Marine Mammal Science

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Saxitoxin Linked to Deaths of Northern Fur Seals in the Southeast Bering Sea

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ABSTRACT

In August 2024, a northern fur seal mortality event was observed on St. Paul Island, AK in the southeast (SE) Bering Sea. Ten seals in good body condition were found dead along with large accumulations of dead fish on Benson Beach located on St. Paul Island. Full necropsies of the five available adult seals, one pup, and several fish did not reveal any overt causes of death. Testing of tissues for the algal neurotoxins domoic acid (DA) and saxitoxin (STX) confirmed the presence of STX in multiple tissues and physiological exposure in all five adult NFS and the two fish available for testing. DA was not detected in any samples. Complimentary samples of the SE Bering Sea ecosystem during the same time frame and location as the die off revealed bloom densities of *Alexandrium catenella* (the dinoflagellate that produces STX), large *A. catenella* cyst beds, and high prevalences of STX in fish (100%, $n = 22$), zooplankton (93%, $n = 28$), clams (100%, $n = 10$) and worms (93% $n = 15$) in the foraging area of NFS. High STX concentrations were observed in fish, clams, worms, and NFS urine, providing compelling evidence for a STX poisoning event.

1 | Introduction

Toxic marine harmful algal blooms (HABs) occur when microscopic algal cells that naturally produce potent neurotoxins proliferate to high cell densities in marine ecosystems. Two HAB species of concern in Alaskan marine environments include *Pseudo-nitzschia* spp., a group of diatoms that produce domoic acid (DA), and *Alexandrium catenella*, a dinoflagellate that produces paralytic shellfish toxins (PSTs) including saxitoxin (STX) (Anderson et al. 2022). During blooms, STX and DA accumulate in filter-feeding organisms and are responsible for the human illnesses known as paralytic shellfish poisoning (PSP) and amnesic shellfish poisoning (ASP), respectively (Wekell et al. 2004). Additionally, these toxins can be found in all trophic layers of food webs, creating exposure risks to marine wildlife on a broad scale (Landsberg et al. 2014; Anderson et al. 2021; Lefebvre et al. 2022). Both of these toxins affect the central nervous system, but via different mechanisms. Domoic acid is a neuroexcitatory amino acid that acts as a glutamate (Glu) agonist and overstimulates nerves (Berman and Murray 1997). Glutamate is the normal excitatory neurotransmitter needed for communication between nerves via Glu receptors (Novelli and Diporzio 1993). The chemical structure of DA contains the structural component of Glu but with an additional proline ring that makes it bind longer to receptors, causing overexcitation and eventually neuronal cell death (Hampson and Manalo 1998). Outward signs of DA poisoning include seizures, gastrointestinal (GI) distress, memory loss, coma, and death (Teitelbaum et al. 1990). Saxitoxin is a voltage-gated sodium channel blocker that prevents nerve function by blocking action potential activity in nerves (Thottumkara et al. 2014). This results in paralysis, particularly of the respiratory system. Clinical signs of STX poisoning in humans include oral and facial paresthesia (tingling of skin/lips), nausea, vomiting, dysphagia (difficulty swallowing), dysarthria (abnormal speech), weakness progressing to paralysis, and death due to respiratory failure (Suarez-Isla 2014; Knaack et al. 2016).

It is well known that marine mammals are exposed to these algal-produced neurotoxins and that they can impact marine mammal health (Landsberg et al. 2014; Lefebvre et al. 2016). Importantly, the differences in the mechanisms of action between DA and STX cause different types of poisoning, with neurobehavioral signs of toxicity varying in visibility. DA was first recognized as a poisoning agent for marine mammals in 1998 in Monterey Bay, CA, when hundreds of California sea lions (CSL; *Zalophus californianus*) came ashore on public beaches exhibiting neuronal excitotoxicity in the form of seizures (Lefebvre et al. 1999; Gulland 2000; Scholin et al. 2000). This highly visible event prompted a large-scale response by scientists and health care professionals that resulted in determining that DA from a toxic *Pseudo-nitzschia* bloom was transferred through filter-feeding northern anchovies (*Engraulis mordax*) to sea lions causing excitotoxicity and death (Lefebvre et al. 1999; Scholin et al. 2000). Since this first recognized event, dozens to hundreds of CSL experience DA poisoning each year, and there has been a statistically significant increasing trend of cases of CSL diagnosed with DA toxicosis recorded at the Marine Mammal Center in Sausalito, CA (Anderson et al. 2021). In addition to CSL, DA has been suspected and confirmed in numerous other mass-mortality events in many marine mammal groups including sea otters (*Enhydra lutris*), dolphins, porpoises, harbor seals (*Phoca vitulina*), whales, and northern fur seals (NFS, *Callorhinus ursinus, Iaaquda$\hat{x}$ in Unangam Tunuu*) in California (Landsberg et al. 2014).

In the case of STX, far fewer poisoning events have been documented for marine mammals. In fact, only a few publications have provided evidence implicating STX poisoning in marine mammal mortalities (Landsberg et al. 2014). The first and strongest documented case occurred in 1987 in Cape Cod Bay, MA, where 14 humpback whales (*Megaptera novaeangliae*) died after consuming Atlantic mackerel (*Scomber scombrus* L.) containing STX, having no other signs of illness (Geraci et al. 1989). Earlier that same year, a mortality event of 60 sea otters (*E. l. lutris*.) in Alaska was highly suspected to have been caused by STX but remains unconfirmed (Degange and Vacca 1989). A third study implicates STX as the cause of the deaths of 117 critically endangered Mediterranean monk seals (*Monachus monachus*) in Western Sahara, Africa (Costas and Lopez-Rodas 1998). More recently, a mass mortality event in 2015 of primarily sei whales (*Balaenoptera borealis*) in Chilean Patagonia was linked to possible STX poisonings due to elevated STXs in the environment attributed to an abnormally strong El-Niño event (Häussermann et al. 2017). The impact of STX on marine mammals has been difficult to document most likely because the toxicological impacts are less visible than those for DA poisoning. Unlike the highly visible stranding and seizures characteristic of DA excitotoxicity observed in CSL, paralysis of the respiratory system that is typical of STX-associated death in mammalian species, including humans, would most likely result in suffocation of marine mammals at sea. As such, these animals may never be observed or sampled for confirmation of poisoning, likely resulting in a gross underestimate of the frequency and severity of STX poisoning in marine mammals.

Saxitoxin poisoning may sometimes be perceived as a coastally associated phenomenon because shellfish are commonly harvested and consumed close to shore. However, offshore blooms of *A. catenella* are significant sources of toxins to marine food webs (Keafer et al. 2005; Martin et al. 2014). These offshore blooms originate from *A. catenella* cyst beds, which are accumulations of resting cysts that lie dormant in continental shelf sediments (McGillicuddy et al. 2003). Germination of *A. catenella* cysts is temperature-dependent, leading to seasonal cycles of bloom activity, generally concentrated in the spring and summer (Anderson 1998; Anderson et al. 2012). Given the crucial role that this life stage plays in bloom initiation, mapping benthic cyst accumulations in shelf sediments is an important component in understanding regional bloom dynamics (Anderson et al. 2014). Offshore blooms originating from these cyst beds are logistically challenging to monitor with routine sampling (Sellner et al. 2003), so while they may be opportunistically detected with shipboard measurements (Fachon et al. 2025), it is likely that many blooms may be missed altogether or not discovered until an illness or mortality has occurred.

In the present study, 10 dead NFS in good body condition, along with hundreds of fish (primarily benthic dwelling fish such as flounder and sole (*Pleuronectidae*), Pacific cod (*Gadus macrocelphalus*), and Pacific halibut (*Hippoglossus stenolepis*)), washed ashore on St. Paul Island, AK in the southeast (SE) Bering Sea

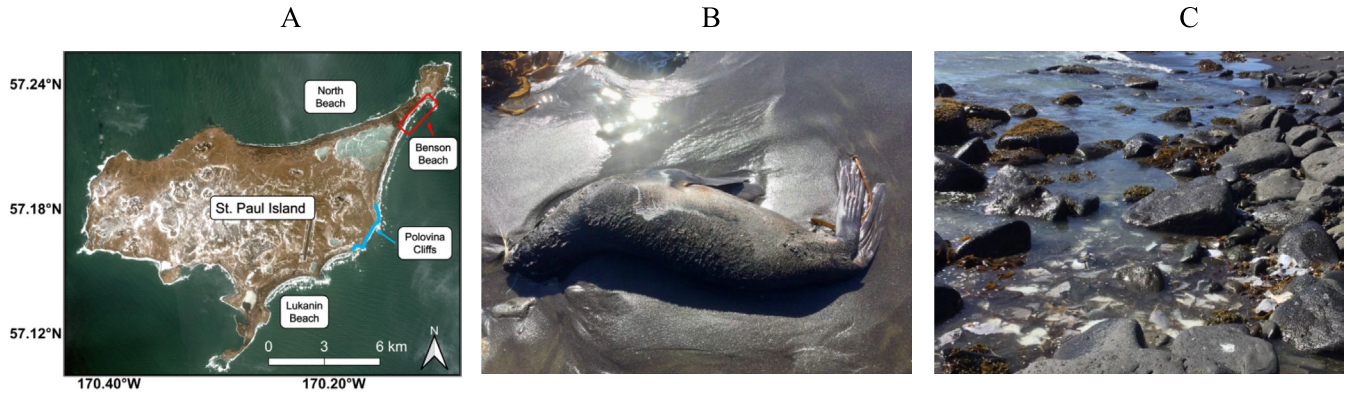

FIGURE 1 | Aggregates of dead unidentified fish and 10 dead Northern Fur seals (NFS) were found on the northeast side of St. Paul Island on Benson Beach, AK on August 18, 2024. Figure panels show (A) map of St. Paul Island with Benson Beach (red square), (B) photo of dead seal, and (C) photo of dead fish.

in August 2024. The animals were first observed by an Aleut Community of St. Paul Island tribal member on August 18, 2024, and tribal environmental staff collected and froze six NFS carcasses (five adults and one pup) and several fish carcasses for later necropsy to determine the cause of death. A thorough investigation of possible causes of death included necropsies of the six frozen NFS and all available fish. Results from necropsies and examinations of dead fish and NFS body tissues, as well as analyses of seawater, sediments, and food web samples that were independently collected by research cruises during the same general time frame in surrounding waters, provided compelling evidence that STX exposure via the food web caused this acute mortality event.

2 | Methods

2.1 | Mortality Event Necropsy and Sampling

In the evening of August 18, 2024, ten dead NFS and hundreds of dead fish were observed by a beachcomber on the shores of the northeast side of Benson Beach, located on St. Paul Island (Figure 1). An immediate report was made to environmental staff of the Aleut Community of St. Paul Island Ecosystem Conservation Office (ECO). ECO staff immediately responded to Benson Beach and observed ten NFS ranging from a pup (born that year) to adult individuals in various stages of decomposition from fresh dead to moderately decomposed, many wrapped in bull whip kelp (*Nereocystis leutkeana*). In addition to NFS carcasses, hundreds of fish carcasses in fresh condition were observed along the wrack line. The following day, ECO staff swabbed all available NFS ($n=5$ adults and $n=1$ pup) for influenza surveillance and froze these NFS carcasses and 5 fish ($n=4$ northern rock sole and $n=1$ Pacific cod (*Gadus macrocephalus*)) for subsequent necropsy. Four NFS carcasses were transferred to Anchorage, AK, and necropsied by Alaska Veterinary Pathology Services (AVPS), and two were necropsied on island according to standard protocols (Geraci and Lounsbury 1993). Organ tissues, stomach contents, urine, and feces were collected into sterile whirl-paks or conical tubes. Swabs were stored in 2 mL cryovials with viral transport media (Remel) or tryptic soy broth with 15% glycerol (Hardy Diagnostics). All necropsy samples were stored at −80°C and shipped for diagnostics on dry ice. Samples from the NFS were also fixed in 10% neutral buffered formalin (VWR) and processed for histopathology at Histological Consulting Services (Everson, WA).

Polymerase chain reaction (PCR) for influenza, SARs CoV-2, and phocine morbillivirus was performed on nasal, rectal, and brain swabs at Tufts University using established methods (Puryear et al. 2023). Blubber ($n=6$), brain ($n=6$), feces ($n=5$), kidney ($n=6$), liver ($n=6$), muscle ($n=3$), gastrointestinal (GI) contents ($n=6$), and urine ($n=2$) from NFS ($n=5$ adults and $n=1$ pup) and intestinal contents and liver from fish carcasses ($n=2$) were sent to the U.S. National Oceanic and Atmospheric Administration's (NOAA) Wildlife Algal-toxin Research and Response Network (WARRN-West) for DA and STX testing.

2.2 | Ecosystem Sampling- Algal Cells, Algal Cysts, Food Web Samples

During July and August 2024, two research cruises conducted comprehensive oceanographic and HAB sampling in the SE Bering Sea: the Arctic Observing Network (AON) cruise aboard the USCGC *Healy* (HLY2401, July 2, 2024–August 1, 2024) and the Bering Sea Aleutian International Survey (BASIS) aboard the NOAA R/V *Oscar Dyson* (DY24-09, August 15–29, 2024). While DY24-09 focused primarily on the SE Bering Sea, HLY2401 only occupied stations in the Bering Sea from July 3 to 9, 2024, after which the ship transited northward for continued operations. During both cruises, near-surface imagery of the phytoplankton community was collected via an Imaging Flow Cytobot (IFCB, McLane Labs, East Falmouth, MA) configured to sample from the underway seawater system aboard each vessel (Figure 2). Each instrument was programmed to analyze ~5 mL of seawater every 20 min throughout the research cruise, and samples were timestamped and assigned a latitude/longitude from the shipboard GPS. The IFCB intakes were covered with a 150 μm mesh to remove larger debris and sediment that would clog the internal plumbing. Imagery produced by the IFCBs was analyzed for the presence of *A. catenella* cells, and cell counts were normalized to cells L^{-1} to evaluate bloom density. In the case of HLY2401, this analysis was conducted in near-real time from the vessel, while the imagery from DY2409 was analyzed post-cruise. Additionally, the IFCB aboard the *Oscar Dyson* was

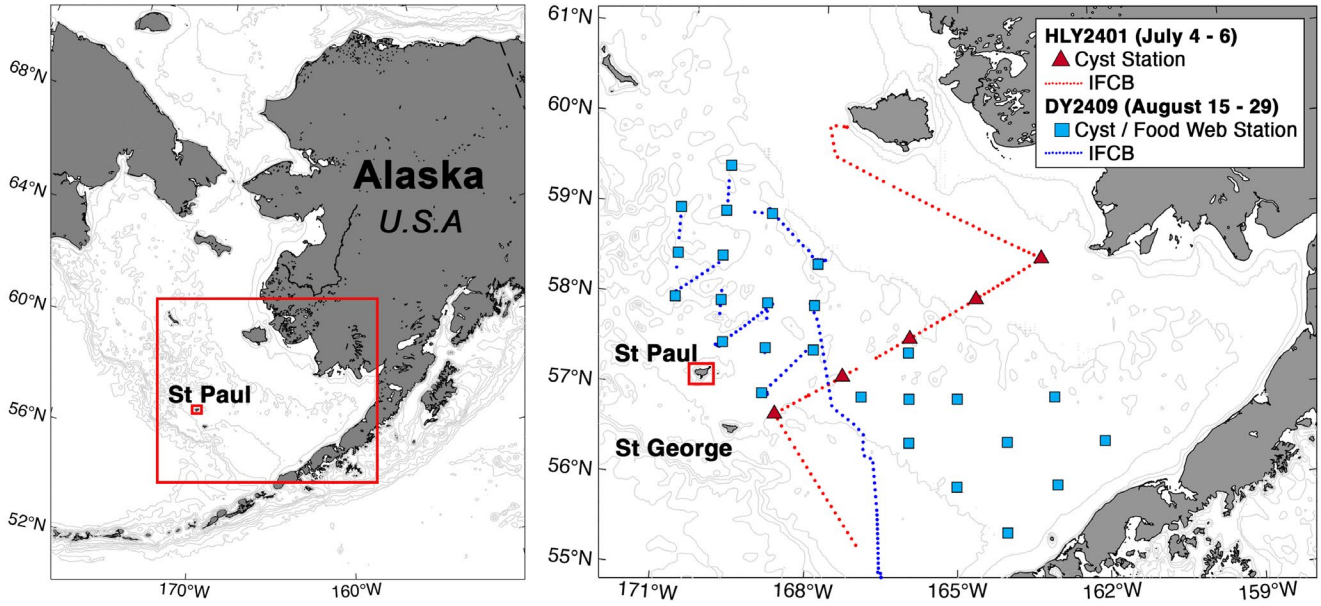

FIGURE 2 | Map of sampling locations for *Alexandrium catenella* cell and cyst counts, and food web samples of live fish, zooplankton, clams and benthic worms (large red rectangle; left panel) in relation to St. Paul Island (small red rectangle; left panel). Sampling locations are detailed in the right panel. *A. catenella* cell abundances were derived from underway Imaging Flow Cytobot (IFCB) sampling (dashed red/blue lines). During the HLY2401 cruise (July 4–6, 2024) stations were sampled for cyst abundance (red triangles), and during DY2409 (August 15–29, 2024) both cyst and food web samples were collected from occupied stations (blue squares).

operational during an earlier expedition (DY2408, June 5–July 20, 2024) dedicated to an acoustic survey of walleye pollock (*Gadus chalcogrammus*) in the southeastern Bering Sea. Due to challenges with instrumental configuration, it was not possible to accurately quantify *A. catenella* from this dataset, but qualitative results are reported.

To quantify *A. catenella* cyst abundance in sediments on the SE Bering Sea shelf, surface sediments were collected from the region during HLY2401 ($n = 5$) and DY2409 ($n = 19$; Figure 2). At each station, a homogenized aliquot of the 0–3 cm layer was collected from a 0.1 m^{-2} Van Veen grab and preserved at 4°C. Cysts were stained and enumerated following protocols outlined in Anderson et al. (2014). Briefly, samples were sonicated and sieved to obtain the 15–80 μm size fraction. This size fraction was resuspended in filtered seawater, preserved with formalin (5% final concentration), and then resuspended in methanol. A series of centrifugation steps were used to remove the methanol, wash the sample, stain with primuline stain (2 mg mL^{-1}), and resuspend stained samples in deionized water. *A. catenella* cysts were enumerated at 10x magnification under an FITC filter set, and counts were normalized to cysts per cubic centimeter of sediment (cysts cm^{-3}). During DY2409, additional food web samples of zooplankton, fish, clams, and worms were collected during mid- to late-August in the same region with collection methods described in Lefebvre 2022 (Figure 2).

2.3 | Algal Toxin Testing

Northern fur seal tissues, zooplankton, fish, clams, and worms were extracted for both DA and STX analyses according to methods described in Lefebvre et al. (2022). Briefly, samples were homogenized and extracted in 50% methanol (1:4 sample-to-methanol; w/v), filtered, and diluted (1:50 extract-to-ELISA kit sample diluent; v/v) to avoid matrix effects and tested using Abraxis Domoic acid (Onsite Technologies) and Abraxis Saxitoxins (PSP) ELISA kits (Gold Standard Diagnostics, Horsham, PA) according to kit instructions. Note: Abraxis Saxitoxins kits are specifically designed to detect STX with 100% reactivity, but the kits have low cross-reactivity with other PST congeners. The next highest congener cross-reactivity is 23%, with others as low as 0.1%. Therefore, these ELISA STX concentrations are likely underestimates of total toxicity, which is described as STX equiv. g^{-1} for seafood safety regulatory purposes using a high performance liquid chromatography (HPLC) method that quantifies all PST congeners, then converts them to toxicity units as related to STX toxicity (Authority EFS 2009). ELISA STX and DA concentrations were interpolated using a 4-parameter logistic curve fit model. The minimum detection limits were 4 ng STX g^{-1} and between 104 and 138 ng DA g^{-1}.

2.4 | Ocean and Atmospheric Reanalysis Fields

To investigate the impact of atmospheric forcing and ocean circulation on HAB progression and the beaching of the NFS and fish, we used the GLORYS12v1 global ocean eddy-resolving reanalysis product from the Copernicus Marine Environment Monitoring Service (CMEMS, https://doi.org/10.48670/moi-00021) and the ERA5 atmospheric reanalysis from ECMWF (https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5). GLORYS12v1 is derived from the Nucleus for European Modeling of the Ocean (NEMO) model, with a horizontal resolution of 1/12°, 50 vertical levels, and a time resolution of 1 day. It is forced at the surface using ERA5, and it assimilates satellite measurements of sea level anomaly, sea surface temperature, sea ice concentration, and in situ vertical profiles of temperature and salinity. ERA5 has

TABLE 1 | Saxitoxin (STX) concentrations (ng STX g^{-1} or mL^{-1}) detected in northern fur seals (NFS) and fish sampled from the mortality event on August 19th, 2024 on the northeast side of St. Paul Island at Benson Beach (Figure 1).

Animal	GI	Feces	Liver	Kidney	Urine	Blubber	Muscle	Brain	Sex	Age class
NFS 1	26	333	21	434	975	bdl	bdl	bdl	F	Adult
NFS 2	21	141	61	22	ns	bdl	ns	bdl	F	Adult
NFS 3	31	596	bdl	148	ns	bdl	ns	bdl	F	Adult
NFS 4	45	56	22	124	ns	bdl	bdl	bdl	F	Adult
NFS 5	21	102	13	55	201	bdl	bdl	bdl	F	Adult
NFS 6	bdl	ns	bdl	bdl	ns	bdl	ns	bdl	F	Pup
Fish 1	810	ns	495	ns	ns	ns	ns	ns		Pacific Cod
Fish 2	117	ns	253	ns	ns	ns	ns	ns		Northern Rock Sole

Note: Red values are above the seafood safety regulatory limit (800 ng STX equiv. g^{-1} or 80 μg STX equiv. 100 g^{-1}).
Abbreviations: bdl = below detection limit of 4 ng STX g^{-1} or mL^{-1}; F = Female; GI = gastrointestinal sample; ns = no sample.

a horizontal resolution of 1/4° and a time resolution of 1 h. ERA5 10-m winds have shown good agreement with wind data from the Utqiaġvik, AK weather station (Lin et al. 2021).

Backward particle trajectories were computed by applying the Ocean Parcels package in Python (https://oceanparcels.org/) to the GLORYS12v1 velocity fields at 0.5 m depth (the shallowest available depth level). Since tides are substantial in the SE Bering Sea and GLORYS12v1 does not include tidal velocities, we supplemented the GLORYS12v1 velocities with barotropic tidal velocities from the TPXO9v3 tidal model [http://volkov.oce.orst.edu/tides; (Padman and Erofeeva 2004)]. To do this, we interpolated the GLORYS12v1 data to an hourly grid to match the hourly tidal data. Calculations were done both with and without tides to assess the impact of the barotropic tides.

3 | Results

3.1 | Mortality Event—Necropsy Results

Grossly, all six NFS (five adults and one pup) were in average to good body condition and were in mild decomposition. Two animals had minor ulcerative skin lesions, likely viral; two had excoriations and hemorrhages on the head, and one had excoriations on the flippers. Four animals had fluid in the pleural and peritoneal cavities thought to be due to freeze artifact. Three had small tan foci on the surface of the liver, and one had a volcano ulcer in the lining of the stomach with nematodes attached. The pup's stomach was distended by milk and no prey items. There were no other significant gross lesions. Nasal, rectal, and brain swabs were negative for influenza A by PCR for all six NFS. Histopathology on the seals showed evidence of terminal aspiration of stomach contents in all of the animals. Mild vacuolar hepatopathy was present in two adults and the pup. Various incidental parasite-related changes, including mild chronic active bronchitis in two adults, ulcerative and nodular granulomatous gastritis related to nematodes in one adult, and mild multifocal random hepatitis and hookworm enteritis in the pup, were noted. One animal had mild pyramidal cell dropout and vacuolation in the hippocampus of unknown significance. The aspiration of stomach contents in the pup combined with hookworm enteritis was thought to be the cause of death, while STX toxicity was likely the cause of death in the adult NFS. All five fish were scavenged and markedly decomposed. Histopathology was not performed on the fish.

3.2 | Mortality Event—Algal Toxin Samples

All five adult NFS and both fish sampled from this event contained detectable concentrations of STX in multiple tissues, while the pup was negative (Table 1). The highest STX concentrations of 975 ng STX mL^{-1} in NFS urine and 810 ng STX g^{-1} in fish GI contents were above the seafood safety regulatory limit of 800 ng STX equiv. g^{-1} or mL^{-1} (Wekell et al. 2004). Saxitoxin was not detected in blubber, muscle, or brain samples analyzed, or in the NFS pup (Table 1). Domoic acid was not detected in any of the samples.

3.3 | Ecosystem Samples—Algal Cell and Cyst Counts

Underway phytoplankton imagery collected aboard the *Healy* (HLY2401) and *Dyson* (DY2408, DY2409) cruises detected *A. catenella* in the Bering Sea (Figure 3). On June 22nd, the IFCB aboard the *Dyson* recorded *A. catenella* concentrations > 1000 cells L^{-1} approximately 26 nautical miles (nmi) north of St. Paul Island, although instrumentation issues experienced during this period prevented full characterization of the bloom. On July 5th, while transiting eastward from the Pribilof Islands towards mainland Alaska, the *Healy* IFCB detected elevated concentrations of *A. catenella* (Figure 3A). Maximum detected concentrations of this harmful species were estimated to be 4600 cells L^{-1} of seawater recorded on July 5th at 10:44 GMT approximately 160 nmi east of St. Paul Island. Six seawater samples with high *A. catenella* cell counts (above 1000 cells L^{-1}) were detected while the vessel transited approximately 35 nmi. Seven weeks later (August 15–29, 2024), when the *Dyson* (DY2409) cruise was occupying the region, low levels of *A. catenella* were still detectable (Figure 3B), with a maximum of 1000 cells L^{-1} recorded on August 28th 170 nmi northeast of St. Paul. Collectively, these observations across several cruises indicate that the *A. catenella* bloom period in the SE Bering Sea extended from late June through the end of August during the summer of 2024.

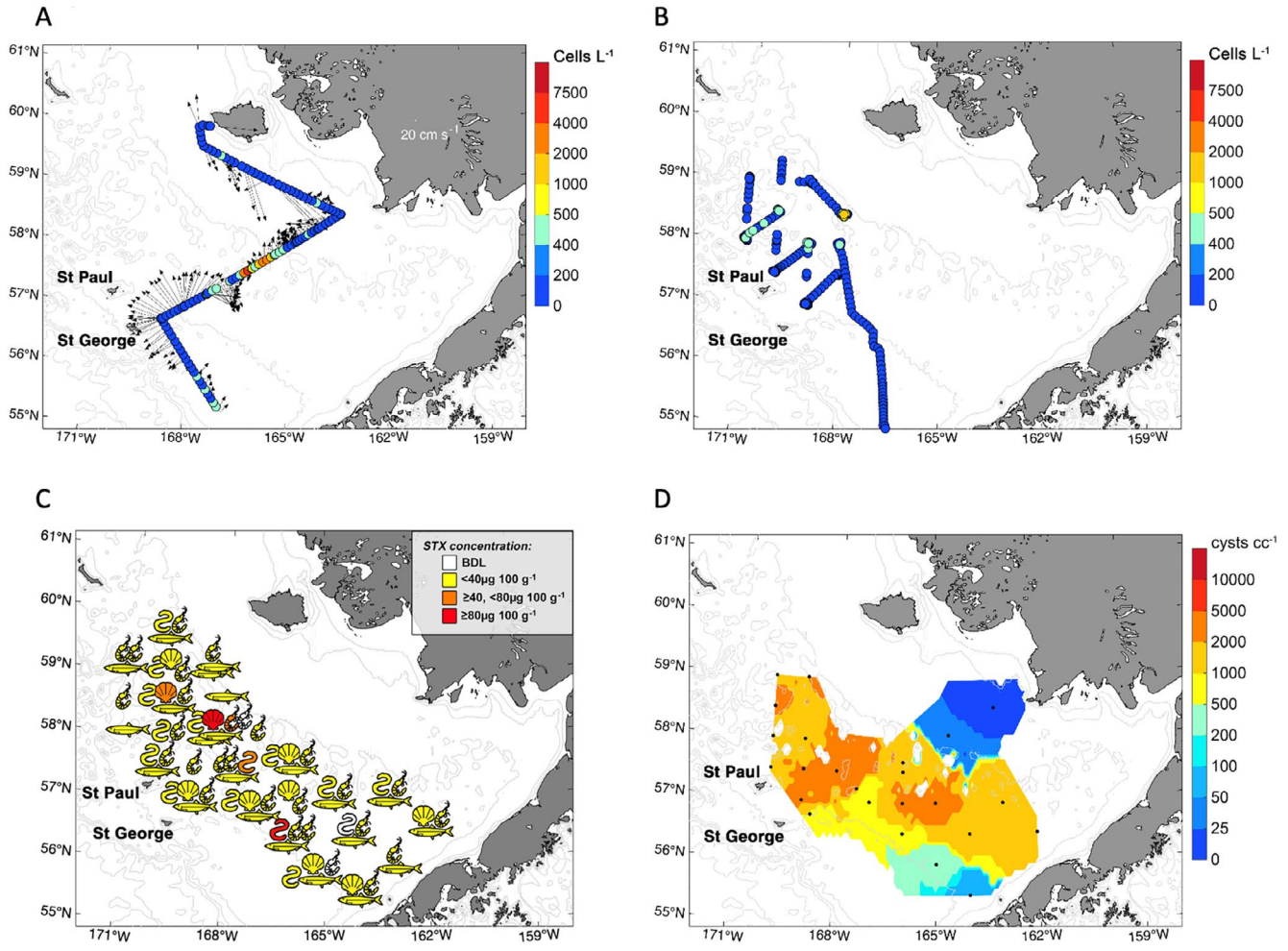

FIGURE 3 | Algal cell and cyst counts, and saxitoxin (STX) concentrations in the food web. Panels show estimated cell densities (cells L^{-1}) of *Alexandrium catenella* (colored dots) sampled via Imaging Flow Cytobot (IFCB) in (A) July 2024 and (B) August 2024. Arrows indicate current direction and strength at the time of sampling, measured by shipboard acoustic Doppler current profiler. (C) Saxitoxin concentrations (ng STX g^{-1}) in fish, clams, worms, and zooplankton samples collected from August 8 to 16, 2024 (red = above the seafood safety regulatory limit of 800 ng STX equiv. g^{-1}; Orange = half of the regulatory limit; Yellow = below half of the regulatory limit; and white = below assay detection limit of 4 ng STX g^{-1}. (D) *A. catenella* cyst densities in the 0–3 cm sediment layer (cysts per cubic centimeter; cm^{-3}) interpolated across sampling locations (black points) during research cruises.

High densities (> 300 cysts cm^{-3}) of *A. catenella* cysts were detected in surface sediments throughout the SE Bering Sea (Figure 3D), at bottom depths ranging from 34 to 98 m. The maximum cyst concentration was 3610 cysts cc^{-1}, found in a sample collected ~70 nmi east of St. Paul Island. Across all samples collected ($n = 24$), the mean ± SD cyst concentration was 1480 ± 920 cysts cm^{-3}. The presence of this dense cyst bed indicates a high potential for bloom activity on the SE Bering Sea shelf.

3.4 | Ecosystem Samples—Algal Toxins in Fish, Zooplankton, Clams, Worms

In addition to the presence of toxigenic *A. catenella* cells and cysts (Figure 3A,B,D), STX was detected in all components of the food web including fish, zooplankton, clams, and benthic worms (Figure 3C). All fish collected during cruises in July/August 2024 from the SE Bering Sea contained detectable concentrations of STX (100% prevalence). Fish species tested included age-0 walleye pollock ($n = 20$), age-1+ Pacific herring (*Clupea pallasii*; $n = 1$), and juvenile capelin (*Mallotus villosus*; $n = 1$). Toxin concentrations ranged from 9 to 157 STX g^{-1} in fish viscera. Toxin prevalences in zooplankton ($n = 28$), clams ($n = 10$), and benthic worms ($n = 15$) were 93%, 100%, and 93%, respectively. The highest concentrations were detected in clams (1020 ng STX g^{-1}) and worms (1423 ng STX g^{-1}), surpassing the seafood safety regulatory limit of 800 ng STX equiv. g^{-1} (Wekell et al. 2004) (Figure 3C).

3.5 | Impact of Ocean Circulation and Atmospheric Forcing

Under the scenario that the poisoned NFS and fish first encountered the *A. catenella* cells in the region east of St. Paul Island prior to beaching on the northeast part of the island, we

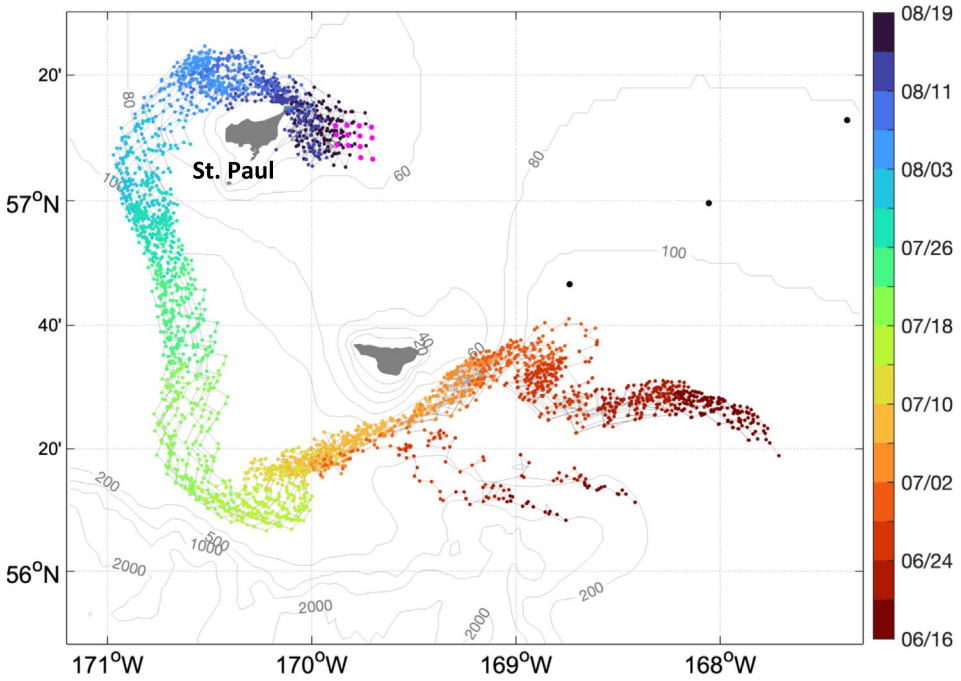

FIGURE 4 | Backward trajectories of particles released on Aug 18, 2024 in the region east of St. Paul Island, color-coded by date going back in time. The magenta circles mark the starting positions of the particles. The black circles are stations occupied by USCGC *Healy* from July 4 to 6, 2024.

computed backward surface (0.5 m) particle trajectories to see where the HAB may have stemmed from. This indicates that, roughly 2 months prior, the water resided east of St. George Island and was subsequently advected in a general anti-cyclonic pathway east of the Pribilofs, finally circulating around the northern side of St. Paul (Figure 4). While the effect of the tides is evident in the dithering of the trajectories, the overall pathway is similar when using the velocity fields with the tides removed (not shown). Such a pathway is consistent with the general circulation of the region (Stabeno et al. 2016); in particular, it corresponds to the outer shelf pathway deduced by the drifter and mooring data presented in Stabeno et al. (2016), which includes the anti-cyclonic flow around St. Paul Island. Notably, the particles are near the western end of the *Healy* transect in late-June/early-July (Figure 4), precisely at the time that the HAB was observed on the cruise. This suggests that the HAB sampled on the *Healy* could have contributed to the mortality event east of St. Paul Island.

To investigate what might have caused the beaching, we considered the atmospheric forcing and wind-driven circulation. Prior to the discovery of the dead NFS on Benson Beach, a succession of two low pressure systems transited the SE Bering Sea, the second of which was the remains of extratropical storm Ampil which progressed past the Pribilofs from Aug 15 to 17 (Figure 5B–D). We created a timeseries of wind-driven flow averaged over a box situated east of St Paul Island (Figure 5A). In particular, we computed the surface Ekman flow (45° to the right of the wind stress). Just prior to when the storm center reached the Pribilofs (time t1, Figure 5B), there was roughly a half-day period when the surface flow was conducive for advecting carcasses onto Benson Beach (i.e., flow to the northwest). The GLORYS12v1 surface velocities without tides are consistent with this result. If, however, the NFS perished after the passage of the storm (i.e., closer to their discovery on the beach), then the tidal flow by itself would be able to cause the beaching. In particular, strong tidal velocities (roughly 15 km/d) are directed shoreward for several hours each day as part of the tidal cycle in this region.

4 | Discussion

Collectively, our data suggest that the accumulation of STX in SE Bering Sea food webs during *A. catenella* blooms in summer 2024 contributed to the deaths of several NFS that washed up on Benson Beach on the Northeast side of St. Paul Island, AK on August 18, 2024 (Figure 1). It has recently been confirmed that STX-producing HABs commonly occur in Arctic waters and that STX is present throughout all layers of food webs in the Beaufort, Chukchi, and Bering seas (Lefebvre et al. 2016; Anderson et al. 2022; Lefebvre et al. 2022). The continued warming of northern ocean bottom and surface waters contributes to increasing cyst germination rates and algal cell growth rates of *A. catenella*. With denser and more frequent blooms come increased toxin accumulation in benthic and pelagic trophic components of the food web, thereby increasing toxin exposure risks to higher trophic level predators such as marine mammals. High-volume filter feeders like clams and planktivorous fish are of particular concern for toxin accumulation. Previous studies have identified higher STX exposure risks to walruses (*Odobenus rosmarus divergens*) and bearded seals (*Erignathus barbatus*) due to their dietary reliance on clams compared to other Arctic marine mammals (Lefebvre et al. 2016; Hendrix et al. 2021; Lefebvre et al. 2022). Exposure risks are determined by multiple ecosystem factors including algal cell toxicity, bloom density and duration, and toxin accumulation in prey. Here we documented several environmental factors that were temporally linked to the deaths of NFS as well as the detection of high concentrations of STX in multiple NFS tissues, confirming

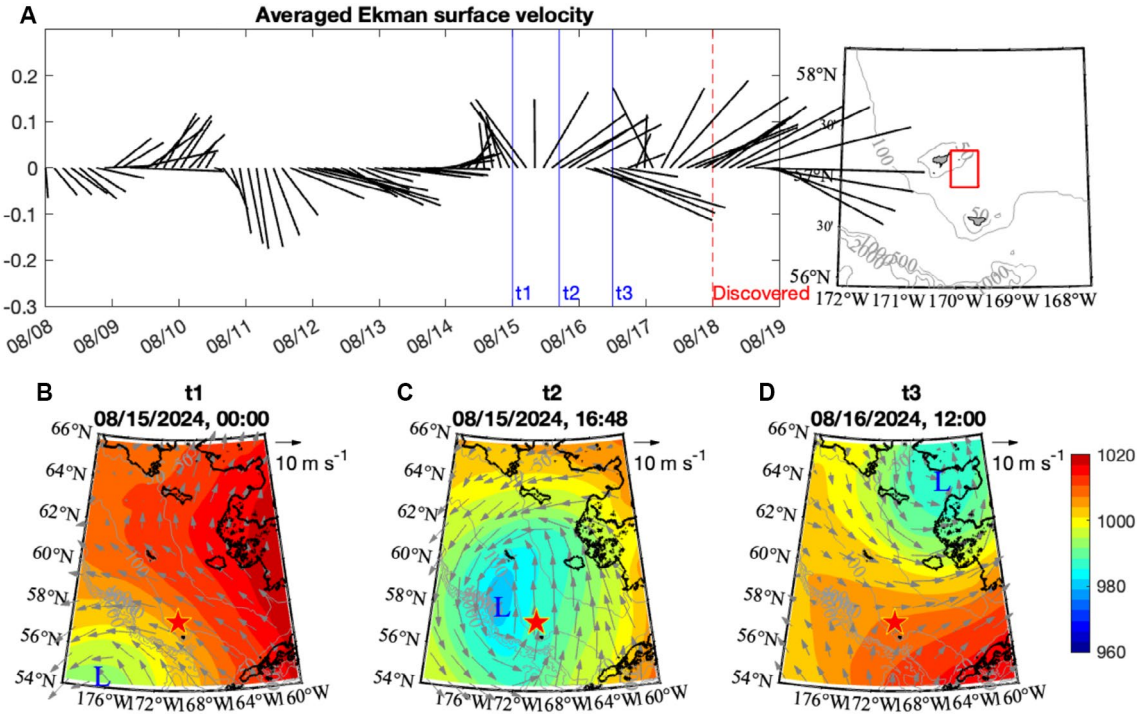

FIGURE 5 | (A) Timeseries of calculated surface Ekman velocity vectors ($m\,s^{-1}$) averaged within the red box east of St. Paul Island (see text for details). The blue lines indicate the times of the snapshots shown in panels (B)–(D). The red dashed line is the time of discovery of the dead northern fur seals (NFS) on Benson Beach. (B)–(D) Sea level pressure (color, hPa) and 10-m wind vectors from ERA5 corresponding to times t1–t3. The red star marks the location of St. Paul Island, and the L marks the center of the extratropical cyclone at the time of the snapshot.

exposure and providing compelling evidence for an acute STX poisoning event.

4.1 | *A. catenella* Blooms and Large Cyst Beds in the SE Bering Sea

A. catenella cells and cysts are the source for STX production and accumulation in multiple layers of marine food webs (Lefebvre et al. 2022). In the time period before and during the NFS mortality event, bloom densities of *A. catenella* were detected in the SE Bering Sea where NFS are known to feed (Figure 3). While the exact relationship between *Alexandrium* cell density and PST accumulation has yet to be rigorously characterized for the SE Bering Sea, cell concentrations above 100–1000 cells L^{-1} are known to cause shellfish toxicity in the Gulf of Alaska and elsewhere (Vandersea et al. 2018). Therefore, for the purposes of this survey, we define bloom densities as anything > 1000 cells L^{-1}. The consistent observation of cells throughout the summer, from late June through August, indicates sustained potential for STX production and accumulation in the food web. Although the cell concentrations detected during these surveys were much lower than the bloom detected further north in the Bering Strait region in 2022 (Fachon et al. 2025), we were unable to characterize the full bloom extent in the SE Bering Sea in 2024 with these observations, and it is possible that higher concentrations of *A. catenella* were missed by the cruise tracks. Indeed, *A. catenella* concentrations of up to 60,000 cells L^{-1} have been observed on the eastern Bering Sea shelf in previous summers (Natsuike et al. 2017) at similar latitudes (57°–58° N) to the observations reported here. In addition to the presence of *A. catenella* cells at bloom densities that were temporally and geographically linked to the die-off, the presence of a large and high-density cyst bed throughout the SE Bering Sea indicates a significant reservoir of resting cysts available to initiate blooms (Figure 3D). This cyst bed is not a new feature; cysts have been observed across this region in the past (Natsuike et al. 2013), but at lower concentrations than the levels reported here.

4.2 | STX Accumulation in Food Webs and Feeding Areas for NFS

In addition to the accumulations of fish found washed ashore and intermixed with the dead NFS on St. Paul Island, other samples of live fish, clams, worms, and zooplankton were acquired at the stations where *A. catenella* cells and cysts were sampled northeast of St. Paul Island in the Bering Sea (Figure 2). All of the dead ($n = 2$) and live ($n = 22$) fish tested contained detectable concentrations of STX. One dead fish (Pacific cod) contained STX above the seafood safety limit of 800 ng STX equiv. g^{-1} in its gastrointestinal tract (Table 1), confirming a potential toxin exposure route to NFS. During the summer pupping and nursing season, NFS are central place foragers (Orians and Pearspon 1979; Gentry 1998). Females give birth to a single pup at terrestrial breeding rookeries (the central place), and then undertake foraging trips at sea, interspersed with regular visits to the central breeding site on land to nurse their pup. This central place foraging behavior continues from July to November annually, at which time most NFS begin overwintering migrations to the broader North

Pacific (Kenyon and Wilke 1953; Ream et al. 2005). Rookeries on the Pribilof Islands are grouped into rookery complexes based on patterns in diet determined from adult female scat samples (Zeppelin and Ream 2006). Foraging ranges associated with these rookery complexes were defined using telemetry (Robson et al. 2004; Call et al. 2008; Kuhn et al. 2014). Zeppelin and Ream (2006) used a primary prey frequency of occurrence analysis to summarize scat samples of adult female NFS across rookeries and found that NFS diets were dominated by walleye pollock (68%–74% of NFS diets) at all St. Paul rookery complexes. NFS consume both juvenile pollock (age 0–2) and adult pollock (e.g., age 3–5+). Gudmundson et al. (2006) also found that larger (i.e., older) pollock and gonatid squid are relatively more common in regurgitation spews (versus scat) samples, and comprise important diet components. Other diet items include Pacific herring, Pacific sandlance (*Ammodytes hexapterus*), and salmonids (*Oncorhynchus* spp.; (Zeppelin and Ream 2006; Tk and Aj 2010).

One of the adult female seals found dead on Benson Beach, uniquely identified as 136X, was tagged in 2023 at Polovina Cliffs rookery as part of NOAA Marine Mammal Laboratory long term vital rates studies. Since NFS are considered to have strong site fidelity (Kuhn et al. 2014), it is safe to assume that NFS136X was hauling out in the vicinity of Polovina Cliffs in the summer of 2024. Seals from Polovina, which are from the eastern rookery complex "St. Paul East", feed on the Bering Sea shelf primarily east and northeast of St. Paul Island (Kuhn et al. 2014). Northeast of St. Paul Island is where high counts of both *A. catenella* cyst densities and STX concentrations in fish, clams, worms, and zooplankton were recorded in 2024 (Figure 3C). Altogether, these data confirm the presence of *A. catenella* blooms (> 1000 cells L^{-1}), high cyst counts, and high STX prevalence and concentrations above the seafood safety limit in fish, clams, and worms in the SE Bering Sea, overlapping with the foraging range of St. Paul NFS.

4.3 | STX Concentrations in NFS

The *A. catenella* bloom and food web STX data provide evidence of potential risk of STX exposure to NFS, and the detection of STX in multiple tissues from all five adult NFS sampled confirms it (Table 1). A previous survey of STX presence in several marine mammal species in Alaska documented that only 5% of 179 live NFS sampled on St. Paul Island, AK, contained detectable concentrations of STX, with a maximum fecal concentration of 42 ng STX g^{-1} (Lefebvre et al. 2016). Interestingly, the pup from the 2024 event reported here did not contain detectable concentrations of STX, consistent with the finding that the pup was still nursing and not yet feeding at sea. The cause of death is consistent with aspirated stomach contents and hookworm enteritis, known causes of death in NFS pups (Spraker and Lander 2010). Comparatively, all adults sampled from the die-off contained STX in at least three tissue types, with fecal STX concentrations ranging from 52 to 333 ng STX g^{-1} (Table 1). The presence of STX in liver, kidney, and urine provides confirmative evidence for physiological exposure to STX.

The urine of two NFS contained high STX concentrations of 201 and 975 ng STX mL^{-1}, the latter being above the seafood safety regulatory limit of 800 ng STX equiv. g^{-1} (Table 1). It is not possible to confirm the doses of STX to these adult NFS via tissue sampling or to determine the dose needed to cause respiratory paralysis and death. However, one study documenting a lethal human PSP event from eating toxic crab reported urine STX concentrations ranging from 100 to 158 ng STX mL^{-1} in the patient that died (Llewellyn et al. 2002). A second mortality event investigation involving two fishermen who consumed toxic bivalves reported a urine concentration of 1800 ng STX mL^{-1} in one of the victims (García et al. 2004). A third non-mortality PSP event that required 1 day on a ventilator reported 499 ng STX mL^{-1} on day one of the incident followed by 6.0 ng STX mL^{-1} on the second day when the ventilator was removed; however, hospitalization continued for an additional 3 days (Watanabe et al. 2024). Each of the human case studies used different analytical methods for STX equiv. quantification (RBA, HPLC, and LC/MS/MS). The ELISA methods used in this study to quantify urine STX concentrations likely provide underestimates of total STX toxicity because of low cross reactivity with other PSP congeners that are accounted for in the other methods, suggesting that the NFS total STX toxicity could be higher in the urine (Costa et al. 2009). Also, considering allometric scaling, a lethal dose to these NFS (31 kg ± 1 kg (SD), $n = 3$ adult NFS) would be 24% higher compared to humans. With these considerations and based on the urine STX concentrations from known human poisonings, the NFS urine values reported here very likely represent lethal exposure.

4.4 | Conclusions

In the present study, we were able to capitalize on multiple HAB sampling studies operating in the SE Bering Sea, together with ocean and atmospheric reanalysis fields, to investigate the potential role of two algal toxins (DA and STX) in the deaths of NFS on St. Paul Island, AK, in August 2024. DA was not detected in NFS involved in the die-off, but STX was detected in all of the adult NFS and in multiple NFS tissues. *A. catenella* bloom densities, high cyst abundance, 100% prevalence of STX in fish, and high STX concentrations in zooplankton, clams, and worms that overlapped temporally and geographically in NFS feeding areas in the SE Bering Sea confirm exposure risks to NFS. Additional analyses of NFS tissues documented STX concentrations in the GI tract, feces, liver, kidney, and urine, confirming physiological exposure. High urine concentrations indicated likely lethal STX exposure when compared to previously known urine STX concentrations from PSP mortality events in humans (Llewellyn et al. 2002). Furthermore, NFS were found in good body condition with no other significant factors present to explain this mortality event. This is consistent with mortality caused by STX poisoning, as there are no known histopathological lesions associated with PSP due to the mechanism of action of STX. Historically, it has been difficult to identify STX as a cause of marine mammal mortality. In this opportunistic study, available HAB data, along with information on the ocean circulation and atmospheric forcing, allowed for a thorough investigation of the role of algal toxins in the deaths of these marine mammals washed ashore on Benson Beach, St. Paul Island, AK.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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