Continental shelf off northern Chilean Patagonia: A potential risk zone for the onset of Alexandrium catenella toxic bloom?

Article *in* Marine Pollution Bulletin · September 2022

DOI: 10.1016/j.marpolbul.2022.114103

Camilo Rodríguez-Villegas
Universidad de Los Lagos

Rosa Isabel Figueroa
Instituto Español de Oceanografia

Iván Ernesto Pérez Santos
Centro i-mar, Universidad de Los Lagos, Puerto Montt

Carlos Molinet
Universidad Austral de Chile

Marine Pollution Bulletin 184 (2022) 114103

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Baseline

Continental shelf off northern Chilean Patagonia: A potential risk zone for the onset of *Alexandrium catenella* toxic bloom?

Camilo Rodríguez-Villegas [a,b,c], Rosa I. Figueroa [d], Iván Pérez-Santos [b,e,f], Carlos Molinet [g,h], Gonzalo S. Saldías [e,i,j,k], Sergio A. Rosales [l], Gonzalo Álvarez [m,n], Pamela Linford [a], Patricio A. Díaz [b,c,*]

[a] *Programa de Doctorado en Ciencias, Mención Conservación y Manejo de Recursos Naturales, Universidad de Los Lagos, Camino Chinquihue km 6, Puerto Montt, Chile*
[b] *Centro i~mar, Universidad de Los Lagos, Casilla 557, Puerto Montt, Chile*
[c] *CeBiB, Universidad de Los Lagos, Casilla 557, Puerto Montt, Chile*
[d] *Centro Oceanográfico de Vigo, Instituto Español de Oceanografía (IEO-CSIC), Subida a Radio Faro 50, 36390 Vigo, Spain*
[e] *Centro de Investigación Oceanográfica COPAS COASTAL, Universidad de Concepción, Concepción, Chile*
[f] *Centro de Investigaciones en Ecosistemas de la Patagonia (CIEP), Coyhaique, Chile*
[g] *Programa de Investigación Pesquera, Instituto de Acuicultura, Universidad Austral de Chile, Puerto Montt, Chile*
[h] *Programa Integrativo, Centro Interdisciplinario para la Investigación Acuícola (INCAR), Concepción, Chile*
[i] *Departamento de Física, Facultad de Ciencias, Universidad del Bío-Bío, Concepción, Chile*
[j] *Instituto Milenio en Socio-Ecología Costera (SECOS), Santiago, Chile*
[k] *Centro de Investigación en Dinámica de Ecosistemas Marinos de Altas Latitudes (IDEAL), Valdivia, Chile*
[l] *Departamento de Biología Marina, Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo, Chile*
[m] *Facultad de Ciencias del Mar, Departamento de Acuicultura, Universidad Católica del Norte, Coquimbo 1281, Chile*
[n] *Centro de Investigación y Desarrollo Tecnológico en Algas (CIDTA), Facultad de Ciencias del Mar, Universidad Católica del Norte, Coquimbo 1281, Chile*

ARTICLE INFO

Keywords:
Alexandrium catenella
Paralytic shellfish toxins (PST)
Cyst beds
Upwelling
Submarine canyons
Chilean Patagonia

ABSTRACT

Harmful Algal Blooms (HAB) pose a severe socio-economic problem worldwide. The dinoflagellate species *Alexandrium catenella* produces potent neurotoxins called saxitoxins (STXs) and its blooms are associated with the human intoxication named Paralytic Shellfish Poisoning (PSP). Knowing where and how these blooms originate is crucial to predict blooms. Most studies in the Chilean Patagonia, were focused on coastal areas, considering that blooms from the adjacent oceanic region are almost non-existent. Using a combination of field studies and modelling approaches, we first evaluated the role of the continental shelf off northern Chilean Patagonia as a source of *A. catenella* resting cysts, which may act as inoculum for their toxic coastal blooms. This area is characterized by a seasonal upwelling system with positive Ekman pumping during spring-summer, and by the presence of six major submarine canyons. We found out that these submarine canyons increase the vertical advection of bottom waters, and thus, significantly enhance the process of coastal upwelling. This is a previously unreported factor, among those involved in bloom initiation. This finding put this offshore area at high risk of resuspension of resting cysts of *A. catenella*. Here, we discuss in detail the physical processes promoting this resuspension.

The narrow transition zone between the ocean and the continent has significant effects on the welfare of society, including health, leisure, and economy (Vila et al., 2021). Chile's coastal system has experienced relevant problems on welfare over the last fifty years. In particular, Harmful Algal Blooms (HABs) have caused important and direct negative economic impacts, since they have led to bans on the extraction of shellfish and massive fish death, affecting the aquaculture industry (e.g. Anderson et al., 2012; Díaz et al., 2019).

The dinoflagellate species *Alexandrium catenella* produces the Paralytic Shellfish Toxins (PST), one of the most potent groups of natural neurotoxins that cause Paralytic Shellfish Poisoning (PSP) (Fraga et al., 2015). Events of PSP are more frequent and intense in the southernmost regions of Chile (Aysén and Magallanes) (Molinet et al., 2003). PST are accumulated in plankton feeders (mainly bivalves) (Bricelj and

* Corresponding author at: Centro i~mar & CeBiB, Universidad de Los Lagos, Casilla 557, Puerto Montt, Chile.
E-mail address: patricio.diaz@ulagos.cl (P.A. Díaz).

https://doi.org/10.1016/j.marpolbul.2022.114103
Received 3 June 2022; Received in revised form 1 September 2022; Accepted 2 September 2022
Available online 15 September 2022

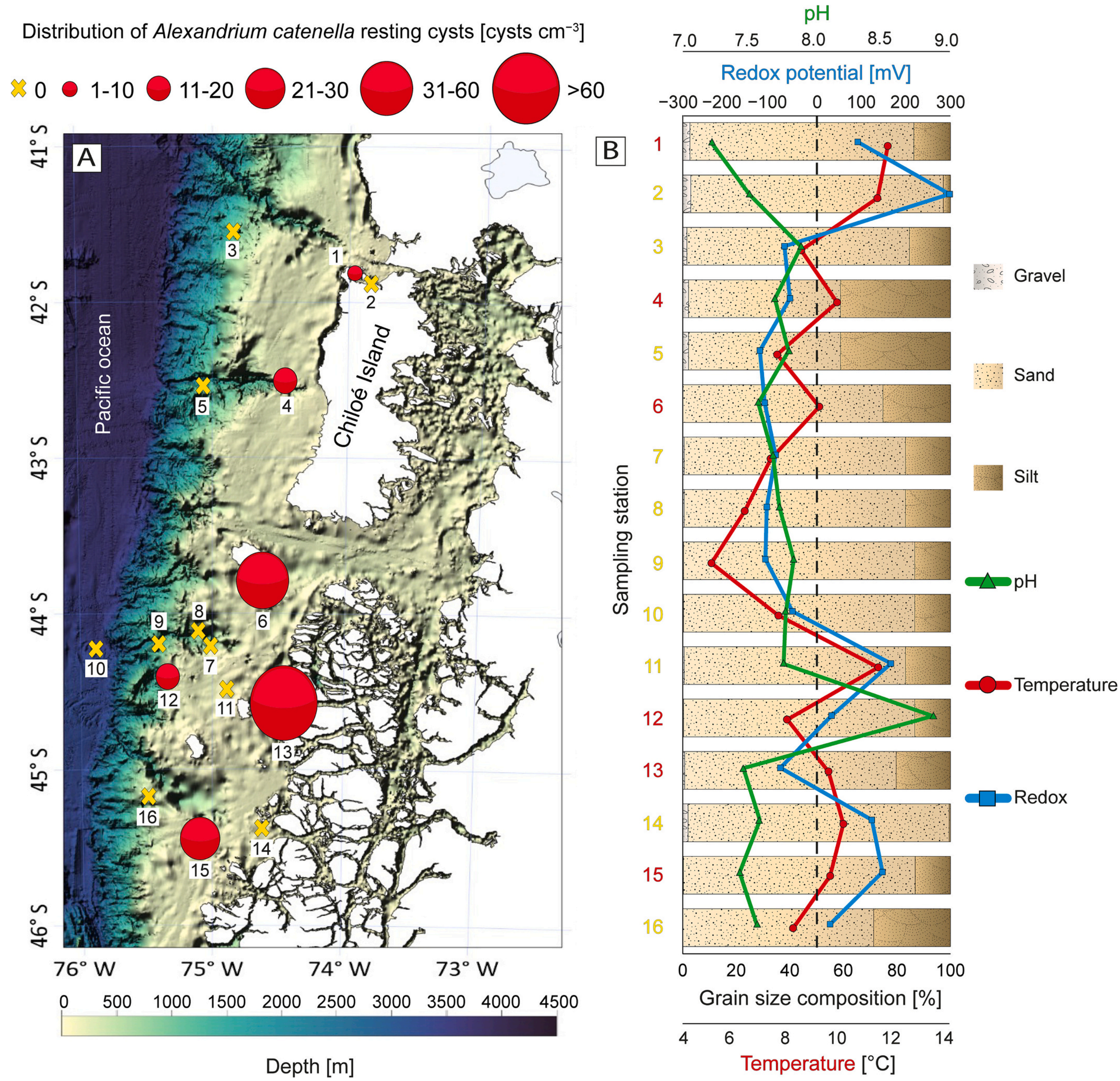

Fig. 1. Study area in the continental shelf off northern Patagonia. A) Bathymetric map showing the spatial variability of *Alexandrium catenella* resting cysts abundance. Red circles and yellow crosses show the sampling stations with the presence and absence of *A. catenella* resting cyst, respectively; B) spatial variability of grain size composition (%), sediment temperature (°C), pH, and redox potential (mV) recorded at each sampling station. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Shumway, 1998; Schantz, 1986; Wiese et al., 2010) and, when regulatory limits for their accumulation are exceeded (~80 μg STX eq. 100 g^{-1} meat), the extraction and commercialization of shellfish are banned to prevent health problems (Fernández et al., 2003). During *A. catenella* blooms, resting cyst are formed through gamete fusion between strains showing sexual compatibility (complex heterothallism) (Rodríguez-Villegas et al., 2021a). After fulfilling their physiological maturation period (mandatory dormancy), and if appropriate environmental conditions are provided (light, temperature, oxygen), the cysts can germinate, potentially leading to a new harmful event (Bravo and Figueroa, 2014; Díaz et al., 2014; Díaz et al., 2018). During the summers of 2009, 2016, and 2018, there were three *A. catenella* blooms in southern Chile, which reached remarkably high cell densities (5.0×10^6, 2.5×10^5, and 1.2×10^6 cells L^{-1}, respectively) (Álvarez et al., 2019; Armijo et al., 2020; Díaz et al., 2014; Hernández et al., 2016; Trainer et al., 2020). This caused an alarm for a possible recrudescence of the PSP events in intensity but, also in space, as blooms seem to spread geographically (Armijo et al., 2020; Guzmán et al., 2002; Molinet et al., 2003; Rodríguez-Villegas et al., 2020). During the summer of 2018, a global historical maximum of 143,000 μg STX eq. 100 g^{-1} was detected in mussels from the Aysén region (Díaz et al., 2019; Guzmán et al., 2018). In this region there are small-scale benthic fisheries (such as the national Management and Exploitation Areas of Benthic Resources, MEABRS) (Castilla and Fernandez, 1998) and marine indigenous areas (such as

Coastal and Marine Spaces of Indigenous People, ECMPO) (Araos et al., 2020). As a consequence of these serious bloom events, aquaculture farms (mussels and salmonids) are expanding towards offshore waters, where these episodes are supposed to be rare. However, not specific risk assessment studies are available for those areas, and thus, it is urgent to specifically evaluate the risk factors meeting in the new cultivation areas in order to establish appropriate measurements, and thus minimize losses for the aquaculture sector.

Current Chilean monitoring programs are principally focused on inland waters (austral fjords and channels); and consequently, the planktonic–benthic dynamic of *A. catenella* cells in the adjacent continental shelf is practically unknown (Espinoza-González et al., 2021). Summarizing, we have addressed here a main question: Is it negligible the risk of resting cyst resuspension and bloom initiation in deep, offshore waters of the Chilean Patagonia, regarding the toxic species *A. catenella*? For answering that question, we present data on the distribution of *A. catenella* resting cysts from the continental shelf off northern Patagonia, and for the first time, we inspect modelling results to understand how resting cysts can be resuspended from deep sediments, to eventually germinate, posing a real risk for *A. catenella* blooms in the coastal waters of the continental shelf of Chilean Patagonia.

The study area is located in the northern area of the Chilean Patagonia (Fig. 1A), which is part of one of the most extensive estuarine regions worldwide (Pantoja et al., 2011), with elevated freshwater inputs from rivers and ice melting (Dávila et al., 2002). This creates a zonal salinity gradient that extends offshore by ~4° (Saldías et al., 2019). The irregular topography/bathymetry is characterized by islands, channels, sills, rivers, glaciers, etc., highlighting the geographic complexity of this remote coastal system. There are just few oceanographic studies of the coastal ocean off northern Patagonia, with most studies conducted in the Inner Sea of Chiloé (e.g., Pantoja et al., 2011, and references therein). The seasonal variability of sea surface temperature reveals a coastal band of cold water during spring-summer off Chiloé Island (Saldías et al., 2021b), which is coherent with the northward wind stress field during summer (Pérez-Santos et al., 2019).

To estimate resting cyst abundance in the analyzed area, recent sediments were sampled at 16 stations (hereafter st.) from the oceanic region off Northern Patagonia, using a 0.1 m^2 Van Veen grab during the austral spring of 2017 ($n = 2$) and 2018 ($n = 14$) (Fig. 1A). Three subsamples for *A. catenella* resting cysts were obtained from the top 3 cm of the grab using a plastic corer of 8 cm length × 6 cm diameter. To avoid stimulating cyst germination by oxygen, light, and temperature changes, air bubbles were manually released from each sub-sample that was then wrapped in aluminum foil and preserved at 4 °C. In the laboratory, the *A. catenella* resting cysts were extracted following the procedures outlined by Matsuoka and Fukuyo (2000), with slight modifications as described by Rodríguez-Villegas et al. (2021b).

Simultaneously, three records of temperature, pH, and redox potential (hereafter redox) were taken at haphazard positions in each Van Veen grab from the sediment surface, using a pre-calibrated multiparameter portable MultiLine® meter (Multi 3620 IDS probe, WTW) with electrodes designed for measuring semisolids. pH was recorded with a conic electrode with Teflon, fiber, and ceramic triple union, and temperature compensation. Redox was determined with a platinum sensor Ag/AgCl saturated (3.5 M KCL) with gel/polymer electrolyte. All measurements were made according to the Chilean standard ISO NCh: 17025 of 2005.

To determine sediment granulometry, three sediment samples were collected (~50 g^{-1}), freeze-dried, and then separated using a series of sieves (500, 250, 150, 90, and 63 μm). Each sample was shaken for 15 min in a mechanical sieve shaker (Gilson Company, Inc.). Then, we recorded the weights of the sediment fractions retained in each sieve and in the pan (<63 μm). These data were then used to calculate the granulometry parameters using the rysgran package in R (De Camargo, 2016). The grain size composition of sediment was categorized using the Wentworth scale chart (Wentworth, 1922) as follows: gravel ≥2000 μm, sand 63–2000 μm, and silt ≤63 μm. To summarize and characterize each sampling station, the three sediment subsamples were averaged.

Finally, we calculated median values with Inter Quartile Range (IQR) for the physical-chemical description of the sediment, and arithmetic mean values with standard deviations for the definition of the abundance of *A. catenella* cyst.

The surface wind dataset was obtained from the ERA5 reanalysis, and the daily gridded (0.25° × 0.25°) ocean surface wind vectors were downloaded from Copernicus Climate Data Store (https://cds.climate.copernicus.eu). This dataset was used to calculate the zonal and meridional components of the wind stress according to Yelland and Taylor (1996). The surface Ekman transport was calculated for each grid point of the ERA5 data (Smith, 1968), and the depth of the surface Ekman layer was computed as in Pond and Pickard (1983) for latitudes outside ±10° from the Equator. Finally, the Ekman pumping velocity was calculated according to Smith (1968).

Hydrodynamic data from the regional model HYCOM (HYbrid Coordinate Ocean Model) were used to perform numerical simulations of particle dispersion. Data for January 2016, 2017, 2018, and 2019 were obtained from the model website (www.hycom.org). The simulations were run with the lagrangian model OpenDrift (Dagestad et al., 2018). Thus, 276 particles distributed in a regular grid were released at the depth of 200, 150, 100, and 0 m, and followed for six days. Finally, the model was configured with outputs every 3 h.

In this study, we used field sampling, oceanographical, and modelling approaches and present conclusive results on the risk of *A. catenella* bloom initiation - through resting cyst resuspension, germination and cell growth - in the adjacent oceanic areas of the fjord system of northern Patagonia. Our risk assessment is based on the following indicators:

Resting cysts were found in 36 % of the sampling stations with abundances ranging from 2 to 68 cysts cm^{-3} (9.6 ± 18.4; $n = 16$; Fig. 1A). The highest abundance was recorded at st.13 and the lowest at st. 1, at 168 m and 18 m depth, respectively (Fig. 1A). St.1 was the only site where we found empty cysts of *A. catenella* even in high abundance (~44 empty cysts cm^{-3}; data not shown). These cysts abundances are relatively low when compared to values reported in sediments from other regions of the world with abundance up to 9000-cyst cm^{-3} (White and Lewis, 1982). Nevertheless, these low *A. catenella* cysts abundance (small inoculum) contrasting with the intense blooms recorded in the last years in the Chilean fjords (Díaz et al., 2022).

All resting cysts were deposited in sediments that were mostly composed of fine sand (median = 82.9 %, IQR = 8.40), followed by silt (median = 16.1 %, IQR = 8.19), and gravel (median = 0.51 %, IQR = 1.68) (Fig. 1B). Moreover, they were found in sediments with a median temperature of 8.74 °C (IQR = 2.73), a pH of 7.68 (IQR = 0.23), and a redox of −57.90 mV (IQR = 197.63) (Fig. 1B).

Previous results revealed that not only cysts are formed in the studied area, but also that germination processes occur and contribute to the population dynamics of this toxic species in the water column (Díaz et al., 2014; Rodríguez-Villegas et al., 2021b, 2022). Indeed, *A. catenella* strains isolated from oceanic areas (Bahía Mansa, ~40.6°S) showed a higher reproductive compatibility index than other strains, and this factor is directly proportional to resting cysts production (Rodríguez-Villegas et al., 2021a). Moreover, cyst germination, either *in situ* or via resuspension into the water column through advective flows, enhances the potential PST outbreak risk. Recent toxins profiles from oceanic strains (Bahía Mansa ~40.6°S and Bahía Coliumo ~36°S) showed a high concentration of toxins per cell. In these strains, there was a prevalence of C2, C1, GTX3, GTX4 (Rodríguez-Villegas et al., 2021a), and GTX5 (Paredes-Mella et al., 2021) toxins, that could be accumulated in different tissues of filter-feeding bivalves. Some of these toxins (principally C1 and C2) could be then biotransformed to more toxic and more thermodynamically stable forms (e.g., GTX1, GTX2, and STX) by enzymatic activities (Oshima, 1995; Oyaneder-Terrazas et al., 2017).

The influence of wind on the ocean surface layer contributes to the vertical mixing of the water column, favoring the input of nutrients to

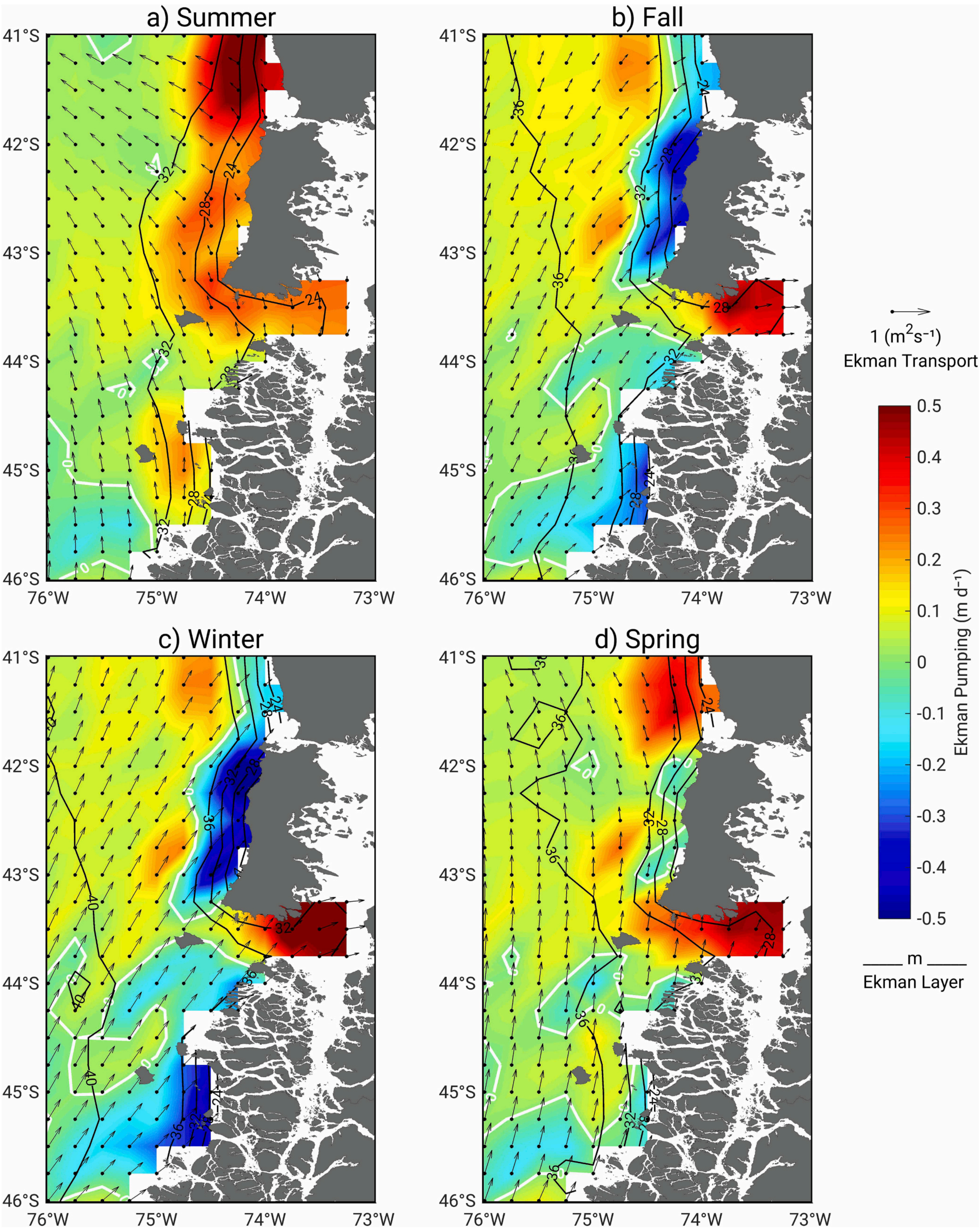

Fig. 2. Long-term mean of the seasonal surface Ekman transport (m^2s^{-1}; grey arrows), Ekman pumping ($m\ d^{-1}$; color-coded), and Ekman layer depth (m; black lines) computed between 2016 and 2020. The white lines represent the 0 values of Ekman pumping, and positive/negative records represent upwelling/downwelling conditions.

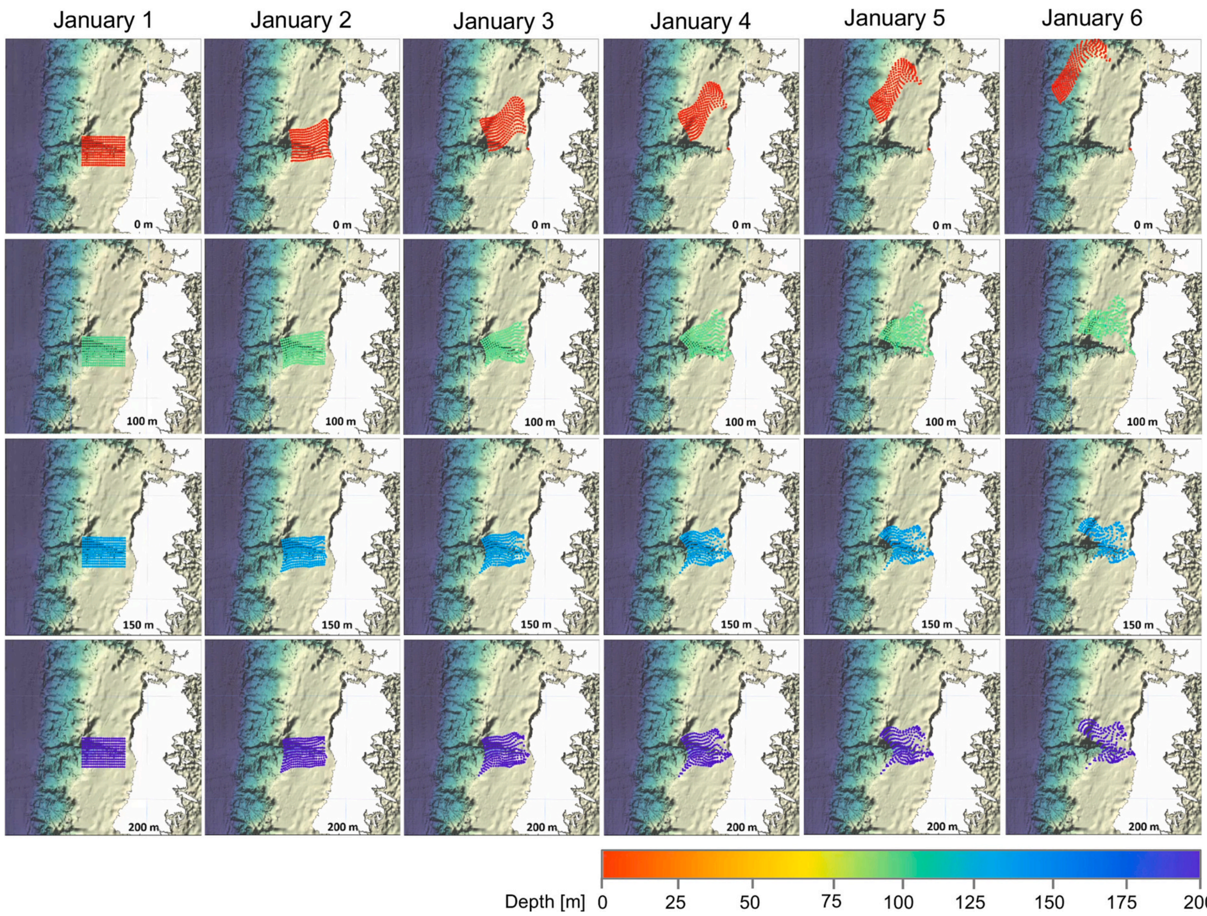

Fig. 3. Six-day evolution of particles released from the continental shelf off Chiloé island over the Cucao submarine canyon at four fixed depths (0, 100, 150, and 200 m) obtained from HYCOM forecast model simulations between January 1–6, 2016.

the photic layer, and therefore, increasing the primary production (Tomczak and Godfrey, 1994). Also, the alongshore wind stress forces the upwelling/downwelling of coastal waters (Bakun, 1973). Therefore, the upwelling process is another mechanism favoring the vertical advection of subsurface waters, activating the biological production of plankton. Along the coastal area of Chile, upwelling conditions by Ekman transport (ET) and Ekman pumping (EP) mainly dominate during spring-summer (Bravo et al., 2016) because of the influence of the southeast Pacific subtropical anticyclone (Rahn and Garreaud, 2013; Schneider et al., 2017). Recently, upwelling was reported up to 44°S, evidencing an increase in chlorophyll-*a* and a decrease in the temperature of the sea surface off Chiloé island (Narváez et al., 2019; Pérez-Santos et al., 2019). The long-term seasonal mean of the offshore ET and upward velocity of EP confirmed the occurrence of upwelling during summer from ~41° to 46°S. The occurrence of these processes extended offshore to ~75°W, showing an Ekman layer depth from 24 to 32 m. The EP was less intense during the spring season, and the ET was parallel to the coastline, whereas downwelling conditions dominate in fall and winter with onshore ET and downward EP flow (Fig. 2).

The analysis of the influence of the surface wind as a process favoring upwelling demonstrated that both ET and EP contribute to the vertical ascent of subsurface waters in summer. Furthermore, the occurrence of these processes in the area where the greatest abundance of toxic cysts of *A. catenella* were detected, despite being relatively small when compared to values reported in sediments from other regions of the world (up to 9000 cysts cm^{-3}; White and Lewis, 1982), supports the hypothesis that ET and EP could favor the deposition and resuspension of the cysts. If *A. catenella* mature cysts are transported into the photic layer, they can found there environmental conditions (temperature, light, nutrients, etc.) are generally compatible to their vegetative growth. Therefore, reaching the photic zone, and the stability and depth of it, determines the chances for bloom initiation, given that a critical number of cells are needed to successfully initiate a bloom (Estrada et al., 2010). Considering an average vertical advection of ~0.2–0.5 m d^{-1} off Chiloé Island in summer (Fig. 2), an accumulated effect with the rise of 2–5 m would occur in only ten days and could transport the cysts to the surface. There, they can germinate and eventually originate a bloom in a couple of months.

The particles, from model simulation, released over the canyon off Chiloé Island showed on the surface a clear relation with the coast and the oceanographic conditions generated by the horizontal gradients of density, wind conditions, and the influence of ET and EP (Fig. 3; Supplementary). At the same time, the particles released at 200, 150, and 100 m showed the effect of the topography in combination with the horizontal gradients of density, and the influence of ET and EP. According to the ET and EP conditions, the particles released at depth approach the coast through the canyon, which would probably cause the cysts to be transported to shallow waters (see Supplementary).

Similarly, Butman et al. (2014) and Amorim et al. (2014) showed that the location of the benthic seed-beds of the PST-producing species *A. catenella* (previously *A. fundyense*) and *Gymnodinium catenatum* could be geographically located far away from where a pelagic bloom was initiated. Moreover, they could be as deep as 100–250 m. In this context, we describe a novel factor increasing the vertical advection of bottom waters: submarine canyons (Fig. 1A). Indeed, in response to alongshore winds, the process of coastal upwelling is significantly increased by the presence of submarine canyons (Saldías and Allen, 2020). This is due to non-linear ageostrophic circulation balancing the cross-shore advection of subsurface waters around a submarine canyon, and the passage of coastal trapped waves over it (Saldías et al., 2021a). The passage of these waves perturbs the sea level promoting a cross-shore pressure gradient and enhancing the onshore transport of subsurface and bottom waters. This process even occurs in the absence of wind forcing. Recent analyses along the Chilean coast estimated the passage of coastal trapped waves with a period of about seven days (Sobarzo et al., 2016). These waves promoted the rise of cold waters with vertical displacements ranging from 29 to 137 m in the head of the Biobio canyon in a few days. Thus, the presence of about six major submarine canyons in the Los Lagos and Aysén regions (Fig. 1A) should promote frequent and strong upwelling events.

However, to better understand the small-scale variability of the circulation and verify the variability of these processes, a specific modelling study should be carried out. Finally we need to study the implications of these events in the resuspension of *A. catenella* resting cysts from sediments and its influence on the dynamics of the water column population for new PST outbreaks in this area.

Our study demonstrated that the offshore ET and upward velocity of EP occurred during summer, favoring upwelling along the coastal zone of the eastern austral Pacific Ocean (41° − 46° S). This contributes to the high abundance and resuspension of cysts of the toxic species *Alexandrium catenella*. This physical transport, in addition to upwelling advection by submarine canyons, can effectively make the cyst that sank to the sediments a source of viable cells able to trigger bloom formation. Our observations highlight the importance to establish the continental shelf off northern Patagonia as a risk zone for PST outbreaks. Management actions must be supported by monitoring programs to assure PST early warnings for all stakeholders in this area.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2022.114103.

CRediT authorship contribution statement

Camilo Rodríguez-Villegas: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization. **Rosa I. Figueroa:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Iván Pérez-Santos:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization. **Carlos Molinet:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization. **Gonzalo S. Saldías:** Methodology, Formal analysis, Writing – review & editing, Visualization. **Sergio A. Rosales:** Formal analysis, Investigation, Software, Writing - original draft, Writing - review & editing. **Gonzalo Álvarez:** Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Pamela Linford:** Software, Formal analysis, Investigation, Visualization. **Patricio A. Díaz:** Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Visualization, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: We have not financial interests/personal relationships which may be considered as potential competing interests.

Data availability

No data was used for the research described in the article.

Acknowledgements

This research has been primarily funded by the Centre for Biotechnology and Bioengineering (CeBiB) (PIA project FB0001, ANID, Chile). Camilo Rodríguez-Villegas was funded by a Ph.D. fellowship from the Universidad de Los Lagos. Rosa I. Figueroa was funded by a national project from the Spanish Ministry of Science and Innovation and the European Community (FEDER) (Project DIANAS-CTM2017-86066-R) and a grant for Galician Networks of Excellence (GRC-VGOHAB IN607A-2019/04) from the Innovation Agency of the Xunta de Galicia (GAIN). Iván Perez-Santos was funded by COPAS Sur-Austral (ANID AFB170006), COPAS COASTAL (ANID FB210021), CIEP R20F002, and FONDECYT 1211037. Carlos Molinet was partially financed by the FONDAP Project N°15110027 (INCAR). Gonzalo Saldías is partially funded by FONDECYT 1220167, the Millennium Science Initiative Program (Code ICN2019_015), and by COPAS COASTAL (ANID FB210021).

References

Álvarez, G., Díaz, P.A., Godoy, M., Araya, M., Ganuza, I., Pino, R., Álvarez, F., Rengel, J., Hernández, C., Uribe, E., Blanco, J., 2019. Paralytic shellfish toxins in *Mesodesma donacium* during an exceptional bloom of *Alexandrium catenella* associated to an intense mass mortality. Toxins 11, 188.

Amorim, A., Nolasco, R., Oliveira, P.B., Silva, T., Silva, A., Domingues, B., Brotas, V., Dubert, J., Moita, M.T., 2014. Seeding of *Gymnodinium catenatum* blooms on the Iberian shelf. In: ICES Annual Science Conference A Coruña, Spain, p. 2.

Anderson, D.M., Alpermann, T.J., Cembella, A., Collos, Y., Masseret, E., Montresor, M., 2012. The globally distributed genus *Alexandrium*: multifaceted roles in marine ecosystems and impacts on human health. Harmful Algae 14, 10–35.

Araos, F., Anbleyth-Evans, J., Riquelme, W., Hidalgo, C., Brañas, F., Catalán, E., Nuñez, D., Diestre, F., 2020. Marine indigenous areas: conservation assemblages for sustainability in southern Chile. Coast. Manag. 48, 289–307.

Armijo, J., Oerder, V., Auger, P., Bravo, A., Molina, E., 2020. The 2016 red tide crisis in southern Chile: possible in uence of the mass oceanic dumping of dead salmons. Mar. Pollut. Bull. 150, 110603.

Bakun, A., 1973. Coastal Upwelling Indices, West Coast of North America, 1946-71. U.S. Dep. Commer., NOAA Technical Report, NMFS SSRF-671.

Bravo, I., Figueroa, R.I., 2014. Towards an ecological understanding of dinoflagellate cyst functions. Microorganisms 2, 11–32.

Bravo, L., Ramos, M., Astudillo, O., Dewitte, B., Goubanova, K., 2016. Seasonal variability of the ekman transport and pumping in the upwelling system off Central-Northern Chile (~ 30° S) based on a high-resolution atmospheric regional model (WRF). Ocean Sci. 12, 1049–1065.

Bricelj, V.M., Shumway, S., 1998. Paralytic shellfish toxins in bivalve molluscs: occurrence, transfer kinetics, and biotransformation. Rev. Fish. Sci. 6, 315–383.

Butman, B., Aretxabaleta, A.L., Dickhudt, P.J., Dalyander, P.S., Sherwood, C.R., Anderson, D.M., Keafer, B.A., Signell, R.P., 2014. Investigating the importance of sediment resuspension in *Alexandrium fundyense* cyst population dynamics in the Gulf of Maine. Deep-Sea Res. II 103, 79–95.

Castilla, J.C., Fernandez, M., 1998. Small-scale benthic fisheries in Chile: on co-management and sustainable use of benthic invertebrates. Ecol. Appl. 8, 124–132.

Dagestad, K.-F., Röhrs, J., Breivik, O., Adlandsvik, B., 2018. OpenDrift v1.0: a generic framework for trajectory modelling. Geosci. Model Dev. 11, 1405–1420.

Dávila, P., Figueroa, D., Muller, E., 2002. Freshwater input into the coastal ocean and its relation with the salinity distribution of austral Chile (35–55°S). Cont. Shelf Res. 22, 521–534.

De Camargo, M.G., 2016. SysGran: um sistema de código aberto para análises granulométricas do sedimento. Rev. Bras. Geosci. 36, 371–378.

Díaz, P.A., Molinet, C., Seguel, M., Díaz, M., Labra, G., Figueroa, R., 2014. Coupling planktonic and benthic shifts during a bloom of *Alexandrium catenella* in southern Chile: implications for bloom dynamics and recurrence. Harmful Algae 40, 9–22.

Díaz, P.A., Molinet, C., Seguel, M., Díaz, M., Labra, G., Figueroa, R.I., 2018. Species diversity and abundance of dinoflagellate resting cysts seven months after a bloom of *Alexandrium catenella* in two contrasting coastal systems of the chilean Inland Sea. Eur. J. Phycol. https://doi.org/10.1080/09670262.09672018.01455111.

Díaz, P.A., Álvarez, A., Varela, D., Pérez-Santos, I., Díaz, M., Molinet, C., Seguel, M., Aguilera-Belmonte, A., Guzmán, L., Uribe, E., Rengel, J., Hernández, C., Segura, C., Figueroa, R.I., 2019. Impacts of harmful algal blooms on the aquaculture industry: Chile as a case study. Perspect. Phycol. 6, 39–50.

Díaz, P.A., Pérez-Santos, I., Schwerter, C., Arenas, S., Navarro, P., Mancilla-Gutiérrez, G., Barrera, F., 2022. Multi-specific harmful algal bloom in a Chilean fjord: a dangerous phytoplankton cocktail. Harmful Algae News 70.

Espinoza-González, O., Guzmán, L., Salgado, P., Carbonell, P., Norambuena, L., Cascales, E., Mardones, J., Paredes, J., Fuenzalida, G., Tardón, H., Espinoza, C., Cáceres, J., Lincoqueo, L., López, L., Labra, G., Correa, K., Olivares, B., González, R., Soto, C., Muñoz, V., Cornejo, M.F., Ramírez, L., 2021. Programa de Manejo y Monitoreo de las Floraciones Algales Nocivas y Toxinas Marinas en el Océano Pacífico del Centro Sur de Chile (36° - 44 °S), Etapa III, 2020 – 2021. Informe Final

(Tomo I y II). Mayo 2021. Subsecretaría de Economía y EMT. Instituto de Fomento Pesquero, 120 pp.
Estrada, M., Solé, J., Anglès, S., Garcés, E., 2010. The role of resting cysts in *Alexandrium minutum* population dynamics. Deep Sea Res. II 57, 308–321.
Fernández, M.L., Shumway, S.E., Blanco, J., 2003. Management of shellfish resources. In: Hallegraeff, G.M., Cembella, A., Anderson, D.M. (Eds.), Manual on Harmful Marine Microalgae. UNESCO Publishing, Paris, pp. 657–692.
Fraga, S., Sampedro, N., Larsen, J., Moestrup, Ø., Calado, A.J., 2015. Arguments against the proposal 2302 by John et al. to reject the name *Gonyaulax catenella* (*Alexandrium catenella*). Taxon 64, 634–635.
Guzmán, L., Pacheco, H., Pizarro, G., Alárcon, C., 2002. *Alexandrium catenella* y veneno paralizante de los mariscos en Chile. In: Sar, E.A., Ferrario, M.E., Reguera, B. (Eds.), Floraciones Algales Nocivas en el Cono Sur Americano. Instituto Español de Oceanografía, Madrid, pp. 235–255.
Guzmán, L., Espinoza-González, O., Pinilla, E., Besoain, V., Calderón, M.J., Cáceres, J., Iriarte, L., Muñoz, V., Martínez, R., Hernández, C., Tocornal, M.A., Carbonell, P., 2018. Atmospheric and oceanographic processes on the distribution and abundance of *Alexandrium catenella* in the North of Chilean fjords. In: The 18th International Conference on Harmful Algae, 21-26 Octubre, Nantes, France.
Hernández, C., Díaz, P.A., Molinet, C., Seguel, M., 2016. Exceptional climate anomalies and northwards expansion of paralytic shellfish poisoning outbreaks in southern Chile. Harmful Algae News 54, 1–2.
Matsuoka, K., Fukuyo, Y., 2000. Technical Guide for Modern Dinoflagellate Cyst Study. WESTPAC-HAB/WESTPAC/IOC, Japan.
Molinet, C., Lafón, A., Lembeye, G., Moreno, C.A., 2003. Patrones de distribución espacial y temporal de floraciones de *Alexandrium catenella* (Whedon & Kofoid) Balech 1985, en aguas interiores de la Patagonia noroccidental de Chile. Rev. Chil. Hist. Nat. 76, 681–698.
Narváez, D., Vargas, C., Cuevas, A., García-Loyola, S., Lara, C., Segura, C., Tapia, F., Broitman, B., 2019. Dominant scales of subtidal variability in coastal hydrography of the Northern Chilean Patagonia. J. Mar. Syst. 193, 59–73.
Oshima, Y., 1995. Chemical and enzymatic transformation of paralytic shellfish toxins in marine organisms. In: Lassus, P., Arzul, G., Erard-Le Denn, E., Gentien, P., Marcaillou-Le Baut, C. (Eds.), Harmful Marine Algal Blooms. Lavoisier Publishing ILP, Paris, pp. 475–480.
Oyaneder-Terrazas, J., Contreras, H.R., García, C., 2017. Prevalence, variability and bioconcentration of saxitoxin-group in different marine species present in the food chain. Toxins 9, 190.
Pantoja, S., Iriarte, J.L., Daneri, G., 2011. Oceanography of the Chilean Patagonia. Cont. Shelf Res. 31, 149–153.
Paredes-Mella, J., Mardones, J.I., Norambuena, L., Fuenzalida, G., Labra, G., Espinoza-González, O., Guzmán, L., 2021. Toxic *Alexandrium catenella* expanding northward along the Chilean coast: new risk of paralytic shell sh poisoning off the Bío-Bío region (36° S). Mar. Pollut. Bull. 172, 112783.
Pérez-Santos, I., Seguel, R., Schneider, W., Linford, P., Donoso, D., Navarro, E., Amaya-Cárcamo, C., Pinilla, E., Daneri, G., 2019. Synoptic-scale variability of surface winds and ocean response to atmospheric forcing in the eastern austral Pacific Ocean. Ocean Sci. Discuss. 15, 1247–1266.
Pond, S., Pickard, G.L., 1983. Introductory Dynamical Oceanography. Pergamon Press, Oxford.
Rahn, D., Garreaud, R., 2013. A synoptic climatology of the near-surface wind along the west coast of South America. Int. J. Climatol. 34, 780–792.
Rodríguez-Villegas, C., Díaz, P.A., Pizarro, G., Salgado, P., Pérez-Santos, I., Díaz, M., Seguel, M., Baldrich, A., Bravo, I., Iriarte, L., Figueroa, R.I., 2020. *Alexandrium catenella* cyst accumulation by passive and active dispersal agents: implications for the potential spreading risk in Chilean Patagonian fjords. Harmful Algae 96, 101832.
Rodríguez-Villegas, C., Díaz, P.A., Riobó, P., Rossignoli, A.E., Rodríguez, F., Loures, P., Baldrich, A., Varela, C., Sandoval-Sanhuesa, A., Figueroa, R.I., 2021a. Latitudinal variation in toxicity and sexual compatibility of Alexandrium catenella strains from southern Chile. Toxins 13, 900.
Rodríguez-Villegas, C., Lee, M., Salgado, P., Figueroa, R.I., Baldrich, A., Pérez-Santos, I., Tomasetti, S.J., Niklitschek, E., Díaz, M., Álvarez, G., Marín, S.L., Seguel, M., Díaz, P. A., 2021b. Drivers of dinoflagellate benthic cyst assemblages in the NW Patagonian Fjords System and its adjacent oceanic shelf, with a focus on harmful species. Sci. Total Environ. 785, 47378.
Rodríguez-Villegas, C., Díaz, P.A., Salgado, P., Tomasetti, S.J., Díaz, M., Marín, S.L., Baldrich, Á.M., Niklitschek, E., Pino, L., Matamala, T., Espinoza, K., Figueroa, R.I., 2022. The role of physico-chemical interactions in the seasonality of toxic dinoflagellate cyst assemblages: The case of the NW Patagonian fjords system. Environ. Pollut. 311, 119901 https://doi.org/10.1016/j.envpol.2022.119901.
Saldías, G., Allen, S., 2020. The influence of a submarine canyon on the circulation and cross-shore exchanges around an upwelling front. J. Phys. Ocenogr. 50, 1677–1698.
Saldías, G.S., Sobarzo, M., Quiñones, R., 2019. Freshwater structure and its seasonal variability off western Patagonia. Prog. Oceanogr. 174, 143–153.
Saldías, G., Ramos-Musalem, K., Allen, S.E., 2021a. Circulation and upwelling induced by coastal trapped waves over a submarine canyon in an idealized eastern boundary margin. Geophys. Res. Lett. 48, e2021GL093548.
Saldías, G.S., Hernández, W., Lara, C., Muñoz, R., Rojas, C., Vásquez, S., Pérez-Santos, I., Soto-Mardones, L., 2021. Seasonal variability of SST fronts in the inner sea of Chiloé and its adjacent coastal ocean, Northern Patagonia. Remote Sens. 13, 181.
Schantz, E.J., 1986. Chemistry and biology of saxitoxin and related toxins. Ann. NY Acad. Sci. 479, 15–23.
Schneider, W., Donoso, D., Garcés-Vargas, J., Escribano, R., 2017. Water-column cooling and sea surface salinity increase in the upwelling region off central-south Chile driven by a poleward displacement of the South Pacific High. Prog. Oceanogr. 151, 38–48.
Smith, R.L., 1968. In: Upwelling. Oceanography and Marine Biology—An Annual Review, 6, pp. 11–46.
Sobarzo, M., Saldías, G.S., Tapia, F.J., Bravo, L., Moffatt, C., Largier, J.L., 2016. On subsurface cooling associated with the Biobio River Canyon (Chile). J. Geophys. Res. Oceans 121, 4568–4584.
Tomczak, M., Godfrey, J.S., 1994. Regional Oceanography: An Introduction. Pergamon, Oxford, UK.
Trainer, V.L., Moore, S.K., Hallegraeff, G., Kudela, R.M., Clement, A., Mardones, J.I., Cochlan, W.P., 2020. Pelagic harmful algal blooms and climate change: lessons from nature's experiments with extremes. Harmful Algae 91, 101591.
Vila, M., Camp, J., Berdalet, E., 2021. Toxic microalgae and global change: why have proliferations increased along the Mediterranean coast? Mètode Sci. Stud. 11, 201–207.
Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. J. Geol. 30, 377–392.
White, A.W., Lewis, C.M., 1982. Resting cysts o the toxic, red tide dinoflagellate *Gonyaulax excavate* in Bay of Fundy sediments. Can. J. Fish. Aquat. Sci. 39, 1185–1194.
Wiese, M., D'agostino, P.M., Mihali, T.K., Moffitt, M.C., Neilan, B.A., 2010. Neurotoxic alkaloids: saxitoxin and its analogs. Mar. Drugs 8, 2185–2211.
Yelland, M., Taylor, P.K., 1996. Wind stress measurements from the open ocean. J. Phys. Ocenogr. 26, 541–558.