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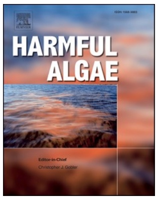

The role of sea temperature in *Ostreopsis* cf. *ovata* blooms in temperate areas—14 years of data gathered along the Northern Mediterranean coast

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ABSTRACT

Ostreopsis cf. *ovata* is a benthic dinoflagellate able to produce toxins of the palytoxin group. It forms harmful blooms affecting marine ecosystems, coastal economies, and human health. Initially reported in tropical areas, this species is now found throughout the Mediterranean coast where, in certain sites, it reaches high cell abundances during the summer and/or fall periods. We analyzed data from long-term monitoring conducted between 2010 and 2023 in the Northwestern Mediterranean along the coasts of Spain, France, Principality of Monaco, and Italy, within the RAMOGE Agreement. Results revealed that *O.* cf. *ovata* is widely distributed and remains stable in historically colonized sites, both as epiphyte on benthic macroalgae and in the plankton. Sea surface temperature recorded during the periods with *O.* cf. *ovata* presence ranged from 15.5 to 34.8°C. Most sites did not exhibit clear temperature–abundance relationships, with significant correlations found at only 23% of the monitored stations (mostly showing higher values at warmer conditions). A few stations displayed significant temporal trends, either positive or negative, in abundances, bloom onset, or duration, with patterns varying by location. Overall, the results suggested that, while global warming may influence the dynamics of *O.* cf. *ovata* (in terms of abundances, time of bloom onset and duration), the response of the species is more complex and site-specific, shaped by local environmental factors. Besides the unquestionable increasing trend of seawater temperature in the Mediterranean Sea, this study highlighted a stabilization of the *O.* cf. *ovata* bloom phenomenon at most stations in the Mediterranean.

1. Introduction

The ecological, economic, and health impacts of Harmful Algal Bloom (HAB) events have become increasingly evident and concerning in recent decades, particularly in coastal regions worldwide (Anderson et al., 2019, Hallegraeff et al., 2021). This increment appears to be primarily driven by global climate change, which facilitated the expansion and accelerated growth of tropical and subtropical harmful dinoflagellates (Tester et al., 2020).

The genus *Ostreopsis*, belonging to the family Ostreopsidaceae (Gonyaulacales, Dinophyceae), includes several species widely distributed across tropical to temperate marine coastal regions worldwide.

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Originally reported in tropical areas, *Ostreopsis* has, over the past two decades, become more common in temperate zones as well (Litaker et al., 2009; Rhodes, 2011; Zingone et al., 2021). In the Mediterranean Sea, *Ostreopsis* blooms are mostly caused by *O.* cf. *ovata*, although *O.* cf. *siamensis* and *O. fattorussoi*, have also been identified (Accoroni and Totti, 2016; Penna et al., 2012).

During the bloom development, *Ostreopsis* forms a biofilm on biotic and abiotic benthic substrates, but cells can also be found in the water column and in highly dense aggregates floating at surface. Several biotic and abiotic factors act to regulate bloom dynamics in terms of cell abundance and onset timing and duration of the proliferation. Key factors include mainly temperature but also hydrodynamics, water depth, concentrations of both inorganic and organic nutrients, substrate availability, and allelochemical interactions (e.g. Accoroni et al., 2017a, Boisnoir et al., 2018; Cohu et al., 2013; Glibert et al., 2012; Larsson et al., 2019; Parsons and Preskitt, 2007; Pavaux et al., 2020; Pichierri et al., 2017; Richlen & Lobel, 2011; Skinner et al., 2013; Ternon et al., 2020; Yong et al., 2018).

Some *Ostreopsis* species produce toxins of the palytoxin group, and their blooms in temperate areas can cause mass mortalities of marine invertebrates (Accoroni and Totti, 2016; Parsons et al., 2012), as well as respiratory diseases due to inhalation of marine aerosols and skin and eye irritations through direct contact with seawater in humans (Berdalet et al., 2022; Vila et al., 2016). *Ostreopsis* toxins can circulate through the marine food webs, as suggested by several studies in some Mediterranean sites, constituting a potential foodborne risk in humans. Indeed, *Ostreopsis* toxin concentrations ranging from 100 to 600 µg kg^{-1} were estimated in diverse seafood products (Accoroni et al., 2011, 2022; Aligizaki & Nikolaidis, 2008; Amzil et al., 2012; Barnouin et al., 2025; Sardo et al., 2020), well above the threshold of 30 µg·kg^{-1} established by the European Food Safety Authority (EFSA Panel on Contaminants in the Food Chain (CONTAM), 2009), for human consumption. However, to the best of our knowledge, cases of intoxication from contaminated seafood (Tubaro et al., 2011) have not been reported so far in this area.

In the Mediterranean Sea, the emergence of *Ostreopsis* blooms has been recorded along many rocky shores of the basin (Zingone et al., 2021). The genus was first documented at Villefranche-sur-Mer, France, in 1972 (Taylor, 1979), and subsequently in Lebanese coastal waters in 1980 (Abboud-Abi, 1989), as well as along the Catalan coast in Spain between 1997 and 1998 (Vila et al., 2001). In Italy, the species was initially detected along the Tyrrhenian Sea in 1994 (Tognetto et al., 1995). The first remarkable episode related to *Ostreopsis* bloom in the Mediterranean Sea occurred in 2005 in Genoa (Ligurian Sea), when more than 200 people sought medical treatment for such as rhinorrhea, cough, fever, bronchoconstriction with mild breathing difficulties, with 20 people requiring hospitalization (Brescianini et al., 2006). In the Adriatic *Ostreopsis* was detected since the early 2000s in the southern Adriatic coasts (Bottalico et al., 2002; Di Turi et al., 2003; Ungaro et al., 2005), and reached the rocky northern Adriatic shores by 2006 (Monti et al., 2007; Totti et al., 2007). Over the past two decades, *Ostreopsis* blooms have been reported in several Mediterranean regions, including Spain, France, Greece, Italy, Algeria, Tunisia, and Turkey (S. Accoroni & Totti, 2016, and references therein). Overall, its proliferation was characterized by a rapid and unexpected surge around the year 2000, followed by a gradual expansion of its distribution and a subsequent decade of relative stability. This sequence represents one of the most prominent examples of range expansion and increasing ecological impact over time in the region (Zingone et al., 2021). Comparable patterns of sudden proliferation and increased influence have also been documented in other temperate regions such as New Zealand (Parsons et al., 2012). Notably, this range expansion has occurred alongside a marked rise in monitoring efforts and scientific studies targeting benthic microalgae (Zingone et al., 2021), which might have significantly influenced the perception of the phenomenon and its apparent intensity.

The potential link between climate change and harmful benthic microalgae has been the subject of considerable debate. While some researchers have proposed that rising temperatures and an increased frequency of hot days may lead to more intense *Ostreopsis* blooms in the future (Asnaghi et al., 2017; Fabri-Ruiz et al., 2024; Tester et al., 2020), others have suggested that the observed pattern in the Mediterranean Sea is more consistent with a stabilization (Accoroni et al., 2024a; Zingone et al., 2021).

The aim of this study was to investigate the temporal dynamics of *Ostreopsis* cf. *ovata* blooms (onset and duration), the potential relationships with sea surface temperature, and the interannual abundance trends. Data were collected between 2010 and 2023 along the Northwestern Mediterranean coasts of Spain, France, Monaco, and Italy, within the RAMOGE working group.

Although this study did not analyze other environmental parameters, such as nutrient concentrations, salinity, light availability, and hydrodynamic conditions, relevant published data support our conclusions. The results of this study will help to better define if this phenomenon has an increasing, stable or decreasing trend, linked or not to certain climate change predictors.

2. Materials and methods

2.1. Study area and sampling

The sampling stations are located along the Mediterranean coasts in the northeast of Spain, France, the Principality of Monaco, and Italy (21, 16, 5, and 612 stations, respectively, Fig. 1 – in Italy, the number of stations has decreased over time, as some have been removed due to a lack of recorded data). Sampling was conducted between 2010 and 2023, from April to December (up to a maximum weekly frequency) within the framework of the RAMOGE Agreement, which compiled data mainly from the national monitoring programs of the aforementioned countries (https://ramoge.org/en/ where most of the data used for this work are also available). Most sampling sites were on rocky coasts, but sampling was also conducted on inconsistent coastal substrata and/or in zones strongly influenced by freshwater input, such as those near the Po River.

At each station, benthic macroalgae and/or seawater samples were collected for the estimation of the epiphytic and/or planktonic *Ostreopsis* cell concentrations, respectively, along with measurements of sea surface temperature.

Undisturbed benthic samples of macroalgae (seaweed species are

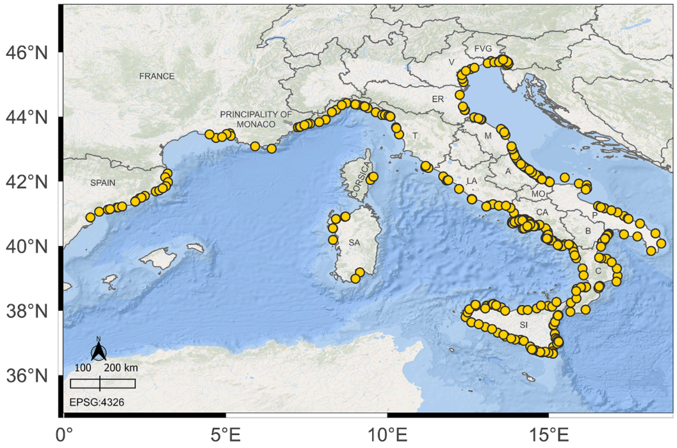

Fig. 1. Map of the study area. The yellow circles mark the locations of all stations monitored during the entire study period (2010–2023) across Spain, France, the Principality of Monaco, and Italy. In Italy, the regions are abbreviated as follows: FVG = Friuli Venezia Giulia, V = Veneto, ER= Emilia-Romagna, M = Marche, A = Abruzzo, MO = Molise, P = Apulia, C = Campania, SI = Sicily, SA = Sardinia, CA = Campania, LA = Lazio, T = Tuscany, L =Liguria.

listed in Table S1) were obtained within the first 2 m of depth, following the common protocol for the sampling of *O.* cf. *ovata* (Accoroni et al., 2024b). Briefly, thalli were collected after hooding in plastic bags which were promptly closed underwater, to avoid the loss of epiphytic cells. The samples were then transferred to plastic jars filled with filtered seawater (FSW). Alternatively, thalli were collected by hand touching only the base of the thallus and placed in a plastic bottle, filled with ca. 200 mL seawater (Jauzein et al., 2018). Samples were kept dark and in situ temperature (using a portable refrigerator) until reaching the laboratory.

Seawater samples for the analysis of *Ostreopsis* cf. *ovata* planktonic cells were collected in the sampling stations following the Intergovernmental Oceanographic Commission guidelines (Reguera et al., 2016).

2.2. *Ostreopsis cf. ovata sample treatment and analysis*

The general procedure to estimate the concentrations of the epiphytic *Ostreopsis* cells consisted in: i) shaking the collected macroalgae in a known seawater volume (to dislodge the microalgae), ii) percolating the seawater containing the released cells through a mesh (to eliminate macroalgae, bigger microorganisms and debris), iii) fixing the percolated seawater with Lugol's solution and iv) measuring the fresh weight of the macroalgae. This general procedure was applied with certain variations by the participant groups (e.g. Jauzein et al., 2018; Accoroni et al., 2024b, Fabri-Ruiz et al., 2024), considering that the comparability of the protocols had been previously tested by intercalibration exercise (Vassalli et al., 2018).

Microalgae from both epiphytic and planktonic samples were counted between one week and one month after collection, following the Utermöhl method (EUROPEAN STANDARD, 2006), using sedimentation chambers (10 mL, 50 mL or 100 mL, depending on the cells densities). The more concentrated benthic samples were processed using 1 mL Sedgewick-Rafter chambers.

The final data were expressed as cells g^{-1} FW of macroalgal thalli, and as cells L^{-1} for epiphytic and planktonic abundances, respectively.

2.3. *Statistical analysis*

All analysis were performed using R software (R Core Team, 2023), version 4.3.2.

Spearman's correlations were made using rcorr function from the Hmisc package version 5.2.3. (Harrell Jr, 2025) to determine monotonic relationships between the epiphytic (cells g^{-1} FW) and planktonic (cells L^{-1}) abundances of *Ostreopsis* cf. *ovata*, as well as between *O.* cf. *ovata* abundances (both cells g^{-1} FW and cells L^{-1}) and seawater temperature values.

To assess the presence of significant increasing or decreasing trends in *Ostreopsis* cf. *ovata* abundances (both cells L^{-1} and cells g^{-1} FW) throughout the studied years, the Mann-Kendall test (Kendall, 1975; Mann, 1945) was applied using the Kendall function from the Kendall package version 2.2.1 (McLeod, 2022). This test was applied using only annual maxima values of cell abundances at each station and was restricted to stations with at least 10 years of data. This criterion ensured the robustness of the correlation score (S) and the reliability of the results. It also confirmed that detected trends reflected actual temporal changes rather than short-term fluctuations due to limited time series length (Hipel and McLeod, 2005; McLeod, 2022). The Mann-Kendall test was also applied to assess if significant (increasing or decreasing) trends over the study period occurred in: (i) bloom duration, calculated as the number of days with positive values (i.e., both cells L^{-1} and cells g^{-1} FW > 0) recorded each year at each station; and (ii) timing of bloom onset and bloom peak, expressed as the number of days between the reference date (i.e. May 18th corresponding to the earliest positive record observed in the entire dataset) and the date of the first observation of abundance > 0 and the date of maximum abundance, respectively, calculated annually for each station (e.g. 44 days correspond to a bloom onset recorded on July 1st and 75 days correspond to a bloom peak recorded on August 1st). When no statistically significant trend —either positive or negative— is detected, the variable can be considered stable over time, and we therefore interpret this as a condition of stabilization.

Spatial maps were produced using both QGIS software version 3.22 and R software.

3. Results

3.1. *Spatial distribution of Ostreopsis cf. ovata*

Although *Ostreopsis* cf. *ovata* blooms are predominantly benthic phenomena, they are also recorded in the water column (Fig. 2). *Ostreopsis* cf. *ovata* has been documented in almost all of the stations considered with the exception of some stations situated in Corsica and several Italian regions (Abruzzo, Basilicata, Calabria, Sicily, Campania, and Lazio). In Veneto and Emilia-Romagna (Italy) *Ostreopsis* has been never observed, except once in a water sample close to Venice. In most stations where the species was detected epiphytic on macroalgae, its presence was also confirmed in the water column as highlighted also by a significant positive Spearman's correlation found between epiphytic and planktonic *O.* cf. *ovata* abundances ($r = 0.825$; $p < 0.001$).

3.2. *Influence of sea water temperature on the Ostreopsis cf. ovata abundances*

During the study period (2010–2023), when *Ostreopsis* cf. *ovata* was detected, sea surface temperature (SST) along the coast of the study area ranged from 15.4 to 34.5°C, with the maximum value recorded on July 12th, 2016, in Liguria (Italy) in a supralittoral rock pool (Fig. 3). The highest epiphytic abundance (21×10^6 cells g^{-1} FW) was recorded in Apulia (Italy) at 25°C on July 8th, 2021, while the highest planktonic abundance (10×10^6 cells L^{-1}) was observed in Liguria (Italy) at 25°C on July 1st, 2010 (Table 1).

Considering the whole dataset, significant Spearman's correlations were observed between the abundances of *O.* cf. *ovata* and seawater temperature values, although with low correlation coefficient values ($r = 0.034$, $p < 0.05$, and $r = 0.086$, $p < 0.001$, for epiphytic and planktonic abundances, respectively). However, focusing the analysis on each station separately, only 23.0 % (epiphytic cells) and 22.8 % (planktonic cells) of the stations showed significant correlations with seawater temperature. Significant positive correlation between the abundances of *O.* cf. *ovata* and water temperature values was found at several stations along the northeastern Spanish coast, in Monaco, and along the Italian shores of the Tyrrhenian and Ionian Seas. On the contrary, significantly negative correlations were observed in some stations in Italy, located in the Marche region (for both epiphytic and planktonic abundances) and in Apulia and Sardinia (only for planktonic abundances) (Fig. 4).

3.3. *Analysis on trends of Ostreopsis cf. ovata bloom: abundance, bloom duration, and timing of bloom onset and peak*

In the stations where *Ostreopsis* cf. *ovata* was detected, a general pattern of consistency was observed: in most stations where *O.* cf. *ovata* had previously been recorded, its presence persisted in subsequent years. The maximum values of *Ostreopsis* cf. *ovata* were of the order of 10^7 both for epiphytic (cells g^{-1} FW) and planktonic (cells L^{-1}) abundances (Table 1).

The Mann-Kendall test was used to analyze temporal trends in *Ostreopsis* cf. *ovata* maximum abundances in each station throughout the study period, i.e. to explore the tendency of bloom intensities over the years. Regarding epiphytic abundances, only 3 out of 35 stations, corresponding to 8.6 % of the total, showed a decreasing trend. These stations were located in Calabria, Sardinia, and Sicily (Italy). Regarding the planktonic abundances, only 8 out of 57 stations, corresponding to

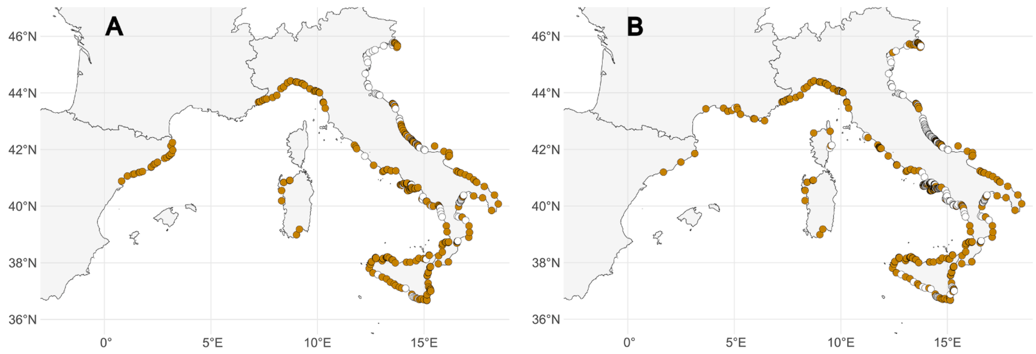

Fig. 2. Spatial distribution of *Ostreopsis* cf. *ovata* based on epiphytic (A) and planktonic (B) records within the entire study period (2010–2023). White dots show the stations where *Ostreopsis* cf. *ovata* was not recorded during the whole study period, while orange dots show where it was recorded, at least on one sampling date.

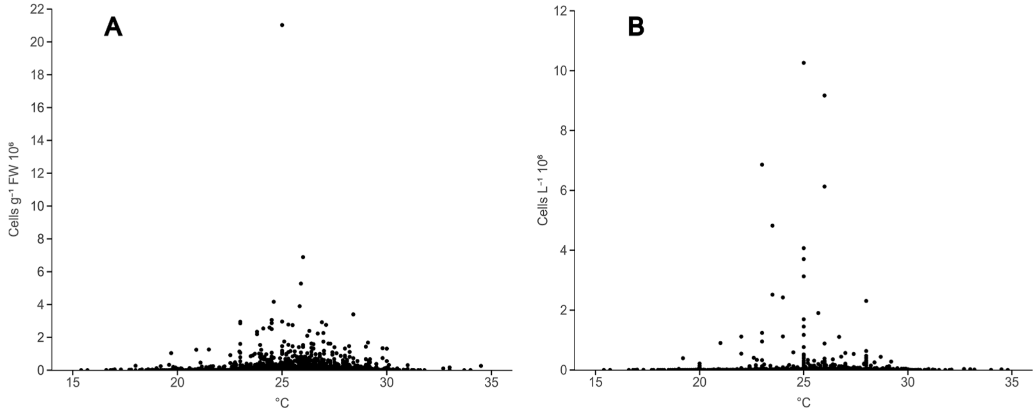

Fig. 3. Epiphytic (A) and planktonic (B) *Ostreopsis* cf. *ovata* abundances (>0) according to seawater temperature.

Table 1
Maximum epiphytic and planktonic abundances of *Ostreopsis* cf. *ovata* recorded in the study area, with associated seawater temperature and date of observation.

Coastal area	Epiphytic *Ostreopsis* maximum abundance			Planktonic *Ostreopsis* maximum abundance		
	Abundances (cells g^{-1} FW)	Temperature (°C)	data	Abundances (cells L^{-1})	Temperature (°C)	data
Spain	6888,055	26	29/07/2021	195,144	26	24/07/2018
France	3897,109	25.8	05/07/2023	44,400	na	28/07/2016
Principality of Monaco	1564,242	na	15/07/2014	30,260	na	19/07/2010
Western Italian coast	2777,889	25.3	24/07/2014	10,262,000	25	01/07/2010
Eastern Italian coast	21,026,175	25	08/07/2021	9170,850	26	06/09/2018

na = not available

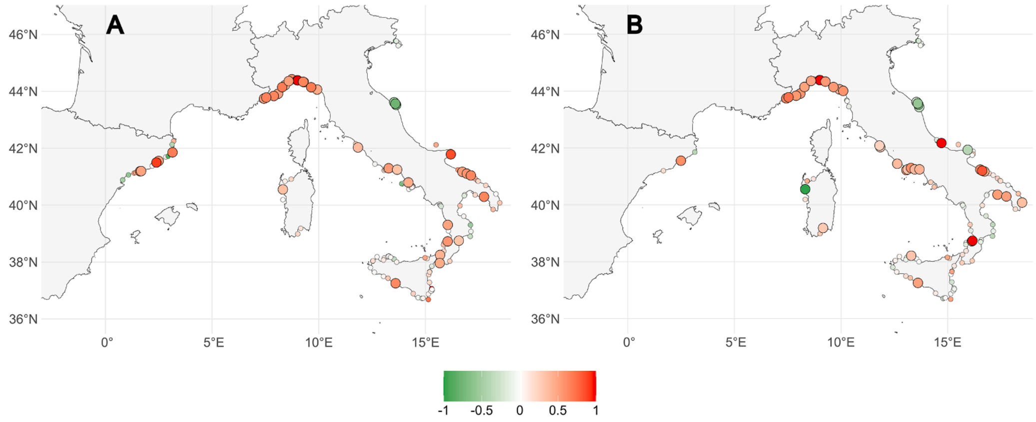

Fig. 4. Spearman's correlation between epiphytic (A) and planktonic (B) abundances of *Ostreopsis* cf. *ovata* and sea surface temperature. The red and green dots indicate the stations where positive and negative correlations were recorded, respectively. Statistically significant correlations are indicated by large dots.

14.0 % of the stations considered, showed significant decreasing trend. These stations were located in Calabria (1), Marche (1), Apulia (1), Sardinia (2), and Sicily (3) (Italy, Fig. 5).

The temporal trends were analyzed (Mann-Kendall test) also on the duration of blooms at each station, with the aim of determining whether the number of bloom days has increased or decreased over time. Considering epiphytic *Ostreopsis* cf. *ovata* cells, only 1 out of 25 stations (2.9 %), located in Lazio (Italy), showed a significant decreasing trend, while 2 out of 35 stations (5.7 %), both in Sicily (Italy), exhibited a significant increase (Fig. 6A). Focusing on planktonic *Ostreopsis* cf. *ovata* cells, 3 out of 57 stations (5.3 %), 1 in Calabria and 2 in Apulia (Italy) showed a significant decreasing trend, whereas 7 out of 57 stations (12.3 %), all located in Italy (Calabria, Friuli-Venezia Giulia, Lazio, and Apulia), showed a significant increasing trend (Fig. 6B).

Furthermore, the Mann-Kendall test was applied to the number of days between the reference date of the earliest positive record (May 18th) and the first observation of abundance > 0 at each station and for each year, in order to detect potential trends indicating an advancement or delay in the onset of the bloom over the study period. Given that in some monitoring programs the sampling of benthic substrate is carried out only when planktonic cells reach a certain threshold (e.g. ISPRA 2024), the timing of bloom onset was assessed based solely on planktonic cells to avoid possible false delayed bloom onsets. Among all the stations considered, 16 out of 63 (25.4 %), all located in Italy (2 in Friuli-Venezia Giulia, 7 in Lazio, 1 in Apulia, and 6 in Sicily), showed a significant negative trend, i.e. a tendency toward an earlier bloom onset. In contrast, 3 out of 63 stations (4.8 %), also in Italy (2 in Apulia and 1 in Sardinia), showed a significant positive trend, indicating a delayed start of the bloom (Fig. 7).

The Mann-Kendall test was applied also to the number of days between the reference date of the earliest positive record and the day on which the maximum abundance value was observed at each station and for each year. Considering *Ostreopsis* cf. *ovata* epiphytic cells, 2.9 % of the stations considered (1 out of 35, located in Sicily, Italy) revealed a significant trend, specifically a tendency toward an earlier timing of peak abundance (Fig. 8A). Regarding planktonic *O.* cf. *ovata* cells, 10 out of 57 stations (17.5 %), located in Apulia (6), Calabria (2), Lazio (1), and Sicily (1) (Italy), showed a significant tendency toward an earlier timing of peak abundance (Fig. 8B).

4. Discussion

This study confirmed the presence of *Ostreopsis* cf. *ovata* at all stations of the northwestern Mediterranean Sea characterized by rocky coasts, while it was not observed in areas with inconsistent coastal substrata and/or in zones strongly influenced by freshwater input, such as those near the Po River. In fact, *Ostreopsis* has never been detected at salinity values below 30 in the Mediterranean Sea, and its preference for hard substrata and macroalgae has been demonstrated in several studies (Accoroni and Totti, 2016; Carnicer et al., 2015; Monserrat et al., 2024; Pavaux et al., 2020) and in studies on habitat complexity related effects (Chiantore et al., 2024). Moreover, *O.* cf. *ovata* generally showed persistence over time: in most stations where it was recorded once, its presence continued in subsequent years. This recurrent detection is consistent with the hypothesis that *Ostreopsis* recruits from benthic resting stages (actually observed in field and culture samples, e.g. Accoroni et al., 2014), which would naturally favor its reappearance at sites where it has been previously observed. However, in some stations, changes in bloom parameters, i.e., maximum abundances, duration and timing of onset and peak were observed.

The first record of *Ostreopsis* in the Mediterranean Sea dates back to 1972 in Villefranche-sur-Mer (France), as reported by Taylor (1979). Later, *O.* cf. *ovata* was detected in 1994 along the Italian coasts of the Tyrrhenian Sea (Tognetto et al., 1995), and in 1997–1998 along the Catalan coast in Spain (Vila et al., 2001). The first large bloom was detected in Italy in 2005 (Mangialajo et al., 2008). Since then, blooms of *Ostreopsis* species have been recorded with increasing frequency and are now widely distributed across many Mediterranean areas (Zingone et al., 2021). The increasing occurrence of the *Ostreopsis* phenomenon has led to a widespread belief that the expansion of *Ostreopsis* cf. *ovata* into new areas is driven by global warming and the general rise in seawater temperature, which is an unquestionable trend in the Mediterranean Sea (https://marine.copernicus.eu/access-data/ocean-monitoring-indicators/mediterranean-sea-surface-temperature-cumulative-trend-map). However, several reports of *Ostreopsis* blooms occurring at low temperatures — even as low as 7°C — challenge this hypothesis (Mangialajo et al., 2011; Monti et al., 2007; Selina & Orlova, 2010; Selina et al., 2014). For this reason, some authors have suggested that global warming may not directly influence the geographic spread of the phenomenon, but could instead affect the dynamics of *O.* cf. *ovata*, for example by increasing bloom magnitude (Fabri-Ruiz et al., 2024) and/or promoting an earlier seasonal onset, as optimal temperature conditions are reached sooner (Drouet et al., 2022; Fricke et al., 2018). This study highlighted that only a few stations (~23 %) showed a significant correlation between temperature and *Ostreopsis* abundances. Among these, most stations exhibited a positive trend (as expected), although some showed a negative one, as observed in the N Adriatic Sea. These conflicting results regarding temperature have also been reported in the literature: while some studies, conducted both in the field and in laboratory, found a positive correlation between *Ostreopsis* abundance and temperature (e.g., Granéli et al., 2011; Yamaguchi et al., 2012), others observed negative responses (Carnicer et al., 2016; Cohu et al., 2011; Scalco et al., 2012).

In this context, it should always be kept in mind that, beyond

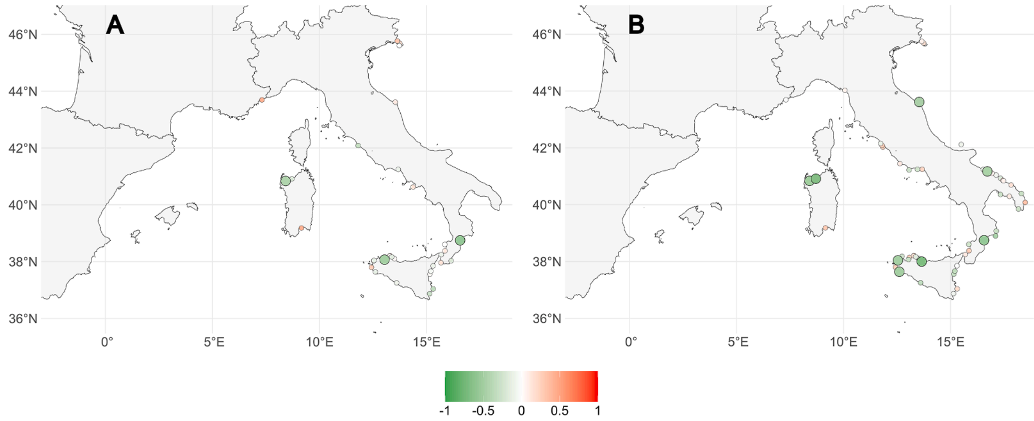

Fig. 5. Temporal trends in annual maximum epiphytic (A) and planktonic (B) abundances of *Ostreopsis* cf. *ovata*. The red and green dots indicate the stations where positive (increase) and negative (decrease) trends (tau) were recorded, respectively. Large dots indicate statistically significant trends ($p < 0.05$).

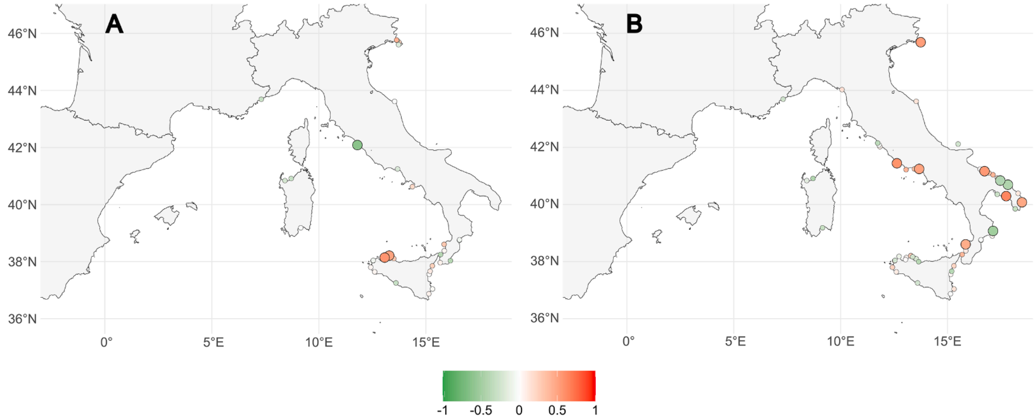

Fig. 6. Temporal trends in the duration of blooms based on the number of consecutive positive days of *Ostreopsis* cf. *ovata* for epiphytic (A) and planktonic (B) abundances. The red and green dots indicate the stations where positive (prolonged) and negative (shortened) trends (tau) were recorded, respectively. Large dots indicate statistically significant trends.

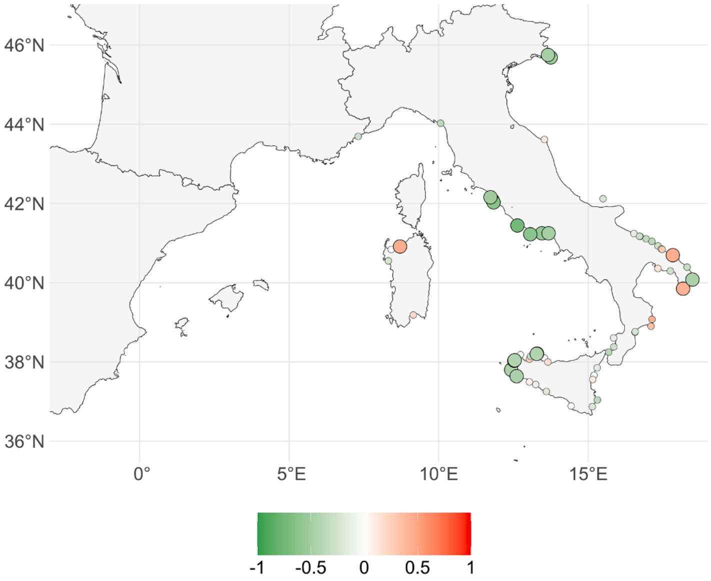

Fig. 7. Temporal trends in the timing of onset blooms of *Ostreopsis* cf. *ovata* based on the number of days from the reference date for planktonic abundances. The red and green dots indicate the stations where positive (delayed onset) and negative (early onset) trends (tau) were recorded, respectively. Large dots indicate statistically significant trends.

temperature, several other biotic and abiotic factors influence the *Ostreopsis* proliferations, such as hydrodynamics, water depth, concentrations of both inorganic and organic nutrients, substrate availability and type, habitat complexity, and allelochemical interactions (Accoroni et al., 2017a,Boisnoir et al., 2018; Cohu et al., 2013; Glibert et al., 2012; Larsson et al., 2019; Parsons and Preskitt, 2007; Pavaux et al., 2020; Pichierri et al., 2017; Richlen & Lobel, 2011; Skinner et al., 2013; Ternon et al., 2020; Yong et al., 2018). Indeed, in the northern Adriatic Sea, a strongly phosphorus-limited environment (Accoroni et al., 2017b), blooms of *Ostreopsis* have historically been delayed due to the low availability of phosphorus in the water. Since the onset of blooms depends on a combination of optimal conditions, i.e. calm sea, temperatures above 25 °C, and optimal nutrient availability (N:P ratios close to the Redfield ratio), and because this last condition is not always found in summer, no direct correlation with temperature has ever been detected (Accoroni et al., 2015).

In other areas where nutrients are not a limiting factor, the increase in seawater temperature could more directly affect the bloom dynamics of *Ostreopsis*. In fact, Fabri-Ruiz et al. (2024), in a study focusing on prediction of *O.* cf. *ovata* dynamics, observed that temperature is the best predictor of blooms. Similar conclusion was achieved by Asnaghi et al. (2017), where sea surface temperature was found to be the strongest predictor, following the “day of the year” (timing linked to seasonality). The study of Fabri-Ruiz et al (2024) suggested that *Ostreopsis* cf. *ovata* abundances is expected to increase along the Mediterranean coasts of France, Spain, and the Adriatic Sea, while a decrease is expected in the Tyrrhenian Sea. Moreover, the bloom period may be extended, starting earlier and persisting later in the year. Indeed, as already suggested by some authors (Drouet et al., 2022; Fricke et al., 2018), rising temperatures in spring appear to promote an earlier seasonal onset and peak reaching in a few locations (only < 25 % of the monitored stations), as optimal temperatures are reached sooner. Temperatures close to 25 °C, together with relative calm sea conditions and optimal nutrient availability, are known to be ideal for the onset of *Ostreopsis* blooms (Accoroni et al., 2015), as they are fundamental for cyst germination and therefore for bloom initiation, and consequently for the attainment of peak abundance. However, the annual abundance maxima did not show a clear trend, which suggests they stabilized over time. In a few locations (just under 14 % of the stations considered) even a decreasing trend in abundance was observed.

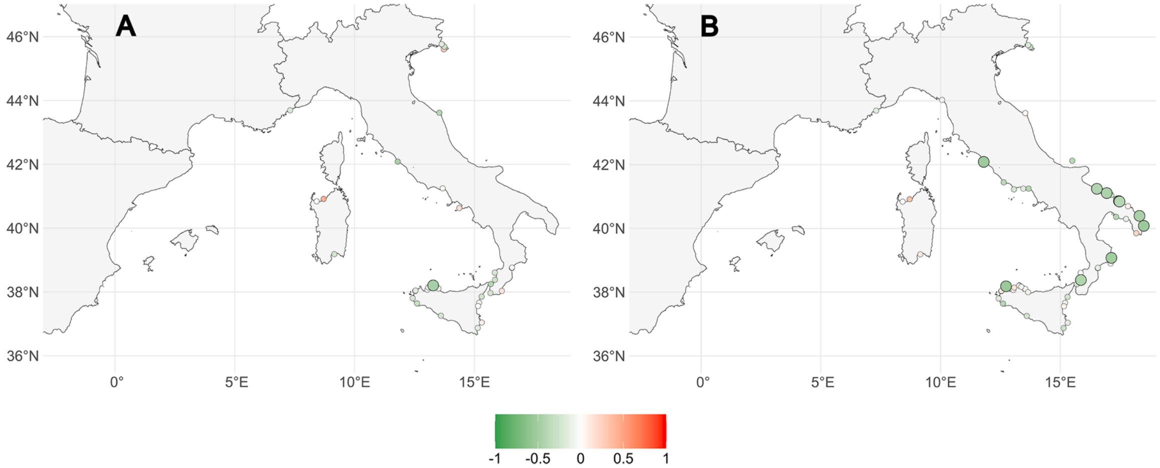

Fig. 8. Temporal trends in the timing of the peak of blooms of *Ostreopsis* cf. *ovata* based on the number of days from the reference date to the annual maximum abundance for epiphytic (A) and planktonic (B) abundances. The red and green dots indicate the stations where positive (delayed peak) and negative (early peak) trends (tau) were recorded, respectively. Large dots indicate statistically significant trends.

This general stabilization of abundances following an abrupt initial increase has been interpreted by some authors as a suggestion that *Ostreopsis* cf. *ovata* may be an alien species in the Mediterranean Sea (Accoroni et al., 2024b; Zingone et al., 2021). Simberloff & Gibbons (2004) observed that an invasive alien species often shows a phase of sudden increase in the new area followed by a decline, probably due to biotic interactions (i.e. competition and/or grazing among others) with other species, or by unidentified factors. However, the origin of *Ostreopsis* cf. *ovata* in the Mediterranean Sea is still unresolved. Even phylogenetic studies did not resolve this issues, as identical *O.* cf. *ovata* strains found in the Atlantic (Brazil) and Mediterranean Sea were also recorded in Malaysia and Japan (Gu et al., 2022; Ngoc et al., 2021; Sato et al., 2011), suggesting that Western Pacific *O.* cf. *ovata* might have migrated into Mediterranean and/or Atlantic oceans, or vice versa (Sato et al., 2011), or that the same strain has been subjected to multiple introductions. In this regard, Fraga et al. (2012) suggested that, although increasing awareness is evident, it is possible that the enhancement of the *Ostreopsis* bloom and biogeographic spread phenomenon observed in the first years from its first records could have been caused by a phase shift in benthic microalgae communities due to anthropogenic or natural environmental change. They hypothesized that the mass mortalities of benthic invertebrates recorded because of the exceptional 2003 heatwave (Garrabou et al., 2009) could have had potential cascade effects in the ecosystems. In the case of *Ostreopsis,* heatwaves could have negatively affected potential predators of *Ostreopsis* leading to an increase in its populations. Another hypothesis is linked to the well-known regime shifts in macroalgal-dominated ecosystems, resulting in the loss of high-complexity large brown marine forests and their replacement by turfs (Filbee-Dexter & Wernberg., 2018: Pessarrodona et al., 2021). In the Mediterranean Sea, an extremely important loss of loss of *Cystoseira sensu lato* forests has been observed in recent decades, together with the consequent increase of turf-dominated ecosystems s (e.g., Monserrat et al., 2022, 2024; Rindi et al., 2024; Verdura et al., 2023 and references therein). As *Ostreopsis* species develop preferentially in such low-complexity macroalgal communities, typical of post-regime shift scenarios such as in urban and degraded areas (Monserrat et al., 2022), this wide-scale phenomenon could have facilitated the increase and stabilization of *Ostreopsis* blooms. The intrinsic reasons of this facilitative process remain poorly understood, but they could be linked both to direct chemical interactions between *Ostreopsis* and the substrate macroalgal species and to other ecological processes, such as grazing, competition and parasitism, and anthropogenic forcings.

The increasing water temperature could have played two opposite roles on the *Ostreopsis* phenomenon in Mediterranean Sea: an indirect facilitation role in years 2000s when blooms became evident, and a disadvantageous role (given the too high values) two decades later. The possibility that high water temperatures may become disadvantageous is subtly suggested both by the Gaussian-like behavior of the correlation between *Ostreopsis* abundance and water temperature, and by the decreasing trend observed in a few locations within a continuously warming Mediterranean Sea, a pattern already documented by Drouet et al. (2022, 2024) along the Monaco-French coast for temperatures exceeding 26°C. Moreover, those apparently contradictory trends in different areas may also be explained by differences in environmental requirements and genetic traits among *Ostreopsis* strains: laboratory studies on Mediterranean strains have shown that optimal growth temperatures are strain-specific, ranging from 20 to 30°C depending on the clone (Carnicer et al., 2016; Gémin et al., 2021; Granéli et al., 2011; Pezzolesi et al., 2012; Scalco et al., 2012).

In this study, a significantly positive correlation between planktonic and benthic *Ostreopsis* cells was confirmed, in agreement with previous findings in the literature (e.g. Accoroni et al., 2015; Chiantore et al, 2024; Jauzein et al., 2018; Mangialajo et al., 2011). This could suggest that, for monitoring purposes and risk management, it might be sufficient to focus on the more easily collected planktonic abundances. However, the *Ostreopsis* phenomenon is highly complex, as planktonic cells are strongly connected to benthic ones. This is due both to hydrodynamic conditions (hydrodynamic events can either increase planktonic cell abundance by resuspension or decrease them by dilution if a hydrodynamic event is very strong, Accoroni et al., 2015), and to the natural daily vertical migration of the *Ostreopsis* cells (Cohu et al., 2013; Pavaux et al., 2021). For this reason, integrated sampling strategies such as the Benthic Dinoflagellates Integrator (BEDI) (Chiantore et al., 2024; Mangialajo et al., 2017) should be recommended (where possible, i.e. relative calm and shallow waters), as it collects both epiphytic and planktonic cells (thereby providing an estimate of the number of cells potentially available in the water column due to detachment or resuspension) with a non-destructive sampling method that does not potentially affect macroalgal communities in the long term in regular monitoring sites.

5. Conclusions

The conclusions of this study are inevitably constrained by the heterogeneous sampling efforts across regions and by the absence, within the time series, of key explanatory variables such as nutrient concentrations, salinity, light availability, and hydrodynamic metrics. Nevertheless, the extensive dataset collected over the years highlights the nonuniform nature of *Ostreopsis* dynamics at the Mediterranean scale, revealing complex local patterns and specificities. While the phenomenon appears largely stabilized at most stations, continuous monitoring remains essential to detect potential hotspots that still exhibit evolving trends.

This underscores the importance of international collaboration in studies of this kind, not only to share data and insights but also to develop and adopt standardized protocols—regarding sampling depth, substrate type, measurement units, and minimum sampling frequency—to enhance comparability across stations and countries.

CRediT authorship contribution statement

Stefano Accoroni: Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Giorgia Montali:** Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Francesca Neri:** Software, Investigation, Data curation. **Patrizia Borrello:** Writing – review & editing, Investigation, Data curation. **Emanuela Spada:** Writing – review & editing, Investigation, Data curation. **Elisa Berdalet:** Writing – review & editing, Resources, Investigation, Data curation. **Magda Vila:** Writing – review & editing, Investigation, Data curation. **Rodolphe Lemée:** Writing – review & editing, Investigation, Data curation. **Julie Davenet:** Writing – review & editing, Investigation, Data curation. **Marie-Yasmine Dechraoui Bottein:** Writing – review & editing, Investigation, Data curation. **Luisa Mangialajo:** Writing – review & editing, Investigation, Data curation. **Mariachiara Chiantore:** Writing – review & editing, Investigation, Data curation. **Valentina Asnaghi:** Writing – review & editing, Investigation, Data curation. **Clara Fricano:** Writing – review & editing, Resources. **Florent Champion:** Writing – review & editing, Resources. **Cecilia Totti:** Writing – review & editing, Validation, Supervision, Resources.

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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.hal.2026.103107.

Data availability

Data will be made available on request.

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