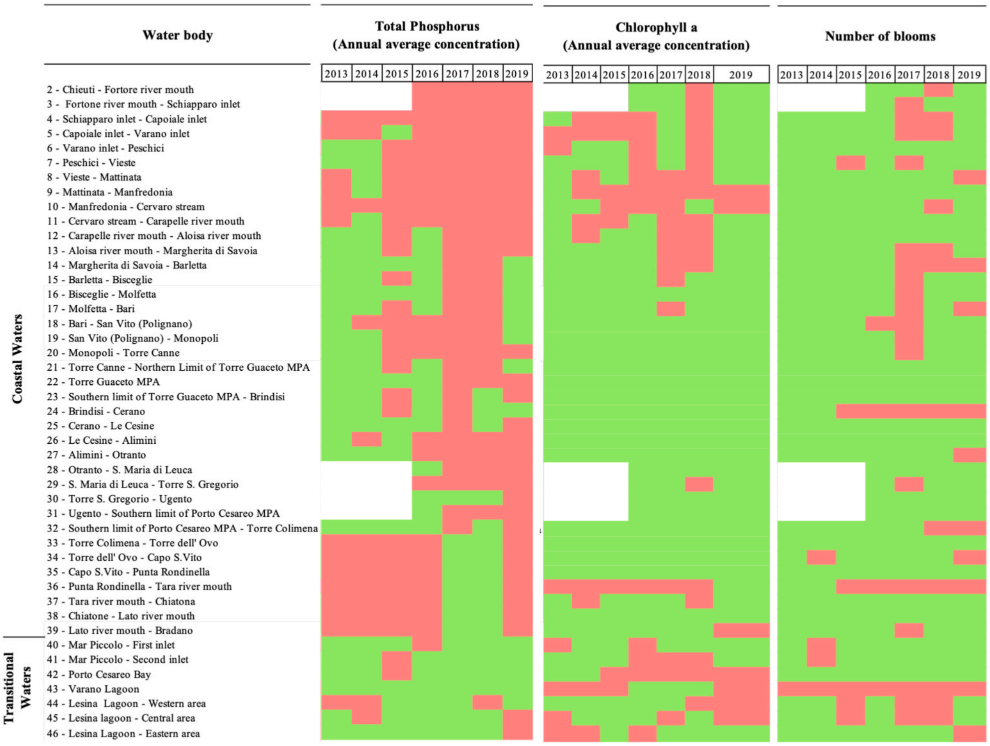
The discovery of potentially toxic species in the Mediterranean Sea has undergone an evident escalation over the years (Zingone et al., 2021; Griffith and Gobler, 2020). The information on their distribution has also markedly increased along with the intensification of monitoring operations and studies on planktonic and benthic microalgae (e.g., Aligizaki et al., 2009; Balkis and Taş, 2016; Fernández et al., 2019; Pistocchi et al., 2012; Zingone et al., 2006; Hallegraeff et al., 2021) 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 HABs species in the Mediterranean Sea is far from being known (Zingone et al., 2021) and most studies are snapshots of isolated toxic episodes (Pistocchi et al., 2012, and references therein). For example, in the Northern Adriatic Sea, where phytoplankton have been extensively studied for decades (Bernardi Aubry et al., 2012; Cerino et al., 2019; Marić et al., 2012; Mozetič et al., 2012; Ninčević-Gladan et al., 2010; Totti et al., 2019), highlighting a number of changes, such as trends or regime shifts in main phytoplankton groups (Mozetič et al., 2010; Totti et al., 2019) and in bloom forming species (Cabrini et al., 2012), no trends specifically related to toxic species emerged from these long-term studies, neither in terms of increased frequency nor of abundance.

We provided evidence that the central and south west coasts of the Adriatic Sea could be a potential hotspot of these phenomena since, as in other coastal regions globally (Anderson et al., 2002; Heisler et al., 2008; Glibert, 2020), the total number of algal blooms and HABs in the studied region has steeply increased over the last decade. As concerning the composition of the high-biomass species, the main responsible were diatoms, as already observed in other sites (Zingone et al., 2021). For example, *Chaetoceros,* which is one of the most representative genus in this study, is an important component of the Adriatic Sea (Bosak and Sarno, 2017) and blooms caused by *Chaetoceros* species were already detected in the Adriatic Sea (Cerino et al., 2012; Caroppo et al., 1999b; Totti et al., 2019) and in the Ionian Sea (Caroppo et al., 2006, 2016). During the period considered in the present study, *Skeletonema* genus occurred with the larger number of bloom events. *Skeletonema costatum* complex is confirmed to be common bloom forming phytoplankters, especially in coastal estuarine and marine environments (Kooistra et al., 2008 and references herein). Also, in the Adriatic Sea this genus produces blooms (Caroppo, 2001b; Cerino et al., 2012; Pfannkuchen et al., 2018; Totti et al., 2019). Another important component of phytoplankton community described in this work is *Pseudo-nitzschia*, genus that was already reported for Southern Adriatic (e.g. Caroppo et al., 2005) and Northern Ionian waters (Caroppo et al., 2016). This potentially producer domoic acid (DA) is considered to be cosmopolite (Hasle, 2002; Lelong et al., 2012) and variable on hydrological preferences depending on their ecosystem inhabited and genetic strains. Several authors have related these blooms, including the production of DA, with changes in nutrient availability and nutrients ratio from the onset to the end of the blooms (Fehling et al., 2005; Palenzuela et al., 2019). We found it blooms mainly in transitional waters and harbours.

During the period considered in this study along the Apulian coasts, dinoflagellates and phytoflagellates were found to produce intense discoloration events (e.g., *Noctiluca scintillans, Prorocentrum shikokuense*, *Margalefidinium* cf. *polykrikoides, Dunaliella salina, Fibrocapsa japonica*). One of the main issues with coastal water discoloration, as already reported for the Mediterranean Sea (Randone et al., 2017), is the potential socio-economic impact on the tourism industry that in Apulia region is about 20 billion US$ annually (Report of the Regional Tourism Promotion Agency, 2016). For example, during this time series we registered blooms of *M.* cf. *polykrikoides* (Roselli et al., 2020) that is a cosmopolitan dinoflagellate notorious for causing fish-killing HABs (Kim, 1998). Despite the high-density blooms and the amount of mucilage on the beach, no fish die-offs were observed in the Porto Cesareo bay. However, local media and Authorities have given a lot of attention to this phenomenon acting as a sounding board of public

Table 2

Pressure – Impact relationships on water bodies during the study period. In red the pressures and impact resulted significant sensu WFD; in green not significant; in white no data available (according to Fiorenza et al., 2018).



	Water body	Total Phosphorus (Annual average concentration)							Chlorophyll a (Annual average concentration)							Number of blooms						
		2013	2014	2015	2016	2017	2018	2019	2013	2014	2015	2016	2017	2018	2019	2013	2014	2015	2016	2017	2018	2019
Coastal Waters	2 - Chieuti - Fortore river mouth				🟥	🟥	🟥	🟥				🟩	🟩	🟥	🟩				🟩	🟩	🟥	🟩
	3 - Fortone river mouth - Schiapparo inlet				🟥	🟥	🟥	🟥				🟩	🟩	🟥	🟩				🟩	🟥	🟩	🟩
	4 - Schiapparo inlet - Capoiale inlet	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟩	🟥	🟥	🟥	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟩
	5 - Capoiale inlet - Varano inlet	🟥	🟥	🟩	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟩
	6 - Varano inlet - Peschici	🟩	🟩	🟥	🟥	🟥	🟥	🟥	🟥	🟩	🟩	🟥	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	7 - Peschici - Vieste	🟩	🟩	🟥	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟥	🟩	🟥	🟩	🟩	🟩	🟥	🟩	🟥	🟩	🟩
	8 - Vieste - Mattinata	🟥	🟩	🟥	🟥	🟥	🟥	🟥	🟩	🟥	🟩	🟥	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥
	9 - Mattinata - Manfredonia	🟥	🟩	🟥	🟥	🟥	🟥	🟥	🟩	🟥	🟥	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	10 - Manfredonia - Cervaro stream	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟩	🟩	🟥	🟥	🟥	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟥	🟩
	11 - Cervaro stream - Carapelle river mouth	🟥	🟩	🟥	🟥	🟥	🟥	🟥	🟩	🟥	🟥	🟩	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	12 - Carapelle river mouth - Aloisa river mouth	🟩	🟩	🟥	🟩	🟥	🟥	🟥	🟩	🟥	🟩	🟩	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	13 - Aloisa river mouth - Margherita di Savoia	🟩	🟩	🟥	🟩	🟥	🟥	🟥	🟩	🟩	🟩	🟩	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	14 - Margherita di Savoia - Barletta	🟩	🟩	🟩	🟩	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟩
	15 - Barletta - Bisceglie	🟩	🟩	🟥	🟩	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟥
	16 - Bisceglie - Molfetta	🟩	🟩	🟩	🟩	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟩	🟩
	17 - Molfetta - Bari	🟩	🟩	🟥	🟩	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟩	🟩
	18 - Bari - San Vito (Polignano)	🟩	🟥	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟩	🟥
	19 - San Vito (Polignano) - Monopoli	🟩	🟩	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟩	🟩
	20 - Monopoli - Torre Canne	🟩	🟩	🟥	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟩	🟩
	21 - Torre Canne - Northern Limit of Torre Guaceto MPA	🟩	🟩	🟥	🟩	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟩	🟩
	22 - Torre Guaceto MPA	🟩	🟩	🟩	🟩	🟥	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	23 - Southern limit of Torre Guaceto MPA - Brindisi	🟩	🟩	🟥	🟩	🟥	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	24 - Brindisi - Cerano	🟩	🟩	🟥	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟥	🟥	🟥
	25 - Cerano - Le Cesine	🟩	🟩	🟩	🟩	🟥	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	26 - Le Cesine - Alimini	🟩	🟥	🟩	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	27 - Alimini - Otranto	🟩	🟩	🟩	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥
	28 - Otranto - S. Maria di Leuca				🟩	🟥	🟥	🟥				🟩	🟩	🟩	🟩				🟩	🟩	🟩	🟩
	29 - S. Maria di Leuca - Torre S. Gregorio				🟥	🟥	🟥	🟥				🟩	🟩	🟥	🟩				🟩	🟥	🟩	🟩
	30 - Torre S. Gregorio - Ugento				🟩	🟩	🟩	🟥				🟩	🟩	🟩	🟩				🟩	🟩	🟩	🟩
	31 - Ugento - Southern limit of Porto Cesareo MPA				🟩	🟥	🟥	🟥				🟩	🟩	🟩	🟩				🟩	🟩	🟩	🟩
	32 - Southern limit of Porto Cesareo MPA - Torre Colimena	🟩	🟩	🟩	🟩	🟥	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟥
	33 - Torre Colimena - Torre dell' Ovo	🟥	🟥	🟥	🟥	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	34 - Torre dell' Ovo - Capo S.Vito	🟥	🟥	🟥	🟥	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟥
	35 - Capo S.Vito - Punta Rondinella	🟥	🟥	🟥	🟥	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	36 - Punta Rondinella - Tara river mouth	🟥	🟥	🟥	🟥	🟩	🟩	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟥	🟥	🟥	🟥	🟥
	37 - Tara river mouth - Chiatona	🟥	🟥	🟥	🟥	🟩	🟩	🟥	🟩	🟥	🟩	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	38 - Chiatone - Lato river mouth	🟥	🟥	🟥	🟥	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	39 - Lato river mouth - Bradano	🟥	🟥	🟥	🟥	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟥	🟩	🟩
Transitional Waters	40 - Mar Piccolo - First inlet	🟩	🟩	🟩	🟥	🟩	🟩	🟩	🟥	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩
	41 - Mar Piccolo - Second inlet	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟥	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩
	42 - Porto Cesareo Bay	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟥	🟥	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩
	43 - Varano Lagoon	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟥	🟩	🟩	🟩	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥
	44 - Lesina Lagoon - Western area	🟥	🟥	🟩	🟩	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟩	🟩	🟥	🟩	🟥	🟥	🟩
	45 - Lesina lagoon - Central area	🟩	🟥	🟩	🟩	🟩	🟩	🟥	🟥	🟩	🟩	🟩	🟥	🟩	🟥	🟩	🟩	🟥	🟩	🟥	🟥	🟩
	46 - Lesina Lagoon - Eastern area	🟩	🟩	🟩	🟩	🟩	🟩	🟥	🟥	🟥	🟩	🟥	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟥

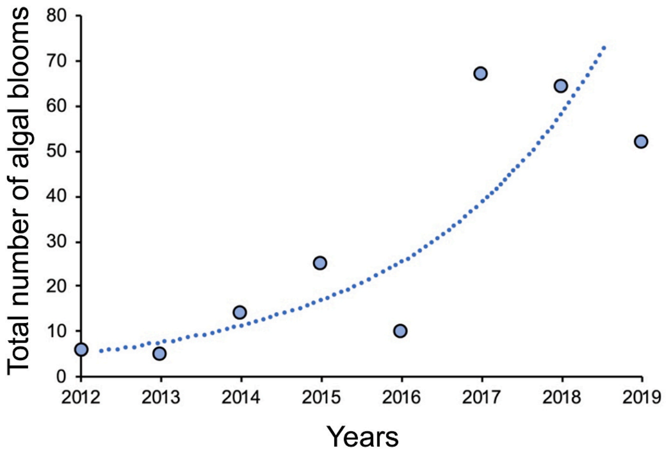


Fig. 4. Temporal trend of the total number of algal blooms (light blue circles) recorded along the whole investigated coast. The exponential model fitted to data is showed (dotted line). (Adj. $R^2 = 0.73$, $P < 0.01$).

opinion during summer with potentially negative consequences for the tourist season in that area.

Others potentially-toxic taxa were detected during this time-series with low occurrence and low cell abundance. A number of *Dinophysis/Phalacroma* species potentially causative agents of diarrhetic shellfish poisoning (DSP) are found in the study area, as already reported in previous studies (Caroppo et al., 1999b, 2001). DSP is the main toxin-related problem in the Mediterranean Sea, where mussel contamination due to okadaic acid and dinophysistoxins has been reported from the Adriatic Sea (Boni et al., 1993; Marasović et al., 1998) and from French (Belin, 1993; Belin et al., 1995), Spanish (Delgado et al., 1996) and Greek (Koukaras and Nikolaidis, 2004) coasts. In our knowledge, these species have not caused health problems for human population due to ingestion of contaminated mussel. All the potential PSP toxin producers (*A. minutum* complex*, A. tamarense* complex) were rather rare in the study area. PSP contamination of is not very common in the whole Mediterranean area, with the exception of a few episodes reported from Italy (Honsell et al., 1996), Morocco (Taleb et al., 2001) and Spain (Vila et al., 2001). The benthic dinoflagellates *Ostreopsis* cf. *ovata,* a palitoxins-like producer giving airborne disease, were occasionally recorded in the samples of the column water during WFD and MSFD monitoring but it reached high abundance in the samples of the *ad hoc* BWD monitoring particularly in the shallow rocky coast sites. Hydrodynamic conditions are referred as the main factor affecting *Ostreopsis* bloom trends, highlighting that higher abundances are observed in sheltered sites compared with exposed ones (Barone, 2007; Shears and Ross, 2010; Totti et al., 2010; Mabrouk et al., 2012) and where high irradiance values and prolonged calm sea conditions occur (Ungaro et al., 2010; Accoroni and Totti, 2016). Potentially producer yessotoxins (YTXs, e.g. *Lingulodinium polyedra*, *Protoceratium reticulatum* and *Gonyaulax spinifera*) that are not considered toxic to humans (Tubaro et al., 2010) and are quite widespread in the Mediterranean Sea (Zingone et al., 2021) causing economic impacts in 2002, 2004 and 2007, when mussel harvesting was halted for a long time in the north-western Adriatic Sea (Poletti et al., 2008), were rarely observed in these data.

Our results showed that occurrence, abundance and richness of HABs species varied along the Apulian coasts. In particular, the occurrence of HABs species over the investigated period was significantly higher in those WBs where most of anthropogenic pressures considered in this study overlap than in those where only a few or no pressures insisted. The whole set of pressures, however, explain only a portion of the variability in HABs occurrence due to the different levels of pressures, suggesting that other factors could play a crucial role in driving their distribution and frequency of appearance. The increase of coastal human

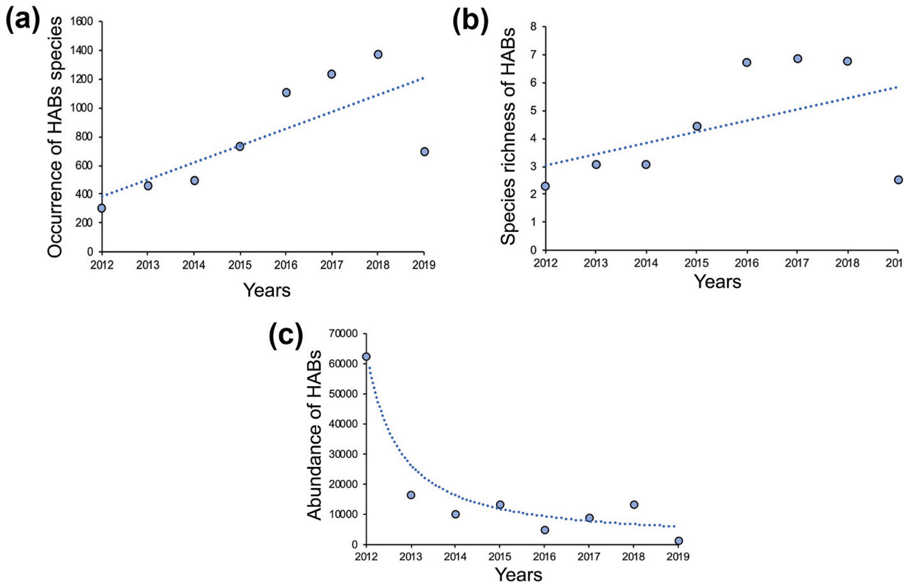


Fig. 5. Temporal trend in the features of HABs. a) Temporal trend in the occurrence of HABs species (light blue circles) recorded along the whole investigated coast. The linear model fitted to data is showed (dotted line), Adj. $R^2 = 0.73$, $P < 0.01$. b) Temporal trend in the species richness of HABs (light blue circles) recorded along the whole investigated coast. The linear model fitted to data is showed (dotted line), Adj. $R^2 = 0.11$, $P < 0.22$. c) Temporal trend in average abundance of HABs (light blue circles) recorded along the whole investigated coast. The power model fitted to data is showed (dotted line), Adj. $R^2 = 0.58$, $P < 0.05$.

Table 3

Summary of ANOVA on occurrence, species richness and average abundance of HABs species in WBs where threshold limits were exceeded for 0–1 (L), 2 (M), and 3–4 (H) anthropogenic pressures. Pairwise *t*-test are reported for variables showing significant difference among pressure levels. ** = $P < 0.01$; NS = not significant. Cochran's *C*-test was not significant for 'Occurrence HABs' and 'Richness HABs'; for 'Abundance HABs' the test was not significant after data transformation [log (x+1)].

Occurrence HABs				Richness HABs				Abundance HABs			
df	SS	MS	*F*	df	SS	MS	*F*	df	SS	MS	*F*
2	12825	6412.3	56.871**	2	35.9	18.0	0.582^{NS}	2	35.7	17.8	0.821^{NS}
75	84564	1127.5		75	231.6	30.9		75	163.0	21.7	
H > M = L				–				–			

Table 4

Summary of DistLM to assess the contribution of the anthopogenic pressures in explain differences in the occurrence of HABs species over the whole coast.

	Pseudo-F	*P*	Proportion of explained variation	Contribution to total variation
Physical alteration	21.30	0.001	0.219	99%
Urban run-off	0.27	0.595	0.003	1%
Agriculture	0.09	0.786	0.000	≪1%
Sewage	0.00	0.981	0.000	≪1%

population, agriculture, aquaculture and sewage all contribute to elevated nutrient concentrations in coastal waters with strong evidence that elevated nutrients have led to increase of phytoplankton biomass, including biomass of harmful species (Gowen et al., 2012; Davidson et al., 2014; Glibert, 2020). It is recognized that the local geography such as catchment characteristics and estuarine, bay and coastal geomorphology is an important factor influencing the HABs development (Wells et al., 2020). Most of the blooms detected during the study period occurred in transitional waters, but also in the harbours. Physiographical and hydrological characteristics of transitional waters as well as human management of coastal lagoons, affect their physical-chemical properties and their buffering capacity against nutrient enrichment and eutrophication risk (Kjerfve, 1994; Roselli et al., 2009, 2013; Wells et al., 2020). Nevertheless, studies demonstrated that is difficult to establish a direct link between increase of nutrient availability and frequency and abundance of harmful species (Glibert, 2020; Davidson et al., 2014). Other factors, such as the interactions with co-occurring organisms, the life strategies of the species and the physical dynamics that alter abiotic conditions and aggregate or disperse cells contribute to the success of HABs (Glibert and Burford, 2017; Glibert, 2020). Our study revealed that the physical alteration of the coasts is the most important pressure determining the HABs occurrence pattern. We highlight that the modification of coastal ecosystems which result in habitat changes, for example due to the increased number of tourists harbours or other coastal infrastructures, can also create new sheltered areas where HABs of cyst forming species have been frequently reported (Garcés and Camp 2012).

Despite the variety and the abundances of the harmful microalgae observed along the Apulian coasts during the time-series of eight years, to our knowledge, no human health problems or risks have been ever recorded, nor were full-blown consequences on marine organisms such as fish kills during algal blooms. In any case, the observed values of the potentially toxic microalgae have been detected below the threshold limits imposed in various early warning systems developed to prevent the risk for human health mainly due to the ingestion of contaminated seafood products (CEMAS, IOC-UNESCO, IPAM). On the other hand, bloom events coupled with water discoloration phenomena could become a big issue to tourism and recreational activities that have locally important socio-economic value.

Long term monitoring activities are the appropriate tool to investigate harmful algae features and to identify areas at higher risk. We highlight the fundamental importance to implement both surveillance monitoring and *ad hoc* alerts during unusual events. Also, the integration of monitoring and anthropogenic pressure impact valuation for an accurate planning policy of the coastal marine resources would prevent harmful algal blooms occurrence and outbreak. However, monitoring phytoplankton is particularly demanding in terms of time and associated costs because of labor-intensive procedures for sample processing and taxonomic identifications. Analysts of the environmental agencies deputed for monitoring often lack adequate instruments and, though carefully trained, have rarely sufficient expertise to identify all taxonomic groups at species-level. In this context we highlight the importance of the role of modern taxonomy that integrates technology advances, on one side, and trait-based approach, on the other side, increasing the opportunity to monitor phytoplankton communities at ecologically relevant scales and to reveal biodiversity patterns (Campbell et al., 2010; Ruppert et al., 2019; Roselli et al., 2022).

Credit author statement

Leonilde Roselli: Conceptualization, Formal analysis, Investigation, Writing - original draft, Writing - review and editing. **Carmela Caroppo:** Investigation, Writing - original draft, Writing - review and editing. **Stanislao Bevilacqua:** Formal analysis, Writing - original draft, Writing - review and editing. **Pierangelo Cosimo Ciciriello:** Formal analysis. **Nicola Ungaro:** Writing - original draft, Writing - review and editing. **Maria Rosaria Vadrucci**: Conceptualization, Formal analysis, Investigation, Writing - original draft, Writing - review and editing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Accoroni, S., Totti, C., 2016. The toxic benthic dinoflagellates of the genus *Ostreopsis* in temperate areas: a review. Adv. Oceanogr. Limnol. 1–15. https://doi.org/10.4081/aiol.2016.5591, 7.1.

Aligizaki, K., Nikolaidis, G., Katikou, P., Baxevanis, A.D., Abatzopoulos, T.J., 2009. Potentially toxic epiphytic *Prorocentrum* (Dinophyceae) species in Greek coastal waters. Harmful Algae 8 (2), 299–311. https://doi.org/10.1016/j.hal.2008.07.002.

Anderson, D.M., Glibert, P.M., Burkholder, J.M., 2002. Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. Estuaries 25, 704–726. https://doi.org/10.1007/BF02804901.

Balkis, N., Taş, S., 2016. Phytoplankton of the sea of marmara: a review. In: Özsoy, E., Çağatay, N.M., Balkıs, N., Öztürk, B. (Eds.), The Sea of Marmara: Marine Biodiversity, Fisheries, Conservation and Governance İstanbul. Turkish Marine Research, pp. 326–343.

Barone, R., 2007. Behavioural trait of *Ostreopsis ovata* (Dinophyceae) in Mediterranean rock pools: the spider's strategy. Harmful Algae News 33, 1–3.

Belin, C., 1993. Distribution of *Dinophysis* spp. and *Alexandrium minutum* along French coasts since 1984 and their DSP and PSP toxicity levels. In: Smayda, T.J., Shimizu, Y. (Eds.), Toxic Phytoplankton Blooms in the Sea: Proceedings of the Fifth International Conference on Toxic Marine Phytoplankton, Newport, Rhode Island, U.S.A. Developments in Marine Biology, 3. Elsevier Science Publishers, Amsterdam, pp. 469–474.

Belin, C., Beliaeff, B., Raffin, B., Rabia, M., Ibanez, F., 1995. Phytoplankton time-series data of the French phytoplankton monitoring network: toxic and dominant species. In: Lassus, P., Arzul, G., Erard-Le Denn, E., Gentien, P., Marcaillou-Le Baut, C. (Eds.), Harmful Marine Algal Blooms. Proceedings of the 6th International Conference on Toxic Marine Phytoplankton. Lavoisier, Intercept Ltd, Nantes, France, pp. 771–776.

Berdalet, E., Fleming, L.E., Gowen, R., Davidson, K., Hess, P., Backer, L.C., Moore, S.K., Hoagland, P., Enevoldsen, H., 2016. Marine harmful algal blooms, human health and wellbeing: challenges and opportunities in the 21st century. J. Mar. Biol. Assoc. U. K. 96 (1), 61–91. https://doi.org/10.1017/S0025315415001733.

Bernardi Aubry, F., Cossarini, G., Acri, F., Bastianini, M., Bianchi, F., Camatti, E., De Lazzari, A., Pugnetti, A., Solidoro, C., Socal, G., 2012. Plankton communities in northern Adriatic Sea: patterns and changes over the last 30 years. Estuar. Coast Shelf Sci. 115, 125–137. https://doi.org/10.1016/j.ecss.2012.03.011.

Boni, L., Milandri, A., Poletti, R., Pompei, M., 1993. DSP cases in the coast of emilia romagna (northwestern Adriatic Sea). In: Smayda, T.J., Shimizu, Y. (Eds.), Toxic Phytoplankton Blooms in the Sea: Proceedings of the Fifth International Conference on Toxic Marine Phytoplankton, Newport, Rhode Island, U.S.A. Developments in Marine Biology, 3. Elsevier Science Publishers, Amsterdam, pp. 475–481.

Bosak, S., Sarno, D., 2017. The planktonic diatom genus *Chaetoceros* ehrenberg (bacillariophyta) from the Adriatic Sea. Phytotaxa 314 (1). https://doi.org/10.11646/phytotaxa.314.1.1, 01–44.

Bravo, I., Garcés, E., Diogène, J., Fraga, S., Sampedro, N., Figueroa, R.I., 2006. Resting cysts of the toxigenic dinoflagellate genus *Alexandrium* in recent sediments from the Western Mediterranean coast, including the first description of cysts of *A. kutnerae* and *A. peruvianum*. Eur. J. Phycol. 41 (3), 293–302. https://doi.org/10.1080/09670260600810360.

Brondi, A., Cicero, A.M., Magaletti, E., Giovanardi, F., Scarpato, A., Silvestri, C., Spada, E., Casazza, G., 2003. Italian coastal typology for the European water framework directive. In: Özhan, E. (Ed.), Proceedings of the Sixth International Conference on the Mediterranean Coastal Environment, MEDCOAST 03, 7-11 October 2003, 2, pp. 1179–1188.

Cabrini, M., Fornasaro, D., Cossarini, G., Lipizer, M., Virgilio, D., 2012. Phytoplankton temporal changes in a coastal northern Adriatic site during the last 25 years. Estuar. Coast Shelf Sci. 115, 113–124. https://doi.org/10.1016/j.ecss.2012.07.007.

Campbell, L., Olson, R.J., Sosik, H.M., Abraham, A., Henrichs, D.W., Hyatt, C.J., et al., 2010. First harmful Dinophysis (Dinophyceae, Dinophysiales) bloom in the US is revealed by automated imaging flow cytometry. J. Phycol. 46, 66–75. https://doi.org/10.1111/j.1529-8817.2009.00791.x.

Caroppo, C., 2001. Autoecology and morphological variability of *Dinophysis sacculus* (dinophyceae: dinophysiaceae) in a mediterranean lagoon. J. Mar. Biol. Assoc. U. K. 11–21. https://doi.org/10.1017/S0025315401003356, 81.1.

Caroppo, C., Congestri, R., Bruno, M., 1999a. On the presence of *Phalacroma rotundatum* in the southern Adriatic Sea (Italy). Aquat. Microb. Ecol. 301–310. https://doi.org/10.3354/ame017301, 17.3.

Caroppo, C., Fiocca, A., Sammarco, P., Magazzù, G., 1999b. Seasonal variations of nutrients and phytoplankton in the coastal SW Adriatic Sea (1995-1997). Bot. Mar. 42, 389–400. https://doi.org/10.1515/BOT.1999.045.

Caroppo, C., Congestri, R., Bruno, M., 2001. Dynamics of *Dinophysis sensu lato* species (dinophyceae) in a coastal mediterranean environment (Adriatic Sea). Continent. Shelf Res. 21 (16–17), 1839–1854. https://doi.org/10.1016/S0278-4343(01)00028-0.

Caroppo, C., Congestri, R., Bracchini, L., Albertano, P., 2005. On the presence of *Pseudo-nitzschia calliantha* Lundholm, Moestrup et Hasle and *P. delicatissima* (Cleve) Heiden in the Southern Adriatic Sea (Mediterranean Sea, Italy). J. Plankton Res. 27 (8), 763–774. https://doi.org/10.1093/plankt/fbi050.

Caroppo, C., Turicchia, S., Margheri, M.C., 2006. Phytoplankton assemblages in coastal waters of the Northern Ionian Sea (eastern Mediterranean), with special reference to cyanobacteria. J. Mar. Biol. Assoc. U. K. 86, 927–937. https://doi.org/10.1017/S0025315406013889.

Caroppo, C., Cerino, F., Auriemma, R., Cibic, T., 2016. Phytoplankton dynamics with a special emphasis on harmful algal blooms in the Mar Piccolo of Taranto (Ionian Sea, Italy). Environ. Sci. Pollut. Control Ser. 23, 12691–12706. https://doi.org/10.1007/s11356-015-5000-y.

Cerino, F., Bernardi Aubry, F., Coppola, J., La Ferla, R., Maimone, G., Socal, G., Totti, C., 2012. Spatial and temporal variability of pico-, nano- and microphytoplankton in the offshore waters of the southern Adriatic Sea (Mediterranean Sea). Continent. Shelf Res. 44, 94–105. https://doi.org/10.1016/j.csr.2011.06.006.

Cerino, F., Fornasaro, D., Kralj, M., Giani, M., Cabrini, M., 2019. Phytoplankton temporal dynamics in the coastal waters of the north-eastern Adriatic Sea (Mediterranean Sea) from 2010 to 2017. Nat. Conserv. 34, 343–372. https://doi.org/10.3897/natureconservation.34.30720.

Davidson, K., Gowen, R.J., Harrison, P.J., Fleming, L.E., Hoagland, P., Moschonas, G., 2014. Anthropogenic nutrients and harmful algae in coastal waters. J. Environ. Manag. 146, 206–216. https://doi.org/10.1016/j.jenvman.2014.07.002.

Delgado, M., Garcés, E., Camp, J., 1996. Growth and behaviour of *Dinophysis sacculus* from NW mediterranean. In: Yasumoto, T., Oshima, Y., Fukuyo, Y. (Eds.), Harmful and Toxic Algal Blooms. UNESCO, Sendai Kyodo Printer, Sendai, pp. 261–264.

Edler, L., Elbrächter, M., 2010. The Utermöhl method for quantitative phytoplankton analysis. In: Microscopic and molecular methods for quantitative phytoplankton analysis, pp. 13–20. https://doi.org/10.25607/OBP-1371, 110.

EEA European Environmental Agency, 2018. Coordination of information of the environment Land cover 2011 seamless vector data (CORINE Land covermap). Available online at. https://land.copernicus.eu/pan-european/corine-land-cover/clc2018.

U Directive, EU Directive 2006/7/EC of the European Parliament and of the Council of 15 February 2006 Concerning the Management of Bathing Water Quality and Repealing Directive 76/160/EEC.

Fehling, J., Davidson, K., Bates, S.S., 2005. Growth dynamics of non-toxic *Pseudonitzschia delicatissima* and toxic *P. seriata* (Bacillariophyceae) under simulated spring and summer photoperiods. Harmful Algae 4, 763–769. https://doi.org/10.1016/j.hal.2004.11.002.

Fernández, R., Mamán, L., Jaén, D., Fernández Fuentes, L., Ocaña, M.A., Gordillo, M.M., 2019. *Dinophysis* species and diarrhetic shellfish toxins: 20 years of monitoring program in Andalusia, South of Spain. Toxins 189. https://doi.org/10.3390/toxins11040189, 11.4.

Ferreira, J.G., Andersen, J.H., Borja, A., Bricker, S.B., Camp, J., Cardoso da Silva, M., Garcés, E., Heiskanen, A.-S., Humborg, C., Ignatiades, L., Lancelot, C., Menesguen, A., Tett, P., Hoepffner, N., Claussen, U., 2011. Overview of eutrophication indicators to assess environmental status within the European Marine Strategy Framework Directive. Estuar. Coast Shelf Sci. 93 (2), 117–131. https://doi.org/10.1016/j.ecss.2011.03.014.

Figueroa, R.I., Estrada, M., Garcés, E., 2018. Life histories of microalgal species causing harmful blooms: haploids, diploids and the relevance of benthic stages. Harmful Algae 73, 44–57.

Fiorenza, A., Casotti, V., Civano, V., Mancaniello, D., Marchesi, V., Menichetti, S., Merlo, F., Piva, F., Spezzani, P., Tanduo, I., Ungaro, N., Venturelli, S., Zorza, R., 2018. Linee guida per l'analisi delle pressioni ai sensi della Direttiva 2000/60/CE – ISPRA –Manuali e Linee Guida 177/2018. Roma, pp. 1–102.

Garcés, E., Camp, J., 2012. Habitat changes in the Mediterranean Sea and the consequences for harmful algal blooms formation. In: Stambler, N. (Ed.), Life in the Mediterranean Sea: a Look at Habitat Changes. Nova Science Publishers Inc., pp. 519–541

Giovanardi, F., Francé, J., Mozetič, P., Precali, R., 2018. Development of ecological classification criteria for the Biological Quality Element phytoplankton for Adriatic and Tyrrhenian coastal waters by means of chlorophyll a (2000/60/EC WFD). Ecol. Indicat. 93, 316–332. https://doi.org/10.1016/j.ecolind.2018.05.015.

Glibert, P.M., Burford, M.A., 2017. Globally changing nutrient loads and harmful algal blooms: recent advances, new paradigms, and continuing challenges. Oceanography 58–69. https://doi.org/10.5670/oceanog.2017.110, 30.1.

Glibert, P.M., Berdalet, E., Burford, M.A., Pitcher, G.C., Zhou, M., 2018. Harmful algal blooms and the importance of understanding their ecology and oceanography. In: Glibert, P.M. (Ed.), Global Ecology and Oceanography of Harmful Algal Blooms. Springer International Publishing, Cham, pp. 9–25. https://doi.org/10.1007/978-3-319-70069-4_2.

Glibert, P.M., 2020. Harmful algae at the complex nexus of eutrophication and climate change. Harmful Algae 91, 101583. https://doi.org/10.1016/j.hal.2019.03.001. January 2020.

Gowen, R.J., Mckinney, A., Tett, P., Bresnan, E., Davidson, K., Harrison, P.J., Milligan, S., Mills, D.K., Silke, J., Crooks, A.M., 2012. Anthropogenic nutrient enrichment and blooms of harmful phytoplankton. Oceanogr. Mar. Biol. 50, 65–126.

Griffith, A.W., Gobler, C.J., 2020. Harmful algal blooms: a climate change co-stressor in marine and freshwater ecosystems. Harmful Algae 91. https://doi.org/10.1016/j.hal.2019.03.008.

Hallegraeff, G.M., 1993. A review of harmful algal blooms and their apparent global increase. Phycologia 79–99. https://doi.org/10.2216/i0031-8884-32-2-79.1, 32.2.

Hallegraeff, G.M., Anderson, D.M., Belin, C., Dechraoui Bottein, M.-Y., Bresnan, E., Chinain, M., Enevoldsen, H., Iwataki, M., Karlson, B., McKenzie, C.H., Sunesen, I., Pitcher, G.C., Provoost, P., Richardson, A., Schweibold, L., Tester, P.A., Trainer, V.L., Yñiguez, A.T., Zingone, A., 2021. Perceived global increase in algal blooms is attributable to intensified monitoring and emerging bloom impacts. Commun. Earth Environ. 1–10. https://doi.org/10.1038/s43247-021-00178-8, 2.1.

Harrison, P.J., Xu, J., Yin, K., Liu, H., Lee, J., Anderson, D., Hodgkiss, I., 2012. Is there a link between N:P ratios and red tides in Tolo Harbour, Hong Kong? In: Pagou, K., Hallegraeff, G. (Eds.), Proceedings of 14th International Conference on Harmful Algae. Hersonissos-Crete, Greece, pp. 90–92.

Hasle, G.R., 2002. Are most of the domoic acid-producing species of the diatom genus *Pseudo-nitzschia* cosmopolites? Harmful Algae 1 (2), 137–146. https://doi.org/10.1016/S1568-9883(02)00014-8.

Heisler, J., Glibert, P.M., Burkholder, J.M., Anderson, D.M., Cochlan, W., Dennison, W. C., Dortch, Q., Gobler, C.J., Heil, C.A., Humphries, E., Lewitus, A., Magnien, R., Marshall, H.G., Sellner, K., Stockwell, D.A., Stoecker, D.K., Suddleson, M., 2008. Eutrophication and harmful algal blooms: a scientific consensus. Harmful Algae 8 (1), 3–13. https://doi.org/10.1016/j.hal.2008.08.006.

Honsell, G., Poletti, R., Pompei, M., Sidari, L., Milandri, A., Casadei, C., Viviani, R., 1996. *Alexandrium minutum* halim and PSP contamination in the northern Adriatic Sea (Mediterranean Sea). In: Yasumoto, T., Oshima, Y., Fukuyo, Y. (Eds.), Harmful and Toxic Algal Blooms. Intergovernmental Oceanographic Commission of UNESCO, Paris, pp. 77–80.

Howarth, R.W., Marino, R., 2006. Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: evolving views over three decades. Limnol. Oceanogr. 51 (1), 364–376. https://doi.org/10.4319/lo.2006.51.1_part_2.0364.

Ignatiades, L., Gotsis-Skretas, O., 2010. A review on toxic and harmful algae in Greek coastal waters (E. Mediterranean Sea). Toxins 2, 1019–1037. https://doi.org/10.3390/toxins2051019.

Kim, H.G., Paiik, J.S., Lix, S.G., AN, K.H., 1993. Population cell volume and carbon content in monospecific dinoflagellate blooms, 769-773. In: Toxic Phytoplankton Blooms in the Sea. Proc. 5th Int. Conf. On Toxic Marine Phytoplankton. Elsevier, Amsterdam.

Kim, H.G., 1998. Harmful algal blooms in Korean coastal waters focused on three fish killing dinoflagellates. In: Lee, H., Lee, S., Lee, C. (Eds.), Harmful Algal Blooms in Korea and China. NFRDI, Pusan, Korea.

Kjerfve, B., 1994. Chapter 1 coastal lagoons. In: Kjerfve, B. (Ed.), Elsevier Oceanography Series, vol. 60. Elsevier, pp. 1–8. https://doi.org/10.1016/S0422-9894(08)70006-0.

Kooistra, W.H.C.F., Sarno, D., Balzano, S., Gu, H., Andersen, R.A., Zingone, A., 2008. Global diversity and biogeography of *Skeletonema* species (bacillariophyta). Protist 177–193. https://doi.org/10.1016/j.protis.2007.09.004, 159.2.

Koukaras, K., Nikolaidis, G., 2004. *Dinophysis* blooms in Greek coastal waters (thermaikos Gulf, NW aegean sea). J. Plankton Res. 445–457. https://doi.org/10.1093/plankt/fbh042, 26.4.

Kudela, R.M., Gobler, C., 2012. Harmful dinoflagellate blooms caused by Cochlodinium sp.: global expansion and ecological strategies facilitating bloom formation. Harmful Algae 14, 71–86. https://doi.org/10.1016/j.hal.2011.10.015.

Lelong, A., Hégaret, H., Soudant, P., Bates, S., 2012. *Pseudo-nitzschia* (Bacillariophyceae) species, domoic acid and amnesic shellfish poisoning: revisiting previous paradigms. Phycologia 168–216. https://doi.org/10.2216/11-37.1, 51.2.

Mabrouk, L., Hamza, A., Mahfoudi, M., Bradai, M.N., 2012. Spatial and temporal variations of epiphytic *Ostreopsis siamensis* on *Posidonia oceanica* (L.) Delile leaves in Mahdia (Tunisia). Cah. Biol. Mar. CBM-Cahiers de Biologie Marine 419–427, 53.4.

Marasović, I., Ninčević, Z., Pavela-Vrančić, M., Orhanović, S., 1998. A survey of shellfish toxicity in the central Adriatic Sea. J. Mar. Biol. Assoc. U. K. 78 (3), 745–754. https://doi.org/10.1017/S0025315400044751.

Marić, D., Kraus, R., Godrijan, J., Supić, N., Djakovac, T., Precali, R., 2012. Phytoplankton response to climatic and anthropogenic influences in the north-eastern Adriatic during the last four decades. Estuarine. Coast. Shelf Sci. 115, 98–112. https://doi.org/10.1016/j.ecss.2012.02.003.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297. https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2.

McGeoch, M.A., Butchart, S.H.M., Spear, D., Marais, E., Kleynhans, E.J., Symes, A., Chanson, J., Hoffmann, M., 2010. Global indicators of biological invasion: species numbers, biodiversity impact and policy responses. Divers. Distrib. 16 (1), 95–108. https://doi.org/10.1111/j.1472-4642.2009.00633.x.

Moestrup, Ø., Akselmann-Cardella, R., Churro, C., Fraga, S., Hoppenrath, M., Iwataki, M., Larsen, J., Lundholm, N., Zingone, A. (Eds.), 2009. IOC-UNESCO Taxonomic Reference List of Harmful Micro Algae. https://doi.org/10.14284/362. Accessed at. http://www.marinespecies.org/hab on 2021-12-20.

Montresor, M., Zingone, A., Sarno, D., 1998. Dinoflagellate cyst production at a coastal Mediterranean site. J. Plankton Res. 2291–2312. https://doi.org/10.1093/plankt/20.12.2291, 20.12.

Mozetič, P., Solidoro, C., Cossarini, G., Socal, G., Precali, R., Francé, J., Bianchi, F., De Vittor, C., Smodlaka, N., Umani, S.F., 2010. Recent trends towards oligotrophication of the northern Adriatic: evidence from chlorophyll *a* time series. Estuar. Coast 33 (2), 362–375. https://doi.org/10.1007/s12237-009-9191-7.

Mozetič, P., Francé, J., Kogovšek, T., Talaber, I., Malej, A., 2012. Plankton trends and community changes in a coastal sea (northern Adriatic): bottom-up vs. top-down control in relation to environmental drivers. Estuar. Coast Shelf Sci. 115, 138–148. https://doi.org/10.1016/j.ecss.2012.02.009.

Ninčević-Gladan, Ž., Marasović, I., Grbec, B., Skejić, S., Bužančić, M., Kušpilić, G., Matijević, S., Matić, F., 2010. Inter-decadal variability in phytoplankton community in the middle adriatic (kaštela bay) in relation to the north atlantic oscillation. Estuar. Coast 33 (2), 376–383. https://doi.org/10.1007/s12237-009-9223-3.

Palenzuela, J.M., González Vilas, L., Bellas, F.M., Garet, E., González-Fernández, Á., Spyrakos, E., 2019. *Pseudo-nitzschia* blooms in a coastal upwelling system: remote sensing detection, toxicity and environmental variables. Water 11 (9). https://doi.org/10.3390/w11091954, 1954.

Pfannkuchen, M.D., Godrijan, J., Smodlaka Tanković, M., Baričević, A., Kužat, N., Djakovac, T., Pustijanac, E., Jahn, R., Pfannkuchen, M., 2018. The ecology of one cosmopolitan, one newly introduced and one occasionally advected species from the genus *Skeletonema* in a highly structured ecosystem, the northern Adriatic. Microb. Ecol. 75, 674–687. https://doi.org/10.1007/s00248-017-1069-9.

Pistocchi, R., Guerrini, F., Pezzolesi, L., Riccardi, M., Vanucci, S., Ciminiello, P., Dell'Aversano, C., Forino, M., Fattorusso, E., Tartaglione, L., Milandri, A., Pompei, M., Cangini, M., Pigozzi, S., Riccardi, E., 2012. Toxin levels and profiles in microalgae from the North-Western Adriatic Sea—15 years of studies on cultured species. Mar. Drugs 140–162. https://doi.org/10.3390/md10010140, 10.1.

Poletti, R., Cangini, M., Ceredi, A., Magnani, F., Milandri, A., Pigozzi, S., Pompei, M., Riccardi, E., Zoffoli, S., 2008. Bioaccumulo di tossine algali liposolubili in *Mytilus galloprovincialis* (Lamarck, 1819) del Nord Adriatico. Biol. Mar. Mediterr. 54–57, 15.1.

Pyšek, P., Jarosik, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffer, U., Vil, M., 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biol. 18 (5), 1725–1737. https://doi.org/10.1111/j.1365-2486.2011.02636.x.

Randone, et al., 2017. Reviving the Economy of the Mediterranean Sea: Actions for a Sustainable Future. WWF Mediterranean Marine Initiative, Rome, Italy, p. 64.

Roselli, L., Fabbrocini, A., Manzo, C., D'Adamo, R., 2009. Hydrological heterogeneity, nutrient dynamics and water quality of a non-tidal lentic ecosystem (Lesina Lagoon, Italy). Estuarine. Coast. Shelf Sci. 84, 539–552. https://doi.org/10.1016/j.ecss.2009.07.023.

Roselli, L., Cañedo-Argüelles, M., Costa Goela, P., Cristina, S., Rieradevall, M., D'Adamo, R., Newton, A., 2013. Do physiography and hydrology determine the physico-chemical properties an trophic status of coastal lagoons? A comparative approach. Estuar. Coast Shelf Sci. 117, 29–36. https://doi.org/10.1016/j.ecss.2012.09.014.

Roselli, L., Vadrucci, M.R., Fanelli, F., Ungaro, N., Caroppo, C., 2019. First bloom event of the small dinoflagellate *Prorocentrum shikokuense* in the Mediterranean Sea: cryptogenic or introduced? Mar. Pollut. Bull. 139, 197–204. https://doi.org/10.1016/j.marpolbul.2018.12.034.

Roselli, L., Vadrucci, M.R., Belmonte, M., Ciciriello, P., Rubino, F., Ungaro, N., Caroppo, C., 2020. Two-stages bloom of *Margalefidinium* cf. *polykrikoides* in a Mediterranean shallow bay (Ionian Sea, Italy). Mar. Pollut. Bull. 151, 110825 https://doi.org/10.1016/j.marpolbul.2019.110825.

Roselli, L., Bevilacqua, S., Terlizzi, A., 2022. Using null models and species traits to optimize phytoplankton monitoring: an application across oceans and ecosystems. Ecol. Indicat. 138 (2022), 108827 https://doi.org/10.1016/j.ecolind.2022.108827.

Ruppert, K.M., Kline, R.J., Rahman, M.S., 2019. Past, present, and future perspectives of environmental DNA (eDNA) metabarcoding: a systematic review in methods, monitoring, and applications of global eDNA. Global Ecol. Conserv. 17, e00547 https://doi.org/10.1016/j.gecco.2019.e00547.

Sarkar, S.K., 2018. Marine Algal Bloom: Characteristics, Causes and Climate Change Impacts. Springer Nature Singapore Pte Ltd, ISBN 978-981-10-8261-0, p. 170.

Satta, C.T., Anglès, S., Lugliè, A., Guillen, J., Sechi, N., Camp, J., Garcés, E., 2013. Studies on dinoflagellate cyst assemblages in two estuarine Mediterranean bays: a useful tool for the discovery and mapping of harmful algal species. Harmful Algae 24, 65–79. https://doi.org/10.1016/j.hal.2013.01.007.

Shears, N.T., Ross, P.M., 2010. Toxic cascades: multiple anthropogenic stressors have complex and unanticipated interactive effects on temperate reefs. Ecol. Lett. 13 (9), 1149–1159. https://doi.org/10.1111/j.1461-0248.2010.01512.x.

Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., Garcia-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vil, M., 2013. Impacts of biological invasions: what's what and the way forward. Trends Ecol. Evol. 28 (1), 58–66. https://doi.org/10.1016/j.tree.2012.07.013.

Smayda, T.J., 1990. Novel and nuisance phytoplankton blooms in the sea: evidence for a global epidemic. In: Graneli, E., Sundstrom, B., Edler, L., Anderson, D.M. (Eds.), Toxic Marine Phytoplankton. Elsevier, New York, pp. 29–40.

Su-Myat, Koike, K., 2013. A red tide off the Myanmar coast: morphological and genetic identification of the dinoflagellate composition. Harmful Algae 27, 149–158. https://doi.org/10.1016/j.hal.2013.05.010.

Taleb, H., Vale, P., Jaime, E., Blaghen, M., 2001. Study of paralytic shellfish poisoning toxin profile in shellfish from the Mediterranean shore of Morocco. Toxicon 1855–1861. https://doi.org/10.1016/S0041-0101(01)00167-2, 39.12.

Tanaka, T., Thingstad, T.F., Christaki, U., Colombet, J., Cornet-Barthaux, V., Courties, C., Grattepanche, J.-D., Lagaria, A., Nedoma, J., Oriol, L., Psarra, S., Pujo-Pay, M., Van Wambeke, F., 2011. Lack of P-limitation of phytoplankton and heterotrophic prokaryotes in surface waters of three anticyclonic eddies in the stratified Mediterranean Sea. Biogeosciences 8, 525–538. https://doi.org/10.5194/bg-8-525-2011.

Tomas, C.R., 1997. Identifying Marine Phytoplankton. Academic Press, San Diego, p. 858.

Totti, C., Accoroni, S., Cerino, F., Cucchiari, E., Romagnoli, T., 2010. *Ostreopsis ovata* bloom along the Conero Riviera (northern Adriatic Sea): relationships with environmental conditions and substrata. Harmful Algae 9 (2), 233–239. https://doi.org/10.1016/j.hal.2009.10.006.

Totti, C., Romagnoli, T., Accoroni, S., Coluccelli, A., Pellegrini, M., Campanelli, A., Grilli, F., Marini, M., 2019. Phytoplankton communities in the northwestern Adriatic Sea: interdecadal variability over a 30-years period (1988–2016) and relationships with meteoclimatic drivers. J. Mar. Syst. 193, 137–153. https://doi.org/10.1016/j.jmarsys.2019.01.007.

Tubaro, A., Dell'Ovo, V., Sosa, S., Florio, C., 2010. Yessotoxins: a toxicological overview. Toxicon 56 (2), 163–172. https://doi.org/10.1016/j.toxicon.2009.07.038.

Underwood, A.J., 1996. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variances. Cambridge University Press, Cambridge. https://doi.org/10.1017/CBO9780511806407.

Ungaro, N., Assennato, G., Blonda, M., Cudillo, B., Petruzzelli, R., Mariani, M., Pastorelli, A.M., Aliquò, M.R., D'angela, A., Aiello, C., Ranieri, S., 2010. Occurrence of the potentially toxic dynoflagellate *Ostreopsis ovata* along the apulian coastal areas (Southern Italy) and relationship with anthropogenic pollution. Fresenius Environ. Bull. 19 (9), 1813–1821.

Vila, M., Delgado, M., Camp, J., 2001. First detection of widespread toxic events caused by *Alexandrium catenella* in the Mediterranean Sea. In: Hallegraeff, G.M., Blackburn, S.I., Bolch, C.J., Lewis, R.J. (Eds.), Harmful Algal Blooms 2000. Proceedings of the 9th International Conference on Harmful Algal Blooms. Intergovernmental Oceanographic Commission of UNESCO, Hobart, Tasmania, Australia, pp. 8–11.

Wells, M.L., Trainer, V.L., Smayda, T.J., Karlson, B.S., Trick, C.G., Kudela, R.M., Ishikawa, A., Bernard, S., Wulff, A., Anderson, D.M., Cochlan, W.P., 2015. Harmful algal blooms and climate change: learning, from the past and present to forecast the future. Harmful Algae 49, 68–93. https://doi.org/10.1016/j.hal.2015.07.009.

Wells, M.L., Karlson, B., Wulff, A., Kudela, R., Trick, C., Asnaghi, V., Berdalet, E., Cochlan, W., Davidson, K., De Rijcke, M., Dutkiewicz, S., Hallegraeff, G., Flynn, K.J., Legrand, C., Paerl, H., Silke, J., Suikkanen, S., Thompson, P., Trainer, V.L., 2020. Future HAB science: directions and challenges in a changing climate. Harmful Algae 91, 101632. https://doi.org/10.1016/j.hal.2019.101632.

Zingone, A., Siano, R., D'Alelio, D., Sarno, D., 2006. Potentially toxic and harmful microalgae from coastal waters of the Campania region (Tyrrhenian Sea, Mediterranean Sea). Harmful Algae 5 (3), 321–337. https://doi.org/10.1016/j.hal.2005.09.002.

Zingone, A., Enevoldsen, H., Hallegraeff, G.M., 2017. Are HABs and their societal impacts expanding and intensifying? A call for answers from the HAB scientific community. In: Proenca, L.A.O., Hallegraeff, G.M. (Eds.), Marine and Fresh-Water Harmful Algae. Proceedings of the 17th International Conference on Harmful Algae 2016. International Society for the Study of Harmful Algae and Intergovernmental Oceanographic Commission of UNESCO, pp. 14–17, 2017.

Zingone, A., Escalera, L., Aligizaki, K., Fernández-Tejedor, M., Ismael, A., Montresor, M., Mozetič, P., Seyfettin, T., Totti, C., 2021. Toxic marine microalgae and noxious blooms in the Mediterranean Sea: a contribution to the global HAB status report. Harmful Algae 102, 101843. https://doi.org/10.1016/j.hal.2020.101843.