

Article

Towards the Prediction of Favourable Conditions for the Harmful Algal Bloom Onset of *Ostreopsis ovata* in the Ligurian Sea Based on Satellite and Model Data

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Abstract: In recent years, the occurrence of *Ostreopsis ovata* (*O. ovata*) Harmful Algal Blooms (HAB) has increased in the coasts of the Ligurian Sea, causing problems to the marine environment and human health. Favourable conditions for *O. ovata* bloom are triggered by many drivers, many of which are still under investigation, but we hypothesize that this phenomenon can be simulated using a reduced number of major meteo-marine factors, namely water temperature and remixing. Satellite and model data obtained and derived from Copernicus service, namely Sea Surface Temperature (SST) and Significant Wave Height (SWH), were therefore investigated as possible proxies of these local factors. A simplified conceptual model, built on such proxies, was developed and applied to yield a synthetic indicator informative on *O. ovata* abundance. The model was tested in two study areas in the Ligurian Sea, Marina di Pisa and Marina di Massa in Tuscany, Italy. The results obtained show that the synthetic indicator is able to account for about 35% of the temporal variability of *O. ovata* bloom occurrence in the two study areas.

Keywords: harmful algal bloom; *Ostreopsis ovata*; Ligurian Sea; satellite; model; sea state conditions; sea surface temperature; significant wave height



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1. Introduction

Ostreopsis is a potentially toxic dinoflagellate which is predominantly benthic [1–3] *Ostreopsis ovata* (*O. ovata*), in particular, is the dominant species in the Mediterranean [4,5]. This algae grows in semi-closed coastal areas; it is preferentially epiphytic on macroalgae [6], and on different substrata [7] where it forms a mucilaginous film [8]. *O. ovata* occurrence in water column is caused by detachment from the substrate and resuspension caused by wave-induced turbulence and/or by exceedingly high abundances [9].

O. ovata was originally widespread in tropical and subtropical areas, but in recent decades it has also been found in temperate zones and in the Mediterranean Sea [10] The cause of the recent increase of bloom occurrence in these areas is actually subject to multiple interpretations, in some cases controversial, invoking climate change and pollution [11,12]. According to the Intergovernmental Panel on Climate Change [13] since the early 1980s, the occurrence of Harmful Algal Blooms (HAB) has increased in coastal areas in response to warming, deoxygenation and eutrophication, depending on species-specific responses to the interactive effects of climate change and other human drivers. In Mediterranean

areas, *O. ovata* blooms occur from spring to autumn, with a certain inter-annual variability. Abundance peaks in the Ligurian Sea are mostly recorded in mid-summer (end of July) [14].

The recent worldwide spread of *O. ovata* harmful algal blooms is causing problems for the marine environment and human health—epidemiological and clinical features of respiratory syndrome [15]—in many seaside resorts. In Italy, the first cases of these harmful effects on humans were observed along the northern coast of Tuscany in 1998 [16]. Exposure to the toxins produced by *O. ovata* can cause bio-intoxication in humans, non-lethal in itself [17], and also suffering or mortality in marine benthic communities [18]. *O. ovata* can be harmful, threatening coastal food web and fisheries [19]. Understanding the environmental conditions that can trigger the bloom can therefore be important not only as an aid to protect marine biodiversity, but also to support the tourism sector. Therefore, after selecting the main environmental and ecological bloom triggering conditions, satellite and model data could be used in sight of detecting and predicting this phenomenon.

The most widely used techniques for algal bloom detection are based on standard data from ocean colour satellites and concern extensive algal blooms, covering sea area large enough to be directly observed by space instruments [20–22]. These techniques are therefore inapplicable to the direct monitoring of *O. ovata* blooms, which usually occur in small areas close to the coastline. An alternative method is provided by products obtained through remote sensing technology and modelling, which are used as proxies of phenomena occurring at a small scale and very close to the coast [23]. The efficiency of this method obviously depends on the selection of satellite or numerical model products informative about the environmental factors most relevant for algal bloom occurrence, that must therefore be known from previous investigations.

Understanding the role of coastal sea drivers in biological phenomena is, however, complicated, because of the complexity of the relationships between the physical, biogeochemical, and biological parameters. The environmental and ecological drivers involved in *O. ovata* growth and bloom dynamics are modulated by complex interactions among biotic (intra- and inter-specific relationships) and abiotic (meteo-marine) drivers, and the chain of factors triggering the bloom is still object of research [24]. In the case of *O. ovata* bloom dynamics, many studies show that the role of environmental drivers is complex and, in some cases, contradictory, with notable differences at basin scales [25].

The relevance of these drivers has been investigated in several studies, which have also provided the basis for the development of specific models e.g. [26]. For example, a conceptual model of annual *O. ovata* bloom was developed by Accoroni et al. [27], who highlighted the synergistic effect between local hydrodynamic conditions, temperature, and nutrients availability as N and P (sampled in situ), suggesting that favourable conditions for bloom onset are when calm sea conditions occur in the days immediately preceding the bloom, after reaching a water temperature threshold necessary for excystment, and when N:P ratio is around Redfield. Some authors [28–30] have elaborated explanatory models performing multiple correlations of bloom dynamics with coastal ocean variables, highlighting the importance of temperature.

The current research was built on these studies but focused on a different objective. Although *O. ovata* bloom is a complex phenomenon driven by many factors, our working hypothesis was that specific, major meteo-marine datasets obtainable by satellite and model techniques are able to explain a significant part of the temporal phenomenon variability. In particular, the possibility of monitoring *O. ovata* HAB triggering conditions via products distributed by Copernicus, the European Union's Earth observation programme [31], could help us better and sustainably manage the environment hosting this species.

In accordance with these premises, the current study is aimed at developing and testing a simplified model to predict *O. ovata* bloom dynamics on the basis of operational Copernicus Marine Service products. This objective was pursued relying on both the findings of previous investigations about this subject and the results of statistical analyses conducted over readily available observations.

The study therefore started with a short review of the most important factors involved in *O. ovata* bloom triggering conditions, in order to select the most suitable.

The results of this bibliographic analysis were then experimentally assessed using observations taken in two study areas along the Tuscany coast (Central Italy) over an eight-year period (2012–2019). This allowed the development of a simplified conceptual model for the prediction of *O. ovata* bloom triggering conditions based on the Copernicus products, which was tested against the same observations.

2. Literature Review on the Main Drivers of *O. ovata* Bloom

In this section, we first analyse the major meteo marine factors involved in *O. ovata* bloom triggering conditions, namely identified in surface temperature and sea state parameters (i.e., waves). Further potential drivers have also been investigated, mainly acting at local scale or at a resolution not addressable by remote coastal observations, and difficult to model in coastal areas: for these reasons, they will not be part of the simplified conceptual model proposed as a reference in this paper for the onset of *O. ovata* bloom.

2.1. Temperature

Temperature is one of the main drivers in *O. ovata* bloom onset, as it affects cyst germination at the beginning of the season [32]. Accoroni et al. [33] hypothesize, from in vitro observations, that a temperature threshold around 25 °C for resting cyst excystment needs to be reached for at least 5 days at the beginning of the season after a 5-month dormancy period. The seasonality of *O. ovata* blooms shows peaks in early summer [34,35] and appears to be related to benthic cysts, as they provide seed stocks for blooms [36,37]. Bloom can persist until temperature values are much lower than that threshold, apparently because once *O. ovata* cysts are germinated, this vegetative form seems to actively proliferate even if temperature values decrease; for the same reason, bloom can also occur after the temperature maximum [38]. Hydroclimatic conditions, and especially spring temperature anomalies, may have an important impact on the period of bloom appearance [39].

Of equal importance, *O. ovata* bloom events occur within an optimal temperature range [40]. In fact, there is a correlation between maximum cell concentrations and water temperature, as is also reported by [41]. Optimal growth temperature ranges are different at the basin level for the Mediterranean Sea, as well as sea temperature allowing bloom occurrence. Specifically, in the north-western Mediterranean Sea, bloom generally occurs when seawater temperature exceeds 24–26 °C [42]. The positive role of water temperature in enhancing the magnitude of the bloom most probably consists of the direct effect on epiphytic cell proliferation; a large source cell stock on benthos is positively correlated with the bloom magnitude in water column [43]. The relationship between *O. ovata* proliferation and temperature is not the same in all geographic areas [44].

In summary, temperature is crucial either at the beginning of the season, in reaching a threshold necessary for excystment, and as an optimal temperature range enhances the bloom magnitude.

2.2. Hydrodynamic Conditions

As previously reported, hydrodynamics is considered a major factor affecting the *O. ovata* abundance in many studies. Low energetic sea conditions, occasionally interrupted by the occurrence of short time events of water remixing, characterizes the environment in which *O. ovata* thrives and blooms: shallow waters in semi-closed areas, such as enclosed gulfs and artificial reefs for coastal erosion containment [45,46]. The removal of the artificial breakwater reefs from an *O. ovata* bloom hot-spot area in Conero Riviera, in fact, led to a marked decrease of *O. ovata* abundances in the following years [47].

Benthic *O. ovata* cells are only lightly attached to the substrata, and can then be easily removed and resuspended in the water column under the effect of wave-induced turbulence; significantly higher abundances (on epiphytic cells) are observed in the sheltered sites compared with the exposed ones [48]. Therefore it is important to underline that

hydrodynamics may as well have an important effect on the temporal variability of bloom occurrence, because stormy events can result in a sudden decrease of cell abundances on the benthic substrata, after which high density of cells is re-established following a few days of calm sea conditions [49].

In particular, some authors [50] observed that in order to have a bloom in water column, an effective short time event of cell resuspension by wave action, followed by a period of calm sea conditions, is needed. The effect of water motion on cell resuspension is stronger on a benthic mat formed by a large number of cells, produced during the intense growth period [27]. A marked effect of hydrodynamic conditions is in fact generally observed in those areas where high abundances are reached, as observed by Richlen and Lobel [51], who also observed a positive correlation of *O. ovata* abundances with water motion. The mechanisms causing cell detachment from the benthic substrate need to be fully understood.

In summary, in areas suitable for *O. ovata* growth, characterized by low water energy and weak water exchange, conditions favouring bloom occurrence are short term episodes of water mixing with resuspension of cells and sediments [52] throughout the surf zone, in most cases driven by wave action, followed by calm sea conditions.

2.3. Other Potential Drivers

As previously noted, *O. ovata* bloom is a complex phenomenon, involving different factors in addition to water temperature and hydrodynamics: the most important ones are briefly reviewed hereinafter.

As for response to nutrients, controversial results are found in literature. Worldwide *O. ovata* appears to proliferate both in eutrophic and oligotrophic areas, and key role seems to be played by the N:P [53].

As *O. ovata* is a benthic species, it is affected by the action of other benthic organisms, and by trophic relations among species, such as allelopathy; Ternon et al. [54] highlighted the allelopathic effect of both benthic and planktonic diatoms on *O. ovata* growth.

Besides that, other drivers could have important roles, such as organic nutrients, substrate characteristics, competitive and trophic interactions, or regulation of dinoflagellates by parasites [55,56].

Regarding the effect of salinity for the bloom development, several authors have suggested that benthic dinoflagellates proliferation is favoured by low salinity waters, while others reported higher values in the north-western Mediterranean Sea, [57,58].

None of these factors are included in the simplified conceptual model proposed here, since, as mentioned previously, standard operational data are not available at the time and spatial scales needed; moreover, the role of some of these factors in bloom onset still needs to be fully investigated.

Consequently, attention was focused on the two major drivers identified, i.e., sea water temperature and hydrodynamic conditions, the importance of which was analysed using observations taken in two study areas.

3. Materials and Methods

3.1. Study Areas and Periods

The study areas are located on the coast of Tuscany, Italy, facing the Ligurian sea (Figure 1a, red squares). The Marina di Pisa study area is located south the Arno river mouth, and belongs to the municipality and province of Pisa (PI) (Figure 1b), and Marina di Massa in the central part of the Apuan coast, east of the port of Marina di Carrara, and belongs to the municipality of Massa (MS), in the province of Massa-Carrara (Figure 1c). Three *O. ovata* ARPAT (Agenzia regionale per la protezione ambientale della Toscana, Tuscan Environmental Protection Agency) sampling sites are found in Marina di Pisa, and four in Marina di Massa [59]. Both areas are subject to recurrent *O. ovata* bloom and are characterized by the geomorphological characteristics suitable for *O. ovata* growth described in Section 2.2. In fact, both study areas are strongly affected by coastal erosion [60], so that

costal defences were built to mitigate that pressure. As a side effect, these structures have created a compartmentation in water mirrors, with a consequent weak water exchange, suitable for algal bloom development. ARPAT samples *O. ovata* during growth and bloom season, from June to September, and data are published by ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale). We selected the years 2012–2019, as in this period the same number of *O. ovata* samplings per year at the same sampling frequency for every monitoring station was available.

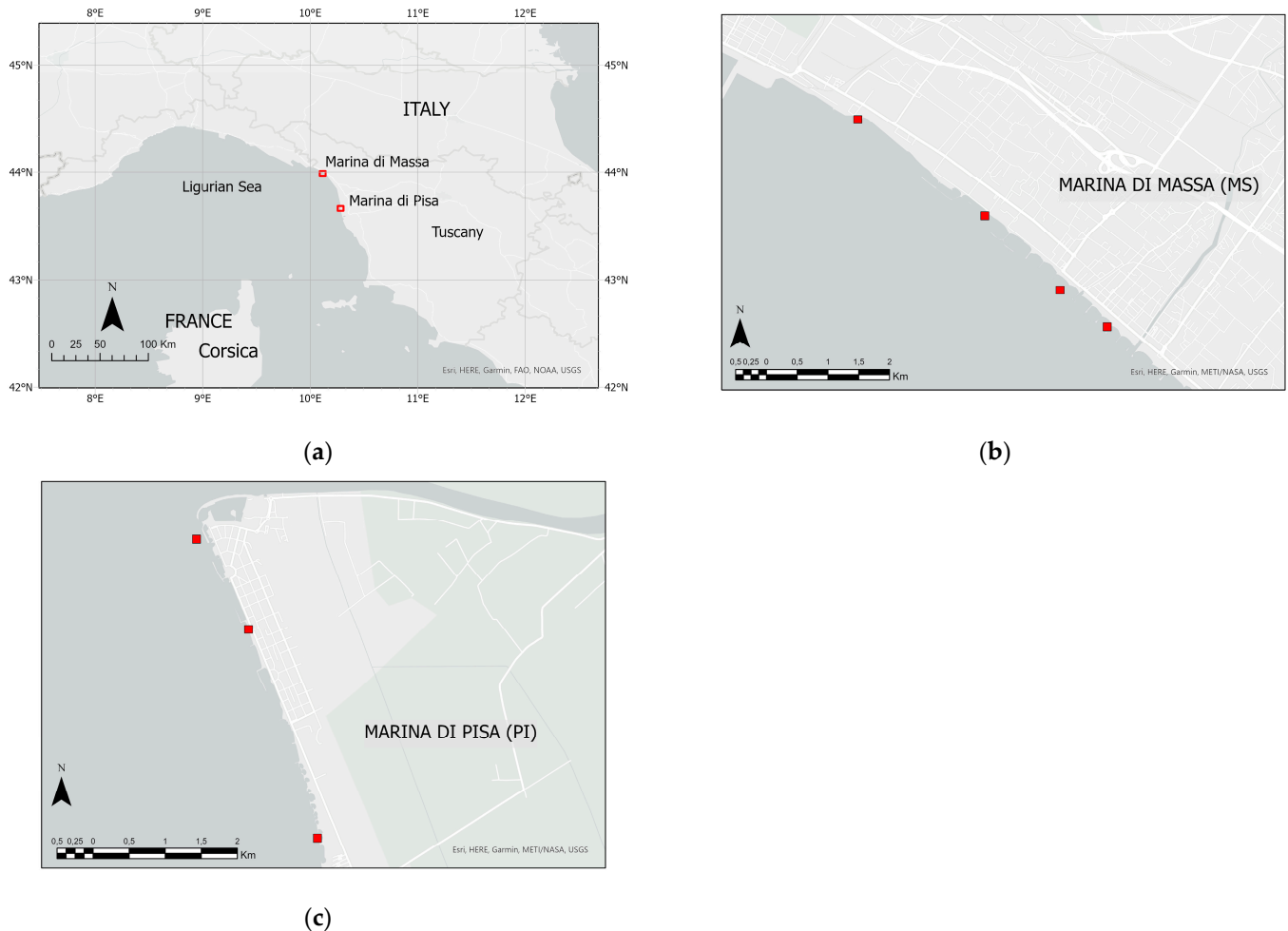


Figure 1. Study areas (a) Marina di Pisa, (b) and Marina di Massa, (c). Sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

3.2. *O. ovata* Measurements

O. ovata cell concentration data in water column as number of cells per litre are here obtained from ARPAT, as they are measured within the national coastal marine monitoring program [61]. Water samples are collected within the first meter of submerged area, in proximity of the substratum [62]. Sampling of water and analyses are performed monthly in June and September, every 10–15 days in July and August, and intensified in case of bloom; eight samples plus the possible additional ones per year are taken for each monitoring station. Data of the period 2012–2019 were selected for this work, in the areas of Marina di Pisa (3 sampling stations) and Marina di Massa (4 sampling stations). For the statistics, we evaluated the accumulated cell/L number and average surface temperature of the stations belonging to each sampling area (Marina di Pisa and Marina di Massa), so that 131 observations of cell/L could be used (67 in Marina di Pisa and 64 in Marina di Massa sampling sites).

Although ecologically the evaluation of abundance of cells on the substrate is more significant, as they provide seed stock for bloom, in this study we considered cell abundances in water column, as blooms of cells that are in the water column are the ones more directly affecting humans by contact or inhalation. Local agencies in fact monitor samples in water column, according to the Ministry of Health guidelines [63]. Moreover, Mangialajo et al. [64] observed a relatively good correlation between epiphytic and planktonic cell abundances. Bloom in water column was defined as number of cells per litre above the threshold of 10,000 according to Italian law [65], indicating the limit to shift from the alert to the emergency phase. These guidelines were recently updated, differentiating thresholds according to environmental conditions [66].

3.3. Satellite and Model Data

The possibility of using a daily continuous dataset of satellite Sea Surface Temperature (SST) is essential, as in situ monitoring data available in this study are only taken on the same *O. ovata* sampling day. Satellite SST refers to a skin temperature, from approximately 10 μm to 1mm below the surface depths, depending on the observation frequency band (e.g., infrared or microwave). Thus, generally speaking, this may not be straightforwardly taken as representative of sub-surface temperature or deeper in the water column ('bulk' temperature). Nevertheless, many studies have shown that under certain meteo-marine conditions (for low sun radiative forcing or when mechanical mixing processes are active), SST values may be representative of water temperatures to depths up to a few meters in the open ocean [67]. In shallow coastal waters where benthic habitats live, additional factors can affect the correspondence between SST and the temperatures experienced by subtidal organisms: however, many studies e.g. [68] apply SST as proxy for temperatures influencing benthic organisms in subtidal habitats. SST data selected for this study are supercollated merged multisensor SST remapped over the Mediterranean Sea at 1/100-degree spatial resolution, daily mean L3S (SST_MED_SST_L3S_NRT_OBSERVATIONS_010_012) [69]. Data are distributed by the Copernicus Marine Service (CMEMS), a European Union service which provides data about the physical and biogeochemical ocean. These SST products are based on the night-time images collected by the infrared sensors mounted on different satellite platforms: ATSR ENVISAT, MODIS (on both Aqua and Terra satellites), AVHRR, on METOP satellite), and NOAA satellites, SEVIRI, installed on MSG.

Similarly, the definition of the hydrodynamic conditions in the days before *O. ovata* sampling requires a daily continuous dataset. Some authors have already used Significant Wave Height (SWH) as a proxy for mechanical energy entering the system for studying plankton dynamics e.g. [70]. SWH is a reference parameter in oceanography; it is a function of the energy associated to any sea state defined as the integral of wave spectrum in the direction/frequency domain. In this work SWH was chosen to define the sea state threshold which brings the energy needed for water remixing, proper for creating the conditions favouring *O. ovata* bloom onset. As for SWH hourly data, the dataset was produced by a numerical model chain based on the fifth-generation atmospheric reanalysis ERA5 dataset, produced by ECMWF and distributed through C3S service (Copernicus Climate Change). The wind forcing for the wave model was based on a dynamical downscaling of the ERA5 reanalysis, obtained through a nested domain configuration based on the BOLAM/MOLOCH atmospheric limited-area models [71]. Wave data were extracted by a wave hindcast, realized using the WaveWatch III model (hereafter WW3) run with an unstructured grid and with a variable resolution up to 500 m in our coastal areas. Wave data were validated on eleven offshore buoys (Alghero, Alistro, Cap Corse, Capo Mele, Civitavecchia, Giannutri, Gorgona, La Revellata, La Spezia, Livorno offshore, Monaco) and three coastal buoys (Castiglione, Gombo and Bastia).

The hindcast data are expanded to cover 40 years in order to provide a dataset for different scopes such as climatological studies and extreme value analysis. They are focused on the wind and wave climates of the Ligurian and Tyrrhenian seas (north-western

Mediterranean Sea). In these areas, the coastal resolution of 500 m is relevant for the analysis of coastal processes.

In this work, SST was extracted from the valid pixel closest to location where *O. ovata* was sampled according to the closest pixel method of Clay et al. [72]; significant wave height (SWH) was extracted from the grid point closest to the same location, similarly to the method of [73].

3.4. Data Analysis

The data analysis consisted of two main steps. Firstly, the environmental conditions that can affect *O. ovata* bloom dynamics in the two study areas were characterized by means of descriptive and statistical methods, focusing on the impact of SST and SWH. It is to be noted that *O. ovata* monitoring is based on water sampling within a few meters from the coast, where direct satellite observations are not possible because of issues due to observation contamination from sea bottom and land contributions to the measured radiation. To evaluate if in our study the use of Copernicus SST as a proxy the coastal values was acceptable, we compared in situ temperature values, measured by ARPAT during *O. ovata* sampling, with the closest available Copernicus data, see Section 3.3. To investigate the role of sea state, SWH is here used as a proxy, and more specifically for local hydrodynamics, since in our area waves, more than other factors such as tides, cause coastal water motion. On the basis of previous works already mentioned and local direct observations, we defined hydrodynamic events able to resuspend the *O. ovata* cells (from here on referred to as “wave remixing events”) according to Douglas scale, excluding severe storms, as at least 10 consecutive hours of SWH major or equal 0.7 m, reaching 2 m at least once. The role of hydrodynamic conditions in *O. ovata* bloom onset was assessed comparing the number of wave remixing events and of blooms, the latter computed cumulating blooms occurring in the *O. ovata* sampling stations for each study area and calendar year (months from June to September), from here on indicated as “cumulated bloom number”.

Secondly, based on the results of the bibliographic analysis and of the previous experimental step, a simplified conceptual model was developed and applied to the data of the two areas in order to assess its capability to explain the cell/L variations referring to bloom events.

The results of the statistical analyses performed are described in the following section. In all cases, the significance level of the correlations found was determined through a standard Student’s t-test.

4. Results

4.1. Environmental Framework and Bloom Occurrence

The climatological wave conditions of the two study areas for the target period are summarised in Figure 2. The model is able to take into account major coastal processes (mainly, refraction), but is still representative of offshore wave conditions (around 500 m from the coastline). Wave conditions in the surf zone and coastal hydrodynamic processes (waves, wave-induced currents and bottom stress) depend on many additional factors such as coastline morphology and human-made structures.

Directional roses of both study areas (Figure 2) from WW3 model show, between 2012 and 2019 (June to September), prevailing wave directions from W to SW (270° to 210°), associated with ‘libeccio’ wind conditions; within these, motions from W-SW (Massa) and S-SW (Pisa) include the highest frequency of high waves (> 1.5 m).

Marina di Pisa and Marina di Massa are 40 km distant from each other with a similar coastline orientation, so, climatologically speaking (especially if considering only temperature and waves), they are close. In spite of that, the blooms occur differently in the two study areas. In Figure 3 the number of blooms for each study area is referred to the sum of *O. ovata* samplings showing a number of cell/L above the threshold in each study year (Figure 3). A slightly negative correlation ($R = -0.35$) is found between the number of blooms in Marina di Pisa and in Marina di Massa. This highlights the complexity of the

bloom occurrence phenomenon, i.e., the fact that most of the bloom interannual variability is due to local factors that cannot be accounted for at the scale we are using in our analysis.

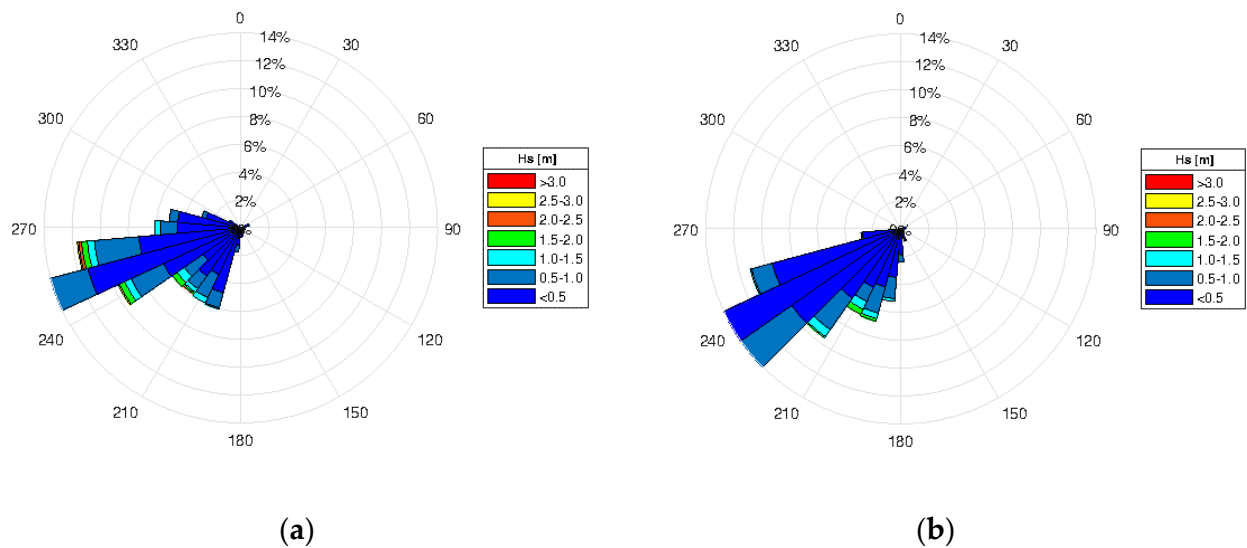


Figure 2. SWH maximum height and peak direction in Marina di Pisa (a) and Marina di Massa (b), period 2012–2019, months from June to September.

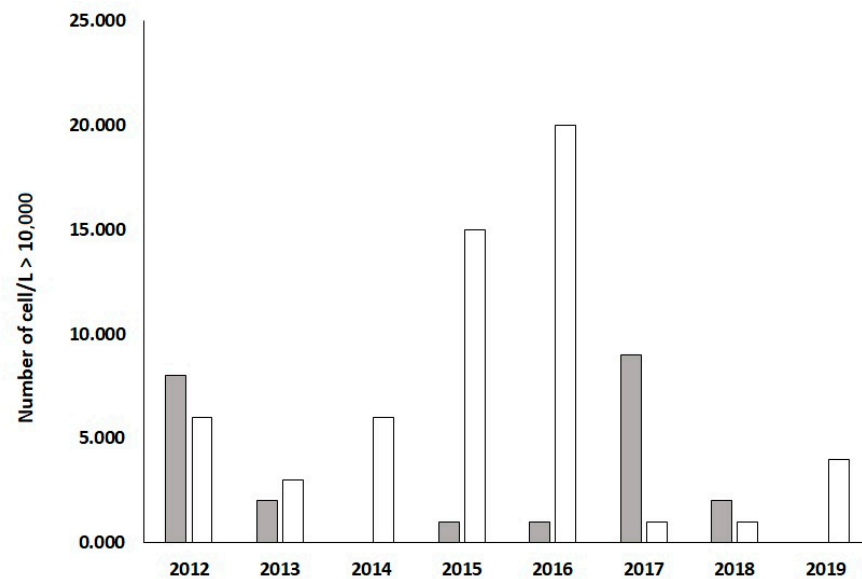


Figure 3. Number of blooms per year. In grey are the averages computed from 3 stations in Marina di Pisa; in white are the averages computed from 4 stations in Marina di Massa. The bars indicate the respective standard deviations.

4.2. Role of Temperature

The correlation between measured and estimated SST shows a significant correlation in both the Marina di Pisa and Marina di Massa sites ($R = 0.71$ in both cases). In addition, in Marina di Pisa, the differences are randomly distributed, with an average value of about $1.5\text{ }^{\circ}\text{C}$; a similar, slightly worse average error is also found in Marina di Massa, but in this case with a systematic tendency to temperature underestimation. However, for our purposes we consider such difference ranges to be largely acceptable, and thus we used CMEMS satellite SST data in the closest pixel to estimate water temperature in *O. ovata* sampling sites.

Marina di Massa shows a higher number of days (413) with an average SST above the threshold (25° , see Section 2.1) compared to Marina di Pisa (349). The SST trend in Marina di Pisa shows a year, 2014, in which the lowest average temperature among all the years was recorded, 23.6°C . Only for 5 consecutive days was SST slightly above the threshold (average: 25.5°C), and this occurred during the first week of August. The average temperature of the period (June to September) in the years 2012–2019 in this study area was 24.6°C . The trend in Marina di Massa SST was more stable, and the average temperature of the period was about 24.6°C (Figure 4).

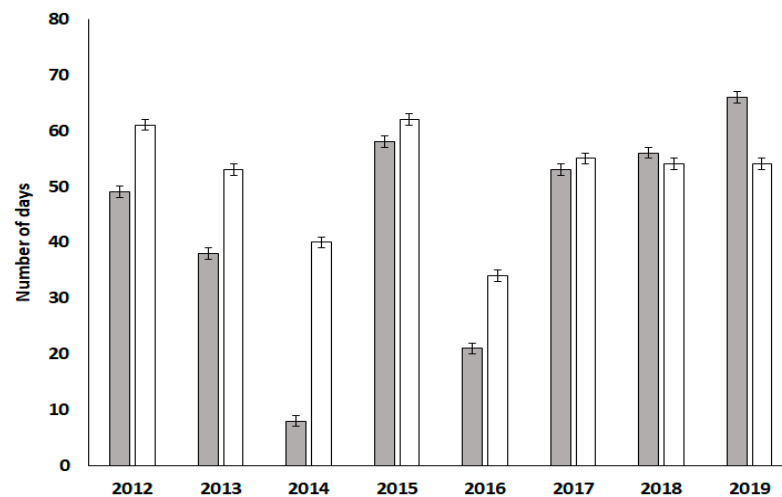


Figure 4. Number of days within the study period, for each year, when SST was above threshold. In grey are the averages computed from 3 stations in Marina di Pisa; in white are the averages computed from 4 stations in Marina di Massa. The bars indicate the respective standard deviations.

Figure 5a,b show the linear regressions of average log accumulated cell/L versus average SST in June, at the beginning of *O. ovata* growth and bloom season for the 8 study years. In both cases, the correlation is highly significant.

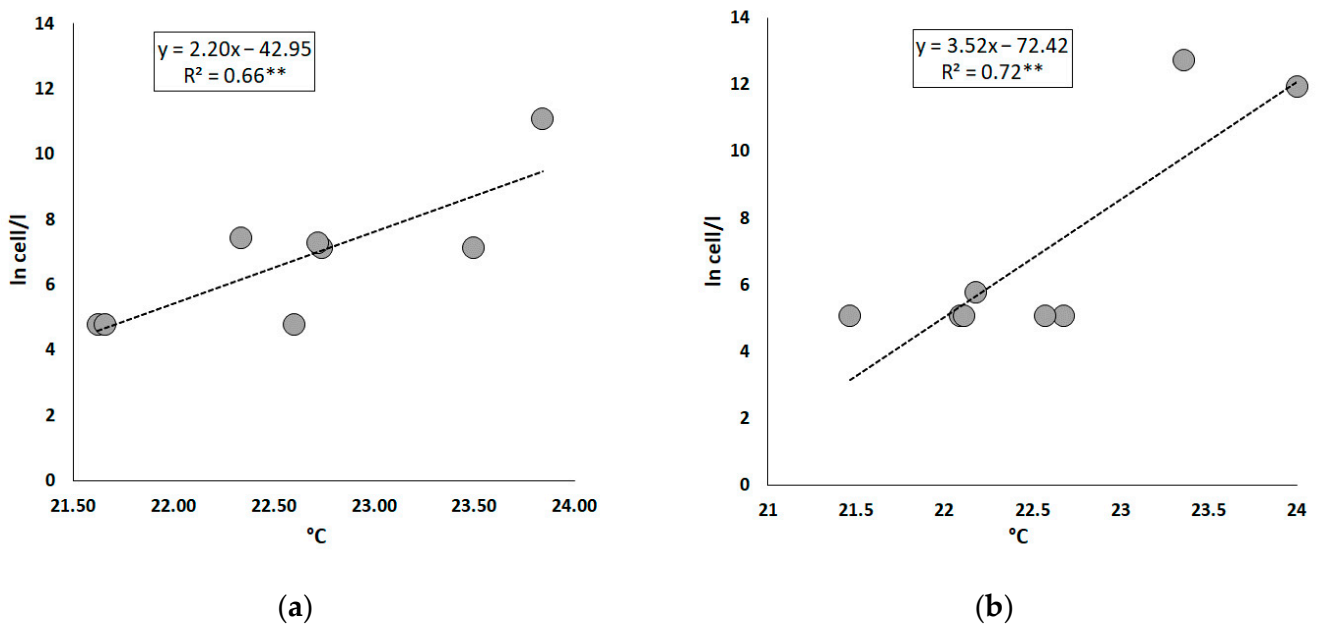


Figure 5. Scatter plot of monthly average temperature in June versus monthly averages of log accumulated cell/L in June, for every year, in Marina di Pisa (a) and Marina di Massa (b) (** = highly significant correlation, $p < 0.01$).

The year 2014 showed the lowest number of days above the temperature threshold in Marina di Pisa (Figure 4).

4.3. Role of Hydrodynamic Conditions

The scatter plot for Marina di Pisa confirms that there is an overall significant statistical correlation between the accumulated bloom number and the wave remixing events number per year (Figure 6a). In Marina di Pisa, the years showing the highest number of blooms are 2012 and 2017 (Figure 3), and they also show the highest periods of number of hours with SWH above the threshold, namely, 50% higher than the average of the whole study period (data not shown). The year 2019 shows no bloom: as temperature conditions were favourable for bloom occurrence, this absence could be explained by a possible lack of water remixing events, in fact the number of hours with SWH above threshold (as defined in Section 3.4) is only the 10% of the average of the whole study period (data not shown).

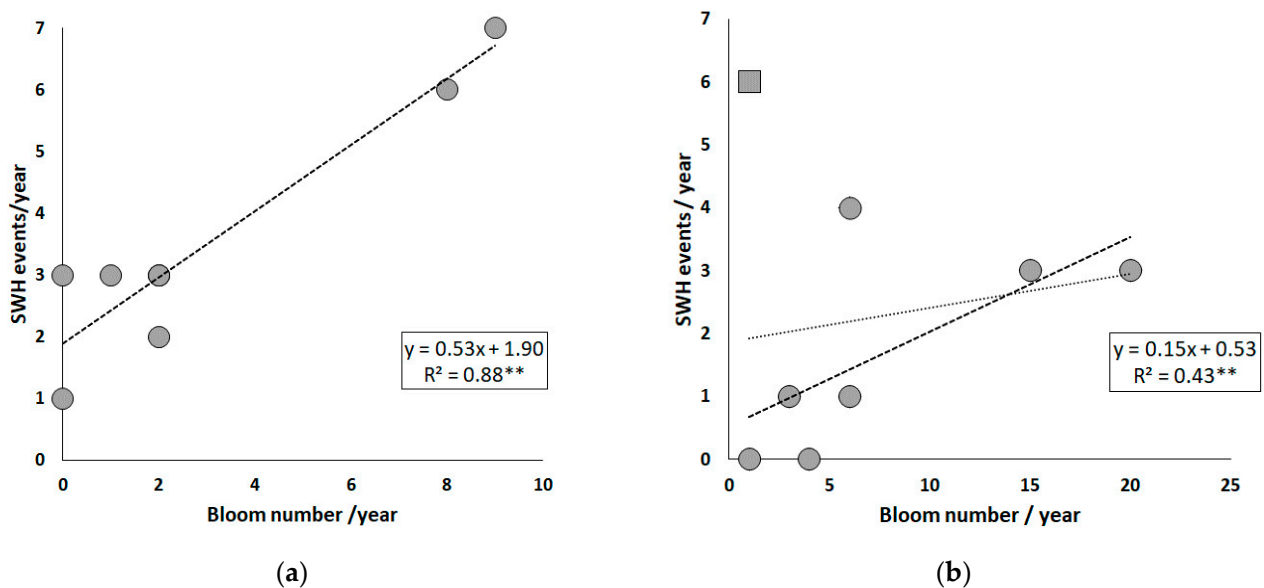


Figure 6. Scatter plots and respective linear regressions of accumulated bloom number versus wave remixing events, per year, in Marina di Pisa (a), and Marina di Massa (b); in (b), the statistics refer to the regression obtained excluding 2017 data (square dot) (** = highly significant correlation, $p < 0.01$); the thin regression line is obtained including 2017 ($R^2 = 0.03$).

This situation is partly different for the second study area, Marina di Massa (Figure 6b). In this case, in fact, the statistical correlation between accumulated bloom number and number of wave remixing events per year is low and not significant (Figure 6b, thin line, $R^2 = 0.03$). On the contrary, the regression obtained excluding 2017 data shows a significant correlation between the two variables (Figure 6b, solid line, $R^2 = 0.43$).

4.4. Simplified Conceptual Model

The current section illustrates a conceptual model of *O. ovata* bloom which is based on the previously reviewed ecological and physiological knowledge of the phenomenon and on the results of the experimental data analysis performed. Such information is used to simulate a significant part of *O. ovata* bloom temporal variability based on the available large-scale drivers obtained from Copernicus products. The possible identification of relationships between *O. ovata* bloom and satellite and model data obtained from Copernicus service could allow to operationally predict the onset of favourable condition for *O. ovata* HAB.

As previously noted, a relevant role of seawater temperature and hydrodynamics in driving the bloom is suggested by several descriptive studies performed in the Ligurian Sea. The model is therefore based on the hypothesis that the bloom temporal variability can be partly described by major meteo-marine drivers correlated with temperature and wave-

induced motion, assumed as the main driver of coastal hydrodynamics in our target areas. We consequently refer to a simplified conceptual model, built on ecological observations and centred around the connected roles of sea temperature and sea state (i.e., wave) in triggering the bloom, as well as in driving bloom development.

The simplified conceptual model developed is schematized in Figure 7. Thresholds were established from the literature above, with some minor adjustments from local direct observations which were defined during the calibration phase (see below).

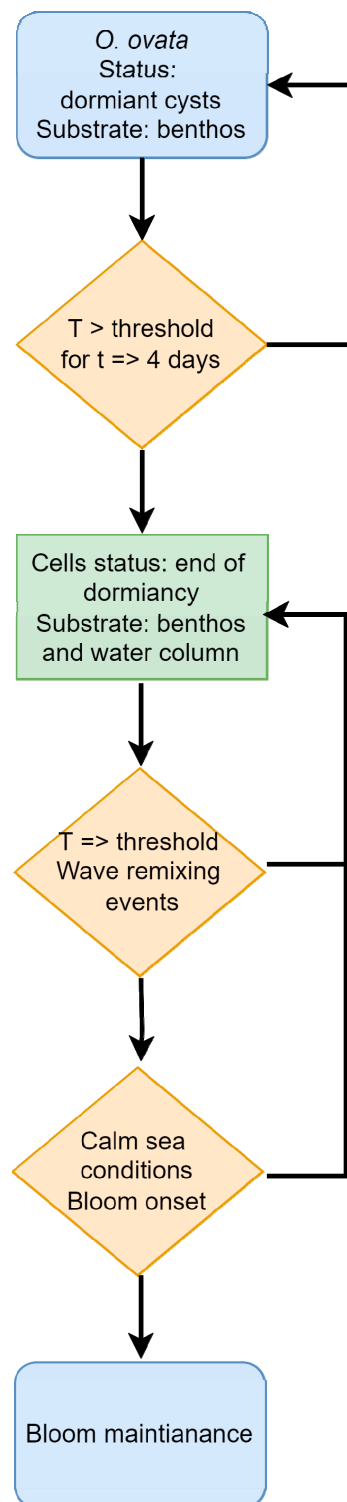


Figure 7. Simplified conceptual model of *O. ovata* bloom onset triggering conditions.

4.5. Identification of *O. ovata* Bloom Triggering Conditions

For the model development, we considered SST and SWH in the two weeks before the *O. ovata* sampling day, and the accumulated number of cell/L for each *O. ovata* sampling site (single day).

The simplified conceptual model therefore yields a synthetic indicator informative on *O. ovata* abundance based on the following evidence: 1. A short period with highly energetic wave-induced hydrodynamics is necessary to promote an *O. ovata* bloom; 2. This period must be followed by some days with relatively calm sea conditions (for us corresponding to SWH below about 0.7 m); 3. The SST during these last days must exceed a threshold (for us corresponding to about 25° C).

The daily maximum wave height averaged over about one week is therefore kept only if followed by a period with relatively calm sea conditions as defined above, and high SST; otherwise, the wave height is set to 0. The selected mean SWH is then regressed versus the logarithm of the cell number in the day following the second period.

The periods and thresholds for SWH and SST were calibrated specifically for Pisa and Marina di Massa based on a trial-and-error strategy. The resulting model parameterization is summarized in Table 1 for the two study areas. The lengths of the periods considered for computing mean SWH and SST are similar in the two cases, and the same is for the SWH and SST thresholds; all these values are close to the reference ones mentioned before. The linear regressions found for the two study areas are shown in Figure 8a,b, respectively; in the latter case, the data of 2017 were excluded, as done previously. Moderate but statistically significant correlations are found in both areas, with *r* around 0.6. The intercepts and slopes of the regressions are slightly different for Marina di Pisa and Marina di Massa.

Table 1. Periods and thresholds for the two study areas obtained by trial error strategy.

Station	Threshold SST (°C)	Days of SST above Threshold	Threshold SWH (m)	Days with SWH under Threshold	Days with SWH above Threshold
Marina di Pisa	24.5	7	0.7	5	7
Marina di Massa	23.5	7	0.77	4	7

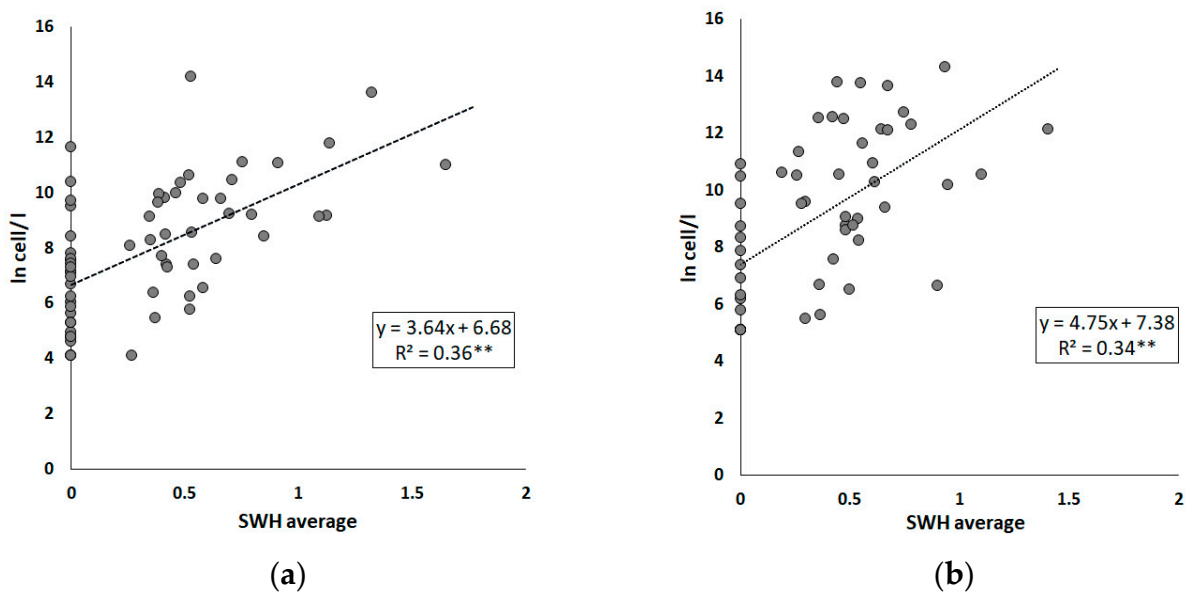


Figure 8. Scatter plots and respective linear regressions of SWH average before sampling day and log of accumulated cell/L in Marina di Pisa (a) and Marina di Massa (b) (** = highly significant correlation, *p* < 0.01).

5. Discussion

The current investigation is based on the results of previous studies which suggested the possibility of predicting a wide part of *O. ovata* bloom occurrence through the use of two main large-scale drivers, SST and SWH patterns, derivable from available satellite and model data. Consequently, our approach differs from purely data-driven statistical methods and cannot account for local factors that affect the timing and intensity of *O. ovata* blooms such as the size of the inoculum present at the beginning of the growth season, intrinsic specific growth under different environmental conditions, loss factors such as grazing, parasite attacks or natural cell death [63]. Conversely, the same approach should reproduce the occurrence of *O. ovata* blooms and, possibly, their temporal variability, using major descriptors of the most effective meteo-marine conditions.

To validate this hypothesis, statistical analyses were first conducted on the relationships between these drivers and *O. ovata* blooms accumulated over relatively long time periods (one to a few months).

Among the meteo-marine conditions, temperature is crucial at the beginning of the *O. ovata* growth and bloom season, as a period of temperature above threshold is needed for the process of excystment, as reported in the previous sections. In the study areas, the beginning of growth occurs in June, when these conditions are particularly variable. In this period, the turn from the weather instability typical of the end of spring to the onset of weather stability characterizing summer takes place. Weather conditions in this period are therefore particularly variable from year to year, in contrast with those of the following, more stable months, when temperature is expected to be stably favourable for *O. ovata* growth and possible bloom. The relevance of June temperature for bloom occurrence is currently demonstrated by Figure 5a,b, which show the linear regressions of average log accumulated cell/L versus average SST in June for the 8 study years. In both cases, the correlation is highly significant. The role of temperature as one of the main drivers is also confirmed by the 2014 Marina di Pisa case: sea state conditions suitable for the bloom occurred, but no bloom was observed. This is probably connected with the fact that, as previously reported, the lowest average temperature among all the years in exam was recorded in this site, 23.6°C. The summer sea temperature threshold of 25°C was reached only for 5 consecutive days, but during the first week of August, probably too late in the season; in fact, the importance of reaching temperature threshold in June for bloom occurrence is shown in Figure 5 and the following comments. Therefore, the fact that no bloom occurred in 2014 in Marina di Pisa may be explained by the temperature almost constantly under threshold, as sea conditions were favourable for bloom occurrence.

A similarly significant correlation was found in the first study area between number of wave remixing events per year and accumulated bloom number in the whole season. This relationship, however, is not able to exhaustively describe the behaviour of *O. ovata*, as it emerges for the second study area. This is mainly due to the bloom occurrence in 2017, which shows a peculiar behaviour with respect to the other years: in spite of favourable conditions both in terms of number of wave remixing events, which is one of the highest in the period (6 events versus an average of 3.5 events in the study period), and temperature (Figure 4), only a single bloom occurred at the beginning of the season (Figure 3).

The relationships found confirm the importance of these major drivers in regulating the bloom, but are of limited utility to predict the phenomenon. Hence, a simplified conceptual model was applied to yield a synthetic indicator based on daily SST and SWH estimates, where the growth of *O. ovata* requires a few days of significant water motion followed by around a week of calm conditions and of temperature above threshold. The indicator had to be calibrated for each site, due to the importance of local factors, and accounted for around 35% of the daily variability in *O. ovata* cell number, with the exclusion of a peculiar year for Marina di Massa (2017). Despite only moderate prediction capability being achieved, this is a promising result, taking into consideration that the model includes only two of the large number of factors involved in the complex *O. ovata* bloom triggering process,

such as organic nutrients, substrate characteristics, competitive and trophic interactions, or regulation of dinoflagellates by parasites.

Marina di Massa 2017 is therefore a case in which local-scale drivers that are not part of the simplified conceptual model seem to have controlled the bloom dynamics. As previously noted, the same local drivers could in any case be determinant in controlling most bloom variability in each specific site. We can only hypothesize about these drivers, as we have no additional data. We know that benthic systems are complex, as they may suffer abrupt alterations due to cascade effects triggered by the action of some organisms and/or environmental changes. Pichierri et al. [74] suggest that, in addition to the abiotic factors causing *O. ovata* blooms, such as hydrodynamics, water temperature and also nutrients, secondary metabolites with allelopathic effects should be considered, to better understand the bloom dynamics. Pfannkuchen et al. [75] suggest that for *O. ovata* minute advantages during the initiation of a mass appearance play a crucial role in determining which species dominates. According to those works, we hypothesize that allelopathy, a prevalent natural phenomenon in terrestrial and aquatic ecosystems, may be one of the factors having caused the 2017 bloom anomaly in Marina di Massa; this, however, remains a hypothesis, as no additional data were available to support experimental trials. Specifically, macrophytes can produce allelochemicals that can be considered as natural algaecides able to suppress the development of plankton and to prevent HAB in water bodies. Gharbia et al. [76], highlighted that some macroalgae can produce allelopathic substances that inhibit *O. ovata* vegetative cells growth. Accoroni et al. [77], examined the allelopathic interactions between *O. ovata* and seaweeds, that compete for space in the same habitat. Fresh and dried thalli of *Dictyota dichotoma* and *Rhodymenia pseudopalmata* were found to significantly inhibit the growth of *O. ovata*; in particular, *Rhodymenia pseudopalmata* is found in the study area of Marina di Massa [78]. Phytoplankton as well can produce allelopathic compounds: Pichierri et al. [79] observed a marked decrease of *O. ovata* growth occurred when cells were exposed to diatom filtrates. We can therefore hypothesize that in 2017 both macrophytes and phytoplankton could have had an allelopathic effect on *O. ovata* in Marina di Massa.

6. Conclusions

The current study investigated if data available from Copernicus core services, i.e., satellite data from CMEMS, as well as model data obtained through downscaling of Copernicus climate services can provide information on drivers of *O. ovata* bloom dynamics, in spite of the fact that it occurs very close to the coast. The study has been conducted in two Tuscany study areas, Marina di Pisa and Marina di Massa, using measurements of *O. ovata* from in situ sampling. We preliminarily verified that Copernicus SST can be used in shallow coastal waters, comparing such variable with in situ observation of sea temperature; we used the state of the art WW3 model for simulating coastal wave conditions.

The analyses performed indicate that the use of SST from satellite and SWH from local models is effective in explaining the main behaviour of *O. ovata* in both study sites, according to a simplified conceptual model derived also from previous works but calibrated with local measurements. In particular, the study demonstrated that: the June temperature trend in relation to the given threshold explains a large part of the respective bloom occurrence, due to the strong dependence of *O. ovata* growth on a favourable start of the summer season. The total number of cells/blooms in a growing season is controlled by local sea state, due to the importance of proper resuspension conditions. Locally calibrated regression models based on SST and SWH patterns as derived from the examined data sources can account for around 35% of the daily variability in *O. ovata* growth.

These findings are more defined for Pisa than for Massa, indicating the importance of local factors which cannot be considered through the examined variables. The latter site, in fact, includes observations from a peculiar year, 2017, when *O. ovata* growth seems to be anomalously inhibited by some factors not included in the analysis, and we argue that could be the combined action of some organisms and benthic conditions (not observed in this work).

It can therefore be concluded that, although *O. ovata* growth and bloom are expected to be sensitive to a large number of drivers, and the role of many of them still needs to be fully understood, temperature and sea conditions are able to explain the main temporal patterns of these phenomena. More particularly, the satellite and model data used in this study carry information useful to identify the onset of favourable conditions for *O. ovata* HAB, in spite of the fact that it occurs very close to the coast, an area which is not usually suitable for satellite observation and where physical variables that determine resuspension are difficult to be precisely modelled unless very detailed ultra-high-resolution hydrodynamic models are implemented at each site. We verified that Copernicus SST can be used in shallow coastal waters, comparing such values with in situ observation of sea temperature; we used the state of the art WW3 model for coastal wave conditions.

These considerations support the possibility to build a more advanced model predicting favourable conditions for *O. ovata* bloom, based on a wider range of standard operational satellite and model data, after having clarified the role of additional drivers such as nutrients, salinity, and also other species interactions. Such analyses will require the extension of the study to other areas and years in which similar environmental issues have been or are being detected.

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