



Unusual red tide of the dinoflagellate *Lingulodinium polyedra* during an upwelling event off the Algarve coast (SW Iberia)



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ABSTRACT

Low biomass, but highly toxic algal blooms are frequent in the Ria Formosa coastal lagoon and adjacent coastal zone (southern Portugal), usually associated with specific oceanographic and nutrient conditions. In June 2019, a massive bloom of the dinoflagellate *Lingulodinium polyedra* developed along the coast, causing water discolouration, and the closure of beaches and of bivalve harvesting, with significant socioeconomic consequences. This study aims to evaluate the relationships between phytoplankton composition and environmental conditions before, during, and after the *L. polyedra* bloom. Water samples were collected in the Ria Formosa coastal lagoon throughout June and July 2019 for determination of nutrient and chlorophyll-a concentration using spectrophotometric methods. Phytoplankton composition and abundance were evaluated using inverted microscopy. Upwelling intensity was estimated considering a wind-based index, the cross-shore Ekman transport. Results show strong relationships between phytoplankton community composition and nutrients, particularly a positive relationship between centric diatoms and nitrogen, and a negative relationship between several dinoflagellate genera, and phosphorus and silicon. *L. polyedra* was not significantly associated with any nutrient variable, most likely due to its mixotrophic capabilities. A clear phytoplankton succession, typical of eastern boundary upwelling locations, was observed throughout the different bloom phases, from dominance of type II dinoflagellates (*Heterocapsa*, *Prorocentrum*) in the pre-bloom period, to dominance of *L. polyedra* (type V) during the bloom, and finally dominance of centric diatoms in the post-bloom period. However, the *L. polyedra* bloom was not associated with upwelling relaxation, but rather with an active upwelling event.

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1. Introduction

Harmful algal blooms (HABs) are natural events caused by microalgae, but they may have serious negative impacts on ecosystem dynamics and human activities (Zingone and Enevoldsen, 2000). The perceived increase in the frequency and magnitude of HABs that has been observed worldwide is most likely the result of intensified monitoring efforts (Hallegraeff et al., 2021). Nonetheless, the deleterious impacts of HABs on ecosystem functioning, public health, tourism, and fisheries are becoming more pronounced (Anderson et al., 2012).

It is widely accepted that, in many ecosystems, HABs are linked to excessive nutrient inputs (Glibert and Burford, 2017; Heisler et al., 2008), and this may also be the case in the Ria Formosa coastal lagoon (southern Portugal), a shallow system of sandy islands and peninsulas subjected to anthropogenic nutrient inputs and frequent upwelling events. HABs and non-harmful

blooms in the Ria Formosa and adjacent coastal waters have been observed in association with other symptoms of eutrophication (e.g., low oxygen, anoxic sediments, fish mortalities), and linked to large inputs of N and P, and unbalanced nutrient ratios (Newton et al., 2014). HABs in this region usually develop along the coastal zone and are imported by tidal currents into the lagoon. Most HABs in the lagoon and adjacent waters are caused by planktonic diatom species of the genus *Pseudo-nitzschia* and the dinoflagellate species *Gymnodinium catenatum*, *Dinophysis acuta* and *D. acuminata* (IPMA, 2020). These organisms produce biotoxins that accumulate in bivalves and are transferred to human consumers, causing a variety of acute toxic symptoms, some potentially lethal. Toxins associated with amnesic, diarrhetic, and paralytic shellfish poisoning have been identified in this ecosystem (IPMA, 2020). Most of these HABs are low-biomass events, but highly toxic, leading to long closures of bivalve harvesting. For instance, in 2019, harvesting of the wedge clam *Donax trunculus* was prohibited for more than 5 consecutive months (IPMA, 2020). Given that 88% of bivalve production in Portugal comes from this region and supports 7000 families (Newton et al., 2014), HABs in this coastal area represent a major socio-economic concern.

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Low-biomass HABs are the most common type of HAB in the Ria Formosa and adjacent coastal waters, but in June 2019, a bloom of the yessotoxin-producing dinoflagellate *Lingulodinium polyedra* caused an extensive red tide in the region, leading to beach and bivalve harvesting closures, and making headlines in news media for a few days (Domingues, 2021). The bloom was transported by tidal currents into the Ria Formosa coastal lagoon, but no water discolouration was observed. Many fundamental questions remain unanswered regarding the relationship between nutrients and HAB development, such as the effects of nutrients from anthropogenic and natural sources on the promotion of high- and low-biomass HABs, or the role of nutrients in the promotion of a particular harmful species (Glibert et al., 2018). Therefore, this study aims to evaluate the relationships between phytoplankton community composition and environmental conditions in the Ria Formosa lagoon before, during, and after the *L. polyedra* bloom in June 2019.

2. Methods

2.1. Study site

The Ria Formosa lagoon is a shallow (mean depth = 2 m), mesotidal system (mean tidal amplitude = 2.1 m) with semidiurnal tides, located on the Southern coast of Portugal (SW Iberian Peninsula; Fig. 1). The lagoon extends 55 km E–W and 6 km N–S (at its widest point), and it is protected from the Atlantic Ocean by sandy barrier islands and peninsulas split by several inlets. The system is subjected to a Mediterranean climate, with hot, dry summers and moderate winters, and is located in an area extremely vulnerable to climate change (Arias et al., 2021). The Ria Formosa wetland has an area of approx. 80 km² and is a National Natural Park, Ramsar site, and Natura 200 site, protected by multiple national and international policies (Barbosa, 2010; Newton et al., 2020).

The coastal region adjacent to the Ria Formosa lagoon is located at the northernmost section of the Iberian Canary Eastern Boundary Upwelling system and is included in the Gulf of Cadiz (Lima et al., 2022). It is a complex coastal domain, subjected to mesoscale and sub-mesoscale features such as upwelling filaments, fronts, and countercurrents (see (Lima et al., 2022) and references therein). Upwelling events are common in the region, especially during early spring to late summer (Relvas et al., 2007), and may extend 6 km upstream through lagoon inlets (Cravo et al., 2014). HABs typically develop in the coastal zone and are transported into the Ria Formosa by tidal currents, through lagoon inlets.

2.2. Sampling strategy

Sampling during the *Lingulodinium polyedra* bloom was undertaken as a part of a weekly sampling programme at an inner location of the Ria Formosa lagoon (Fig. 1). Water samples were collected during June and July 2019, namely: 4th and 11th June (pre-bloom), 17th and 18th June (bloom), and 26th June and 1st July (post-bloom). Owing to the well mixed water column in the Ria Formosa lagoon (Domingues et al., 2021), samples were collected at 0.5 m from a pier by means of a 5 L bottle. Water samples were maintained in cool, dark conditions while transported to the laboratory (approx. 15 min).

2.3. Nutrient and phytoplankton analyses

Water samples for determination of the concentration of dissolved inorganic macronutrients (nitrate, nitrite, ammonium, phosphate, silicate) were immediately filtered through a cellulose

acetate membrane (nominal pore diameter = 0.45 μm) and frozen (−20 °C) until analysis. Colorimetric methods (Hansen and Koroleff, 1999) were used to determine nutrient concentrations, using an autoanalyzer Skalar for nitrate and nitrite and a spectrophotometer Hitachi U-2000 for ammonium, phosphate, and silicate.

Water samples for determination of chlorophyll-a concentration were filtered through glass fibre filters (Whatman GF/F, retention >0.7 μm) and pigments were extracted with acetone 90% for 24 h. After centrifugation, absorbance of the supernatant was measured at 750 nm and 665 nm, before and after acidification with HCl 1 M (Parsons et al., 1984).

Water samples for microphytoplankton (>20 μm) identification were preserved immediately after collection with acid Lugol's solution (final concentration approx. 0.003%), settled in sedimentation chambers, and observed at 400x magnification with a Zeiss Axio Observer A1 inverted microscope under phase contrast and bright field illumination. A minimum of 50 random visual fields, at least 400 cells in total, and 50 cells of the most common genus were counted, for a counting precision of ±10%, assuming random distribution of cells (Venrick, 1978). Phytoplankton identification was based on Dodge (1982) and Tomas (1997).

2.4. Oceanographic data

Upwelling intensity between the pre- and post-bloom phases was estimated considering a wind-based index, the cross-shore Ekman transport (CSET). Daily sea surface zonal (U) and meridional (V) wind fields, at 0.25° spatial resolution, between May and July 2019, were obtained from the new version of the Blended Sea Winds dataset, NBS v2.0, available at NOAA CoastWatch (<https://oceanwatch.noaa.gov/cwn/products/noaa-ncei-blended-seawinds-nbs-v2.html>). BSW data is generated by blending observations from multiple sources (satellites), including scatterometers and microwave radiometers/imagers. However, to overcome the inability of resolving strong storm winds, a multi-sensor data fusion technique based on random errors was incorporated in this new version of the BSW (Saha and Zhang, 2022). Due to the coarse spatial resolution of wind data, CSET was computed for two locations off the south Portuguese coast, both at ~8 km from the coastline, on the western and eastern sectors of Cape Santa Maria (CSET_{wCSM} and CSET_{eCSM}; see Fig. 1). For each location, CSET values represent the average of a 0.75° × 0.75° box centred at the target location. Since the south coast of Portugal is zonally (west–east) oriented, CSET_{wCSM} and CSET_{eCSM} were estimated from the meridional component of the Ekman transport, induced by the zonal component of wind-stress ((Bakun, 1973); for more information see Alvarez et al. (2011), Krug et al. (2017)). No significant differences were observed between CSET_{wCSM} and CSET_{eCSM} (p < 0.05), hence average values were used to represent the cross-shore Ekman transport on the south coast. Negative CSET values indicate offshore Ekman transport and upwelling-favourable conditions, whereas positive values represent onshore Ekman transport and downwelling-favourable conditions.

2.5. Data analysis

Differences in phytoplankton composition between the three periods were assessed with one-way permutational multivariate analyses of variance (PERMANOVA) based on Bray–Curtis dissimilarities, using 999 unrestricted permutations of raw data. Similarity percentages (SIMPER) were used to detect which taxa contributed the most to the dissimilarities. Pearson's correlations were used to evaluate significant associations between the main

Table 1

Mean \pm standard deviation nutrient (μM) and chlorophyll-a ($\mu\text{g L}^{-1}$) concentrations, and abundance of microphytoplankton, dinoflagellates, and diatoms (cells L^{-1}) in the pre-bloom ($n = 2$), bloom ($n = 2$), and post-bloom ($n = 2$) periods. DIN – dissolved inorganic nitrogen; DRP – dissolved reactive phosphorus; DSi – dissolved silicon; N:P – nitrogen:phosphorus molar ratio; Chl-a – chlorophyll-a concentration; microphyto – microphytoplankton.

	DIN	DRP	DSi	N:P	Chl-a	microphyto	dinoflagellates	diatoms
pre-bloom	2.15 \pm 0.60	0.18 \pm 0.10	4.95 \pm 2.28	20.00 \pm 14.25	0.77 \pm 0.35	7.44 $\times 10^4$ \pm 3.09 $\times 10^4$	6.11 $\times 10^4$ \pm 3.15 $\times 10^4$	9.04 $\times 10^3$ \pm 1.26 $\times 10^3$
bloom	1.26 \pm 0.17	0.22 \pm 0.03	8.80 \pm 1.28	6.08 \pm 1.62	0.48 \pm 0.07	2.24 $\times 10^5$ \pm 5.79 $\times 10^4$	2.06 $\times 10^5$ \pm 4.20 $\times 10^4$	9.89 $\times 10^3$ \pm 7.21 $\times 10^3$
post-bloom	2.87 \pm 1.90	0.43 \pm 0.14	10.69 \pm 1.67	9.10 \pm 7.35	0.18 \pm 0.18	8.02 $\times 10^4$ \pm 5.37 $\times 10^4$	1.48 $\times 10^4$ \pm 2.35 $\times 10^3$	6.44 $\times 10^4$ \pm 5.16 $\times 10^4$

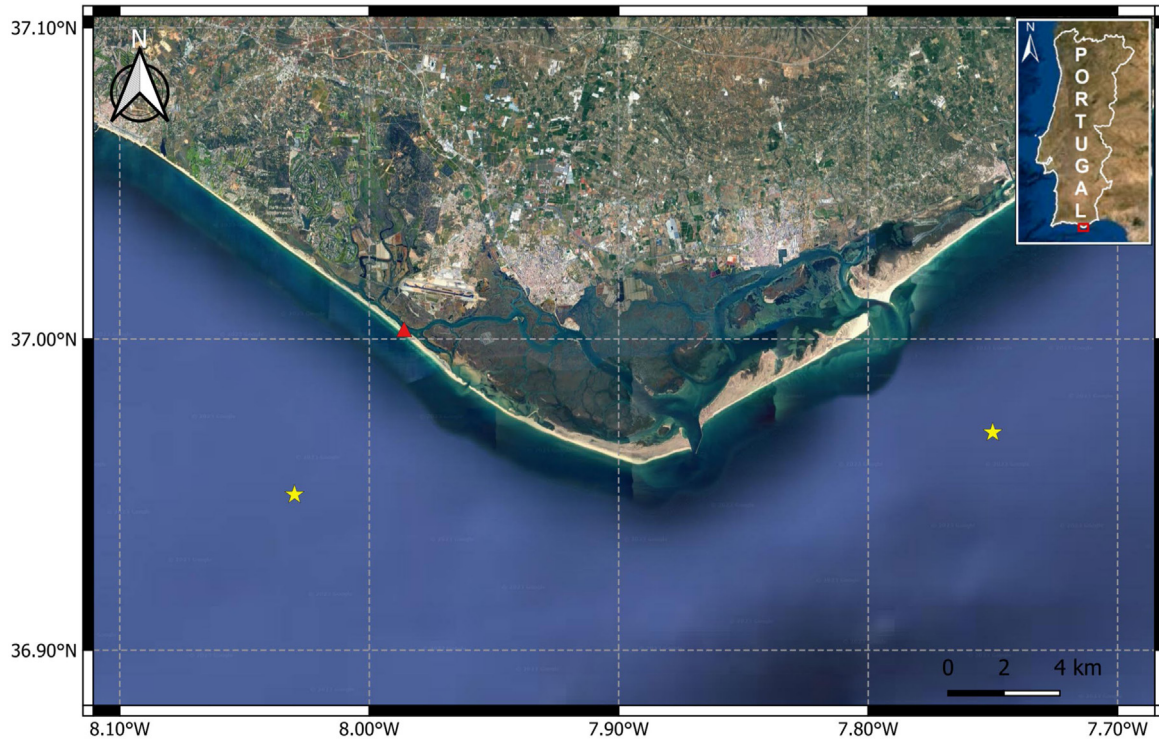


Fig. 1. Map of the Ria Formosa coastal lagoon; red triangle indicates sampling station and yellow stars show two sites, west and east of Cape Santa Maria, used for the calculation of the wind-based upwelling index at the adjacent coastal area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

phytoplankton taxa and the nutrient environment. Finally, redundancy analysis (RDA) was used to examine relationships between nutrient variables (nutrient absolute concentrations and molar ratios) and phytoplankton composition. By combining regression and principal component analysis, RDA allows the determination of which predictor variables (nutrient absolute concentrations and ratios) explain the most variation in multiple response variables (phytoplankton composition) (Borcard et al., 2018). Species data was Hellinger-transformed and environmental data was centred and normalised. Analyses were carried out using IBM SPSS Statistics 28 and the “vegan” package (Oksanen et al., 2022) for R (R Core Team, 2022), using the RStudio environment (RStudio Team, 2022).

3. Results

3.1. Environmental conditions

Nutrient absolute concentrations and molar ratios, chlorophyll-a concentration (Chl-a), and microphytoplankton abundance at

the inner location of the Ria Formosa coastal lagoon for the period June–July 2019 are depicted in Table 1 (see also Fig. 2 for Chl-a and abundance of *L. polyedra* and diatoms). In early June 2019, before the onset of the *Lingulodinium polyedra* bloom, dissolved inorganic nitrogen (DIN), dissolved reactive phosphorus (DRP), and dissolved silicon (DSi) varied between 1.55–2.74 μM , 0.08–0.27 μM , and 2.67–7.23 μM , respectively. Chlorophyll-a concentrations during this period ranged between 0.42 $\mu\text{g L}^{-1}$ and 1.11 $\mu\text{g L}^{-1}$. During the bloom event, DIN, DRP, DSi, and Chl-a presented values between 1.09–1.43 μM , 0.19–0.25 μM , 7.52–10.08 μM , and 0.42–0.55 $\mu\text{g L}^{-1}$, respectively, within the range of values observed during the initial period. In the week following the bloom, nutrient concentrations varied between 0.98–4.77 μM , 0.29–0.56 μM , and 9.03–12.36 μM for DIN, SRP, and DSi, respectively, and Chl-a concentrations ranged between undetectable values and 0.32 $\mu\text{g L}^{-1}$. A nitrogen:phosphorus molar ratio (N:P) below 20 indicated potential limitation by nitrogen during all periods, with N:P in the N and/or P limitation zone ($20 < \text{N:P} < 50$) (Fig. 3).

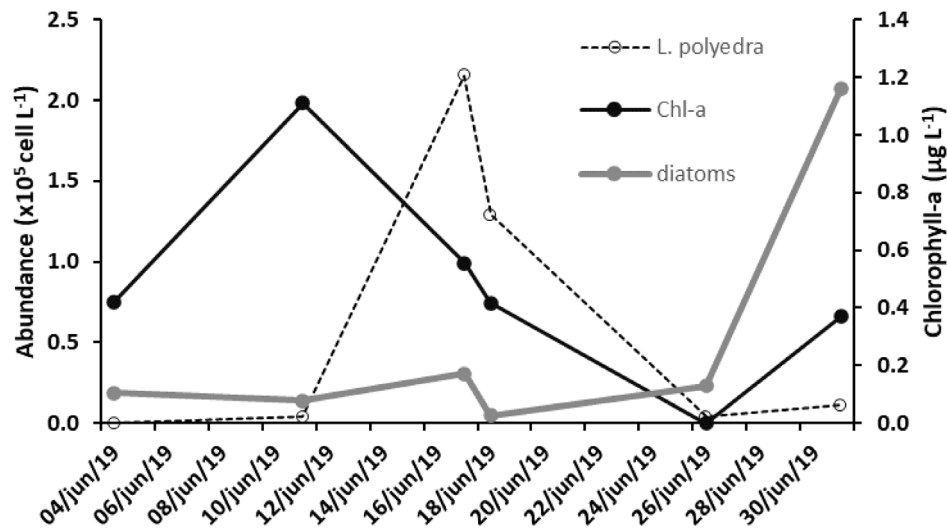


Fig. 2. Temporal evolution of chlorophyll-a concentration, and abundance of *Lingulodinium polyedra* and diatoms in the Ria Formosa coastal lagoon.

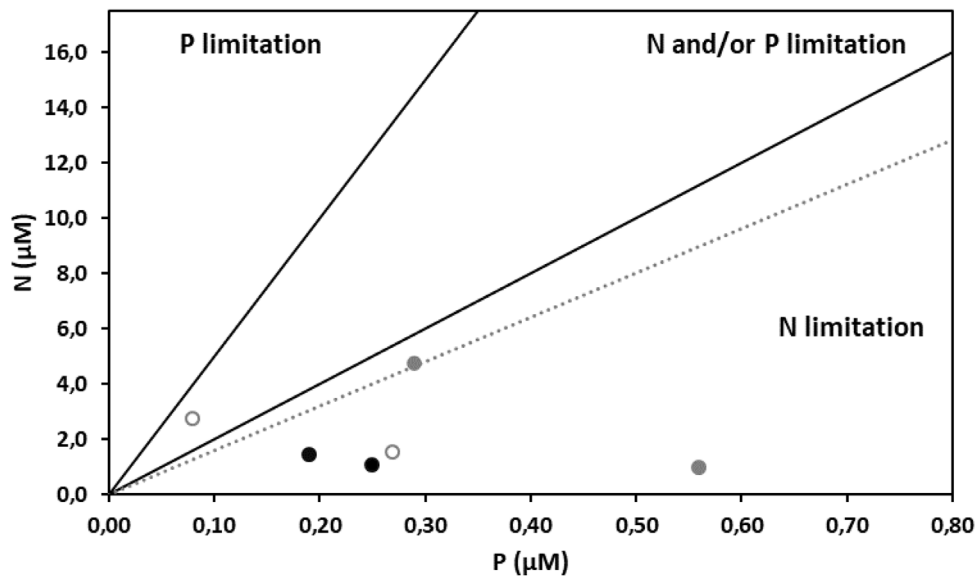


Fig. 3. Application of the resource-ratio hypothesis to ambient nutrient concentrations of nitrogen (N) and phosphorus (P) in the Ria Formosa coastal lagoon for the period June–July 2019. N:P = 20 and N:P = 50 solid lines define three areas within the plot: N:P < 20 – N limitation; 20 < N:P < 50 – N and/or P limitation; N:P > 50 – P limitation (thresholds according to Guildford and Hecky, 2000). Dashed line is N:P = 16. Empty circles – pre-bloom (4 and 11 June); black circle – bloom (17 and 18 June); grey circles – post-bloom (26 June and 1 July)

Concerning the oceanographic regime, the mean CSET ranged from $-998.51 \pm 199.21 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ coastline to $-321.64 \pm 76.12 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ coastline, during the pre-bloom and bloom phases, respectively (Fig. 4). The post-bloom phase was characterised by a mean CSET value of $-363.71 \pm 175.81 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$ coastline.

3.2. Phytoplankton community composition

During the pre-bloom phase (early June), microphytoplankton abundance ranged between $4.20 \times 10^4 \text{ cells L}^{-1}$ and $8.56 \times 10^4 \text{ cells L}^{-1}$ and it was mostly composed by dinoflagellates, which contributed between 68% and 85% to total abundance (Fig. 5). The most abundant dinoflagellates belonged to the Orders Prorocentrales (*Prorocentrum micans* and *Prorocentrum triestinum*) and Peridiniales (*Heterocapsa circularisquama* and *Heterocapsa* spp.); *Lingulodinium polyedra* was already present during the pre-bloom period, at numbers lower than $3.89 \times 10^3 \text{ cells L}^{-1}$. During

this period, diatoms contributed less than 18%, mostly due to *Cylindrotheca closterium* and other pennate diatoms.

In mid-June, during the bloom phase, phytoplankton abundance reached $2.64 \times 10^5 \text{ cells L}^{-1}$ and the causative dinoflagellate *Lingulodinium polyedra* contributed up to 82% ($2.15 \times 10^5 \text{ cells L}^{-1}$) of total cell numbers. The contribution of all dinoflagellates varied between 93% and 98% during the bloom, whereas diatoms did not exceed 7% of total microphytoplankton numbers (Fig. 3).

After the dissipation of the bloom (early July), total microphytoplankton numbers remained at similar levels as during the bloom (1.32×10^5 – $1.75 \times 10^5 \text{ cells L}^{-1}$), but a shift to diatom dominance was observed. In the post-bloom phase, diatoms represented between 58% and 88% of total abundance, with dinoflagellates decreasing to 11% (Fig. 5). *L. polyedra* was still the most abundant dinoflagellate, but species belonging to the orders Prorocentrales and Peridiniales were not detected in the samples. Diatoms were mostly represented by small, centric *Thalassiosira* and *Chaetoceros* species.

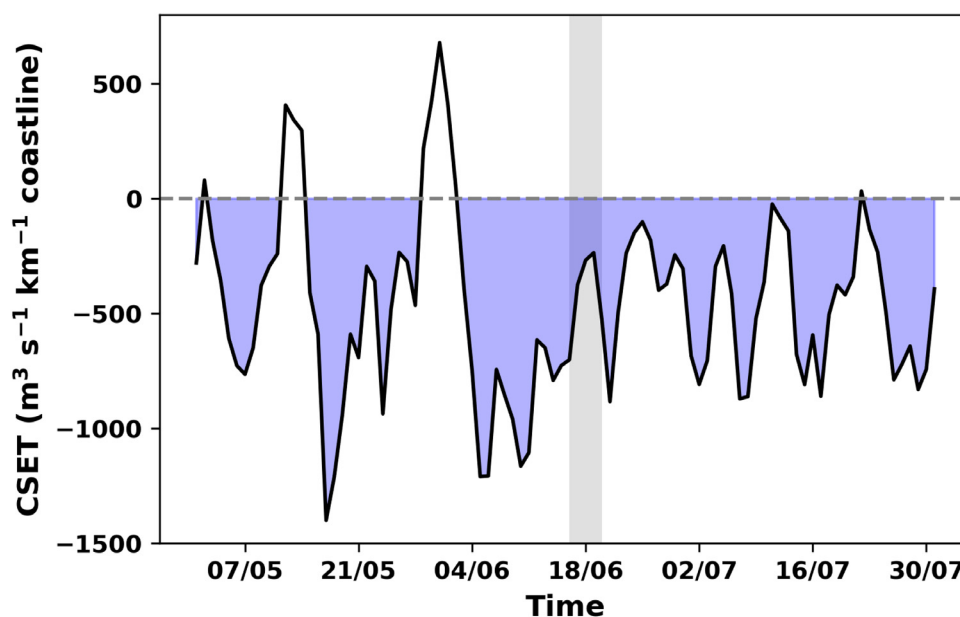


Fig. 4. Time series of cross-shore Ekman transport during the period May–July 2019, averaged over two locations off the south Portuguese coast (see Fig. 1). Blue-labelled negative values represent upwelling-favourable periods. The grey shaded region represents the bloom period (16 June–20 June). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

PERMANOVA results testing the differences in phytoplankton community structure between pre-bloom, bloom, and post-bloom periods, based on Bray–Curtis similarity matrices.

	DF	SS	F	p
Model	1	0.68848	3.0268	0.017
Residual	7	1.59223		
Total	8	2.28071		

PERMANOVA revealed significant differences ($p = 0.017$) in phytoplankton community composition between pre-bloom, bloom, and post-bloom periods (Table 2). Major dissimilarities between the pre-bloom and bloom periods were mostly due to *L. polyedra*, but also due to *Heterocapsa*, *Scripsiella*, and other small, unidentified dinoflagellates, with a cumulative contribution of 78%, as revealed by SIMPER analysis. As for differences between bloom and post-bloom periods, the most influential taxa were centric diatoms and *L. polyedra*, with a cumulative contribution of 81% to the dissimilarities observed. Centric diatoms and *L. polyedra* were also the most important contributors to the dissimilarities observed between the pre- and post-bloom phases, with a cumulative contribution of 62%.

3.3. Relationship between nutrients and phytoplankton community composition

An exploratory correlation analysis detected significant correlations between specific taxa and environmental variables (Table 3). Dinoflagellate genera *Scripsiella*, *Heterocapsa*, *Dinophysis*, and *Prorocentrum* were all positively correlated among each other ($r > 0.7$, $p < 0.05$). All these genera, except *Dinophysis*, were negatively correlated with DRP and DSi ($r > -0.7$, $p < 0.05$). DRP and DSi were strongly and positively correlated ($r = 0.822$, $p = 0.007$). Centric diatoms were strongly and positively correlated with DIN ($r = 0.951$, $p < 0.001$). Fig. 6 shows the results of the RDA ordination, in which phytoplankton taxa are associated with absolute nutrient concentrations and nutrient ratios. The model explains 94.34% of constrained variance, with an adjusted R^2 of 0.77 ($p = 0.003$). Dissolved inorganic nitrogen (N) and the N:P

ratio were the variables more strongly associated with the first axis (scores for constraining variables were -0.68 and -0.50 , respectively), whereas dissolved silicon (Si) and dissolved reactive phosphorus (P) were associated with the second axis (scores of 0.35 and 0.31, respectively). Centric diatoms were strongly associated with the first axis (species scores = -0.74) and with N and N:P, whereas *Lingulodinium polyedra* was strongly associated with the second axis (species score = 0.55).

4. Discussion

This study aimed to analyse the relationships between phytoplankton community composition and environmental conditions, before, during, and after a bloom of the dinoflagellate *Lingulodinium polyedra* off the southern coast of Portugal, which was imported from adjacent coastal waters, through lagoon inlets, into the Ria Formosa coastal lagoon. Overall, strong relationships between the composition of phytoplankton assemblage and nutrients were detected, particularly a positive relationship between centric diatoms and nitrogen, and a negative relationship between several dinoflagellate genera, and phosphorus and silicon. The *L. polyedra* bloom was associated with an upwelling event, but no relationships with the nutritional environment were found.

The occurrence of *L. polyedra* along the southern and western coasts of Portugal is common, but the development of blooms of *L. polyedra* is unpredictable and geographically limited (Amorim et al., 2004). Only 5 bloom events caused by *L. polyedra* have been reported on the Portuguese coast (3 events at the South coast and 2 at the West coast) (IOC-UNESCO, 2021a). Maximum abundances of *L. polyedra* were observed during a bloom in 2012 on the southern coast (Faro-Olhão region), with values surpassing 1.12×10^7 cells L^{-1} (IOC-UNESCO, 2021b). The *L. polyedra* bloom in June 2019 reached an abundance of 6.62×10^5 cells L^{-1} on the southern coast adjacent to the Faro-Olhão region (IOC-UNESCO, 2021c), whereas inside the Ria Formosa lagoon the maximum recorded abundance was 2.16×10^5 cells L^{-1} . These values were above alert levels for yessotoxin-producing species (1×10^3 cells L^{-1}) and below maximum legal levels (1×10^6 cells L^{-1}) (Serret et al., 2019), but still resulted in the closure of bivalve harvesting

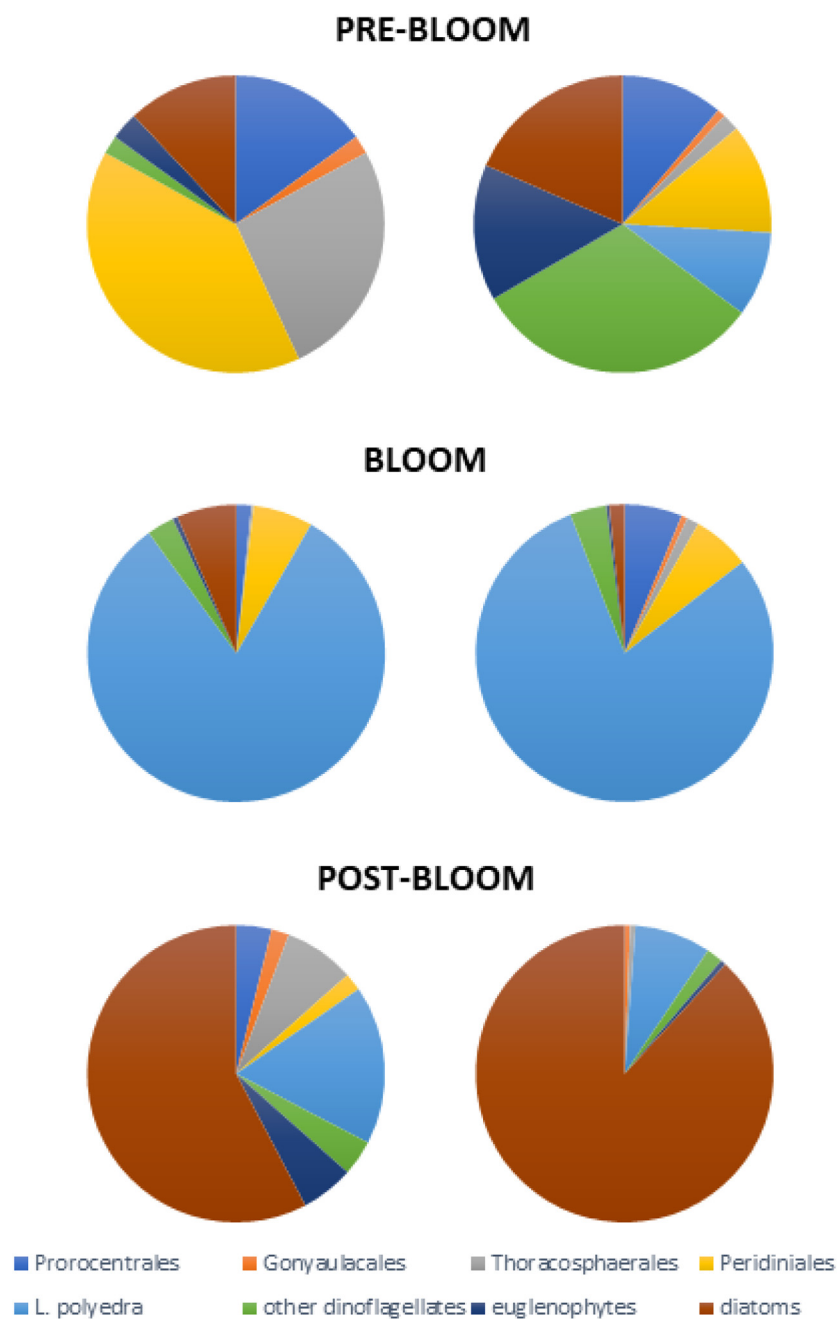


Fig. 5. Relative abundance of different microphytoplankton groups during the pre-bloom (4 June and 11 June), bloom (17 June and 18 June), and post-bloom (26 June and 1 July) periods.

Table 3
Correlation coefficients between the main phytoplankton taxa and nutrient concentrations throughout the sampling period (June–July 2019). Scrip – *Scrippsiella*; Hetero – *Heterocapsa*; Dinop – *Dinophysis*; Proro – *Prorocentrum*; Lingul – *Lingulodinium polyedra*; Centric – centric diatoms; DIN – dissolved inorganic nitrogen; DRP – dissolved reactive phosphorus; DSi – dissolved silicon.

	Scrip	Hetero	Dinop	Proro	Lingul	Centric	DIN	DRP
Hetero	.935**							
Dinop	.935**	.949**						
Proro	.773*	.853**	.854**					
Lingul	.393	-.072	-.174	.219				
Centric	-.308	-.353	-.533	-.481	.345			
DIN	-.252	-.302	-.501	-.416	-.249	.951**		
DRP	-.687*	-.701*	-.612	-.807**	-.043	.263	.135	
DSi	-.765*	-.731*	-.657	-.730**	-.036	-.049	-.138	.822*

*P-values: < 0.05.
**P-values: < 0.001.

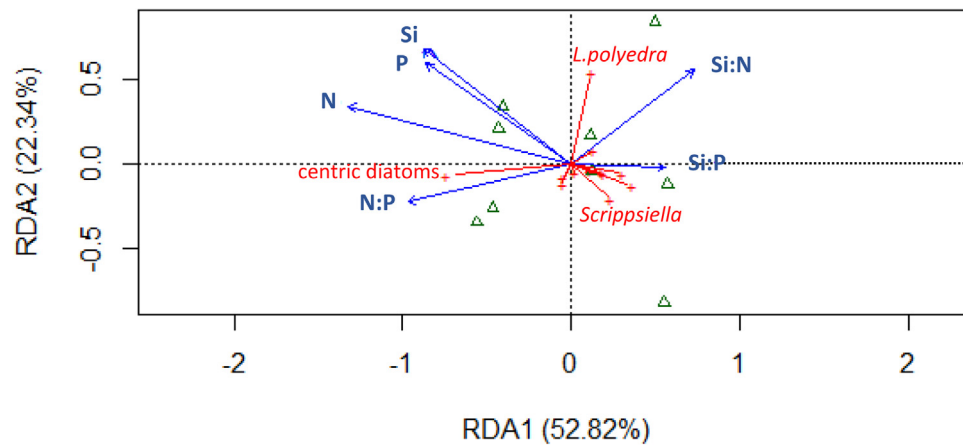


Fig. 6. Redundancy analysis triplot showing the effects of explanatory variables (nutrients) on phytoplankton community structure. Green triangles = samples; red lines = phytoplankton taxa; blue arrows = nutrient variables. The percentage of total variance explained by the first two canonical eigenvalues are indicated in the axes (RDA1, RDA2). The length of the blue arrows (nutrient variables) is indicative of the importance of the variable as a driver of variation in the phytoplankton community matrix. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

in the Ria Formosa and in the adjacent coastal zone, as well as the closure of beaches in the area (Domingues, 2021). In late June 2019, 10 days after the detection of the bloom on the Algarve coast, another *L. polyedra* bloom developed in the Gulf of Cadiz, in coastal waters adjacent to the Guadiana estuary, with abundances reaching 8.5×10^5 cells L^{-1} (Caballero et al., 2020).

Other massive *L. polyedra* blooms observed on the southern coast of Portugal include an event in the Albufeira region in 2004 with a maximum abundance of 1×10^6 cells L^{-1} ; massive blooms along the West coast include an event in Setúbal Bay (7.2×10^5 cells L^{-1}) in 1996 and a bloom in the Lisbon area (4.0×10^6 cells L^{-1}) in 2005 (IOC-UNESCO, 2021a). The magnitude of these blooms is comparable with *L. polyedra* blooms typical of other geographical areas, such as in the California Current system (9.17×10^6 cells L^{-1} : (Kahru et al., 2021)), and in the Black Sea ($0.8\text{--}1.3 \times 10^6$ cells L^{-1} : (Terenko and Krakhmalnyi, 2022)).

Blooms of *L. polyedra* are a common occurrence in many coastal ecosystems, particularly during summer and early autumn (Lewis and Hallett, 1997), with bloom duration dependent on oceanographic conditions. The Algarve bloom in 2019 was preceded by the dominance of the dinoflagellates *Prorocentrum* and *Heterocapsa*, which were negatively associated with nutrient concentrations. These are type II dinoflagellates, which bloom in summer and are associated with somewhat lower, but still elevated, nutrient concentrations (Smayda and Reynolds, 2001). The bloom of *L. polyedra* followed these type II dinoflagellates and dominated the community for several days, leading to discoloration of the water. *L. polyedra* is considered a type V dinoflagellate adapted for survival within upwelling habitats and tends to bloom during upwelling relaxation periods (associated with positive cross-shore Ekman transport) (Smayda and Reynolds, 2001). However, in this case, the bloom phase did not coincide with positive cross-shore Ekman transport values representative of downwelling (outside the upwelling season) or relaxation events (during the upwelling season), but rather with smaller negative values indicative of a weak upwelling event (see Fig. 4). This decrease in upwelling intensity likely promoted the shallowing of the thermocline depth and weakening of horizontal advection which sustained dinoflagellate growth. *L. polyedra* was negatively associated with phosphorus concentration, suggesting that it does not require high nutrient concentrations to bloom. Indeed, increased water column stratification and lower nutrient availability provide a competitive advantage for mixotrophic and motile dinoflagellates (Smayda and Trainer, 2010).

The bloom in the Algarve coast was short-lived and dissipated within less than a week, but other blooms have been known to persist for longer periods and to impact extensive areas. For example, *L. polyedra* was responsible for an extensive bloom on the south and southwest coasts of South Africa, persisting for several months over the summer of 2014 and impacting nearly 1000 km of shoreline (Pitcher and Louw, 2021); (van der Lingen et al., 2016)). After dissipation of the Algarve bloom, small centric diatoms became dominant, but continued to co-exist with *L. polyedra* and other dinoflagellates. The switching between dinoflagellate blooms during periods of upwelling relaxation and mini-blooms of diatoms during active upwelling is common in eastern boundary upwelling systems (Smayda and Trainer, 2010).

L. polyedra blooms in Portugal have never been linked to events of mortality and although lipophilic yessotoxins are commonly detected in shellfish along the Portuguese coast, their levels remain below regulatory limits (Vale et al., 2008) and there are no reported cases of human poisoning (see review by Alfonso et al., 2016 and references therein). However, associations with fish and invertebrate mortalities have been found in other ecosystems (Terenko and Krakhmalnyi, 2022). For instance, in South Africa, the widely distributed 2014 bloom resulted in localised anoxic conditions and the mortality of various marine organisms; a significant decrease in sardine catches was also observed (van der Lingen et al., 2016). In 2017 a bloom dominated by *L. polyedra* and *Gonyaulax spinifera*, both known yessotoxin producers, was responsible for the death of several million abalone on the southwest coast of South Africa (Pitcher et al., 2019).

In conclusion, the *L. polyedra* bloom in southern Portugal was associated with an upwelling event, rather than an upwelling relaxation phase as typically described for type V dinoflagellates. The large biomass of *L. polyedra* caused water discoloration that persisted for a few days and led to the closure of beaches and of bivalve harvesting, although no toxicity was reported. Successional changes in phytoplankton community were observed with the dominance of type II dinoflagellates before the bloom, and the dominance of centric diatoms after the *L. polyedra*. This short-term succession from bloom-forming dinoflagellates to diatoms is commonly found in eastern boundary upwelling systems. There was a significant association of the diatoms and type II dinoflagellates with higher nutrients, but no relationship was evident between the nutrient environment and *L. polyedra*, owing to the mixotrophic nature of this dinoflagellate.

CRediT authorship contribution statement

Rita B. Domingues: Conceptualization, Formal analysis, Funding acquisition, Investigation, Writing – original draft, Writing – review & editing. **Maria João Lima:** Formal analysis, Writing – review & editing.

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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