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Marine mammal mortality during a harmful algal bloom in the Southwestern Atlantic reveals trophic phycotoxin transfer and fetal exposure in sea lions

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In spring 2022, a harmful algal bloom in Golfo Nuevo, Argentina, coincided with widespread exposure to phycotoxins. Here we examined trophic transfer of toxins spanning from phytoplankton to higher trophic levels to quantify toxin transfer and bioaccumulation. High toxin levels were detected in phytoplankton, and elevated levels in mesozooplankton, mussels, and fish confirmed trophic transfer. The highest toxin levels in mesozooplankton occurred in southern right whale feeding areas, and fecal samples confirmed toxin uptake by whales. We also documented a mass mortality event in sea lions associated with algal-derived toxins, including evidence for maternal toxin transfer. During this period, ~10% of the local population was treated for gastrointestinal symptoms potentially linked to the bloom. These findings provide field-based evidence of harmful algal bloom-derived toxin dynamics in the Southwestern Atlantic, highlighting the need for sustained interdisciplinary monitoring and environmental risk assessment.

Marine Harmful Algal Blooms (HABs) are naturally occurring events caused by toxic phytoplankton species that can be lethal to both marine organisms and humans. HABs are a global issue and their records are increasing in frequency and geographic extent, thereby posing a substantial threat to ecosystem health[1,2]. During blooms, toxic algae are consumed by filter-feeding bivalves, zooplankton, and planktivorous fish, presenting substantial risks to marine wildlife, human health, and food safety[3,4]. Certain species associated with HABs produce neurotoxins that can cause severe neurological effects in marine mammals, including impaired sensory functions, seizures, loss of muscle coordination, respiratory failure, ataxia, and alterations in hematologic and endocrine parameters, potentially resulting in death[5–9]. During intense HAB events, the widespread distribution of toxic phytoplankton and the subsequent accumulation of toxins throughout marine food webs often lead to mass mortality events (MMEs), affecting multiple species across extensive geographic areas[10]. Two phycotoxins known to cause marine wildlife morbidity and mortality on a global scale are amnesic shellfish toxins (ASTs; domoic acid [DA] and its isomers) and paralytic shellfish toxins (PSTs; saxitoxin [STX] and its analogues)[11].

In the gulfs bordering Península Valdés in Argentina—Golfo San José (GSJ) in the north and Golfo Nuevo (GN) in the south (Fig. 1)—PSTs, ASTs, and lipophilic toxins (LTs; a toxin group that includes diarrheic shellfish toxins) are of primary concern due to their harmful effects on human health, particularly because of the artisanal harvesting of bivalve mollusks in GSJ. These toxins, especially PSTs, are frequently detected above regulatory limits in shellfish from these gulfs, leading to harvesting closures that cause major economic losses. Dinoflagellates of the genus *Alexandrium* are the primary producers of PSTs in South America[12], which are among the most potent phycotoxins known[13]. In higher mammals, acute exposure to PSTs can cause severe neuropathological effects, including death due to muscle paralysis, by blocking sodium channel activity involved in neuromuscular coordination[14]. Repeated exposure can, in turn, impair respiratory function in cetaceans and pinnipeds, disrupt feeding behavior, and affect the

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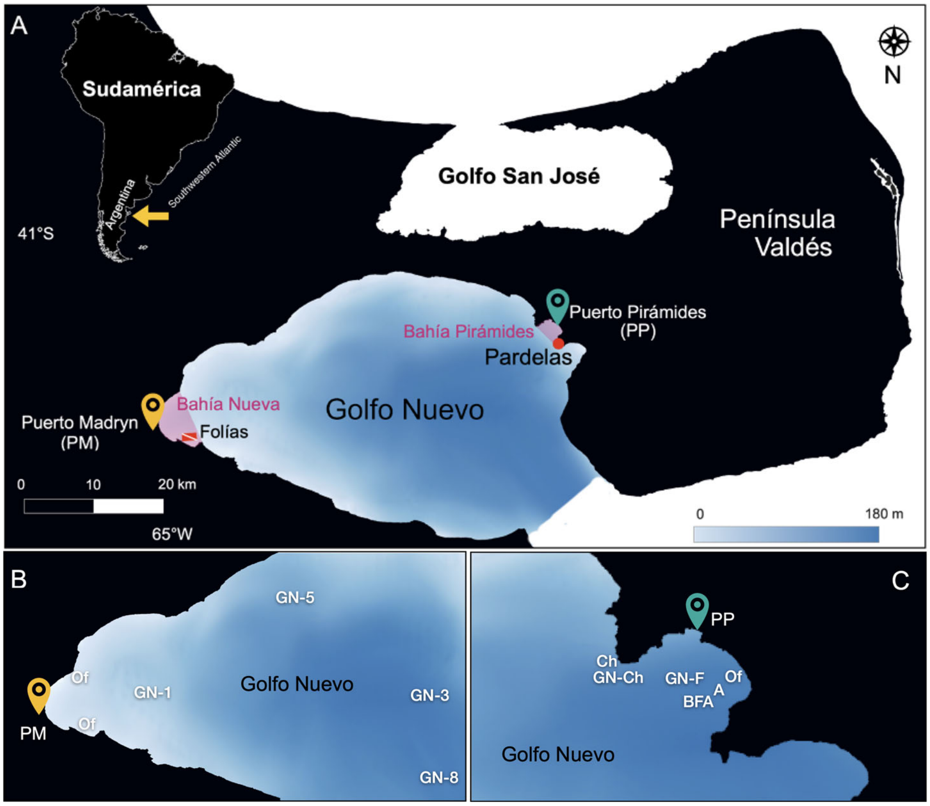

Fig. 1 | Study area and sampling locations. A Map of the study site, Golfo Nuevo, Patagonia, Argentina. **B** Zoom-in of Bahía Nueva and (**C**) Bahía Pirámides, showing sampling stations for phytoplankton and mesozooplankton (GN-1, GN-3, GN-5 and GN-8), mussels (Ch), anchovies (A), dead sea lions (*Otaria flavescens*, Of) and whale feces (*Eubalaena australis*, BFA). GN-F phytoplankton and mesozooplankton samples collected at the southern right whale feeding area. GN-Ch phytoplankton and mesozooplankton samples collected near the mussel sampling site.

reproductive health of populations[15]. Domoic acid is a potent neurotoxin produced as a secondary metabolite by several species of the diatom *Pseudo-nitzschia*. This toxin has been linked to numerous fatal incidents in marine mammals due to its transfer and bioaccumulation through the food web via planktivorous organisms[16–19]. In addition to its acute effects, chronic exposure to DA in sea lions can result in sublethal consequences, such as degenerative heart disease, persistent epileptic conditions, and reproductive issues, including abortions, in-utero fatalities, and premature births[7,20–22]. Lipophilic toxins have not been widely linked to morbidity or mortality in marine mammals; however, compounds of this toxin complex are increasingly recognized as emerging risks for high-trophic-level species[23]. Dinophysistoxins (DTXs) and pectenotoxins (PTXs), produced by planktonic dinoflagellates of the genus *Dinophysis* and by *Prorocentrum* spp.[24,25], can accumulate in marine food webs and have been detected in marine mammals[26,27]. Additionally, spirolides (SPX), produced by *Alexandrium ostenfeldii*[28,29], are fast-acting neurotoxins capable of inducing rapid death in laboratory rodents[30].

Marine mammals have been proposed as sentinel species for monitoring ocean and human health due to their role as top predators, their susceptibility to bioaccumulation of toxicants, and their shared coastal habitats with humans[15,31]. Furthermore, as charismatic megafauna, marine mammals often elicit strong public interest, making changes in their populations more noticeable than those of other marine species, which enhances their utility as sentinels of environmental change[32]. While monitoring algal toxins in shellfish and other seafood helps protect humans from toxin-related health risks, marine mammals and other animals in coastal and oceanic environments are inevitably exposed, as they must continue feeding even during toxic blooms. The impact of phycotoxins on marine mammals is mostly observed as acute intoxication; however, the effects of chronic exposure to sublethal levels of these toxins on animal health are increasingly being investigated[23]. In early austral spring 2022, a shellfish poisoning event in GN (Fig. 1), caused by the dinoflagellate *Alexandrium catenella/tamarense* complex, a known producer of PSTs, resulted in the deaths of 30 southern right whales (*Eubalaena australis*) between 24 September and 11 October, including 28 adults and two juveniles[33] (Supplementary Fig. 1). Notably, on 23 September 2022, we documented several southern right whales feeding at the surface in the same area, immediately preceding the first reported dead whale of the event (Supplementary Movie 1). To investigate the trophic transfer and exposure of marine mammals to phycotoxins, we analyzed PST, DA, and LT levels in samples collected in GN from late winter through spring 2022, including phytoplankton, mesozooplankton, mussels, pelagic fish, and marine mammals. Additionally, we gathered information from the local hospital in Puerto Pirámides (Fig. 1) and from the Harmful Algae Monitoring Program (Ministry of Fisheries, Chubut Province, Argentina) to determine whether any individuals exhibiting clinical signs potentially associated with these toxins had been reported, and to verify whether harvesting bans on bivalve mollusks in GN were in effect.

Results

Environmental conditions during sample collection

Satellite chlorophyll-a (Chl-a) data for 2022 showed monthly variations, reaching lower values in July, August, November, and December, with the highest values recorded in September and October (3.87 ± 1.83 and 4.85 ± 0.58 mg m^{-3}, respectively; Fig. 2). The surface Chl-a levels, used as a proxy for phytoplankton biomass, increased in coastal areas close to Bahía Nueva (BN) and Bahía Pirámides (BP) during September and then spread toward the center of the Gulf in October (Fig. 2).

No statistically significant differences were observed in Chl-a climatological data between the year of the MME (2022) and the complete time series (Supplementary Fig. 2 and Supplementary Table 1). The results of the Mann-Whitney test for sea surface temperature (SST) data indicated significant differences between the climatological mean (2018–2024) and 2022 only for the months of July ($p = 0.03$) and August ($p = 0.02$) (Supplementary Fig. 2 and Supplementary Table 1). Salinity showed significant differences up to July (Supplementary Table 1), with values above the temporal mean (Supplementary Fig. 2). Nitrate (NO_3^-) concentrations were significantly different in January and February of 2022, with values below the temporal

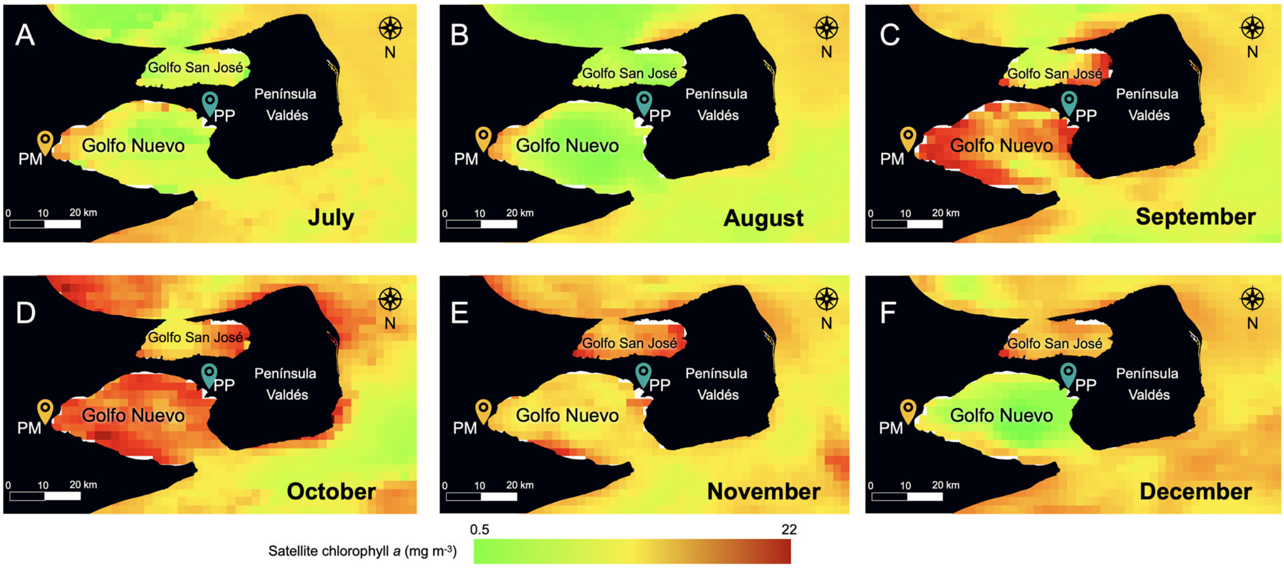

Fig. 2 | Satellite-derived sea surface chlorophyll-a in the waters surrounding Península Valdés, Argentina. Monthly averages of sea surface chlorophyll-a (in mg m^{-3}) from July to December 2022 are shown for panels **A**–**F**, respectively, including Golfo San José and Golfo Nuevo. Pins indicate the locations of Puerto Pirámides (PP; green), and Puerto Madryn (PM; orange) as shown in Fig. 1.

mean. Phosphate (PO_4^{3-}) showed significant differences up to October (Supplementary Table 1), with values exceeding the average (Supplementary Fig. 2). Silicate (SiO_4), on the other hand, exhibited significant differences up to August and again in October (Supplementary Table 1), with values above the temporal mean (Supplementary Fig. 2). No significant differences were found for either photosynthetically available radiation (PAR) or precipitation rate in any of the climatological months when comparing 2022 with the 2018–2024 time series (Supplementary Fig. 2 and Supplementary Table 1).

Pearson correlation revealed differences in the relationships between Chl-a and environmental variables when comparing climatological data from 2018–2024 with data from the year 2022. The correlation between Chl-a and SST was weak and not significant in both periods (Supplementary Table 2). A statistically significant negative correlation was found between Chl-a and PAR in 2022 ($r^2 = -0.71$, $p = 0.009$), which was not significant in the climatological record. Similarly, Chl-a showed significant positive correlations in 2022 with PO_4^{3-} ($r^2 = 0.62$, $p = 0.03$) and SiO_4 ($r^2 = 0.66$, $p = 0.02$). Salinity showed a significant positive correlation with Chl-a in the 2018–2024 period ($r^2 = 0.79$, $p = 0.002$), but this relationship was absent in 2022 (Supplementary Table 2). Other variables, such as NO_3^- and rain precipitation rate, did not show significant correlations in either dataset (Supplementary Table 2).

Phytoplankton abundance and toxicity

Alexandrium cells exhibited a wide range of sizes, suggesting the presence of both *A. catenella*/*A. tamarense* (25–50 μm) and *A. minutum* (20–25 μm). Similarly, *Pseudo-nitzschia* cells belonging to both the *delicatissima* complex (width < 3.5 μm) and *seriata* group (width > 3.5 μm) were observed. Among the lipophilic toxin–producing dinoflagellates targeted, only *Dinophysis acuminata* was detected in the phytoplankton samples. The dinoflagellate genus *Alexandrium* spp. and the diatom genus *Pseudo-nitzschia* spp. were present in all analyzed samples, although *Pseudo-nitzschia* was not detected in the sample collected on 5 October (Table 1). Abundance estimates ranged from 5 to 1760 cells L^{-1} for *Alexandrium* spp. and from 2 to 1668 cells L^{-1} for *Pseudo-nitzschia* spp. The highest values of both genera were recorded in samples taken on 28 September at the site where whales were observed feeding at the surface, with 1760 cells L^{-1} of *Alexandrium* spp. and 1668 cells L^{-1} of *Pseudo-nitzschia* spp. (Table 1). PSTs were detected in all phytoplankton samples collected during the study period, except for the one collected on 23 August (Table 1). In several samples collected in August, toxin levels were relatively low, with some falling below detection limits. Toxin levels increased markedly by late September, coinciding with the period of highest abundances of toxic phytoplankton observed in the study area (Table 1). The highest PST levels were recorded at the whale-feeding site (140 ng STX eq. L^{-1}; Table 1). The toxin profiles included C1/C2, B1, dcGTX2/3, GTX2/3, GTX1/4, NEO, and STX. Among these, GTX1/4 were the most abundant, followed by GTX2/3 and C1/C2, whereas B1, NEO, dcGTX2/3, and STX were present at lower levels. Domoic acid was detected in all phytoplankton samples at trace levels, with only three samples exceeding the detection limit, coinciding with those showing the highest abundances of *Pseudo-nitzschia* spp. (0.061 ng L^{-1} at the whale-feeding site, 0.0052 ng L^{-1} near the mussel-sampling site, and 0.048 ng L^{-1} on 30 September; Supplementary Table 3). Among LTs, PTX-2 was detected in two samples (0.040 ng L^{-1} at the whale-feeding site and 0.013 ng L^{-1} near the mussel-sampling site; Supplementary Table 3), and DTX-1 was found in samples collected near the mussel-sampling site (0.79 ng L^{-1}) and on 30 September (0.039 ng L^{-1}) (Supplementary Table 3).

Mesozooplankton toxicity and main vectors

PSTs were detected in all mesozooplankton samples collected from late winter to early spring 2022 (Table 1). PSTs were represented by C1/C2, B1, dcGTX2/3, GTX2/3, GTX1/4, dcSTX, NEO, and STX. In general, GTX1/4 and GTX2/3 were the dominant analogues. Low PST levels were recorded in August and early October (Table 1). The highest toxin levels in mesozooplankton were quantified in samples collected on 28 September, both at the whale-feeding site (38,000 ng STX eq. g^{-1}) and near the mussel-sampling site (24,000 ng STX eq. g^{-1}). These samples also exhibited high levels of B1, NEO, C1/C2, dcGTX2/3, and STX, indicating a complex toxin profile (Table 1). Domoic acid and LTs were not detected in any mesozooplankton samples. Overall, the most abundant taxa across all sampling dates and potential vectors of phycotoxins were cladocerans, large and small calanoid copepods (CI–CVI), and calyptopis-stage euphausiids (Fig. 3).

PST in mussels and fish

PSTs were detected in both whole Argentine anchovy specimens and mussel samples collected in late September 2022. PSTs in these samples were represented by GTX2/3, GTX1/4, and STX (Table 1). In mussels, the most abundant toxins were GTX2/3 (13,000 ng g^{-1}), followed by GTX1/4 (12,000 ng g^{-1}) and STX (120 ng g^{-1}). In anchovies, GTX1/4 were the most abundant toxins (6700 ng g^{-1}), followed by GTX2/3 (800 ng g^{-1}), whereas

Table 1 | Paralytic shellfish toxin (PST) levels in phytoplankton (P; ng L^{-1}), mesozooplankton (Z; ng g^{-1}), Argentine anchovy (A; ng g^{-1}), and mussel (Ch; ng g^{-1}) samples, as well as toxic phytoplankton abundance (cells L^{-1}) and mesozooplankton vector abundance (ind. m^{-3}), collected in Golfo Nuevo (GN) during late austral winter and spring 2022

Sample	Location	Sample date	C1/C2	B1	dcGTX2/3	GTX2/3	dcSTX	GTX1/4	NEO	STX	ng STX eq. L^{-1}	*Alexandrium* spp. cells L^{-1}	*Pseudo-nitzschia* ssp. cells L^{-1}
P	GN1	1-Aug-22	0.05	bdl	0.01	0.12	bdl	0.29	bdl	bdl	bdl	20	14
P	GN5	3-Aug-22	0.16	bdl	bdl	0.34	bdl	bdl	bdl	bdl	0.14	28	2
P	GN3	11-Aug-22	0.05	bdl	bdl	0.10	bdl	bdl	bdl	bdl	0.04	5	2
P	GN8	23-Aug-22	bdl	bdl	bdl	bdl	bdl	bdl	bdl	bdl	bdl	13	3
P	GN-F	28-Sept-22	21	13	2.40	30	bdl	170	2.20	0.63	140	1760	1668
P	GN-Ch	28-Sept-22	2.20	bdl	0.94	5.60	bdl	27	1.60	0.27	23	56	120
P	GN1	30-Sept-22	0.70	bdl	0.04	1.40	bdl	6	0.16	0.03	5	37	170
P	GN3	5-Oct-22	0.05	bdl	bdl	0.37	bdl	0.42	bdl	bdl	0.44	22	0
Sample	Location	Sample date	C1/C2	B1	dcGTX2/3	GTX2/3	dcSTX	GTX1/4	NEO	STX	ng STX eq. g^{-1}	Ind. m^{-1}	
Z	GN1	1-Aug-22	0.08	bdl	0.48	3.80	bdl	12	0.42	0.07	10	135.38	
Z	GN5	3-Aug-22	bdl	0.05	0.04	0.16	0.02	0.51	bdl	0.03	0.49	14.96	
Z	GN3	11-Aug-22	0.00	bdl	0.06	0.63	bdl	1	0.04	0.03	1.10	33.12	
Z	GN8	23-Aug-22	0.15	bdl	0.25	2.90	bdl	5	0.19	0.05	5	1694.44	
Z	GN-F	28-Sept-22	400	8500	1100	6200	bdl	43,000	3600	460	38,000	7883.86	
Z	GN-Ch	28-Sept-22	1100	2200	170	2600	bdl	29,000	2000	130	24,000	5002.22	
Z	GN1	30-Sept-22	0.30	bdl	0.84	2.30	bdl	24	0.83	0.06	19	787.98	
Z	GN3	5-Oct-22	0.02	bdl	0.02	0.83	bdl	0.37	bdl	0.01	0.61	2486.72	
Sample	Location	Sample date	C1/C2	B1	dcGTX2/3	GTX2/3	dcSTX	GTX1/4	NEO	STX	ng STX eq. g^{-1}		
A	BP (GN)	24-Sept-22	bdl	bdl	bld	800	bdl	6700	bdl	51	5100		
Ch	BP (GN)	28-Sept-22	bdl	bdl	bld	13,000	bdl	12,000	bdl	120	13,000		

GN-F Phytoplankton and mesozooplankton samples collected at the southern right whale feeding area, GN-Ch Phytoplankton and mesozooplankton samples collected near the mussel sampling site, *BP* Bahía Pirámides, *bdl* below detection limit/not detected.

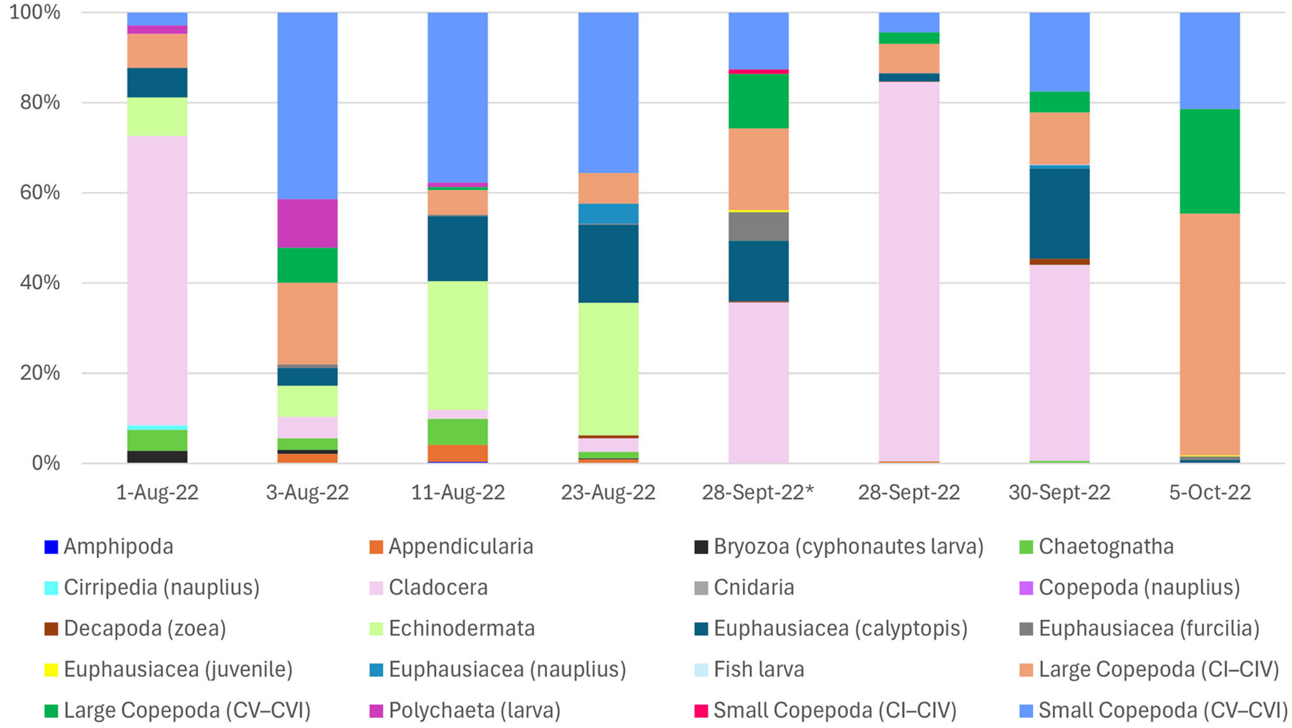

Fig. 3 | Relative abundances (ind. m^{-3}) of potential phycotoxin vectors in mesozooplankton samples from Golfo Nuevo, based on their feeding ecology. The sample collected on 28 September 2022* corresponds to the site where southern right whales were observed feeding.

STX was present at lower levels (51 ng g^{-1}). Mussels exhibited higher PST levels than anchovies (Table 1). The STX-equivalent levels measured in mussels (13,000 ng STX eq. g^{-1}) exceeded the regulatory limit for human consumption (800 ng STX eq. g^{-1}). Domoic acid and LTs were not detected in either anchovy or mussel samples.

PSTs in sea lions and southern right whales

PSTs were detected in various tissues (lungs, kidneys, liver, muscle, and placenta) as well as in fecal samples from adult female sea lions found dead between October and November 2022 along the coast (Table 2). The pregnant female Of1491 showed the highest PST levels, with 2600 ng g^{-1} of STX and 180 ng g^{-1} of dcSTX in feces, and 60 ng g^{-1} of STX in the liver (Table 2 and Supplementary Table 3). Notably, dcSTX was detected only in this individual, while the other females showed only STX. In addition, STX was the only analogue detected in fetal samples. Two of the three fetuses tested positive: STX was found in the amniotic fluid of Of1490 (19 ng g^{-1}) and in both the umbilical cord (110 ng g^{-1}) and amniotic fluid (66 ng g^{-1}) of Of1492 (Table 2). No STX was detected in the blood, heart, brain, or bladder of the adult females, nor in the lungs, kidneys, liver, muscle, heart, or meconium of the fetuses. Similarly, STX was the only analogue detected in all fecal samples from live southern right whales, collected between mid-October and late November, with levels ranging from 102 to 1,800 ng g^{-1} (Table 2). Domoic acid was not detected in any marine mammal samples. Among LTs, SPX-1 was detected in two fecal samples from whales (BFA49: 162 ng g^{-1} and BFA50: 33 ng g^{-1}; Supplementary Table 3).

Public gastrointestinal disorders and shellfish closures

During spring 2022 (September–December), approximately 52 people (about 10 % of the local population) with gastrointestinal illness (diarrhea) were treated at the hospital in Puerto Pirámides. Affected individuals ranged from 5 to over 75 years old (Supplementary Table 4), with the highest number of cases occurring among those aged 20–24 years. It is worth noting that diarrhea alone, without associated neurological symptoms, is not a specific clinical sign of phycotoxin exposure via contaminated seafood or water; therefore, the available data do not permit establishing a direct causal link with these cases. However, reporting gastrointestinal disorders occurring during the same period as the intense bloom of *Alexandrium* spp. in GN remains relevant, as it may help evaluate potential impacts on public health, particularly in a community such as Puerto Pirámides, where drinking water is sourced from desalination.

In GN, shellfish harvesting closure was determined by the local government in late September 2022 and continued until mid-March 2023, due to elevated levels of PSTs in mussels (Table 3). The highest levels were detected on 28 September in Bahía Pirámides (37,410 µg STX eq. kg^{-1}) and Pardelas (28,943.73 µg STX eq. kg^{-1}), as well as on 16 November in the shipwreck point called Folías (18,273.06 µg STX eq. kg^{-1}) (Table 3 and Fig. 1). These values exceeded the regulatory limit for human consumption by more than an order of magnitude (800 µg STX eq. kg^{-1}). It is important to note that under the Chubut Monitoring Program, if elevated phycotoxin levels are detected at any sampling point in GN, the entire Gulf is closed to bivalve and gastropod harvesting and consumption. PST levels varied markedly among sampling sites and dates throughout the monitoring period. For instance, Pardelas presented high levels in late September and early October, while Folías showed a peak only in mid-November. Although toxin levels remained below the regulatory limit for human consumption since late February, the closure continued until 28 March 2023 (https://marearoja.chubut.gov.ar/).

Discussion

Harmful algal blooms have become increasingly frequent in coastal areas[34–36]. Although this rise is partly attributed to enhanced monitoring efforts in coastal waters[1,37], there is growing evidence that global warming is also playing a substantial role in the intensification of HAB events worldwide[38]. In GN, recurrent and intense blooms of *A. catenella* and associated PSTs have been reported[39,40]. However, to the best of our knowledge, this study provides the first well-documented case of PSTs transfer involving both live and dead marine mammals in the Southwestern Atlantic, linked to PST bioaccumulation in plankton, mussels, and fish, and potentially associated with cases of human gastrointestinal illness.

Table 2 | Paralytic shellfish toxin (PST) levels (ng g-1) in dead South American sea lions (*Otaria flavescens*; Of) and live southern right whales (*Eubalaena australis*; BFA) collected during austral spring 2022 in Golfo Nuevo (GN)

ID	Location	Sample date	Sex/Age Class	Saxitoxin (ng STX g^{-1})												
				Feces	Lung	Kidney	Liver	Blood	Muscle	Heart	Brain	Placenta	Bladder	Umbilical cord	Meconium	Amniotic fluid
Of1487	BP	13-Oct-22	Adult Female	ns	34	57	51	bdl	25	ns	ns	na	ns	na	na	na
Of1489	BN	25-Nov-22	Adult Female	280	bdl	67	bdl	bdl	bdl	bdl	bdl	na	ns	na	na	na
Of1490	BN	27-Nov-22	Adult Female Pregnant	bdl	bdl	bdl	bdl	bdl	bdl	bdl	bdl	46	bdl	na	na	na
Of1490	BN	27-Nov-22	Fetus	na	bdl	bdl	bdl	ns	bdl	bdl	ns	na	ns	bdl	bdl	19
Of1491	BN	28-Nov-22	Adult Female Pregnant	2600	bdl	bdl	60	bdl	bdl	bdl	bdl	ns	ns	na	na	na
Of1491	BN	28-Nov-22	Fetus	na	bdl	bdl	bdl	ns	bdl	bdl	ns	na	ns	ns	bdl	bdl
Of1492	BN	25-Nov-22	Adult Female Pregnant	110	bdl	bdl	67	ns	27	bdl	bdl	bdl	ns	na	na	na
Of1492	BN	25-Nov-22	Fetus	na	bdl	bdl	bdl	ns	bdl	ns	ns	na	ns	110	bdl	66
BFA48	BP	18-Oct-22	Adult Female	102												
BFA49	BP	15-Nov-22	Adult Female	1800												
BFA50	BP	23-Nov-22	Adult Female	406												

BP: Bahía Pirámides, *BN*: Bahía Nueva (Fig. 1). *na* not applicable for the age class or individual sampled, *ns* not sampled, *bdl* below detection limit/not detected. Note: Only STX was detected, except in sample Of1491, where dcSTX was also detected (180 ng g^{-1}). Other detected toxins, including the lipophilic toxin spirolide SPX-1, are reported in Supplementary Table 3 and described in the text.

Table 3 | Samples collected during shellfish harvesting closures due to paralytic shellfish toxins (PSTs), as reported by the Harmful Algal Bloom and Shellfish Toxicity Monitoring Program in Golfo Nuevo

Sample	Date	Location	µg eq. STXdi HCl Kg^{-1}	Fisheries closures
Mussel	27-Sept-22	Folías	1,656.9	Yes
Mussel	28-Sept-22	BP	37,410	Yes
Mussel	28-Sept-22	Pardelas	28,944	Yes
Mussel	4-Oct-22	Pardelas	5,598.4	Yes
Mussel	19-Oct-22	Folías	44.505	Yes
Mussel	16-Nov-22	Folías	18,273	Yes
Mussel	16-Nov-22	Pardelas	40.42	Yes
Mussel	27-Jan-23	Pardelas	710.7	Yes
Mussel	28-Jan-23	Pardelas	984.7	Yes
Mussel	27-Feb-23	Pardelas	575.8	Yes
Mussel	27-Feb-23	Pardelas	560.1	Yes
Mussel	15-Mar-23	Pardelas	567	Yes

ND Not detected, *BP* Bahía Pirámides (Fig. 1).

Environmental context of the 2022 harmful algal bloom in Golfo Nuevo

While satellite-derived Chl-a is widely recognized as a good proxy for phytoplankton biomass, its correlation with toxic groups —such as dinoflagellates, which generally have lower chlorophyll concentrations per cell and form part of the mixoplankton community[41]— has not yet been established[42]. Previous studies have examined the influence of temperature and nutrient conditions on HAB dynamics. High temperatures can promote cell growth, while cold shocks may increase toxin production, with the latter factor being more important than nutrients or salinity[43]. In this study, significant differences in some environmental variables were found in 2022 compared to previous or subsequent years, although these differences were not always aligned with the timing of the toxin-producing phytoplankton bloom. Notably, Chl-a in 2022 was correlated with phosphate, silicate, and PAR, suggesting that bottom-up control might have played a pivotal role in bloom occurrence during that year. Interestingly, the absence of a strong correlation between salinity and Chl-a in 2022, relative to the broader 2018–2024 period where it was significant, indicates a potential shift in the environmental drivers of phytoplankton biomass during the anomalous bloom event. Our findings suggest that the MME associated with HAB-forming microalgae was likely driven by multiple interacting environmental factors rather than a single trigger. Many HAB-forming protists exhibit complex trophic strategies, and their occurrence cannot be explained solely by resource availability (e.g., nutrients and light), but rather by interactions among physical, chemical, and biological processes. By integrating satellite-derived environmental data with toxin measurements across multiple trophic levels, this study adopts an ecosystem-level approach to examine the conditions associated with the 2022 event and highlights the importance of continued, coordinated monitoring in the region.

Toxic phytoplankton and mesozooplankton vectors

In this study, *Alexandrium* and PSTs were detected from winter through spring 2022, with the highest abundances in early spring coinciding with the highest PST levels in both phytoplankton and mesozooplankton samples at the site where whales were observed feeding. The wide size range of *Alexandrium* cells observed in the samples suggests the coexistence of both *A. catenella/tamarense* and *A. minutum*, as previously reported in other regions of the Argentine Sea[44]. In phytoplankton, seven PST analogues were detected, and eight were identified in mesozooplankton (from most to least toxic): STX, NEO, dcSTX (only in mesozooplankton), GTX1/4, GTX2/3, dcGTX2/3, B1, and C1/C2. In phytoplankton, the PST profile was dominated by GTX1/4, followed by GTX2/3 and C1/C2, while minor components included B1, NEO, dcGTX2/3, and STX. This profile differs from the typical field profile reported for *A. catenella* in the Argentine Sea[45,46], which was characterized by GTX1/4 as the most abundant toxin, followed by C1/C2, GTX2/3, and NEO. However, it is more similar to that described by Reyero et al. [47] for samples from GN, where profiles were dominated by GTX1/4 and GTX2/3 followed by C1/2, although in our study a wider range of analogues was detected. Notably, our results also differ from those of Montoya et al. [48], who analyzed phytoplankton samples collected in the same area during the 2022 MME of southern right whales in GN and reported PST profiles consistent with the typical field profile previously described for the Argentine Sea. This discrepancy between the profiles may partly reflect differences in analytical resolution, toxin epimerization, or genetic diversity among strains[49]. *Pseudo-nitzschia* spp. were also present in most samples, and low levels of DA were detected in three phytoplankton samples. In Argentina, 16 species of *Pseudo-nitzschia* have been described, of which half have been identified as DA-producing[50]. Additionally, two LTs (PTX-2 and DTX-1) were detected at low levels in phytoplankton. Their occurrence highlights a broader suite of phycotoxins present during the 2022 HAB event. This finding suggests that the bloom occurring in GN involved multiple classes of phycotoxins, even when PSTs dominated trophic transfer and ecological impact.

This study provides clear evidence that mesozooplankton act as vectors of PSTs within pelagic marine food webs, facilitating toxin transfer to planktivorous fish and marine mammals. The mesozooplankton taxa identified as the main potential vectors of phycotoxins included cladocerans, large copepods (mainly CI–CIV), small copepods (mainly CV–CVI), and euphausiids (mainly calyptopis and furcilia stages). In mesozooplankton, the PST profile was dominated, in decreasing order of abundance, by GTX1/4, B1, GTX2/3, NEO, C1/2, dcGTX2/3, STX, and dcSTX. To the best of our knowledge, this constitutes the most toxic profile reported to date for mesozooplankton samples from GN. Our results differ from previous research, which reported only low levels of the GTX2/3 epimers in mesozooplankton from this area[51]. Several studies have reported that gonyautoxins GTX1–GTX4 are highly toxic (acting as sodium channel-blocking agents in mammals), whereas *N*-sulfocarbamoyl toxins, such as B1, are among the least toxic derivatives[52,53].

The samples collected on 28 September 2022 at sites where whales were feeding and near the mussel collection site exhibited the highest total PST levels recorded in this study (38,000 and 24,000 ng STX eq. g^{-1}, respectively). Moreover, the site where whales were observed feeding showed the highest mesozooplankton densities (7,883.87 ind. m^{-3}), dominated by cladocerans (>2800 ind. m^{-3}) and large copepods (CI–CVI, >2,380 ind. m^{-3}), along with a high abundance of euphausiids (calyptopis, furcilia, and juveniles, >1600 ind. m^{-3}). Consistent with the present study, previous research has shown that in GN, southern right whales primarily feed on calanoid copepods and euphausiids[54–56]. This dense, energy-rich mesozooplankton aggregation likely represents a favorable feeding patch, increasing the risk for whales to ingest prey species capable of accumulating high levels of phycotoxins. Field observations during blooms of dinoflagellates that produce PSTs[57,58] and laboratory experiments with cultures of *Alexandrium* spp. have shown that mesozooplankton—mainly copepods—accumulate maximum levels of PSTs within a few hours, without apparent adverse effects, and retain them for at least several days after the bloom peak, even when no dinoflagellates are present in the phytoplankton[57–59]. In this study, higher PST levels were found in all mesozooplankton samples compared to those in phytoplankton samples collected simultaneously at the same site. The occurrence of the highest PST levels and profiles dominated by highly toxic PST derivatives in mesozooplankton highlights their strong potential as vectors for PST transfer to higher trophic levels. Therefore, the high toxicity observed in mesozooplankton in our study, together with our observations of whales feeding in the area on the day before the first dead whale was found (23 September 2022) and during the mortality event (28 September 2022), suggests that the MME of southern right whales was caused by the accumulation of high PST levels in copepods and euphausiids, their main prey in Península Valdés[54–56].

Trophic accumulation of PSTs in mussels and fish and potential implications for human health

Shellfish rapidly bioaccumulate PSTs and are often used as sentinel species in toxin monitoring programs. Live mussels collected in GN during the MME of southern right whales revealed high PST levels (13,000 ng STX eq. g^{-1}). The PST profile was dominated, in decreasing order of abundance, by GTX2/3, GTX1/4, and STX. Notably, PST levels in mussels were lower than those measured in mesozooplankton collected on the same day, both near the mussel bed from which the mussels were obtained and at the site where whales were feeding. Since 2000, when the Chubut Monitoring Program was established in Chubut Province, GN has been subject to periodic annual closures due to PST levels exceeding the regulatory limit of 800 ng STX eq. g^{-1} (equivalent to 80 μg STX eq. 100 g^{-1}) in mussel tissue. During spring 2022, the Chubut Monitoring Program detected high levels of STX in mussels and established harvesting closures from 27 September 2022 to late March 2023 at all shellfish harvesting sites in GN. In addition, on 29 September 2022, the Secretaría de Salud de Chubut issued a recommendation against the consumption of desalinated tap water in Puerto Pirámides for approximately three days, pending toxicity analyses (which yielded negative results). This event gained both local and national relevance, with extensive media coverage. Furthermore, at least 52 people—approximately 10% of Puerto Pirámides' small population of 524 inhabitants—were admitted to the local hospital with gastrointestinal disorders. Although these cases, which did not present neurological symptoms, could not be exclusively linked to PST intoxication, they are important to consider because diarrhea, the most frequently reported symptom among affected individuals, is associated with the ingestion of STX in humans[60]. For context, during a typical austral spring in GN, when PST-related shellfish harvesting closures commonly occur, as in 2025, hospital records indicate that 13 patients were treated for diarrhea, providing a point of comparison with the higher number of cases reported in 2022. Moreover, human intoxications are often misdiagnosed, underdiagnosed, and underreported to public health authorities, hampering proper management and epidemiological data[61]. Additionally, many residents of Puerto Pirámides were reluctant to drink or use tap water due to the potential risk of exposure to phycotoxins from the desalinated seawater supply. This highlights the broad implications of this HAB event, particularly given the temporal overlap of marine fauna mortalities, shellfish harvesting closures, and public concern over drinking water quality, emphasizing the risks posed to both wildlife and human communities in coastal areas.

This study documents, to the best of our knowledge, the first report of dead *E. anchoita* individuals associated with PSTs in the Argentine Sea. Dead anchovies sampled in this study contained high levels of PSTs (5,100 ng STX eq. g^{-1}). The PST levels detected here were higher than those reported by Montoya et al. [62], who found PST levels in anchovy viscera of up to 1010 ng STX eq. g^{-1} in live specimens collected in Argentine waters. In our samples, the PST profile was dominated, in decreasing order of abundance, by GTX1/4, GTX2/3, and STX. The Argentine anchovy is a zooplanktivorous species throughout its life cycle, feeding primarily on cladocerans, copepods, and euphausiids[63–65]. These taxa were also the dominant mesozooplankton groups in our study. Therefore, the present study provides direct evidence that PST-accumulating mesozooplankton are linked to anchovy mortality in GN. Several studies have reported the trophic transfer of PSTs via zooplankton vectors leading to fish mortality events[9,66,67]. In the Argentine Sea, *E. anchoita* plays a key role in the pelagic ecosystem. Its importance lies not only in its high biomass but also in the fact that it constitutes the main component of the diet of several commercially important species, such as hake, squid, and mackerel[64,68], as well as marine mammals such as female South American sea lions[69]. Investigations of South American sea lions have reported sex-specific differences in prey preferences, with anchovies being more important for females than for males[69]. Although males also feed on anchovies, they are a less important prey item. These female preferences for anchovies may explain why all South American sea lions recorded during the MME in this study were females, suggesting that prey selection played a key role in their exposure to PSTs.

Exposure and transfer of PSTs to marine mammals

The present study documents elevated PST levels in both live and dead marine mammals from the Argentine Sea. Marine mammals are recognized as important sentinels of harmful algal toxins and are often used to anticipate potential human health risks linked to ocean deterioration[70]. In late September 2022, in GN, an MME of southern right whales alerted provincial authorities in Chubut, leading to phycotoxin analyses and the establishment of a ban on shellfish consumption and harvesting throughout the Gulf due to high PST levels, along with a precautionary advisory recommending against drinking desalinated tap water until toxicity analyses were completed. This underscores the sentinel role of marine mammals in protecting public health.

During October–November 2022, we collected six adult female South American sea lions in good body condition, with no visible signs that could explain the acute mortality event. An additional six carcasses were reported in GN based on reports from local divers, but we could not locate them: four were submerged at approximately 8 m depth (reported on 13 October) and could not be found later, while the other two were reported on the coast on 17 October and were likely carried away by the tide. This study provides quantitative evidence that STX may have been involved in the deaths of South American sea lions in GN. A previous report mentioned the presence of PSTs in sea lions found dead simultaneously with the whale mortality event in the same area[33], but no toxin levels were provided. In fact, while one study reported exposure of an apparently healthy South American sea lion to saxitoxin-like activity detected by a receptor binding assay in feces from Peru (133 ng STX eq. g^{-1} [71];), no studies have documented mortality in this species linked to PST exposure, nor reported its exposure in Argentine waters. Furthermore, only one study has associated this phycotoxin with sea lion *Callorhinus ursinus* mortality events, based on supporting data[9]. In our study, all females examined were exposed to PSTs. Only STX was detected in most samples, with levels ranging from 25 to 2600 ng STX g^{-1}. Interestingly, in the pregnant adult female with the highest levels of STX (2600 ng STX g^{-1}), dcSTX (180 ng dcSTX g^{-1}) was also detected. These levels are notably high, exceeding those previously reported in sea lions (e.g.[9,71],) and highlighting the severity of PST exposure during this mortality event.

This study demonstrates the maternal transfer of STX to South American sea lion fetuses. Of the three sea lion fetuses examined, two tested positive for STX: one in the amniotic fluid and the other in both amniotic fluid and umbilical cord samples. Importantly, the fetus that tested negative for STX was from the female with the highest STX levels, in which dcSTX was also detected. This finding may reflect the rapid death of the mother due to acute exposure to very high PST levels, possibly occurring before substantial transfer of toxins to the fetus could take place. Cases of sudden mortality associated with STX have been reported in other marine mammals (e.g., humpback whales[72];). Alternatively, transplacental transfer may vary depending on toxin congeners, stage of gestation, or the health status of the placenta, which may influence whether toxins reach the fetus[73]. Whereas several studies have reported that DA crosses the placenta in California sea lions (*Zalophus Californianus*), thereby exposing the fetus to this toxin (e.g[20,21,74].), no previous studies have detected PSTs in sea lion fetuses. However, STX has been detected in liver samples from a bottlenose dolphin mother and her fetus (*Tursiops truncatus*), providing evidence that this phycotoxin can cross the placenta in marine mammals[75]. In our study, no STX was detected in fetal tissues; nevertheless, its presence in amniotic fluid and the umbilical cord indicates that it entered the fetal compartment, likely through transplacental transfer. Studies have reported that phycotoxins, such as DA, accumulate in the amniotic fluid of California sea lions, causing recirculation of the toxin and leading to continuous exposure of the developing brain[20,74]. In addition, experimental studies in rodent models have shown that DA can cross the placenta, accumulate in amniotic fluid, and reach the fetal brain[76]; however, no equivalent studies have been conducted with PSTs, and the risks associated with maternal–fetal transfer of these toxins in mammals remain entirely unknown. Therefore, further research is needed to better assess the risks of PST exposure for marine mammal health at the earliest stages of development.

Here we report, to the best of our knowledge, the first detection of STX in live southern right whales. To date, only two studies have reported PSTs in dead southern right whales: Wilson et al. [77], who found saxitoxin-like activity using a receptor binding assay in feces, liver, and stomach tissue from four calves from GN; however, LC/MS analyses in that study did not confirm the presence of PSTs, and Uhart et al. [33], who detected PSTs in dead whales stranded in GN during spring 2022. Uhart et al. [33] reported detectable levels of PSTs in seven whales (six adult females and one juvenile male) that died between 24 September and 3 October 2022, across a variety of tissues and fluids. The reported levels ranged from 2.7 ng STX eq. g^{-1} to 694.3 ng STX eq. g^{-1}, with the intestinal content from an adult female that died on 24 September showing the highest concentration (694.3 ng STX eq. g^{-1}). In the present study, we analyzed three fecal samples from live adult female whales collected between 18 October and 23 November 2022. Although PSTs are primarily eliminated via urine after systemic absorption[78], fecal samples provide a practical, noninvasive matrix to assess exposure in live marine mammals. Only STX was detected in the samples, with levels ranging from 102 to 1,800 ng STX g^{-1}. Direct comparison between fecal and tissue toxin levels should be interpreted with caution, as these matrices reflect distinct toxicokinetic processes: fecal samples largely represent the unabsorbed and excreted fraction of the ingested dose, whereas tissue levels reflect the absorbed, distributed, and retained fraction of the toxin. In addition, post-mortem processes may alter toxin distribution and stability, potentially leading to lower toxin levels in decomposing tissues[14]. However, when comparing fecal samples from live whales in the present study with fecal samples from dead whales previously reported for GN[33], STX levels in live whales were, except for one individual (BFA48), higher than those reported in feces from dead whales[33]. It is worth noting that the maximum level of STX detected in the present study (1800 ng STX g^{-1}) was similar to the highest levels reported in fecal samples from apparently healthy, feeding North Atlantic right whales (*E. glacialis*, 1763 ng STX eq. g^{-1} [79]), highlighting comparable exposure ranges across right whale populations. Moreover, the detection of STX in fecal samples of live whales in late November—despite the MME occurring between late September and early October—indicates that exposure to PSTs persisted until the end of the whale season in 2022. Therefore, this study provides evidence that southern right whales are exposed to both lethal doses, as reported by Uhart et al. [33], and sublethal doses of PSTs (this study) through their feeding at Península Valdés. Although whale mortality associated with PSTs has been documented only once[33], sublethal exposure is likely more frequent[80,81]. This is because whales feed throughout their stay in the area, with particularly high frequency in spring[82], and *Alexandrium* blooms are recurrent during this period[39], which could lead to chronic exposure to PSTs during their stay at Península Valdés. Thus, such recurrent sublethal exposure may contribute to chronic physiological or behavioral effects[15], which should not be underestimated. In fact, studies on North Atlantic right whales have suggested that sublethal exposure to PSTs can affect respiratory physiology, leading to abnormal diving and feeding behavior that may compromise body condition and potentially reduce fecundity as well as the overall health of the population[58,83]. Moreover, the detection of STX in lactating females in the present study, along with the low levels of STX reported in the milk of southern right whales by Uhart et al. [33], indicates the potential for maternal transfer, which could expose calves to PSTs during the nursing period—a phenomenon that has been previously documented for other phycotoxins in marine mammals, such as domoic acid[84]. This highlights an additional pathway through which HABs may affect early life stages and overall population health of southern right whales.

In addition, the neurotoxin spirolide (SPX-1) was detected in fecal samples of two live whales. To our knowledge, this represents the first report of a spirolide in southern right whales and potentially the first documented

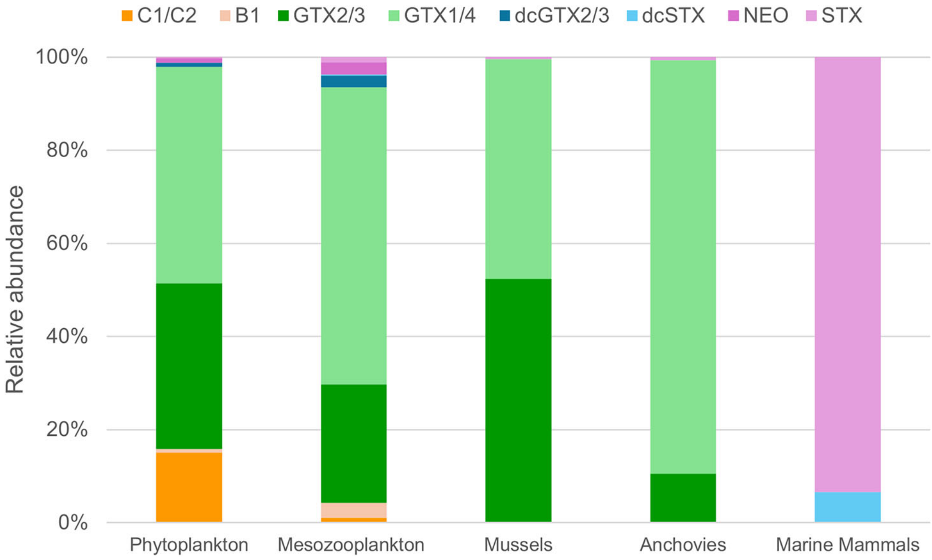

Fig. 4 | Relative PST (paralytic shellfish toxin) profiles across five trophic levels in Golfo Nuevo during 2022: phytoplankton (*n* = 7), mesozooplankton (*n* = 8), mussels (*n* = 1), anchovies (*n* = 1), and marine mammals (*n* = 18). Profiles represent the relative abundance of PST analogues calculated from all toxin-positive samples analyzed for each trophic level. *N*-sulfocarbamoyl toxins (B1 and C1/2) are shown in orange, gonyautoxins (GTX-1 to −4) in green, dicarbamoyl toxins (dcGTX-2/3, dcSTX) in blue, and carbamoyl toxins (NEO, STX) in pink.

exposure in any marine mammal. The individuals in which SPX-1 was detected were also those with the highest STX burdens (BFA49 and BFA50), indicating that exposure to both phycotoxins occurred simultaneously. Spirolides are highly potent, fast-acting neurotoxins in laboratory rodents[30]. Although their effects on marine mammals remain unknown, their occurrence reveals an additional and previously overlooked neurotoxic exposure pathway during HAB events. While spirolides have been previously reported in Argentine waters[13,28,44,85], the present study constitutes only the second record of these phycotoxins in samples from Golfo Nuevo, after D'Agostino et al. [51]. Until now, *A. ostenfeldii*—the only known producer of spirolides — had not been documented in the northern Patagonian gulfs[28,29,44]. However, the earlier detection of SPX-1 in both phytoplankton and mesozooplankton from GN[51] and in whale feces in the present study strongly suggests the presence of *A. ostenfeldii* in the study area. Additionally, the detection of SPX-1 in whales supports that this toxin can be transferred through the local food web.

Metabolism of PSTs between trophic levels

The comprehensive sampling during the paralytic shellfish poisoning event in GN in 2022, from phytoplankton to marine mammals, allowed a unique in situ study of PST metabolism across five different trophic levels, i.e., phytoplankton, mesozooplankton, bivalves, fish (anchovies), and marine mammals. Especially the latter have been challenging to link to plankton toxicity, as in many cases, stranded marine mammals are detected and sampled long after harmful algal blooms; for this reason, a direct comparison is hampered. Whereas the toxin profiles of *Alexandrium* spp[29,45,86,87]. and metabolic biotransformation of PSTs in bivalves have been investigated in detail for decades[78,88–91], less is known about biotransformation in zooplankton[92] and fish, and even less in marine mammals.

Bivalves have been shown to epimerize β-mers (e.g., C2, GTX3) to the corresponding α-mers (e.g., C1, GTX2), in addition to the desulfonation of *N*-sulfocarbamoyl toxins (e.g., C1 to GTX2). This trend is also observed in the field data of the 2022 event (Fig. 4), where the *N*-sulfocarbamoyl toxins B1 and C1/2 (dark and light orange bar sections) are present in phytoplankton samples but completely absent in the analyzed mussels.

The same metabolic activity, although to a lesser extent, was observed in mesozooplankton; but in contrast to mussels, mesozooplankton also displayed desulfatation activity, transforming sulfated gonyautoxins-1 to −4 into NEO and STX, which had a lower relative abundance in phytoplankton. Another metabolic pathway not seen in mussels is the decarbamoylation of GTX2/3 and STX to the dicarbamoyl toxins dcGTX2/3 and dcSTX, and a hydroxylation of the 1N- position partially converting GTX2/3 into GTX1/4. The latter metabolic pathway was also observed in anchovies, which had even higher GTX-1/4 (and accordingly lower GTX2/3) ratios than mesozooplankton. Otherwise, the PST profile was similar to that of mussels, which implies that 1N-oxidation and desulfonation were the metabolic pathways of these fish.

However, the most drastic PST profile transformation occurred in marine mammals, which contained only the desulfonated and desulfated carbamoyl toxins saxitoxin (STX) and dicarbamoyl saxitoxin (dcSTX). The modification of the PST composition in marine mammals is noteworthy from a toxicological perspective, as dcSTX and STX are among the most potent PSTs[93]. These findings highlight that relatively low-toxic PSTs produced during an *Alexandrium* bloom can be transformed into the most toxic PST variants by metabolic and/or selective depuration processes in marine mammals, thereby drastically increasing the harmful impact on these animals and possibly also on human seafood consumers.

Our data show that changes in PST composition strongly depend on the consumer organism, and that top predators exhibit the highest toxicity load due to their metabolic activity.

Conclusions

The present study contributes to understanding how PSTs move through marine food webs from protists to top predators and provides evidence that sea lion fetuses can be exposed to these phycotoxins through maternal transfer during gestation. Our results demonstrate that during HAB, marine mammals are exposed to both sublethal and acute toxicity. For southern right whales, our data provide evidence of sublethal exposure to PSTs even after the MME, which occurred between late September and early October in GN. The highest PST levels detected in mesozooplankton prey during the peak abundances of *Alexandrium* spp. at the site where whales were observed feeding provide direct evidence of trophic transfer at Península Valdés. The presence of high STX levels in lactating females further raises concerns about the potential transfer of these phycotoxins to their calves, as has been demonstrated for DA in other marine mammal species. Moreover, the detection of SPX-1 in fecal samples from live whales reveals an additional neurotoxic exposure pathway that has not previously been documented in this species.

This study demonstrates that PSTs were involved in pinniped mortality in the Argentine Sea. Analyses of tissues from dead sea lions revealed STX in feces, lungs, kidneys, liver, muscle, and placenta, supporting the conclusion that trophic transfer of PSTs led to the mortality event. Furthermore, during the periods of highest abundances of *Alexandrium* spp. in GN, high levels of PSTs were detected in mesozooplankton and in anchovies, a zooplankton-feeding species that constitutes a key prey item for South American sea lion females in the Argentine Sea. Importantly, our results demonstrate that fetuses can also be exposed to these toxins during gestation. The detection of STX in amniotic fluid suggests a potential mechanism of recirculation and re-exposure within the fetal compartment, raising concerns about possible developmental impacts.

Overall, this work provides quantitative evidence of PST exposure in South American pinnipeds and live southern right whales in the Argentine Sea, revealing both trophic and maternal transfer pathways. By demonstrating how toxins originating in phytoplankton can accumulate through the food web and reach top predators—including pregnant and lactating females—this study highlights a critical conservation concern for marine mammal populations in the Southwest Atlantic. In the context of increasingly frequent HABs driven by global warming, these findings underscore the urgent need for continued monitoring and interdisciplinary research to assess the long-term impacts of PST exposure on marine wildlife health and population dynamics. Given that PSTs can also pose serious risks to human health through seafood consumption, the local government should strengthen early-warning systems and public health advisories to mitigate potential impacts on coastal communities.

Methods

Study site

Golfo Nuevo is a key marine ecosystem located along the northeastern coast of Patagonia, Argentina (Fig. 1A). This semi-enclosed basin is part of the Península Valdés region, a UNESCO World Heritage Site recognized for its ecological significance and biodiversity. It has an average depth of 80 m and reaches a maximum depth of 180 m[94]. The Gulf, with an area of 2400 km^2, connects to the Southwestern Atlantic through a 16-km-wide opening facing southeast. As a result, the circulation in GN is primarily influenced by atmospheric forces rather than by those of the adjacent shelf[95,96]. The Gulf is a critical breeding and calving ground for southern right whales (*E. australis*), which annually migrate to the area to mate, give birth, and nurse their calves in its calm, sheltered waters[97]. Furthermore, recent studies have demonstrated that southern right whales forage on zooplankton throughout their seasonal residency in the area (June–December), mainly during spring, targeting calanoid copepods and euphausiids in the waters off Península Valdés, thus making this area a multi-use habitat for this whale species[54–56,82]. The Gulf also serves as an important feeding and nursery habitat for the South American sea lion (*Otaria flavescens*), which forms breeding colonies along its coasts during the reproductive season (December–February) and remains as a permanent resident year-round[98]. The South American sea lion in Patagonian waters is a broad-spectrum predator, feeding mainly on Argentine hake (*Merluccius hubbsi*), Argentine shortfin squid (*Illex argentinus*), and Argentine anchovy (*Engraulis anchoita*)[69]. This combination of reproductive and foraging habitats makes GN a vital area for the conservation of marine mammals in the Southwest Atlantic.

Environmental variables

Satellite data were used in this study to assess the environmental conditions before and after the MME and during the sampling period. The data source was the MODIS (Moderate Resolution Imaging Spectroradiometer) sensor aboard the Aqua Satellite (Aqua MODIS). Level 3 data with a 4 km spatial resolution, 8-day composite time-period, and covering four years (1 January 2018) period previous to 2022 MME until 31 December 2024, were obtained from https://oceancolor.gsfc.nasa.gov/. Data for chlorophyll-a (Chl-a), sea surface temperature (SST), photosynthetically available radiation (PAR), and precipitation rate were gathered for this period. In addition, weekly averages of salinity and nutrients (nitrate, phosphate, and silicate) were determined based on the ARMOR3D reanalysis data downloaded from the Copernicus CMEMS portal for the same period (https://doi.org/10.48670/moi-00052). Pearson correlation analyses were performed between Chl-a and the other variables to identify potential drivers of phytoplankton blooms and to detect potential differences between spring 2022 and the other years. Moreover, Mann-Whitney U tests were conducted to assess differences in climatological surface Chl-a and all the environmental variables between 2022 and the complete time series (2018-2024).

Plankton samples collection

Samples of phytoplankton and mesozooplankton were collected simultaneously at six sites in GN from late austral winter to late spring 2022 (Fig. 1B and C). Water samples for phytoplankton analysis were obtained at 10 m depth using a 5 L Niskin bottle. Subsamples of 250 mL were preserved with Lugol's solution (final concentration ~3%) and stored for species identification and enumeration. Additional phytoplankton samples for enumeration and phycotoxin determination were collected via oblique net tows (20 µm mesh, equipped with a flowmeter [General Oceanics Model 2030 R] at the mouth) from 20 m depth to the surface over a 7-minute period at a speed of 2 knots. Samples were stored in 500 mL plastic bottles. Those intended for taxonomic identification were preserved in 4% formaldehyde and kept at 4 °C until microscopic analysis, while samples for phycotoxin extraction were placed in portable coolers and processed immediately upon return to the laboratory. Mesozooplankton samples for quantitative taxonomic and phycotoxin analyses were collected using a 333 µm mesh net equipped with a flowmeter (General Oceanics Model 2030 R) at the net mouth. Tows were conducted horizontally at a depth of 30 m for 7 min at a speed of 2 knots, and samples were stored in 250 mL plastic flasks. On 28 September 2022, phytoplankton and mesozooplankton samples were collected near the mussel sampling site (see Mussel sample collection section, Fig. 1C). On the same day, four adult whales were observed feeding at the surface; therefore, samples were also taken at that site (Fig. 1C). At both locations, phytoplankton and mesozooplankton were collected and preserved following the standard procedure described above, with minor depth-related adjustments to mesozooplankton sampling at the site where whales were feeding. At this site, mesozooplankton samples for enumeration and phycotoxin determination were collected from surface waters. Surface tows were conducted over a 7-minute period at a speed of 2 knots in a direction parallel to the feeding whales.

Mussel sample collection

Mussels (*Aulacomya atra*) for phycotoxin analysis were collected on 28 September 2022 from natural beds by scuba diving at depths of 5–10 m. Samples were taken in GN (Fig. 1C), placed in plastic bags, and stored at −20 °C until processing.

Fish sample collection

Dead specimens of Argentine anchovy (*E. anchoita*) were opportunistically collected on 24 September 2022 in Bahía Pirámides (BP), GN (Fig. 1C). No fish mortality was recorded at that time; only a few dead individuals were observed, from which a subset was collected for analysis. Whole fish were stored at −20 °C in plastic containers until processing.

Marine mammal sample collection

Samples were collected from October to November 2022 in GN. Various samples, including feces, lung, kidney, liver, blood, muscle, brain, bladder, and placenta, were collected from five stranded adult female South American sea lions (three of which were pregnant) during necropsies (Fig. 5A and B). Not all sample types were available for each individual due to differences in age class or state of decomposition (Table 2); animals ranged from freshly dead to moderately decomposed[99]. Fetuses with intact placentas and fetal membranes were retrieved from the adult female sea lions (Fig. 5B and C) that were found dead along the coastline (Fig. 1B and C). Subsequently, meconium, lung, muscle, liver, kidney, heart, amniotic fluid, and umbilical cord samples were collected by dissection from the three South American sea lion fetuses (Table 2). Furthermore, three fecal samples from live southern right whales were collected using a 125 µm mesh net in BP, between October and November 2022 (Fig. 5D and E; Table 2). All samples were stored at −20 °C until phycotoxin extraction procedures were performed. The sex of adult female whales was inferred based on close and prolonged association with a calf.

Fig. 5 | Collection of marine mammal samples in Golfo Nuevo. A Adult female South American sea lion (*Otaria flavescens*), (**B**) pregnant adult female, (**C**) fetus, (**D**) southern right whale (*Eubalaena australis*), and (**E**) fecal sample from a southern right whale.

Public health records in Puerto Pirámides and shellfish closures in Golfo Nuevo

In Puerto Pirámides (Fig. 1), a small coastal town of 524 inhabitants[100] located within Península Valdés, drinking water is primarily sourced from reverse osmosis desalination of seawater from GN. The process includes a pre-treatment stage (e.g., chlorination and filtration), followed by membrane-based desalination, in which high-pressure pumps force water through semi-permeable membranes that retain salts and most organic compounds. Although this method effectively removes a broad range of contaminants, the final water quality may vary depending on operational conditions. Reverse osmosis membranes can degrade over time due to fouling (colloidal, organic, biological, or inorganic), mechanical damage, or improper cleaning[101]. Notably, during HAB events, high concentrations of dissolved phycotoxins in the water may pose a theoretical risk if membrane integrity is compromised[101,102]. On 29 September 2022, during the intense HAB event in GN, the Secretaría de Salud (Health Secretariat) of Chubut issued a precautionary advisory against consuming desalinated tap water in Puerto Pirámides for 72 to 96 h, pending toxicity analyses. During this period, the water could only be used for bathing and cleaning. This event gained national media attention (Supplementary Fig. 3) and raised concern among the local population of Puerto Pirámides regarding the quality of the drinking water. On 3 October 2022, the authorities confirmed that the desalinated water was safe for human consumption. In this context, we gathered information from the local hospital in Puerto Pirámides regarding cases of human gastrointestinal illness potentially associated with the consumption of contaminated shellfish or desalinated water during spring 2022.

Chubut Province has implemented the Harmful Algal Bloom and Shellfish Toxicity Monitoring Program (hereafter referred to as the Chubut Monitoring Program; https://marearoja.chubut.gov.ar/). This program involves the collection and analysis of both phytoplankton and shellfish to detect the presence of PSTs, DA, and diarrheic shellfish toxins by the mouse bioassay. During winter, when toxigenic taxa are generally scarce, shellfish sampling is conducted monthly. Once potentially harmful species appear in phytoplankton samples, the sampling frequency increases to weekly. If toxin levels exceed regulatory thresholds (PSTs = 80 µg STX eq. 100 g^{-1}; DA = 20 µg g^{-1}; diarrheic shellfish toxins = 160 µg OA eq. kg^{-1}), fisheries are closed and monitoring frequency is reduced to monthly until toxins are no longer detected. At that point, weekly sampling resumes. In this study, we compiled data on shellfish harvesting bans due to PSTs in GN during winter and spring 2022 from the Chubut Monitoring Program.

Plankton analysis and phycotoxin extraction

Phytoplankton samples were analyzed primarily to identify and quantify *Pseudo-nitzschia* spp. and *Alexandrium* spp. Additional lipophilic toxin-producing taxa known from the Argentine Sea—such as *Dinophysis* spp., *Gymnodinium catenatum*, *Prorocentrum lima*, *Protoceratium reticulatum* and *Gonyaulax spinifera*[37]—were also specifically targeted during the analysis. To evaluate potential methodological differences, two traditional counting approaches were used and compared. Samples collected with the Niskin bottle were analyzed using the Utermöhl method under an inverted ZEISS Axioskop 2 microscope (at magnifications of 20× and 40×), testing different sedimentation volumes ranging from 10 to 50 mL. Samples collected with the phytoplankton net were analyzed using a Sedgwick–Rafter counting chamber (1 mL) under a standard upright light microscope (Leica DM500, 20× magnification). The estimation of target organism abundance was more accurate using the Sedgwick–Rafter technique, particularly in cases where protistan plankton density was very high, as the dilution required for Utermöhl counts could introduce variability. Abundance of *Alexandrium* and *Pseudo-nitzschia* spp. was calculated using Sedgwick–Rafter chamber counts combined with the volume of filtered seawater, as determined by the flowmeter attached to the phytoplankton net. This approach accounts for sample concentration during processing and provides more accurate estimates of in situ phytoplankton cells per Liter. In addition, species morphology was examined in more detail using a Nikon Eclipse 80i microscope, and pictures were taken with a Nikon DXM1200F digital camera. Mesozooplankton samples were divided into aliquots to analyze at least 300 zooplankters per sample. Organisms were identified and counted under a stereoscopic microscope (Leica S8 APO). Copepods were assigned to two arbitrary categories, namely 'Small' and 'Large' copepods, according to their body size (up to 1.8 mm and 3.50 mm, respectively), as previously described by Nocera et al. [103] Results were expressed as individuals per cubic meter, based on the total number of organisms in the sample and the volume of water filtered by the net. In this study, the analysis of mesozooplankton focused on the abundance of species that could act as potential vectors of phycotoxins according to their diet (i.e., herbivorous, omnivorous, and carnivorous taxa).

Phytoplankton and mesozooplankton samples were extracted for DA, LT, and PST analyses following the method described by D'Agostino et al. [104] Briefly, phytoplankton samples for phycotoxin extraction were filtered through GF/F filters (47 mm diameter, 0.7 µm pore size) and stored at −20 °C until analysis. Filters were cut into small pieces and placed into cryovials containing 0.9 g of Lysing Matrix D (Thermo Savant). Subsequently, 1 mL of 100% methanol (for the extraction of DA and LTs) or 1 mL of 0.03 M acetic acid (for the extraction of PSTs) was added. Samples were homogenized by reciprocal shaking at maximum speed (6.5 m s^{-1}) for 45 s using a cell disruptor (Bio101 FastPrep instrument, Thermo Savant). After homogenization, samples were centrifuged (Eppendorf model 5415 R) at 16,100 × *g* for 15 min at 4 °C. The residues were re-extracted twice using 0.5 mL of 100% methanol or 0.03 M acetic acid as described above. Supernatants of the same samples were combined, dried under a gentle stream of nitrogen, and reconstituted in 100% methanol or 0.03 M acetic acid to a final volume of 1 mL. The extracts were then filtered through centrifuge filters (0.45 µm pore size; Millipore Ultrafree) by centrifugation (Eppendorf 5415 R) at 16,100 × *g* for 30 s at 4 °C and transferred to autosampler vials.

Mesozooplankton samples for phycotoxin extraction were also filtered through GF/F filters (47 mm diameter, 0.7 µm pore size) and stored at −20 °C until analysis. Filters were cut into small pieces and transferred to centrifuge tubes, where phycotoxins were extracted using 15 mL of 100% methanol (for the extraction of DA and LTs) or 0.03 M acetic acid (for the extraction of PSTs), aided by ultrasonication (Sonopuls HD 2070; Bandelin; 2 min / 7 cycles / 96% power). Samples were vortexed (Heidolph Reax Top Vortex Mixer) for 2 min and then centrifuged (Eppendorf 5810 R) at 3,220 × *g* for 15 min at 4 °C. The resulting supernatant was transferred to clean centrifuge tubes and kept at 4 °C until further processing. The residues were re-extracted twice with 5 mL of 100% methanol or 0.03 M acetic acid as described above. The combined extracts were then dried using a vacuum concentrator equipped with a refrigerated vapor trap until complete dryness (at least 6 h) (SpeedVac, Thermo Scientific), and the final volumes were adjusted to either 1 mL with 100% methanol or 0.03 M acetic acid. Finally, the concentrates were filtered through centrifuge filters (0.45 µm pore size; Millipore Ultrafree), centrifuged (Eppendorf 5415 R) at 3000 × *g* for 30 s at 4 °C, and transferred to autosampler vials.

Phycotoxins in mussels, fish, and marine mammal samples

Samples of whole mussels, whole fish specimens, and tissues/fluids from South American sea lions, and feces from southern right whales were lyophilised (OPERON FDU-8606, Korea) to remove water and then stored at −20 °C until phycotoxin extraction, following the procedure previously described by D'Agostino et al. [104] The samples were thawed at room temperature prior to processing. Aliquots of approximately 1.5 g of each sample were placed in 50 mL centrifuge tubes, and 8 mL of 100% methanol for the extraction of DA and LTs, or 8 mL of 1% (v/v) acetic acid for the extraction of PSTs, were added. The mixtures were vortexed for 2 min (Heidolph Reax Top) and then sonicated (Bandelin Sonopuls HD 2070) for 8 min (7 cycles at 96% power). Each mixture was subsequently vortexed again for 2 min and centrifuged (Eppendorf 5810 R) at 3220 × *g* for 15 min at 4 °C. The supernatants were then transferred to clean centrifuge tubes and stored at 4 °C. The residues were re-extracted twice with 5 mL of 100% methanol or 1% (v/v) acetic acid, following the same procedure. The combined extracts were then dried in a vacuum concentrator equipped with a refrigerated vapor trap until complete dryness (at least 6 h) (SpeedVac, Thermo Scientific), and the final volumes were adjusted to 1 mL with either 100% methanol or 1% (v/v) acetic acid. Finally, the concentrates were filtered through centrifuge filters (0.45 µm pore size; Millipore Ultrafree), centrifuged (Eppendorf 5415 R) at 3000 × *g* for 30 s at 4 °C, and transferred to autosampler vials.

Phycotoxin analysis and data normalization

DA and LT analyses were performed using liquid chromatography–tandem mass spectrometry (LC–MS/MS), as described by Krock et al. [105] and Linke[106]. PSTs were analyzed by high-performance liquid chromatography with post-column derivatization and fluorescence detection (HPLC-FLD), following the method described by Krock et al. [90] Phycotoxin levels in plankton were expressed in ng L^{-1} for phytoplankton and in ng g^{-1} for mesozooplankton samples. Conversions were performed using the filtered water volume, as determined by the flowmeter, and the wet weight of mesozooplankton samples. For mussels, anchovies, and marine mammals, phycotoxin levels were expressed on a wet-weight basis (ng g^{-1}), calculated using the mean water content of each sample type. The levels of the PST analogs gonyautoxins (GTX1/GTX4, GTX2/GTX3) and N-sulfocarbamoyl toxins (C1/C2) were combined by adding the individual values together to account for possible epimerization of the toxin pairs. For plankton samples, anchovies, and mussels, total HPLC-FLD results were also expressed as STX equivalents, calculated using experimentally derived toxicity factors for each congener[54]. The detection limits of PSTs for phytoplankton and mesozooplankton samples were as follows: C1/C2, 0.01; *N*-sulfocarbamoyl toxin (B1), 0.03; decarbamoyl toxins (dcGTX2/GTX3 and decarbamoyl saxitoxin [dcSTX]), 0.01; GTX2/3, 0.01; GTX1/4, 0.11; neosaxitoxin (NEO), 0.04; and saxitoxin (STX), 0.01 ng L^{-1} or ng g^{-1}. For anchovy, mussel, and marine mammal samples, the detection limits were 4.50 ng STX g^{-1} and 6.10 ng dcSTX g^{-1}. The detection limit of DA for all samples was 0.0044 ng L^{-1} or ng g^{-1}. The detection limits of LTs in phytoplankton and mesozooplankton samples were 0.032 (DTX-1) and 0.0087 (PTX-2) ng L^{-1} or ng g^{-1}. For marine mammals, the detection limit of SPX-1 was 0.70 ng g^{-1}. Calibration was performed using certified reference standards purchased from the Metrology Research Centre (NRC, Halifax, NS, Canada).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Environmental data used in this study were obtained from publicly available repositories. Satellite data (chlorophyll-a, sea surface temperature, photosynthetically available radiation, and precipitation rate) from the MODIS Aqua sensor were obtained from the NASA Ocean Color database (https://oceancolor.gsfc.nasa.gov/). Salinity and nutrient data (nitrate, phosphate, and silicate) were obtained from the Copernicus Marine Service

ARMOR3D reanalysis dataset (https://doi.org/10.48670/moi-00052). Toxin data generated during this study are provided in the main article and its Supplementary Information. Statistical analyses were performed using R (version 2024.09.0 + 375).

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Author contributions

V.C.D. conceived the study, designed the methodology, conducted the fieldwork and formal analysis, and contributed to data visualization, project administration, and resource and funding acquisition; wrote the original draft and reviewed and edited the manuscript. M.D. contributed to the methodology, fieldwork, project administration, resource and funding acquisition, and reviewed and edited the manuscript. M.A. contributed to the formal analysis, methodology, and reviewed and edited the manuscript. A.C.N. contributed to the formal analysis, methodology, data visualization, and reviewed and edited the manuscript. V.G. contributed to the formal analysis, methodology, and funding acquisition and reviewed and edited the manuscript. C.F. contributed to the formal analysis and methodology. B.K. provided resources, supervised the study, contributed to funding acquisition, and reviewed and edited the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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