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Ecology

Prorocentrum lima complex associated with macrophytes at two eastern boundary upwelling sites: Estero de Urías Lagoon (Mexico) and Paracas Bay (Peru)

Complejo Prorocentrum lima *asociado a macrofitas en dos sitios de afloramiento de borde oriental: laguna Estero de Urías (México) y bahía de Paracas (Perú)*

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Abstract

Benthic or epibenthic dinoflagellates (EDs) are a potential risk to the environment and human health due to the production of toxins by some species. This study explored for the first time the presence of EDs mainly associated with macrophytes (macroalgae and seagrass) at 2 sites influenced by upwellings: Estero de Urías Lagoon (EUL), at the entrance of the Gulf of California, and Paracas Bay (PB), on the southern Peruvian coast. *Prorocentrum lima* complex was present at low abundances: ≤ 25 cells g^{-1} wet weight in EUL and ≤ 867 cells g^{-1} wet weight in PB. It was recorded in a wide range of temperatures from 22.2 to 31.6 °C in EUL and from 18.0 to 22.2 °C in PB. Despite its low abundance, monitoring the EDs community is essential to detect changes in the distribution patterns of harmful species in the context of climate change.

Keywords: Macroalgae; *Caulerpa*; Artificial substrate; California Current; Humboldt Current

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Resumen

Los dinoflagelados epibentónicos (DE) representan un riesgo potencial al ambiente y a la salud del ser humano debido a la producción de toxinas por parte de algunas especies. En este estudio, se exploró por primera vez la presencia de DE principalmente asociados a macrofitas (macroalgas y pastos marinos) en 2 sitios con influencia de afloramientos: laguna Estero de Urías (LEU), localizado en la entrada del golfo de California y la bahía de Paracas (BP) en la costa sur de Perú. El complejo *Prorocentrum lima* estuvo presente con bajas abundancias: ≤ 25 células g^{-1} peso húmedo en LEU y ≤ 867 células g^{-1} peso húmedo en BP. La especie se registró en un amplio intervalo de temperatura de 22.2 a 31.6 °C en LEU y de 18.0 a 22.2 °C en BP. A pesar de las bajas abundancias encontradas, el monitoreo de la comunidad de DE es importante para detectar cambios en los patrones de distribución de las especies nocivas en un contexto de cambio climático.

Palabras clave: Macroalgas; *Caulerpa*; Sustrato artificial; Corriente de California; Corriente de Humboldt

Introduction

Benthic or epibenthic dinoflagellates (EDs) are common in shallow waters. They are frequently attached to many substrate types, such as algal turf, macroalgae, rocks, coral rubble, sand, or seagrasses (Honsell et al., 2013; Yong et al., 2018). Although they prefer substrate attachment, the vegetative cells of free-living species are flagellated and are fully capable of detachment and motility (Durán-Riveroll et al., 2019). The excessive growth of these species, particularly the toxigenic ones, can produce benthic harmful algal blooms, and toxins can be transferred along the food web; in humans, consumption of contaminated seafood with these toxins can cause diarrhetic shellfish poisoning (DSP) or ciguatera fish poisoning (Berdalet et al., 2016).

Although EDs have a high relative cell abundance and diversity in subtropical and tropical waters, they are found globally, including in temperate, sub-arctic, and polar environments (Álvarez et al., 2022; Tester et al., 2010). In recent decades, evidence suggests a shift in biogeographical distribution patterns for some species (Gobler et al., 2017; Tester et al., 2020), such as *Gambierdiscus*, previously considered tropical or sub-tropical. Recent studies have shown that it is well established in temperate areas such as Korea, Japan, New Zealand, Australia, the northern Gulf of Mexico, and the Mediterranean Sea (Chinain et al., 2021). Furthermore, there is concern that floating plastics in the ocean can act as global vectors for transporting algal cells and transferring toxins along marine food webs (do Prado-Leite et al., 2022).

In Mexico, about 60 species from 18 EDs genera have been identified. The species that form dense benthic blooms with potentially harmful consequences are *Prorocentrum rhathymum*, *Blixaea quinquecornis*, and *Amphidinium* cf. *carterae* (Okolodkov et al., 2022). In South America, 31 EDs taxa have been reported (Mafra et al., 2023). The most frequent and widespread species was the *P. lima* complex (Mafra et al., 2023). On the Peruvian coast, the cold coastal waters of the Humboldt Current System could restrict the presence of these species (Durán-Riveroll et al., 2019). The *P. lima* complex has been frequently observed over the past ~ 50 years, though studies have primarily focused on the planktonic community (Mafra et al., 2023).

Benthic microalgae are expected to benefit from climate change conditions, such as warmer waters and changes in marine current patterns, which could promote their invasive colonization and range of expansion (Tester et al., 2010). Estero de Urías Lagoon (EUL) and Paracas Bay (PB) host harbors with high levels of activity (i.e., the harbors of Mazatlán and San Martín, respectively), which may represent a potential risk since ballast waters remain a vector for the introduction of non-native and potentially harmful aquatic species (Lee et al., 2021). This study aimed to explore the EDs associated with macrophytes in Estero de Urías Lagoon, Mazatlán (Mexico), and Paracas Bay, Pisco (Peru), and the environmental variables associated with the presence of these species.

Materials and methods

Estero de Urías Lagoon (EUL; 23.2° N) is located at the entrance to the Gulf of California (Fig. 1) and covers an area of 18 km^2 with water depths of 1-3 m except in the navigation channel where it is up to 13 m (Montaño-Ley et al., 2008). It is surrounded by the industrialized city and harbor of Mazatlán (Raygoza-Viera et al., 2014). It is influenced by seasonal coastal upwelling events (Herrera-Becerril et al., 2022). EUL does not receive continuous freshwater, for which it exhibits an inverse estuarine circulation, and during the warmest months high salinity occurs in the upper lagoon (Cardoso-Mohedano et al., 2018).

The climate in the area is warm and humid, with a mean annual temperature of 21.4-29.6 °C (1951-2017) and

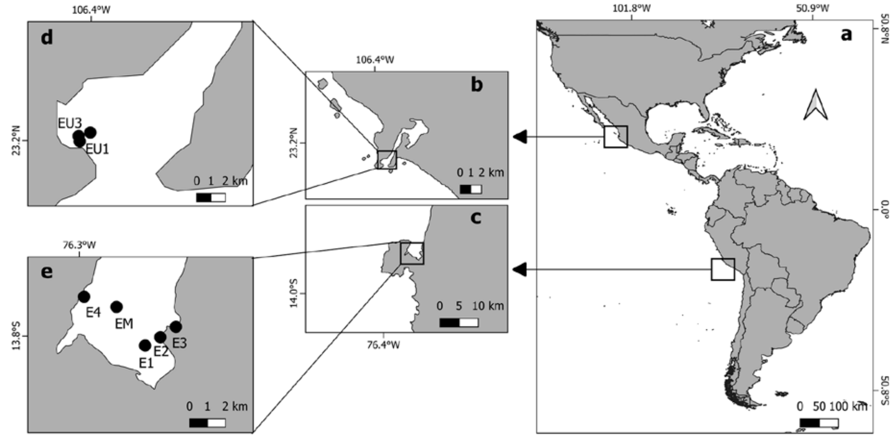

Figure 1. a, Map of the study sites; b, d, sampling sites in Estero de Urías (EU1, EU2, EU3), Mexico; c, e, Paracas Bay (E1, E2, E3, E4, EM), Peru.

a mean annual precipitation of 372 mm (SMN, 2024). EUL is an anthropized coastal lagoon affected by urban development, shrimp farming, and discharges of domestic, industrial, and wastewater (Hernández-Cornejo & Ruiz-Luna, 2000; Méndez, 2002). The Mazatlán harbor is the second largest on the Mexican Pacific coast, and in 2023 it received almost 500,000 cruise ship passengers from the largest cruise ships navigating the globe (API, 2024).

Paracas Bay (PB; 13.8° S) is located in Pisco, off South-Central Peru (Fig. 1), with an area of 30 km^2 and < 15 m of depth (Merma-Mora et al., 2024). The southern part of the bay is included in the Paracas National Reserve (Sernanp, 2019). It is influenced by one of the main upwelling cells of the highly productive Peruvian Upwelling System (Chávez et al., 2008). PB is seasonally influenced by river discharge, and monthly averages range from 0.7 to 282 $m^3 s^{-1}$, with the higher values in austral summer (Cuellar-Martinez et al., 2023).

The climate in the region is arid, with an average annual rainfall of 1.83 mm and air temperatures ranging from 15 to 22 °C (Reyes, 2009). Anthropogenic activities around the bay include artisanal and industrial fishing, tourism, bay scallop *Argopecten purpuratus* aquaculture, fish processing industries, non-metallic minerals, and guano extraction (Reyes, 2009). The Terminal Portuario General San Martín, the country's third most important port for cargo traffic (APN, 2018), is in the surroundings.

The most abundant macrophytes were collected manually or by diving and placed in polypropylene bags; the macrophyte masses ranged from 5 to 342.2 g in wet weight. The 3 sampling sites at EUL were close to the lagoon mouth, where a greater diversity of macroalgae species is found (Ochoa-Izaguirre et al., 2002). The sites were located in a total area of 0.01 km^2 with fish cage cultures (~ 8 m depth). The most abundant macroalgae attached to the floating cage frames were collected monthly between August and November 2018 and in January, February, April, and June 2019. A total of 25 samples were collected, including species of *Gracilaria* sp., *Hynea* sp., *Sargassum* sp., *Padina* sp., *Grateloupia* sp., and *Gelidium* sp. In general, 1 to 4 samples were collected per sampling station. In addition, between August and October 2018, artificial substrates consisting of rectangular pieces (3 x 33 cm) of fiberglass screen fixed on a rigid frame were used (Jauzein et al., 2016). The artificial substrates were collected using scissors. For retrieval, 24 hours after installation, the substrate was cut on one side and carefully placed into a plastic bottle filled with 250 ml of ambient seawater. Then, the other side of the substrate was cut and placed inside the bottle, which was capped underwater (Jauzein et al., 2016).

In PB, the most abundant macrophytes, such as *Caulerpa filiformis*, *Chondracanthus chamissoi,* and *Ruppia maritima* were collected at 5 sites during June and November 2021, and April 2022. The sites were shallow (~ 1 m depth), whereas E1 and EM were 5 m and 10 m deep, respectively. A total of 24 samples were obtained. Additionally, surface water was sampled daily in E1 to evaluate the presence of EDs in the water (cells L^{-1}), and HOBO data loggers (Onset UA-001-64) recorded surface and bottom temperatures every 20 minutes.

Environmental parameters (temperature, salinity, dissolved oxygen, and chlorophyll a) were measured in both PB and EUL using EXO (YSI) multiparameter

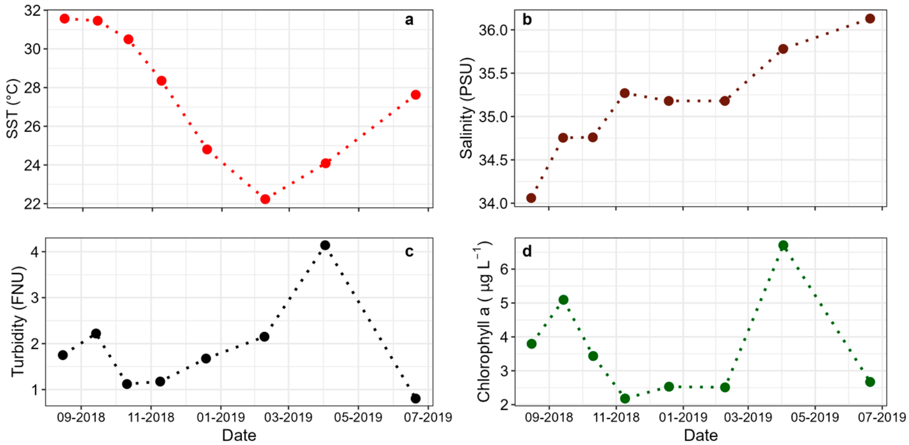

Figure 2. Mean values of the sea surface temperature (SST in °C). a) Salinity (PSU; b), turbidity (in nephelometric turbidity units, NTU); c) chlorophyll a concentration (in µg L^{-1}; d) in the Estero de Urías Lagoon, at the entrance of the Gulf of California.

sondes. In EUL, the chlorophyll a sensor was calibrated using rhodamine standards according to the manufacture's guidelines (YSI Inc., 2014), allowing chlorophyll a concentrations to be expressed in absolute units (µg L^{-1}). In contrast, no calibration was performed in PB; thus, chlorophyll a values are reported in RFU (relative fluorescence units), reflecting the raw sensor response. Although not directly comparable to absolute concentrations, RFU values are widely used to identify temporal patterns in relative chlorophyll a concentrations (Foster et al., 2022). In the EUL, measurements were taken near the sampling sites (1-2 km) at stations 3 and 4 for the coastal observatory of global change in Mazatlán (Fig. 1 in Sanchez-Cabeza et al., 2019) and at station E1 for PB.

In the laboratory, the bags with macrophytes and bottles with artificial substrates were vigorously agitated for 2 minutes. The suspension was filtered through sieves with 250 µm, 150 µm, and 20 µm mesh to remove larger particles. The fraction retained in the 20 µm sieve was concentrated and transferred to a vial of 50 ml filled with seawater filtered through Whatman GF/F filters (nominal pore size ~ 0.7 µm), and preserved with 1% acidic Lugol's iodine fixative. The EDs counting was performed on 3 replicate subsamples from the same macrophyte sample, using a Sedgwick-Rafter chamber in an optical microscope (LM Leica DMR, Wetzlar, Germany) with 200× magnification. Cell abundances were reported as cells per g w.w. of macrophyte (Reguera et al., 2011). The reported uncertainty is the standard deviation of the mean of 3 replicate counts.

The Shapiro test confirmed that species densities were not normally distributed. Therefore, Kruskal-Wallis one-way ANOVA and Dunn's multiple comparison post hoc tests were used to assess whether abundances and environmental variables exhibited significant variations during the study period. The significance level (α) was set at < 0.05. All analyses and plots were performed with R version 2024.04.2 (R Core Team, 2024).

Results

Estero de Urías Lagoon

During the study period, the sea surface temperature (SST) varied from 22.2 to 31.6 °C, salinity from 34.0 to 36.1, turbidity from 0.8 to 4.1 NTU, and chlorophyll a from 2.2 to 6.7 mg L^{-1}. The highest SST was observed in August-September, 2018 (Fig. 2).

No EDs were observed attached to the artificial substrates in the EUL. Macroalgae were not found in EU2 in November 2018 and June 2019. Dinoflagellates on the EUL macroalgae belonged to the genus *Prorocentrum*; the highest abundances corresponded to *P. micans* (Supplementary material; Fig. S1). *Prorocentrum lima* complex was frequently observed in the samples, with abundances ranging from 0 to 78±45 cells g^{-1}. No significant differences in the abundances were observed between seasons or among stations (Fig. 3a, b). Spearman's correlation between the abundances of EDs and environmental variables was not significant.

Paracas Bay

During the study period, temperatures were from 14.1 to 22.2 °C. The sea surface and bottom temperatures were significantly higher in autumn (surface temperatures: 18.0-22.2 °C; bottom temperatures: 17.5-21.6 °C) than

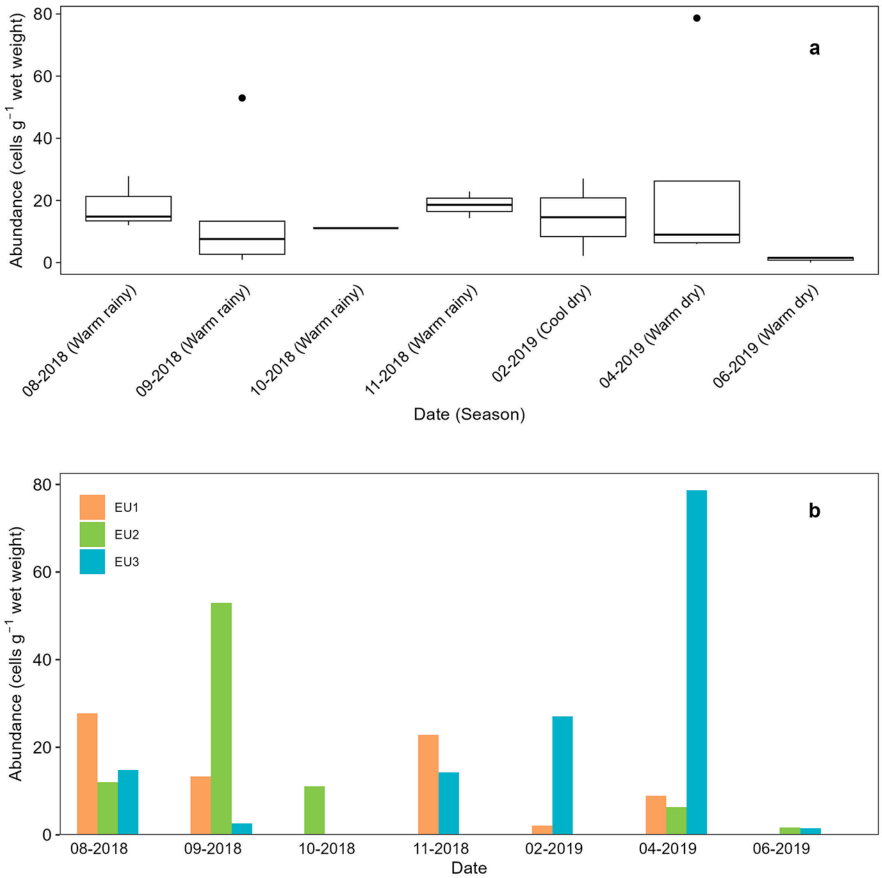

Figure 3. a) Abundance of the *Prorocentrum lima* complex, with seasons indicated in parentheses. Boxplots show the median (horizontal line), the interquartile range (the difference between the third and first quartile; box). Whiskers extend to values within 1.5 times the interquartile range, and data beyond this range are shown as outliers (dots); b, total abundance by station sites in the Estero de Urías Lagoon, located at the entrance of the Gulf of California.

in summer and spring (surface temperatures: 14.5-22.1 °C; bottom temperatures: 14.1-19.7 °C; Fig. 4a). In the 3 seasons, the surface temperatures were significantly higher than the bottom temperatures. When the *P. lima* complex was observed in the water column and associated with macrophytes (May 14-Jun 04), SST ranged from 18.0 to 22.2 °C. Chlorophyll a ranged from 0.45 to 7.12 RFU. The highest values were observed in autumn, while spring and summer values were similar. The salinity varied between 34.4 and 35.2, with higher values in autumn than in spring and summer (4b).

In Paracas Bay, EDs were absent during most of the study period, and the *P. lima* complex was detected only in the austral autumn (June 2-4, 2021; Fig. 5, Table 1) with the highest abundances (867±172 cells g^{-1} in station E3). The *P. lima* complex was attached mostly to *C. filiformis* (Table 1).

According to the high-frequency monitoring of *Prorocentrum* species in surface water, *P. micans* was a common dinoflagellate in austral autumn and summer, and its abundances were from 40 to 1,840 cells L^{-1} (Supplementary material; Fig. S2). The *P. lima* complex was observed only in the austral autumn with a maximum abundance (1,360 cell L^{-1}) on May 14, and between May 17 and June 01, its abundances were ≤ 280 cells L^{-1} (Fig. 4c).

Discussion

Artificial substrates have been successfully used for quantifying and monitoring EDs, particularly in sheltered, shallow, and subtidal sites (Tester et al., 2022). The lack of EDs attached to the artificial substrates in EUL is likely related to the low abundance of these organisms and the lagoon's turbulent hydrodynamics.

Table 1
Abundance of *Prorocentrum* species in Paracas Bay in the austral autumn.

Species	Date	Season	Station	Macrophyte species	Abundance (cells g wet weight)*
Prorocentrum lima complex	2021-06-02	Autumn	E3	*Caulerpa filiformis*	861±172
Prorocentrum lima complex	2021-06-02	Autumn	E3	*Caulerpa filiformis*	250±17
Prorocentrum lima complex	2021-06-02	Autumn	E3	*Caulerpa filiformis*	13±3
Prorocentrum micans	2021-06-02	Autumn	E3	*Caulerpa filiformis*	6±5
Prorocentrum lima complex	2021-06-04	Autumn	E3	*Chondracanthus chamissoi* +*Ulva* sp.	0
Prorocentrum lima complex	2021-06-04	Autumn	E3	Red algae	0
Prorocentrum lima complex	2021-06-04	Autumn	E3	Red algae	0
Prorocentrum lima complex	2021-06-04	Autumn	E4	*Chondracanthus chamissoi*	1±1
Prorocentrum lima complex	2021-06-04	Autumn	E4	*Ruppia marítima*	5±5
Prorocentrum lima complex	2021-06-04	Autumn	E4	*Ruppia maritima*	5±2

* Abundances represent the average of 3 independent counts performed on the same sample. Values are reported as the mean ± standard deviation.

Low abundances of EDs were also observed associated with macroalgae. These results agree with observations from the coast of Tonga in an area exposed to high wave action, where Argyle (2018) detected low abundances of *Gambierdiscus* cells in association with macrophytes, but the artificial substrate failed to collect them. In contrast, *Gambierdiscus* concentrations were high on natural and artificial substrates deployed at sheltered, shallow, and subtidal sites. Despite EUL mouth having the highest macroalgae diversity (Ochoa-Izaguirre et al., 2002), it is not a sheltered zone. It is influenced by the tidal regime since the energy available for water circulation is primarily provided by tidal pumping, with tidal velocities of up to 0.60 m s^{-1} at the main channel (Montaño-Ley et al., 2008). The EDs can be attached by coating mucus or can live freely within the macroalgae interstices, so the turbulence and currents make them vulnerable to cell dispersal. They are mainly found in areas with low to moderately low energy environments (Foden et al., 2005).

Among the *Prorocentrum* species associated with macrophytes in this study, only *P. lima* complex is recognized as a benthic species (Okolodkov et al., 2022), and it is the first time that *P. lima* complex is reported attached to macrophytes in EUL and PB. This cosmopolitan taxon is widely distributed in South America (Mafra et al., 2023). Although low abundances were observed in PB, *P. lima* has been recorded in the water column with abundances of up to $4.5x10^4$ cells L^{-1} (Cuellar-Martinez et al., 2023). *Caulerpa filiformis* is the most representative species in the macroalgae assemblage of PB (Olivas-Valverde, 2013), and the highest abundances of *P. lima complex* were observed on this species. Although information about the toxicity of *P. lima* complex is not available in strains from PB or EUL, reports worldwide reveal that all studied *P. lima* strains produce toxins related to DSP, such as okadaic acid, and several strains produce dinophysistoxins-1 (DTX1; Nishimura et al., 2020). Thus, monitoring this species on different substrates is relevant.

The presence of *P. lima* complex in both the water column and on macroalgae in Paracas Bay coincided with the highest temperatures recorded during the study period. Aissaoui et al. (2014) mentioned that this species

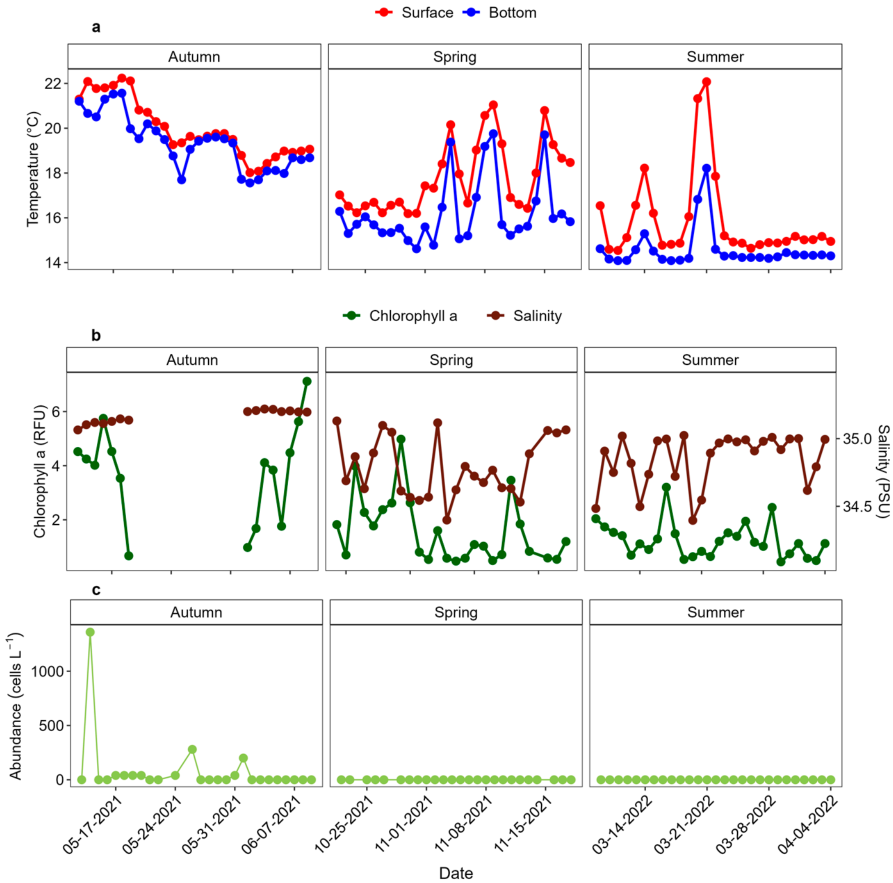

Figure 4. Surface and bottom temperatures (in °C). a) Surface salinity (PSU) and chlorophyll a (in relative fluorescence units, RFU; b), and seasonal abundances of *Prorocentrum lima* complex in surface waters (c) at the E1 station in Paracas Bay, Peru.

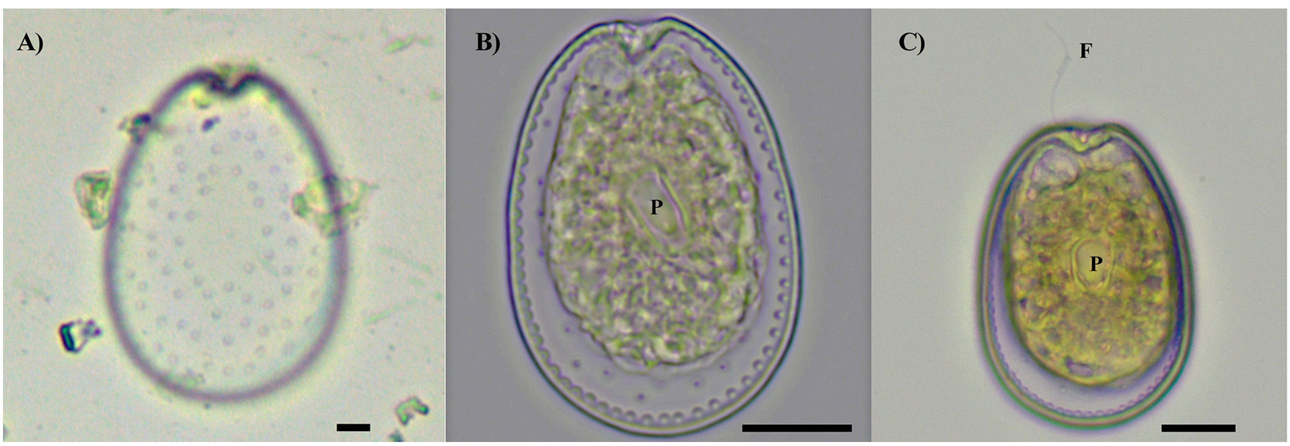

Figure 5. Vegetative cells of *Prorocentrum lima* complex collected from Paracas Bay, Peru, observed under light microscopy. A) Surface focus on a vegetative cell showing the pore pattern, B) cell showing pyrenoid (P), C) cell showing pyrenoid and flagellum. Scale bar: 10 µm.

appears to be eurythermal and euryhaline, as it grows over a wide interval of temperatures and salinities. In this work, *P. lima* complex was observed over a wide range of temperatures (18.0-31.6 °C), suggesting a remarkable ecological plasticity and ability to colonize diverse niches. Although *P. lima* complex was previously observed in PB at temperatures ranging from 15 to 25 °C (Mafra et al., 2023), in this study it was detected during autumn, when the highest temperatures reached 17.5-22.2 °C. Aquino-Cruz et al. (2018) highlighted the importance of temperature on cell growth rates, toxin levels, and photosynthetic efficiency. They determined that the optimum growth of *P. lima* strains from the United Kingdom occurred at 15-25 °C, with an increment in the production of okadaic acid at 15 °C.

Temperatures also affect the range of species distribution. It is expected that warmer temperatures associated with climate change could benefit harmful benthic dinoflagellate species, expanding their geographical distribution range (Tester et al., 2020). Another factor associated with distribution expansion is the artificial introduction of discharged ballast ship water (Park et al., 2021). The sampling period of this study limits the potential for making strong extrapolations regarding the temporal dynamics of the DEs and their ecological dynamics. Nevertheless, the detection of DEs with potential toxin production is a relevant finding that highlights the need for longer-term monitoring to better understand their ecological dynamics and potential harmful implications for environmental health and human activities.

The epibenthic dinoflagellate community was explored at 2 sites influenced by upwellings: Estero de Urías Lagoon, at the entrance to the Gulf of California, and Paracas Bay, off south-central Peru. The *Prorocentrum lima* complex was commonly found with low abundances, mainly associated with macrophytes in Estero de Urías Lagoon and sporadically detected in Paracas Bay (mainly on *Caulerpa filiformis)*. In the water column of Paracas Bay, the *P. lima* complex was observed during the period with the highest recorded temperature in the study, suggesting potential environmental influences. These initial findings highlight the need for long-term studies with higher temporal resolution and increased detection frequency to better understand the environmental relationships of the benthic dinoflagellate at the studied sites. Given the known production of diarrhetic shellfish toxins by *P. lima*, its possible sensitivity to climate-related changes, and the anthropogenic pressures present in both study areas —such as intense marine traffic— further monitoring and multidisciplinary research, including toxicological, physiological, and molecular studies, are strongly recommended to assess the potential risks posed by *P. lima* to marine ecosystems and public health.

Acknowledgments

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