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Ice seals as sentinels for algal toxin presence in the Pacific Arctic and subarctic marine ecosystems

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Abstract

Domoic acid (DA) and saxitoxin (STX)-producing algae are present in Alaskan seas, presenting exposure risks to marine mammals that may be increasing due to climate change. To investigate potential increases in exposure risks to four pagophilic ice seal species (*Erignathus barbatus*, bearded seals; *Pusa hispida*, ringed seals; *Phoca largha*, spotted seals; and *Histriophoca fasciata*, ribbon seals), this study analyzed samples from 998 seals harvested for subsistence purposes in western and northern Alaska during 2005–2019 for DA and STX. Both toxins were detected in bearded, ringed, and spotted seals, though no clinical signs of acute neurotoxicity were reported in harvested seals. Bearded seals had the highest prevalence

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of each toxin, followed by ringed seals. Bearded seal stomach content samples from the Bering Sea showed a significant increase in DA prevalence with time (logistic regression, $p = .004$). These findings are consistent with predicted northward expansion of DA-producing algae. A comparison of paired samples taken from the stomachs and colons of 15 seals found that colon content consistently had higher concentrations of both toxins. Collectively, these results suggest that ice seals, particularly bearded seals (benthic foraging specialists), are suitable sentinels for monitoring HAB prevalence in the Pacific Arctic and subarctic.

KEYWORDS
domoic acid, exposure risks, harmful algal blooms, marine mammals, saxitoxin

1 | INTRODUCTION

1.1 | Changing ocean conditions

Arctic and subarctic seas are experiencing dramatic changes in the persistence, extent, and quality of sea ice due to changing weather patterns and warming ocean temperatures. This is particularly true in the Alaskan Arctic (N. R. Bates et al., 2014; Stevenson & Lauth, 2019) where inputs of Pacific water advected through the Bering Strait are fresher, warmer, and higher in volume (Hu et al., 2012) and where upwelling-favorable winds have also increased (Pickart et al., 2013). Warmer air temperatures and consequently larger negative air-sea heat fluxes have compounded conditions, leading to earlier snowmelt and elevated radiative forcing (Bintanja & van der Linden, 2013; Johannessen et al., 2004; Stone et al., 2002; Turner & Overland, 2009). These changes have affected the ecology and biogeography of species at multiple trophic levels (Capotondi et al., 2012; Stevenson & Lauth, 2019; Tremblay & Gagnon, 2009), and as a result, many temperate organisms are predicted to increase their distribution into or increase their numbers within Arctic waters. In the context of impacts to human, wildlife, and ecosystem health, D. M. Anderson et al. (2018) argue that one of the most significant emerging threats is the expansion of harmful algal bloom (HAB) species, particularly diatoms of the genus *Pseudo-nitzschia* and the dinoflagellate *Alexandrium catenella* that produce the potent neurotoxins domoic acid (DA) and saxitoxin (STX), respectively.

1.2 | Health effects of harmful algal blooms

Harmful algal blooms of DA-producing *Pseudo-nitzschia* and STX-producing *Alexandrium* species are common throughout the temperate world oceans and cause adverse human and wildlife health impacts and mortality. In humans, acute exposure leads to neurologic illnesses known as amnesic shellfish poisoning, caused by DA (S. S. Bates, 2000; S. S. Bates & Trainer, 2006; Berman & Murray, 2002; Perl et al., 1990; Todd, 1993), and paralytic shellfish poisoning, caused by the suite of paralytic shellfish toxins (PSTs) including STX (Etheridge, 2010; Usup et al., 1994). Both toxins accumulate in filter-feeding marine organisms and are transferred through food webs with significant health consequences to animals at multiple trophic levels (Cembella & Desbiens, 1994; Kvitek et al., 2008;

Lefebvre, Bargu, et al., 2002; Lefebvre et al., 2010; Lefebvre, Silver, et al., 2002; Scholin et al., 2000; White, 1980, 1981). Domoic acid exposure causes illness, stranding, and death in seabirds and marine mammals (Fritz et al., 1992; Gulland et al., 2005; Peery et al., 2006; Work et al., 1993). Persistent effects of recurrent DA exposures also lead to long-term neurotoxic effects and epilepsy in California sea lions (*Zalophus californianus*; Cook et al., 2015; Goldstein et al., 2008). Exposures to STX also cause illness and death in marine mammals, although less frequently than those reported for DA. However, STX has been documented to cause massive kills of fish and invertebrates (Shumway, 1990; White, 1980, 1981), and has been linked to a mass mortality of humpback whales (*Megaptera novaeangliae*) off the eastern U.S. coast of Cape Cod, Massachusetts (Geraci et al., 1989). Together, these algal toxins result in significant economic losses in coastal communities relying on commercial and recreational seafood harvesting (C. R. Anderson et al., 2010; D. M. Anderson et al., 2000; Shumway, 1990; Trainer et al., 2007).

1.3 | Marine mammal exposure to harmful algal bloom toxins

In the last two decades, almost half of the marine mammal unusual mortality events in the contiguous U.S. have been attributable to algal toxin exposure (Flewelling et al., 2005; Gulland & Hall, 2007; Landsberg et al., 2014; Scholin et al., 2000), and there is concern that wildlife exposure to HAB toxins may be growing. Domoic acid is known to be particularly common on the west coast of the contiguous U.S., where the first documented marine mammal DA poisoning event occurred in Monterey Bay, California, in 1998. During this event, several hundred California sea lions exhibited seizures and/or died over a short period due to consumption of DA-contaminated anchovies (Gulland, 2000; Lefebvre et al., 1999; Scholin et al., 2000). Since then, dozens to hundreds of sea lions have been affected annually in coastal California (Bargu et al., 2010). In 2015, DA-induced seizures were first observed in sea lions north of California in Long Beach, Washington, during the largest recorded *Pseudo-nitzschia* bloom in coastal waters of North America (McCabe et al., 2016). This bloom was linked to a warm water anomaly that affected oceanic waters northward into the Gulf of Alaska, providing evidence for a potential northward expansion of conditions favorable for *Pseudo-nitzschia* growth (Zhu et al., 2017). Saxitoxin has been a marine mammal health concern since suspected poisonings in the late 1980s affected humpback whales in New England and sea otters (*Enhydra lutris*) in Alaska (DeGange & Vacca, 1989; Geraci et al., 1989; Landsberg et al., 2014). In a recent analysis of HAB events on the Pacific coast of Canada from 1988 to 2017, it was found that STX events occurred on the Canadian Pacific coast with regularity, while DA events occurred infrequently (McKenzie et al., 2021). Algal toxins have been reported in Alaskan Arctic marine mammals; however, algal toxin exposure has not been definitively linked to morbidity and mortality events in the region, and few data exist regarding these events in Alaskan pagophilic seal species (Lefebvre et al., 2016).

1.4 | Ice seal exposure to harmful algal bloom toxins

Bearded (*Erignathus barbatus*), ringed (*Pusa hispida*), spotted (*Phoca largha*), and ribbon (*Histriophoca fasciata*) seals represent critical components of the Pacific Arctic and subarctic marine ecosystems. Collectively referred to as ice seals due to the integral role that ice plays as a substrate for pupping, nursing, and molting, these seals are an important subsistence resource for coastal Alaska Native communities in western and northern Alaska (Nelson et al., 2019). They are also an important component of the Arctic marine ecosystem. In December of 2012, NOAA Fisheries listed ringed and bearded seals as threatened under the Endangered Species Act, citing climate change and resultant sea ice declines as significant threats to the seals' survival (U.S. Federal Register, 2012a, 2012b). Previous analyses of gastrointestinal (GI) samples collected during 2006–2013 detected DA in all four of these ice seal species, and STX in all species except ribbon seals (Lefebvre et al., 2016). As environmental conditions in western and northern Alaska continue to transition, the potential for HAB toxins to increase in prevalence and concentration in the Bering and Chukchi Seas is an increasing health threat for ice seals (D. M. Anderson et al., 2018; Laidre et al., 2015). The objective of this study was to quantify DA and STX prevalence and assess temporal trends therein in four ice seal species in the Bering, Chukchi, and Beaufort Seas. Gastrointestinal samples were collected during 2005–2019 in partnership with coastal Alaska Native communities that harvest ice seals for subsistence purposes (Nelson et al., 2019).

2 | METHODS

2.1 | Collection of gastrointestinal samples from harvested ice seals

During 2005–2019, samples were collected from ice seals harvested for subsistence purposes between May and September from coastal communities along the coast of the Bering, Chukchi, and Beaufort Seas (Figure 1). Information collected included age, sex, length, girth, blubber thickness, and date and location of harvest. General health assessments for body condition and signs of neurotoxicity were noted by samplers and harvesters. Locations in the Bering Strait and southward were considered to be in the Bering Sea, locations north of the Bering Strait and south of Utqiaġvik were considered to be in the Chukchi Sea, and Utqiaġvik was considered to be in the Beaufort Sea (Logerwell et al., 2011, 2018; Moore & Stabino, 2015; Woodgate et al., 2015).

In the field, whole stomachs were collected in Ziploc bags and shipped frozen to laboratories where they were stored at −20°C until they were subsampled. In the laboratory, stomachs were thawed, and 5 ml of semiliquid content was removed and placed in centrifuge tubes with screw caps before being refrozen. Samples removed from stomachs will hereafter be referred to as “stomach contents.” Samples were also collected from the rectum during routine postmortem examination as part of the North Slope Borough Department of Wildlife Management ice seal health monitoring program in Utqiaġvik, Alaska. These samples were stored in 55 cc centrifuge tubes with screw caps and frozen at −20°C. Samples removed from the rectum will hereafter be referred to as “colon contents.” All samples were shipped to the Northwest Fisheries Science Center's Wildlife Algal-Toxin Research and Response Network (WARRN-West) laboratory (NOAA Fisheries, Seattle, Washington) for algal toxin testing.

FIGURE 1 Harvest locations (black pins) are shown within circles indicating regional classifications (Bering, Chukchi, and Beaufort Seas). Next to each harvest location, icons represent the number of each seal species that tested positive for DA (yellow), STX (red), and both toxins (orange). Map generated in Google Earth.

2.2 | Quantification of domoic acid (DA) and saxitoxin (STX)

Toxins were extracted from stomach and colon contents via standard procedures using a 1:3 volume:volume ratio of sample to extraction solvent (Lefebvre et al., 2016). Extraction solvent was 50% methanol for all DA samples, and for 591 STX samples; extraction solvent was 80% ethanol for all other STX samples. Differences in STX concentrations quantified from 50% methanol and 80% ethanol extractions were not found to be statistically significant in $n = 8$ marine mammal GI samples and are therefore not expected to influence trend analyses (data not shown). Final extracts were further diluted 50-fold for stomach contents and 100-fold for colon contents in dilution buffer prior to DA quantification and 50-fold for both stomach contents and colon contents in dilution buffer prior to STX quantification (Lefebvre et al., 2016). These minimum dilutions were chosen to eliminate matrix effects (Frame & Lefebvre, 2013). Samples and solvent were mixed for 1 min, homogenized for 60 s (Omni ES homogenizer), and centrifuged for 20 min at 3,100 rcf (max) at 4°C (Sorvall RC 5C Plus centrifuge). Finally, supernatant was filtered through a spin filter (Millipore Ultra-Free MC-GV centrifugal filters) spun at 13,870 rcf (max) for 3 min in a desktop centrifuge (Fisher Scientific accuSpin Micro 17). All extracts thus obtained were stored at 4°C prior to analysis. Concentrations of DA and STX equivalents in nanograms/gram (ng/g) were quantified in extracts using commercially available enzyme-linked immunosorbent assay (ELISA) kits for DA (Biosense) and for STX equivalents (Abraxis) as per kit instructions. Detection limits for DA in sample material were 4 ng/g for colon contents and 2 ng/g for stomach content. The detection limit for STX in all sample material was 3 ng/g.

It must be noted that the Abraxis STX ELISA kit was specifically designed to detect STX and has limited cross-reactivity with other PST congeners (as listed in the Abraxis product documents). As such, STX concentrations reported here underestimate total potential PST presence. In the absence of data regarding the PST congener profiles in ice seal GI contents, it is difficult to estimate the magnitude of this underestimation. Future studies will include HPLC analyses to characterize the suite of PSTs present in marine mammal tissues as part of our continued research on the trophic transfer of algal toxins in Arctic and subarctic food webs and will be useful for better total PST exposure estimates.

2.3 | Analysis of trends

Temporal trends in each HAB toxin during 2012–2019 were assessed for bearded seals only and the Bering and Chukchi Seas only, due to sample size limitations for the other three ice seal species and the Beaufort Sea. For consistency, only samples from stomach contents were analyzed for trends. Furthermore, samples were restricted to those collected from May to September, when toxins are expected to be present. First, we examined trends in the prevalence or probability of detection for each HAB toxin. We modeled the probability of occurrence for each toxin using logistic regression. Detections were coded as having a value of 1 and non-detections were coded as having a value of 0. Second, given that a toxin was detected, we examined the trends in the concentration of each toxin using simple linear regression. All analyses were performed using the statistical program R (R Core Team, 2018).

3 | RESULTS

Samples were analyzed for the HAB toxins DA and STX from 998 ice seals representing four seal species. Sample collection locations in the Bering, Chukchi, and Beaufort Seas are shown in Figure 1. Sex ratios for all species sampled were approximately 1:1, and all age classes (pup, subadult, and adult) were represented for each species.

3.1 | Toxin prevalence and maximum concentrations in ice seals

Both DA and STX were detected in all regions sampled (Bering, Chukchi, and Beaufort Seas). Bearded seals had the highest prevalence of DA (46%), followed by ringed (21%), spotted (5%), and ribbon seals (4%) (Table 1). Although bearded seals had the highest DA prevalence, ringed seals had the highest DA concentration recorded (1,740 ng DA/g) followed by bearded seals (1,353 ng DA/g) (Table 1). Maximum DA concentrations in spotted and ribbon seals were two orders of magnitude lower at 90 and 33 DA ng/g, respectively. Bearded seals also had the highest prevalence of STX (24%), followed closely by ringed seals (18%). Saxitoxin was only detected in 4% of spotted seals and was not detected in any of the ribbon seals sampled (Table 1). Bearded seals had the highest STX concentration (464 ng STX equivalents/g) followed by ringed (180 ng STX equivalents/g) and spotted seals (66 ng STX equivalents/g). Prevalence of co-occurrence (detectable levels of both DA and STX in the same individual) were highest in bearded (17%) and ringed seals (12%) (Table 1).

3.2 | Temporal trends of toxin prevalence in bearded seals

The large number of stomach-content samples and the greater geographic span of collection locations for bearded seals allowed for the use of logistic regression to test for temporal trends in toxin prevalence in the Bering and Chukchi seas (Table 2). The temporal trend for increasing DA in the Bering Sea was the only significant trend (Figure 2, Table 2; $p = .004$). The logistic regression model estimates for the probability of DA presence in 2012 and 2019 were 5% [0%, 22%] and 94% [63%, 99%], respectively (Table 2 and Figure 2a). The empirical proportions of DA presence were 0% in 2012 and 100% in 2019 (Figure 2a), providing evidence that the regression model accurately describes the trend. No significant trends in the prevalence of STX were observed over the surveyed period (Figure 2).

3.3 | Comparison of toxin concentrations in stomach and colon content samples

To determine if DA and STX concentrations were consistent throughout the GI tract, we compared samples from the same individual at two GI tract locations (stomach and colon) in a subset of bearded ($n = 10$) and ringed ($n = 5$) seals. Domoic acid concentrations were higher in colon content samples compared to corresponding stomach content samples in 9 of 10 bearded seals and 5 of 5 ringed seals (Table 3). In one bearded seal and two ringed seals, stomach content samples were below detection limits (BDL) for DA, but colon content ranged from 12 to 1,293 ng/g (Table 3). The findings for STX concentrations were even more dramatic. Saxitoxin was BDL in stomach content samples from all 15 seals sampled, however, 8 of 10 bearded seals had detectable concentrations in colon content, as did 4 of 5 ringed seals (Table 3).

4 | DISCUSSION

Results from this study confirm previous findings that ice seals are regularly exposed to DA and STX in the Bering, Chukchi, and Beaufort Seas (Lefebvre et al., 2016) (Figure 2, Table 1). The maximum DA concentration reported here (1,740 ng DA/g in ringed seal feces) is an order of magnitude higher than the maximum concentration of DA previously reported (127 ng DA/g in ringed seal feces; Lefebvre et al., 2016). The maximum STX concentration reported here (464 ng STX equivalents/g in bearded seal feces) was also higher than the maximum STX concentration previously reported (172 ng STX equivalents/g in ringed seal feces). However, these new maximum values are still well below the seafood safety regulatory limits for humans for both toxins (Table 1).

TABLE 1 Prevalence of domoic acid (DA) and saxitoxin (STX) in gastrointestinal samples by species. Maximum concentrations did not reach regulatory limits for either DA (regulatory limit = 20,000 ng DA/g shellfish[a]) or STX (regulatory limit = 800 ng STX equivalents/g shellfish[a]).

Species	Collection years	*n* DA positive/*n* DA tested (%DA positive)	*n* STX positive/*n* STX tested (%STX positive)	*n* DA and STX positive (%co-occurrence)	Maximum DA concentration (ng/g)	Maximum STX concentration (ng/g)
Bearded seal, *Erignathus barbatus*	2005–2019	157/344 (46%)	96/404 (24%)	69 (17%)	1,353	464
Ringed seal, *Pusa hispida*	2005–2019	61/289 (21%)	47/263 (18%)	31 (12%)	1,740	180
Spotted seal, *Phoca largha*	2005–2016	14/268 (5%)	9/257 (4%)	1 (0%)	90	66
Ribbon seal, *Histriophoca fasciata*	2008–2016	1/28 (4%)	0/28 (0%)	0 (0%)	33	0

Note: n = number of animals.

[a] Regulatory limit units have been converted to match those reported in the table above.

TABLE 2 Proportion of bearded seal stomach content samples collected in the Bering Sea that were found to have domoic acid (DA) by year and fitted logistic regression probabilities by year with 95% confidence intervals (CI). Fewer than three samples were collected in 2018 from the Bering Sea, therefore it was excluded from analysis.

Year	Samples collected	Samples positive for DA	Proportion positive for DA	Logistic regression estimates of DA probability [95% CI]
2012	4	0	0	0.05 [0.01, 0.22]
2013	7	1	0.14	0.10 [0.03, 0.30]
2014	8	4	0.50	0.20 [0.09, 0.40]
2015	14	2	0.14	0.37 [0.22, 0.54]
2016	6	3	0.50	0.57 [0.36, 0.75]
2017	3	3	1.00	0.75 [0.46, 0.91]
2018	NA	NA	NA	0.87 [0.55, 0.97]
2019	5	5	1.00	0.94 [0.63, 0.99]

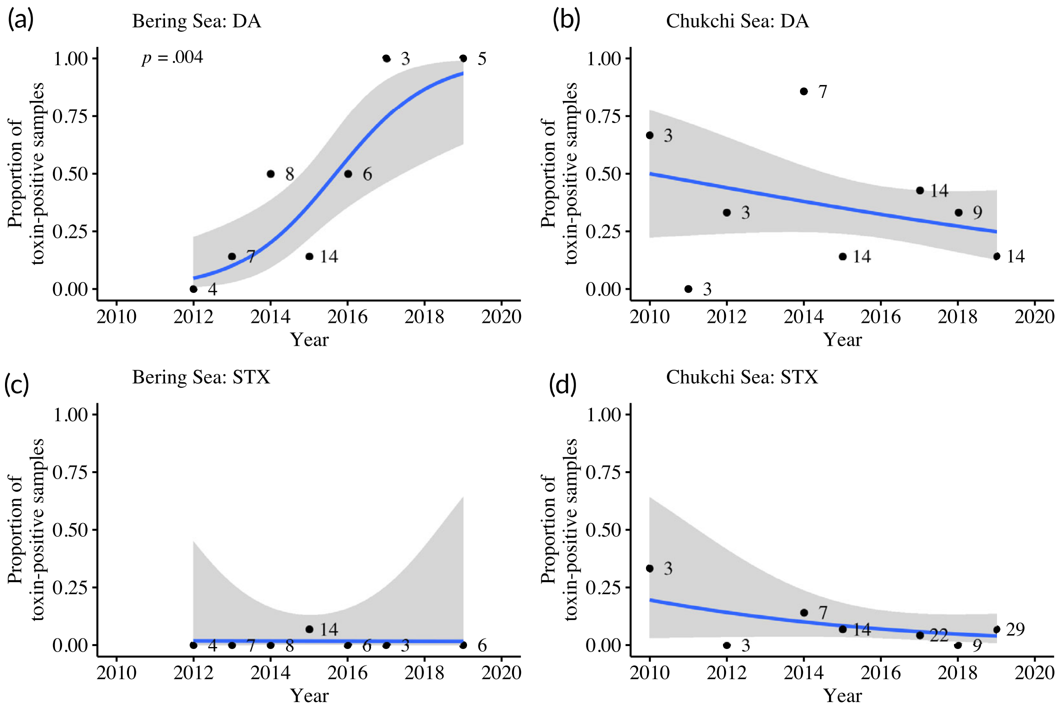

FIGURE 2 The proportion of bearded seal stomach content samples with detectable concentrations of domoic acid (DA) (a, b) and saxitoxin (STX) (c, d) from May–September in the Bering (a, c) and Chukchi (b, d) Seas by year. Sample size is listed to the right of each corresponding data point. Lines represent logistic regressions comparing presence/absence of toxin over the years, and shaded areas represent associated 95% confidence intervals. The only significant trend ($p = .004$) was in the Bering Sea (a).

4.1 | Diet and algal toxin prevalence in ice seals

Algal toxin accumulation and prevalence in ice seals occurs through diet. Bearded seals, primarily benthic foragers (Table 4), had the highest prevalence of both DA (46%) and STX (24%) of the four species examined (Table 1). Ringed

TABLE 3 Comparison of toxin concentrations detected in samples from two gastrointestinal tract locations (stomach and colon) collected simultaneously in 15 seals.

		DA concentration (ng/g)		STX concentration (ng/g)	
Animal ID	Species	Stomach content	Colon content	Stomach content	Colon content
2012BS07	Bearded seal	2	**4**	BDL[a]	**8**
09BS2	Bearded seal	10	**156**	BDL	**10**
09BS20	Bearded seal	7	**23**	BDL	BDL
09BS21	Bearded seal	BDL	**12**	BDL	**15**
09BS22	Bearded seal	138	**887**	BDL	BDL
09BS3	Bearded seal	3	**7**	BDL	**3**
09BS4	Bearded seal	3	**11**	BDL	**6**
09BS7	Bearded seal	**5**	BDL	BDL	**8**
09BS8	Bearded seal	6	**136**	BDL	**108**
09BS9	Bearded seal	8	**12**	BDL	**23**
09RS8	Ringed seal	7	**15**	BDL	**180**
2011RS2	Ringed seal	6	**19**	BDL	**29**
2015-RS-10	Ringed seal	7	**113**	BDL	**6**
2015RS12	Ringed seal	BDL	**142**	BDL	**4**
2015RS13	Ringed seal	BDL	**1,293**	BDL	BDL

Note: For each seal, the highest toxin concentration is in bold.

[a] BDL = below detection limits.

seals, primarily pelagic fish and invertebrate consumers (Table 4), had the second highest prevalence of DA (21%) and STX (18%; Table 1). Toxin prevalence was lower in the spotted and ribbon seal species, for which pelagic fish are a large part of the diet (5% and 4% for DA and STX in spotted seals, respectively, and 4% and 0% for DA and STX in ribbon seals, respectively; Tables 4 and 1). In general, filter-feeding species (benthic and pelagic) accumulate higher concentrations of algal toxins than particulate feeding species due to the direct consumption of algae (Lefebvre, Silver, et al., 2002). A study comparing DA levels in anchovies and sardines collected simultaneously during a toxic *Pseudo-nitzschia* bloom in Monterey, California revealed that anchovies had significantly higher toxin levels than sardines (Lefebvre, Silver, et al., 2002). Although both anchovies and sardines can feed on phytoplankton and zooplankton via filter-feeding or particulate/selective feeding modes (Loukashkin, 1970; Radovich, 1952), comparative mouth morphology and feeding behavior suggests that anchovies feed more generally on diatoms, whereas sardines likely target zooplankton, thereby accumulating *Pseudo-nitzschia* secondarily or in lower quantities (Lefebvre, Silver, et al., 2002). Additionally, during toxic *Alexandrium* blooms, benthic shellfish can accumulate high concentrations of STX via both direct consumption of vegetative algal cells and via consumption of benthic cysts of *Alexandrium spp*. from disturbed sediments, allowing for exposure to occur even in the absence of vegetative blooms in surface waters (Persson et al., 2006). Abundant *Alexandrium* cyst beds are present in the sediments of the Chukchi Sea and the eastern Bering Sea (Natsuike et al., 2013). This is consistent with the higher toxin levels and prevalence observed here in bearded seals that primarily consume benthic prey (e.g., flatfish, sculpins, shrimp, crab, gastropods, and clams) and ringed seals that consume filter-feeding invertebrates and planktivorous fish, compared to spotted and ribbon seals that primarily feed on particulate-consuming pelagic fish (Table 4). In a previous study, Pacific walruses (*Odobenus rosmarus divergens*), the most benthic-dependent feeding pinnipeds in the Bering and Chukchi Seas, had the highest toxin concentrations and prevalence for both DA and STX, further suggesting that benthic prey may be the most significant route for exposure (Lefebvre et al., 2016). The fact that planktivorous-fish-consuming

TABLE 4 Primary known prey species for bearded, ringed, spotted, and ribbon seals.

Species	Feeding preferences	Invertebrate prey	Fish prey	References
Bearded seals (*Erignathus barbatus*)	Benthic fish and invertebrates	Bivalves Gastropods Cephalopods Isopods Amphipods Shrimps Crabs Echiurids Polychaetes	Pelagic Arctic cod (*Boreogadus saida*) Saffron cod (*Eleginus gracilis*) Benthic Sculpins (Cottidae) Snailfish (Liparidae) Pricklebacks (Stichaeidae) Pacific sand lance (*Ammodytes hexapterus*) Flatfish (Pleuronectidae)	Antonelis et al., 1994; Crawford et al., 2015; Lowry et al., 1980a; ADF&G, unpublished data
Ringed seal (*Pusa hispida*)	Pelagic fish and invertebrates	Mysids Amphipods Shrimp	Pelagic Arctic cod (*Boreogadus saida*) Saffron cod (*Eleginus gracilis*) Walleye pollock (*Gadus chalcogramma*) Rainbow smelt (*Osmerus mordax*) Benthic Sculpins (Cottidae)	Crawford et al., 2015; Dehn et al., 2007; Johnson et al., 1966; Lowry et al., 1980b; ADF&G, unpublished data
Spotted seal (*Phoca largha*)	Pelagic fish	Not a significant dietary component	Pelagic Arctic cod (*Boreogadus saida*) Saffron cod (*Eleginus gracilis*) Pacific herring (*Clupea pallasi*) Capelin (*Mallotus villosus*) Rainbow smelt (*Osmerus mordax*)	Bukhtiyarov et al., 1984; Lowry & Frost, 1981; ADF&G, unpublished data
Ribbon seals (*Histriophoca fasciata*)	Pelagic fish and invertebrates	Shrimp Octopus	Pelagic Arctic cod (*Boreogadus saida*) Saffron cod (*Eleginus gracilis*) Walleye pollock (*Gadus chalcogramma*)	Dehn et al., 2007; Frost & Lowry, 1980; ADF&G, unpublished data

ringed seals had the maximum concentrations of both DA and STX reported in previous studies and the maximum STX concentration reported in this study provides further evidence that planktivorous fish are potent vectors of algal toxins.

4.2 | Comparison of toxin concentrations in stomach vs. colon contents

Colon content samples consistently had higher toxin levels than corresponding stomach content samples for both DA and STX (Table 3). Multiple factors may influence this distribution pattern, including less water content, potential absorption and reabsorption patterns, and that colon content represents more than one stomach's worth of digested material. Regardless, sampling colon contents enhances the ability to detect toxins and is preferable for monitoring toxin prevalence in marine mammals. These results suggest that our previous analyses (Lefebvre et al., 2016) greatly underestimated the prevalence of DA and STX in seals and other marine mammals where stomach content was analyzed. Future monitoring efforts should collect and analyze colon content samples for better estimates of prevalence and concentration even though results will not be directly comparable to past stomach content analysis.

4.3 | Temporal trends of toxin prevalence in bearded seals

The significant temporal trend for DA prevalence in bearded seals from 2012 to 2019 reported above in the Bering Sea (Figure 2a) is consistent with a northward expansion of warmer ocean conditions that are favorable for *Pseudo-nitzschia* growth (D. M. Anderson et al., 2018; McCabe et al., 2016). In 2015, a strong link was made between anomalously warm ocean conditions along the U.S. West Coast and Canada, and the development of the largest DA-producing *Pseudo-nitzschia* bloom ever recorded. During this coast-wide bloom, *Pseudo-nitzschia australis* thrived north of its typical range in the warm water that spanned the northeast Pacific (McCabe et al., 2016). Unprecedented levels of DA were found in the northeast Pacific Ocean food web causing coast-wide closures of commercial and recreational fisheries for clams, mussels, Dungeness crab, rock crab, anchovy, and sardine from May to November (McCabe et al., 2016). Unfortunately, concurrent phytoplankton samples were not obtained in the Gulf of Alaska or the Bering Sea, however, warmer ocean conditions were also reported in those regions (McCabe et al., 2016). In fact, sea surface temperature data from the Bering Sea show a significant warming trend of 0.22°C ± 0.10°C per decade during 1966–2018 (Danielson et al., 2020). Although increasing DA was not observed in bearded seals harvested farther north in the Chukchi Sea, continued northern expansion and increases in *Pseudo-nitzschia* may eventually reach the Chukchi Sea. Additionally, changes in ice seal behavior and regional feeding patterns in response to changing ocean conditions may influence toxin prevalence in the future.

4.4 | Exposure risks for ice seals

Official regulatory limits are 20 μg DA/g (equivalent to 20,000 ng DA/g) shellfish and 80 μg STX equivalents/100 g (equivalent to 800 ng/g) shellfish (Table 1) (Wekell et al., 2004). Regulatory limits were established in seafood for the protection of human health to prevent amnesic shellfish poisoning and paralytic shellfish poisoning from DA and STX, respectively (Wekell et al., 2004). All values reported here were below the seafood safety regulatory limits for both toxins (Table 1). Although the concentrations in prey that would be toxic to marine mammals are unknown, regulatory limits can be used as estimates for concentrations in prey that could be harmful to mammalian species.

While some values reported here fall within the range of toxin concentrations quantified in fecal and GI samples from stranded California sea lions diagnosed with acute DA toxicosis (Lefebvre et al., 2016), those levels in sea lions were highly variable (i.e., ranging from 0.001 μg/g to well above seafood safety regulatory limits of >20,000 ng/g; Figure 2 in Lefebvre et al., 2016) and are not a reliable proxy for actual doses of toxin consumed. Consequently, secondary signs of excitotoxicity such as seizures, ataxia, and head weaving are necessary for a positive clinical diagnosis of DA poisoning in marine mammals (Scholin et al., 2000). No clinical signs of DA-induced excitotoxicity or STX-induced paralysis were reported for these seals by the hunters who harvested them. This suggests that algal toxins may not yet be a significant health threat to ice seals, but raises valid concerns about future exposure risks with continued ocean warming as a result of continuing sea ice loss. Because warmer ocean temperatures foster increased harmful algal growth, and Arctic and subarctic regions are undergoing rapid rates of ocean warming, concern for increasing impacts of harmful algal toxins on important marine resources is high (D. M. Anderson et al., 2018). Such impacts are of particular concern for communities where there is a substantial reliance on marine mammals as a food resource (D. M. Anderson et al., 2018; Braund & Associates, 2018; Garlich-Miller & Burn, 1999; MacCracken et al., 2017; Nelson et al., 2019).

4.5 | Summary

Ice seals (i.e., bearded, ringed, spotted, and ribbon seals) are regularly exposed to both DA and STX in the Bering, Chukchi, and Beaufort Seas. Colon content samples are more sensitive indicators for DA and STX prevalence than stomach content samples and should be used in future monitoring efforts. Nonetheless, stomach content analyses in bearded seals were sufficient to identify a significant increase in DA prevalence from 0% in 2012 to 100% in 2019 in the Bering Sea, consistent with warming ocean conditions fostering a northward expansion and increase of *Psuedo-nitzschia* spp. Differences found in toxin prevalence and concentration among ice seal species are most likely due to diet differences, with filter feeding benthic prey and planktivorous fish likely presenting the greatest exposure risks for ice seals. Observable health impacts for the harvested seals sampled in this study were not reported by hunters. However, consequences of chronic low-level exposure are of concern, as is the possibility that toxin concentrations may increase to harmful levels as Alaskan waters continue to respond to the continuing reduction in seasonal sea ice coverage. Ice seals in general, and bearded seals in particular, can be valuable sentinels for changes in DA and STX prevalence in Pacific Arctic and subarctic marine ecosystems.

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AUTHOR CONTRIBUTIONS

Alicia Hendrix: Conceptualization; data curation; formal analysis; investigation; methodology; software; validation; visualization; writing-original draft; writing-review & editing. **Kathi Lefebvre:** Conceptualization; data curation; funding acquisition; methodology; project administration; resources; supervision; validation; writing-original draft; writing-review & editing. **Lori Quakenbush:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; writing-original draft; writing-review & editing. **Anna Bryan:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; writing-original draft; writing-review & editing. **Raphaela Stimmelmayr:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; writing-original draft; writing-review & editing. **Gay Sheffield:** Conceptualization; funding acquisition; investigation; methodology; project administration; resources; writing-original draft; writing-review & editing. **Gabriel Wisswaesser:** Data curation; investigation; writing-review & editing. **Maryjean Willis:** Data curation; project administration; writing-review & editing. **Emily Bowers:** Data curation; investigation; visualization; writing-review & editing. **Preston Kendrick:** Data curation; investigation; writing-review & editing. **Elizabeth Frame:** Data curation; investigation; writing-review & editing. **Thomas Burbacher:** Funding acquisition; project administration; supervision; writing-review & editing. **David Marcinek:** Funding acquisition; project administration; supervision; writing-review & editing.

CONFLICTS OF INTEREST

The authors declare that there are no conflicts of interest.

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