Seasonal warming coincides with loss of epidermal diatoms in northern bottlenose whales

Charlotte L. Riddle[1], Chad Steverding[1], Laura J. Feyrer[1], Hal Whitehead[1*], Sam F. Walmsley[1*]

[1]Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada

*HW and SFW contributed equally.

Correspondence

Sam F. Walmsley, sam.walmsley@dal.ca

Department of Biology, Dalhousie University
1355 Oxford Street
Halifax, Nova Scotia, B3H 4R2
Canada

Abstract

Animals move for access to better conditions, resources, or mating opportunities. However, evidence from cetaceans suggests that some long-distance travel to warmer waters may be primarily related to physiological maintenance, specifically the shedding of epidermal diatoms and parasites. Here we test this “physiological maintenance hypothesis” for cetacean movement from a new angle, asking whether changes in temperature influence epidermal diatoms (microalgae) in a localized, resident population. We used a long-term dataset of northern bottlenose whales (*Hyperoodon ampullatus*) on the Scotian Shelf to test whether large seasonal changes in sea surface temperature predict levels of diatom coverage. Generalized linear mixed models and generalized additive mixed models showed that a seasonal change in SST from 8° to 21° Celsius was associated with a decrease in diatom coverage from approximately 26% to 11%. We also found that males had slightly less diatom coverage than females overall, though the corresponding effect size was very small. Our results support the hypothesis that sea surface temperature can be a driving factor in the epidermal condition of cetaceans. This is consistent with a growing understanding of links between environmental conditions, movement behaviour, and individual health in wild populations.

KEYWORDS

Movement – Health – Physiological maintenance – Skin molt – Diatoms – Northern Bottlenose Whales – Cetaceans

1 | INTRODUCTION

Migration has been documented in numerous species worldwide and refers to the movements of animals from one region to another (Fudickar et al., 2021). While some consider migration necessarily seasonal (Teitelbaum & Mueller, 2019: nomadic-movement), we follow Lefort et al. (2025) in also including significant aseasonal movements as part of migratory behaviour. Migration is common in birds (Barcante, 2017), mammals (Avgar, 2013), fish (Bronmark, 2013), and insects (Holland, 2006). Migratory distances can differ dramatically between populations and species, depending on the biological needs of the individuals (Fudickar et al., 2021). Migration is advantageous, allowing species to benefit from the use of multiple habitats (Alerstam & Backman, 2018). Migration is primarily believed to serve the purpose of finding better seasonal conditions, food availability, predator avoidance, or due to reproductive needs (Alerstam & Backman, 2018; Chapman et al., 2014).

However, research from cetaceans suggests that health maintenance may be an underappreciated motivator for migration. Orcas (*Orcinus orca*) of Antarctic waters have been documented travelling non-stop round trips of 9,400km to warmer waters (Durban & Pitman, 2012). This rapid migration indicates that it is unlikely influenced by foraging or breeding purposes. Instead, it has been attributed to the need for physiological skin maintenance (Durban & Pitman, 2012; Pitman et al., 2020). Various epidermal conditions and diseases in cetaceans have been associated with environmental features such as water temperature (Wilson et al., 1999). It is often hypothesized that increased epithelial shedding in warmer waters is driving these patterns (Gaydos et al., 2023). For example, beluga whales (*Delphinapterus leucas*) undergo epidermal shedding in warmer and less salty summer habitats, resulting in marked changes in colouration

(St. Aubin et al., 1990). Other mechanisms may play a role (e.g., changes in rates of disease or parasites acquisition, or effects mediated through overall stress and health of the host individual).

Diatoms are photosynthetic microalgae commonly found growing on aquatic vertebrates and are linked to their host's biology, behaviour, and environment (Ashworth et al., 2022). For example, *T. dicentrarchi*, a pathogen that is associated with tail and fin rot as well as skin lesions, was positively correlated with high diatom abundances in orcas (Hooper et al., 2019). Antarctic orcas spending more time in the Southern Ocean, where water temperatures are cooler, were found to have a higher diatom abundance than individuals that primarily reside in warmer waters (Hooper et al., 2019). Thus, the observed short-term, "spa day", migration patterns suggest an important link between individual health and spatial behaviour in cetaceans and possibly other mammals.

Northern Bottlenose whales (*Hyperoodon ampullatus*) are deep-diving beaked whales found in high latitude offshore waters of the North Atlantic around Canada, Greenland, Iceland, Great Britain and Europe (Moors-Murphy, 2018). In 2019, a northern bottlenose whale fitted with an animal-borne recording device (tag) travelled 7,281 km in 67 days, from Arctic waters of 4ºC to 23ºC off Newfoundland (Lefort et al., 2025). In warmer waters, the whale remained at the surface rather than foraging at depth, which was hypothesized to facilitate epidermal shedding. Similar, directed short-stay migrations by northern bottlenose whales from the waters around Iceland and Jan Mayen to the Azores are also consistent with an epidermal maintenance hypothesis (*pers. comm.*, Paul Wensveen, University of Iceland, March 2026).

The Scotian Shelf population of northern bottlenose whales resides in and around the Gully, a submarine canyon off the east coast of Canada. Following substantial whaling in the 1970s, the population is listed as Endangered but now appears to be recovering, with a population of approximately 200 individuals (Feyrer et al., 2025). These animals exhibit bisexual philopatry and are highly social, forming specific long-term relationships with conspecifics within a generally fluid or “fission-fusion” social structure (Walmsley et al., 2026). This population displays an unusual degree of site-fidelity compared to other offshore cetaceans, using the Gully and adjacent canyons year-round (Feyrer et al., 2024). Despite clear evidence of residency, nothing is known about whether this population conducts physiological maintenance migration trips (or other longer-distance movements), although, like other cetaceans, northern bottlenose whales accrue visible diatoms.

However, unlike the orcas of the Antarctic, or northern bottlenose whales of the Arctic whose primary habitats are cold year-round, the Scotian Shelf population experiences a major seasonal shift in sea surface temperatures, with an increase from ~3ºC in March to ~20ºC in August. This raises the question of whether local changes in sea surface temperature allow northern bottlenose whales in the Gully to have a “spa day at home” without a long migration. It is also unclear whether susceptibility to epidermal diatoms varies between individuals or sexes. For example, one might expect greater diatom coverage on older individuals (Leone et al., 2019), or those in poor body condition, as their skin regeneration processes may be reduced.

Here we explore how environmental conditions, sex, and minimum age impact epidermal diatoms on northern bottlenose whales. We predict that as sea surface temperature increases, diatom coverage will decrease, supporting the idea that “spa day” trips function as a form of physiological maintenance. This would also suggest that the Scotian Shelf’s annual surface temperature fluctuations are an important component of the population’s habitat. This study provides a new context for testing the hypothesis that water temperature is a driver of epidermal pathologies in cetaceans.

2 | METHODS

2.1 | Study area and data

Data for this study were collected as part of a long-term study of northern bottlenose whales focused on the Gully, a submarine canyon off Eastern Canada (approximately 44° N, 59° W; Figure 1). As part of this project, data on cetaceans and their environment has been collected during most summers between 1988-2024 from ocean-going sailing vessels. Observations from June 14th through September 7th were included in this analysis, though most observations came from July and August. Photographs were taken targeting the dorsal fins of individual whales, allowing for the re-identification of individual whales and sex-classification based on morphological differences between male and female foreheads or "melons" (See Feyrer et al., 2021 or Feyrer & Walmsley, 2024 for more details).

For the present analysis, we focused on individual whales with two or more high-quality photographs (quality rating 3 or 4 on a 1-4 scale) taken at least five days apart within at least one summer field season. Only left-sided photographs were used to prevent duplicated data from the same ID. We restricted our analysis to digital colour images (years 2007-2019), avoiding potential difficulties in classification resulting from black and white film photographs used in earlier years of the project.

For a consistent measure of sea surface temperature (SST), we used the Daily Optimum Interpolation Sea Surface Temperature dataset (DOISST, Version 2.1; Huang et al., 2021), made available by the National Oceanic and Atmospheric Administration (NOAA). This dataset combines measurements from both remote and *in situ* methods (e.g., satellite, vessel-based sampling, oceanographic buoys), and is available at a resolution of 0.25 degrees. While temperatures in our study exhibited clear seasonal variation, measures from each of the three canyon sites were nearly identical (Figure S1), so we proceeded to use measures from the Gully alone for subsequent analyses. Most of our northern bottlenose whale observations came from this canyon (approx. 86%), and whales are known to move back and forth between these sites (Wimmer and Whitehead 2004).

2.2 | Assessing diatom coverage

Levels of diatom coverage on individual whales were assessed visually, using a five-point scale representing estimated coverage of 0-20%, 20-40%, 40-60%, 60-80%, and 80-100%. To assess the reliability of these classifications, an additional 5 independent observers ranked the diatom coverage for 50 random photographs. Interobserver reliability for diatom coverage was calculated using Fleiss' kappa statistic for ordinal data with the *irrCAC* package in R (Kilem, 2019). While classifications for the final dataset were done by one observer, interobserver reliability was assessed to measure the degree to which these estimates are subjective.

2.3 | Modelling the effects of sea surface temperature on diatom coverage

Photographs with diatom classifications were assigned a corresponding SST value based on the date that the photograph was taken. We then used generalized linear mixed-effects models (GLMMs) to test whether levels of diatom coverage were predicted by sea surface temperature. Here, diatom coverage was the response variable while sea surface temperature was the linear predictor. Levels of diatom coverage were converted to the mean proportion of each observer-determined class prior to modelling (i.e., 0.1 for 0-20% coverage, 0.3 for 20-40% coverage, and so on). Given that the response variable represented a proportion, we used a Beta family with canonical link function for each of the following models. We also included random effects to estimate individual-specific variation (Model 1). Next, we used a generalized additive mixed-effects model (GAMM) to test for the presence of a non-linear relationship between diatom coverage and SST. Here, diatom coverage was the response variable while SST was the predictor (Model 2). A non-linear relationship is expected if, for instance, there is a specific threshold at which SST affects diatom coverage with little effect after. To test how well season alone predicted diatom coverage, we also fit a GAMM with a smooth effect for day of year (Model 3). This allowed us to assess whether diatom levels began to increase again following the peak in SST in August (Figure 1). Finally, we fit an additional GLMM (Model 4) and GAMM (Model 5) to explore the effects of sex on diatom coverage. Simplified expressions representing each model are as follows:

$$Diatom_{\%Cover} \sim SST + (Individual) \tag{Model 1}$$

$$Diatom_{\%Cover} \sim smooth(SST) + (Individual) \tag{Model 2}$$

$$Diatom_{\%Cover} \sim smooth(DayOfYear) + (Individual) \tag{Model 3}$$

$$Diatom_{\%Cover} \sim SST + sex + \ (Individual) \tag{Model 4}$$

$$Diatom_{\%Cover} \sim smooth(SST) + sex + \ (Individual) \tag{Model 5}$$

GLMMs were fit using the *glmmTMB* package in R (Brookes et al., 2017), while the GAMM was fit using the *mgcv* package in R (Wood, 2011), using default settings for the basis dimension. Data visualizations were made using the *ggplot2* package in R (Wickham, 2016). Data and code are publicly available at the following link: https://osf.io/8wd29.

3 | RESULTS

3.1 | Summary of data

The final dataset consisted of 1,775 observations of photo-identified whales between August 2007 and August 2019. Of these photographs, 137 were unable to be assessed for diatom coverage due to too little of the area adjacent to the dorsal fin being visible, and were excluded. Right-sided photographs were also excluded, leaving 849 measures of diatom coverage. Most of these were from the Gully ($N = 734$), with smaller numbers from the Shortland and Haldimand canyons ($N = 88$ and 27 respectively). These observations included 257 unique individuals, including 52 males, 90 females, and 115 individuals of unknown sex. Approximately 61% of individuals in the present dataset were included for a single year, with a range of 1-6 years of diatom observations. The corresponding sea surface temperature (SST) was variable across observations of northern bottlenose whales, ranging from 8.11 – 21.05 ºC with a mean of 18.0 ºC. Temperature changed predictably with season, warming gradually between April and August (Figure 1B). The interobserver reliability test resulted in a Fleiss' Kappa of 0.52 with 90% agreement on diatom coverage values between observers ($p < .001$), indicating that classifications were reliable. Levels of diatom coverage tended to be low overall (< 20%), but levels up to 80-100% were observed (Table 1).

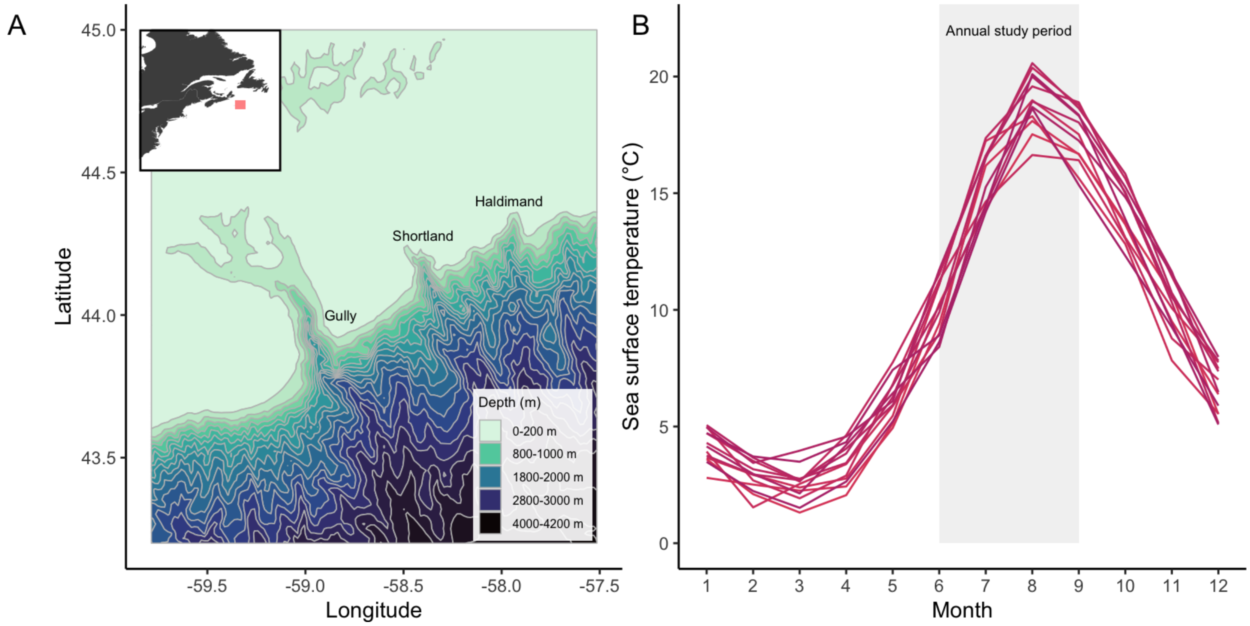

Figure 1 | (A) Map showing the Gully and surrounding canyons with depth. (B) Annual changes of sea surface temperature (°C) in the Gully with annual study period shaded. Lines represent different years between 2007 and 2019.

Table 1 | Counts of all diatom coverage values from 2007 to 2019 for left- and right-sided photographs.

Diatom Coverage (%)	**Left-sided**	**Right-sided**
0-20	796	736
20-40	25	31
40-60	14	12
60-80	8	7
80-100	6	3
Not discernable	63	74

3.2 | Effect of sea surface temperature on diatom coverage

Of individuals with multiple observations in a given year, most showed no change in diatom coverage (89%, often simply stable the lowest levels of coverage), while 8% showed declining coverage over the season, and 2% showed increasing coverage. See Figure S2 for examples of changes in diatom coverage within individuals in a given year.

The main GLMM testing for a relationship between SST and diatom coverage indicated that SST has a significant negative effect on diatom cover (coefficient $\beta = -0.106$, $p < 2 \times 10^{-16}$, AIC = -2148.1, Figure 2). The effect of SST on diatom cover was similarly negative and significant in GLMMs controlling for the effect of sex. The GAMMs exploring the non-linear relationship between SST and diatom coverage also indicated a significant effect of the smooth term of SST on diatom coverage, suggesting that the relationship may be slightly non-linear (for Model 2: effective degrees of freedom (e.d.f.) = 2.03, $p < 2 \times 10^{-16}$, AIC = -2132.37, Figure 2). Unsurprisingly, we also found that diatom coverage tended to decrease as the study season progressed (i.e., with day of year; Figure S3). More specifically, mean predicted diatom coverage fell from approximately 30% at the start of the study season to the lowest level of coverage by early August. We detected no evidence of a positive increase in diatom loading in the later summer as temperatures cooled.

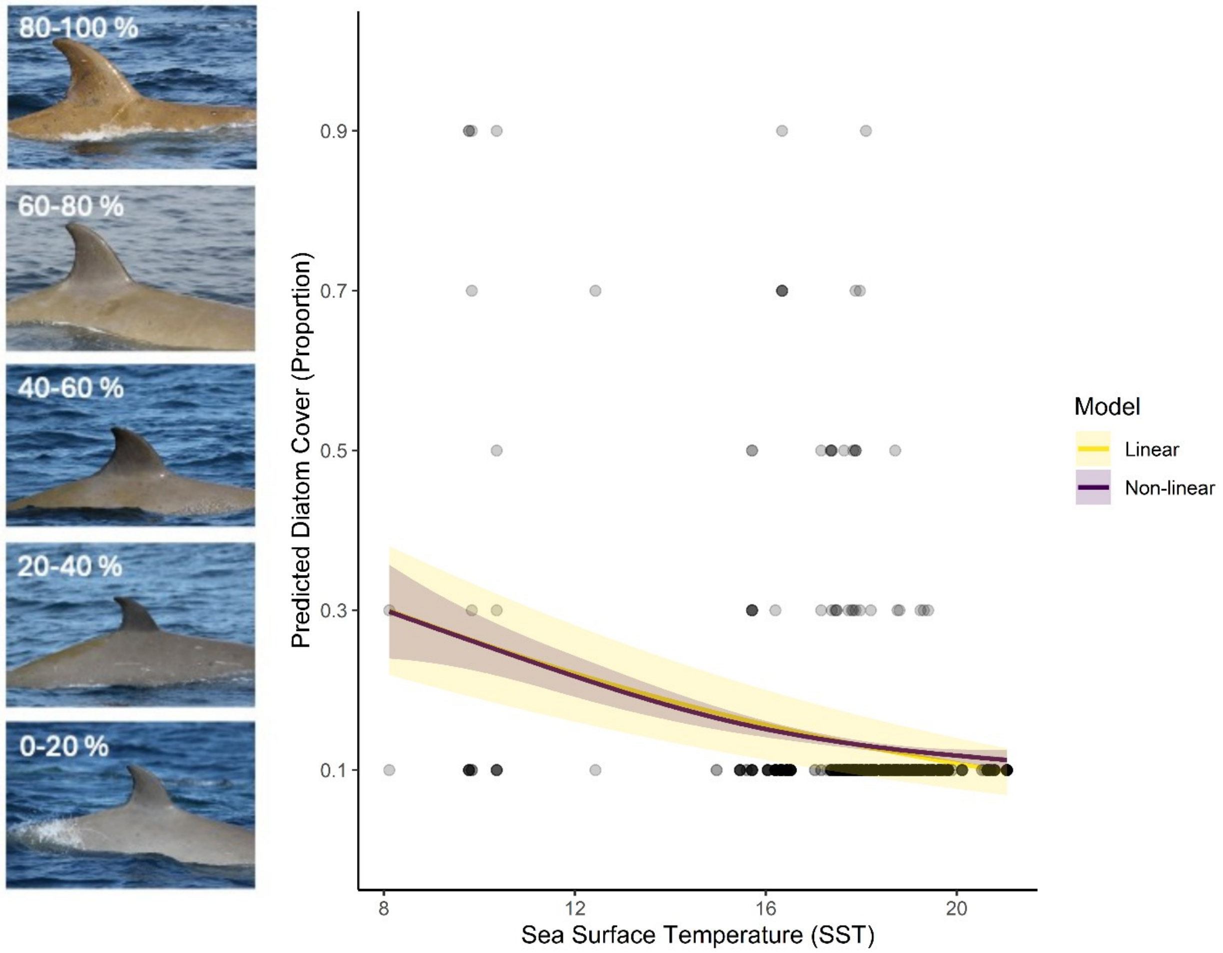

Figure 2 | *Left*: Examples of different levels of diatom coverage on northern bottlenose whales. *Right*: Predicted effects of sea surface temperature on diatom coverage from linear (GLMM – yellow) and non-linear (GAMM – purple), estimated using mixed-effects models. Shaded areas representing the 95% CI around the mean prediction. Points represent specific observations and are partially transparent meaning that darker points imply more observations.

3.3 | Effects of sex, age, and individual variation on diatom coverage

The random effect of individual-specific variation in the first GLMM (Model 1) indicated some variability across individuals in baseline diatom coverage, however, this effect did not appear to have a major contribution to variation in diatom cover (variance = 0.074). Males appeared to have lower diatom coverage than females, though the difference between sexes was very small (GLMM: $\beta = -0.16$, $p = 0.016$; GAMM: $\beta = -0.16$, $p = 0.001$; Figure 3). Numerical summaries of all GLMMS and GAMMs are available in supplemental Tables S2-S6.

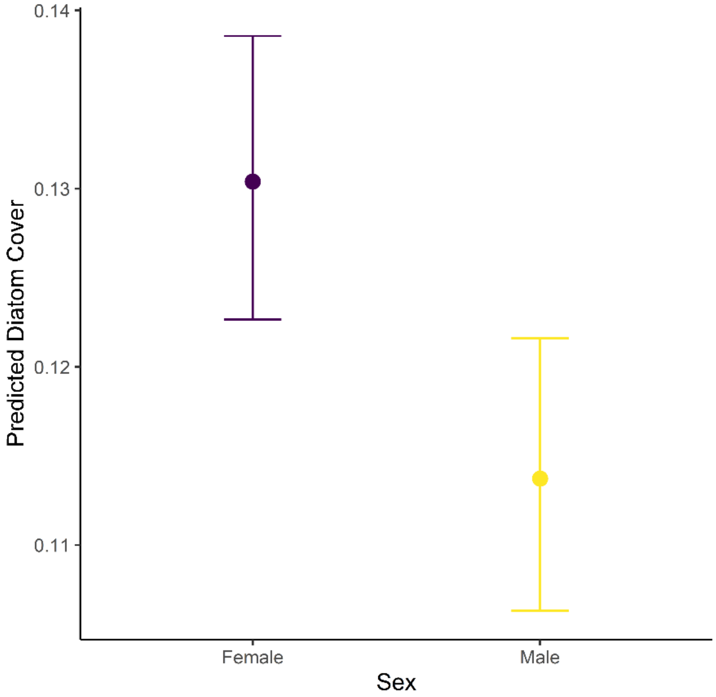

Figure 3 | Predicted probabilities of diatom coverage as a function of sex, highlighting a significant (but small) reduction in diatom coverage for males compared to females. Error bars representing 95% CIs.

4 | DISCUSSION

Migration has primarily been thought to serve the purpose of finding better conditions for food availability or reproductive needs (Chapman et al., 2014). However, a growing body of evidence suggests that migration in cetaceans is also used for physiological maintenance. These findings support a key assumption underpinning the physiological maintenance hypothesis, demonstrating that warmer sea temperatures also predict loss of epidermal diatoms in resident populations.

Our findings are consistent with the expectation that sea surface temperature directly influences diatom coverage on cetaceans. We reviewed photographs of the Scotian Shelf population of northern bottlenose whales between summer field seasons from 2007 –2019. Throughout the observation period, the SST in the Gully ranged from 8.11 – 21.05ºC, with the warmest temperatures similar to those experienced by cetaceans during rapid movements thought to be associated with physiological maintenance (e.g., 20.9-24.2°C, Durban & Pitman, 2012; 22°C, Lefort et al., 2025; 22.8–24.2°C, Pitman et al., 2020). Whales in these previous studies often experienced waters colder than those observed in the Gully during our study period, which may reflect the finding that diatom coverage was often limited in our analysis (0-20%; Table 1). Although it is unclear whether the Scotian Shelf population undertakes physiological maintenance migrations, the large seasonal temperature shifts in their habitat suggests such movements may be unnecessary in spring and summer.

Recent studies have pointed to the putative relationship between sea temperature and epidermal condition to explain movements in northern bottlenose whales specifically (Lefort et al., 2025; Haas et al., 2026). In these cases, time spent in warmer waters was brief, animals were often at the surface, and the trips were not obviously associated with breeding or foraging behaviour, consistent with a role in epidermal maintenance. Similar patterns have been documented in orcas, which undertake long-distance migrations from polar Antarctic waters to warmer regions (Durban & Pitman, 2012; Hooper et al., 2019). In contrast, the Scotian Shelf population of northern bottlenose whales has not (yet) been observed making such migratory trips, raising the possibility that local temperature changes may be sufficient to support physiological maintenance, at least for a portion of the year. Future work using animal-attached tags, especially during the winter months, would help to assess whether the Scotian Shelf animals conduct similar trips to warmer waters, despite the predictable warming each summer.

We found that diatom coverage varied between sexes, with males showing slightly less diatom coverage than females. Similar patterns have been identified in other cetaceans. For example, female bottlenose dolphins (*Tursiops truncatus*) had more severe epidermal lesions, possibly due to a reduced immune system during pregnancy or nursing (Leone et al., 2019; Wilson et al., 1997). Behavioural differences in males versus females, such as social or rubbing behaviour, may also contribute to sex differences in diatom coverage (Hooper, et al., 2019). These differences could affect the rate at which diatoms are removed during physical interactions with conspecifics or their environment.

These results underscore the importance of environmental factors in shaping the health and physiological maintenance of cetaceans. Similar to the present study, research to determine what oceanographic factors impact epidermal lesions on bottlenose dolphins found that individuals in lower water temperatures, as well as lower salinity, experienced higher prevalence and severity of epidermal diseases (Wilson et al., 1999). A greater number of diatoms on whales were found in areas with damaged epidermal tissue in comparison to areas with healthy skin (Henk & Mullan, 1996). Skin maintenance is a balancing act with trade-offs between thermal regulation, pathogen load, foraging, and movement (Hooper et al., 2019). We expect that for the northern bottlenose whale population on the Scotian Shelf this balancing act has been made easier as the surface temperatures in their habitat vary dramatically between seasons.

More broadly, physiological maintenance (i.e., maintaining individual health) may be an underappreciated aspect of movement behaviour across species. Since temperature can impact immune function (Martin et al., 2010) as well as the prevalence of pathogens, seasonal movements can play an important role in minimizing health risks (Altizer et al., 2011; Love et al., 2024). Migrations have been shown to reduce the rate of spreading of infectious diseases, allowing hosts, such as mammals, insects, birds and fish, to escape from a contaminated habitat and return when conditions are more favourable (Altizer et al., 2011). Reindeer (*Rangifer*) undergo post-calving migrations, and Folstad et al. (1991) found that an increase in migration distance from calving grounds resulted in a decrease of parasitic infections. Migration is important for physiological maintenance across species with the potential to influence health directly, over and above the broader effects of moving to areas with improved conditions and access to resources.

This study provides new evidence in support of the physiological maintenance migration hypothesis in whales. Our longitudinal data suggest that higher sea surface temperatures reduce epidermal diatom loading on northern bottlenose whales. In regions where seasonal temperature variation is limited, whales may need to undertake short-term migrations to warmer waters to maintain their health, perhaps via changes in rates of epidermal shedding, as has been hypothesized for other cetaceans. These findings reinforce the idea that physiological maintenance, alongside feeding and breeding, can drive whale movement patterns (Hooper et al., 2019; Lefort et al., 2025).

Understanding individual and population-level differences in susceptibility to diatoms, and their links to habitat-use, health, and climate conditions, may be important when managing cetacean populations, particularly in the context of spatial protections. As ocean temperatures shift under climate change, some populations may need to initiate or adapt migratory behaviour to meet physiological needs. Animals in regions that have cooled may face new pressure to migrate, while others may need to shift existing migratory routes. Our results contribute to a broader understanding of how environmental change shapes animal behaviour and highlights the role of non-reproductive drivers in migration.

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Supplementary Material

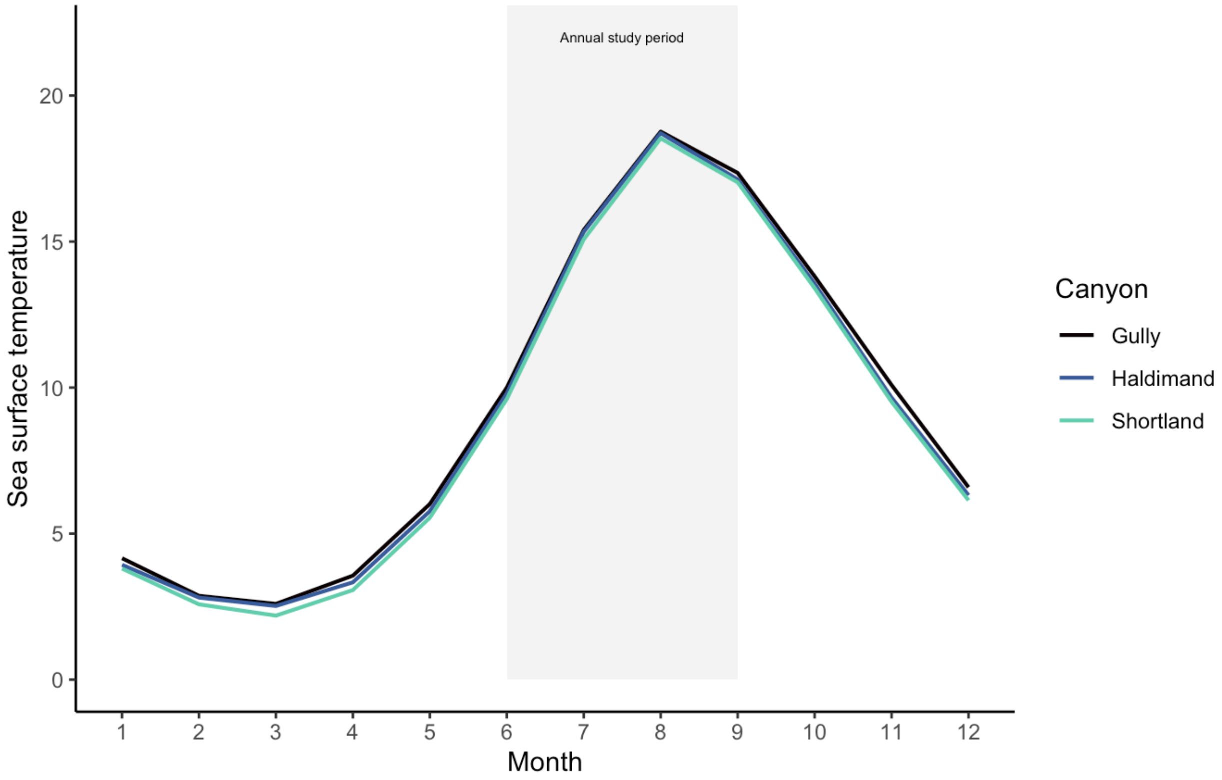

Figure S1 | Sea surface temperatures (SST) from all three canyons where observations took place. Temperatures were very similar across canyons. Data were extracted from the Daily Optimum Interpolation Sea Surface Temperature dataset (DOISST, Version 2.1; Huang et al., 2021), for the period of 1988-2025.

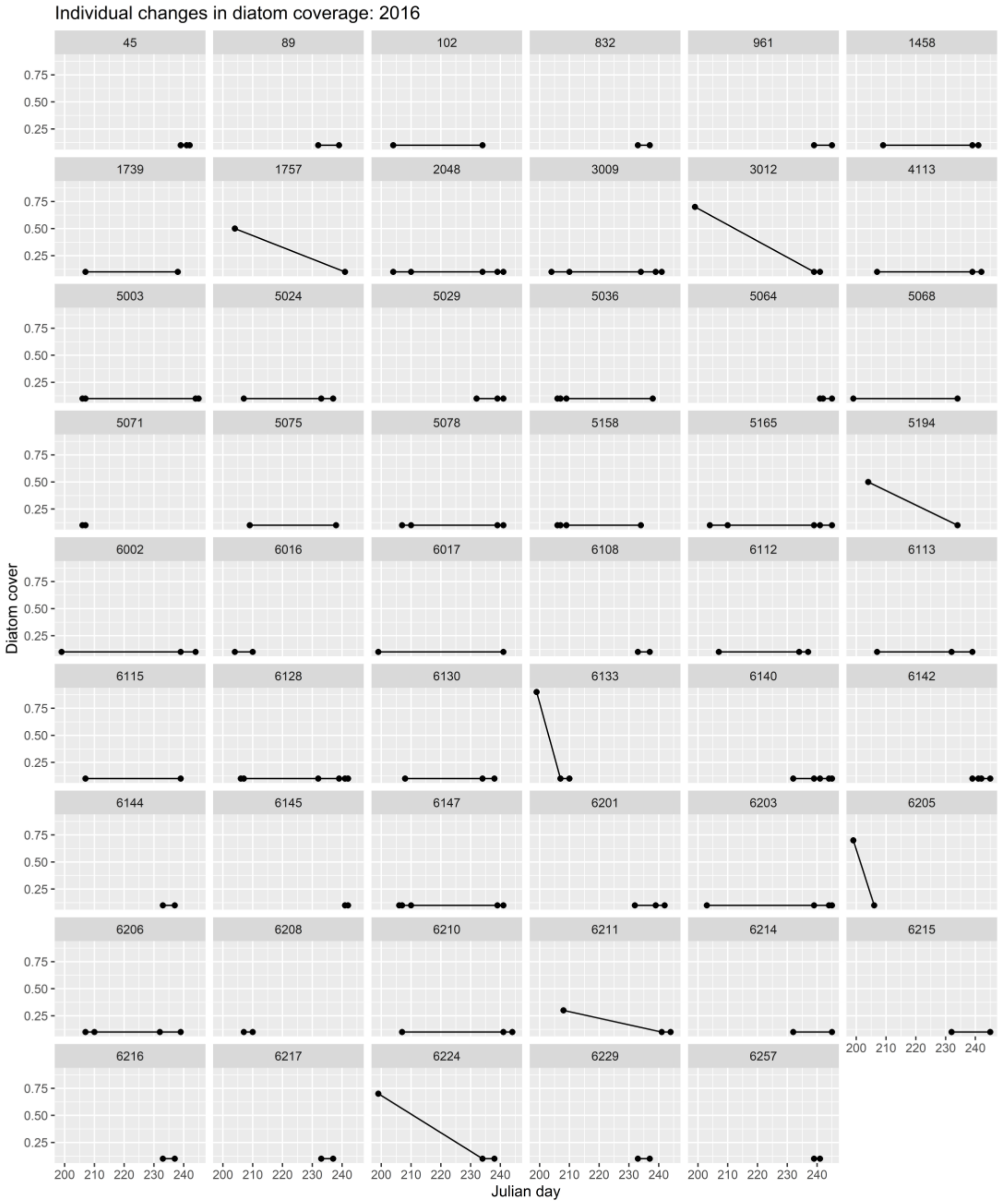

Figure S2 | Examples of individual trajectories in diatom coverage within a year (2016). Most individuals consistently showed few diatoms (<20%), while several showed a decline over the study season.

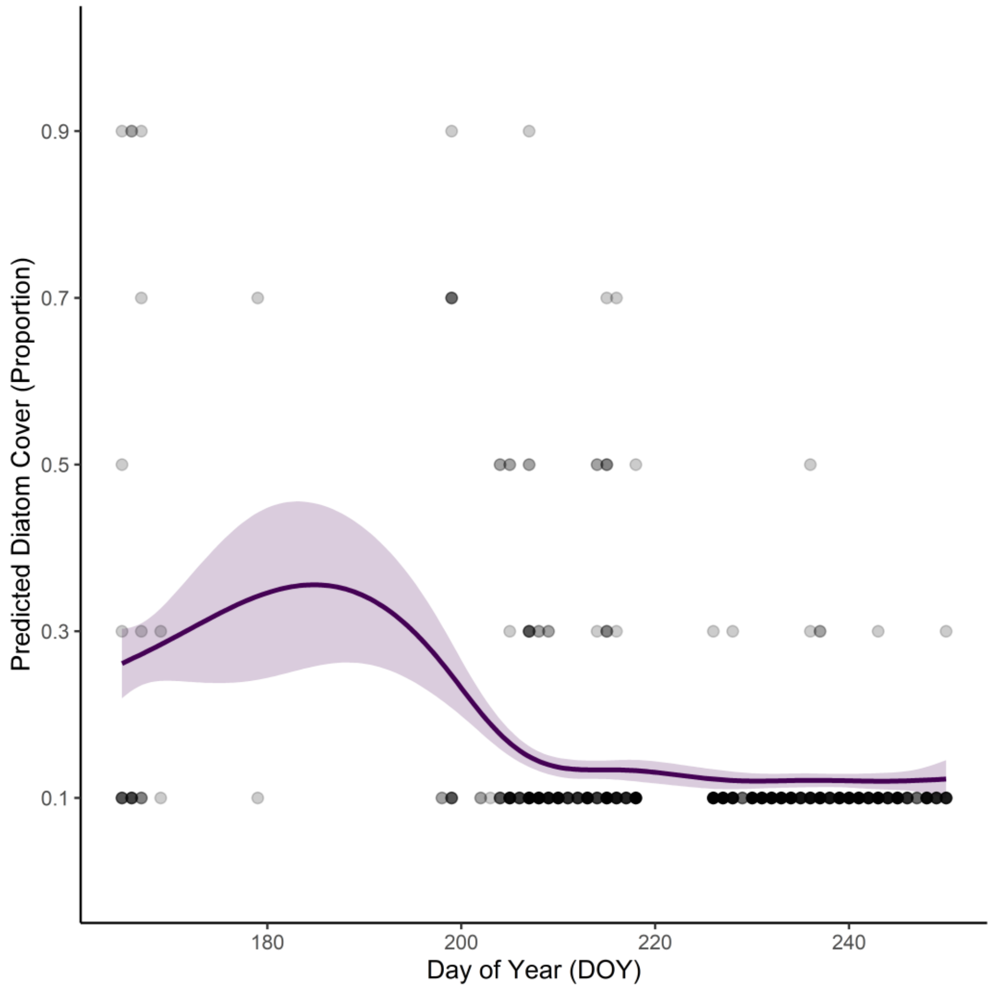

Figure S3 | Predicted effects of day of year on diatom coverage estimated using generalized additive mixed-effects model. Shaded areas representing the 95% CI around the mean prediction. Points represent specific observations and are partially transparent meaning that darker points imply more observations.

Table S1 | Number of left-sided observations of diatom coverage on northern bottlenose whales in the Scotian Shelf between 2007-2019.

Year	**June**	**July**	**August**	**September**
2007	0	0	8	0
2008	0	0	2	2
2009	0	0	2	0
2010	0	39	68	0
2011	2	18	201	0
2013	0	0	17	58
2015	24	0	104	0
2016	0	64	114	9
2017	0	0	14	0
2019	0	31	72	0
Total	**26**	**152**	**602**	**69**

Table S2 | Summary of GLMM explaining diatom coverage on northern bottlenose whales as a function of sea surface temperature (Model 1).

Coefficient	**Estimate**	**Std. Error**	***p***
Intercept	-0.017	0.175	0.924
Sea surface temperature	-0.106	0.010	$< 2 \times 10^{-16}$
Random effect variance (Individual): 0.074			

Table S3 | Summary of GAMM explaining diatom coverage on northern bottlenose whales as a non-linear function of sea surface temperature (Model 2).

Coefficient	**Estimate**	**Std. Error**	***p***
Intercept	-1.922	0.045	$< 2 \times 10^{-16}$
Sea surface temperature	e.d.f = 2.028	--	$< 2 \times 10^{-16}$
Individual	e.d.f = 0.562	--	0.135

Table S4 | Summary of GAMM explaining diatom coverage on northern bottlenose whales as a non-linear function of day-of-year (Model 3).

Coefficient	**Estimate**	**Std. Error**	***p***
Intercept	-1.885	0.021	$< 2 \times 10^{-16}$
Day-of-year	e.d.f = 6.511	--	$< 2 \times 10^{-16}$
Individual	e.d.f = 0.001	--	0.651

Table S5 | Summary of GLMM explaining diatom coverage on northern bottlenose whales as a function of sea surface temperature and sex (Model 4).

Coefficient	**Estimate**	**Std. Error**	***p***
Intercept	0.114	0.214	0.593
Sea surface temperature	-0.110	0.012	$< 2 \times 10^{-16}$
Sex: Male	-0.160	0.067	0.016

Random effect variance (Individual): 0.057

Table S6 | Summary of GAMM explaining diatom coverage on northern bottlenose whales as a non-linear function of sea surface temperature and sex (Model 5).

Coefficient	**Estimate**	**Std. Error**	***p***
Intercept	-1.824	0.057	$< 2 \times 10^{-16}$
Sex: Male	-0.156	0.048	0.001
Sea surface temperature	e.d.f = 2.481	--	$< 2 \times 10^{-16}$
Individual	e.d.f = 0.524	--	0.149