Seasonal warming drives epidermal shedding in northern bottlenose whales

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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 shedding 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 less diatom coverage than females overall, and that diatom coverage tended to increase with estimated (minimum) age. Epidermal shedding is important in health maintenance for cetaceans as diatoms and skin lesions are thought to be linked to immune function. Our results support the hypothesis that health can be a driving factor in animal movements and demonstrates how environmental change can have major effects on behaviour.

KEYWORDS

Movement – Health – Physiological maintenance – 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., 2019). Cetaceans undergo epidermal shedding due to an accumulation of diatoms and other lesions on their skin (Gaydos et al., 2023; Wilson et al., 1999). Diatoms are photosynthetic microalgae commonly found growing on aquatic vertebrates and are highly affected by 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). Crucially, water temperature can affect the rate at which epidermal shedding takes place. 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 (Hooker et al., 2012). 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 forage at depth, which was hypothesized to facilitate epidermal shedding. Similar, directed short-stay migrations by five northern bottlenose whales from the waters around Iceland and Jan Mayen to the Azores are also consistent with an epidermal maintenance function (Wensveen et al., 2025).

The Scotian Shelf population of northern bottlenose whales resides in the Gully, a marine canyon off the east coast of Canada. 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, 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 or northern bottlenose whales in poor body condition, as their skin regeneration processes may be reduced (Leone et al., 2019).

Here we explore how environmental conditions, sex, and 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 temperature fluctuations play an important component of the population’s habitat. We further predict that older individuals will have a reduced capacity for epidermal shedding. Lastly, we expect that sex

may have a modest effect as males may have lower diatom coverage due to more frequent physical interactions and scarring, which could facilitate increased epidermal turnover or mechanical removal of diatoms (Macleod, 1998; Feyrer et al., 2021). This study provides a new context for testing the hypothesis that the effect of temperature on epidermal parasites is a driver of whale movements.

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). 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. 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 at., 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) taken at least five days apart within at least one summer field season. Both left- and right-sided photographs were used. When possible, left- and right-sided IDs were linked based on distinctive markings. However, some IDs were not able to be linked meaning that some side-specific IDs may in fact represent the same individual. 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 photos. Interobserver reliability for diatom coverage was calculated using Fleiss' kappa statistic for ordinal data with the *irrCAC* package R (Kilem, 2019). While classifications for 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 epidermal shedding with little effect after.

$$Diatom_{\%Cover} \sim SST + (1|Individual) \quad \text{(Model 1)}$$

$$Diatom_{\%Cover} \sim smooth(SST) + (1|Individual) \quad \text{(Model 2)}$$

To explore the effects of sex and age on diatom coverage, we fit additional GLMMs incorporating sex as a predictor (Model 3) as well as minimum age of individuals as a predictor (Model 4). Minimum age was determined based on yearly re-sightings in the long-term database (i.e., individuals were assigned a minimum age of "1" in the first year they were encountered, "3" if encountered two years later, and so on). While minimum age will underestimate true age given incomplete sampling in the population, it serves as a simple proxy to estimate age-related changes within individuals. Lastly, we fit GAMMs incorporating the sex of individuals (Model 5) and another GAMM incorporating the minimum age of the individuals (Model 6).

$$Diatom_{\%Cover} \sim SST + sex + (1|Individual) \quad \text{(Model 3)}$$

$$Diatom_{\%Cover} \sim SST + minimumAge + (1|Individual) \quad \text{(Model 4)}$$

$$Diatom_{\%Cover} \sim smooth(SST) + sex + (1|Individual) \quad \text{(Model 5)}$$

$$Diatom_{\%Cover} \sim smooth(SST) + minimumAge + (1|Individual) \quad \text{(Model 6)}$$

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 analyses are available at github.com/CharlotteR42/NBW.git

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, leaving 1,638 measures of diatom coverage. Most of these were from the Gully (N = 1,406), with smaller amounts in the Shortland and Haldimand canyons (N = 163 and 69 respectively). These observations included 428 unique individuals, including 69 males, 159 females, and 213

individuals of unknown sex. 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 18.09 ºC. Temperature changed predictably with season, warming dramatically between July 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).

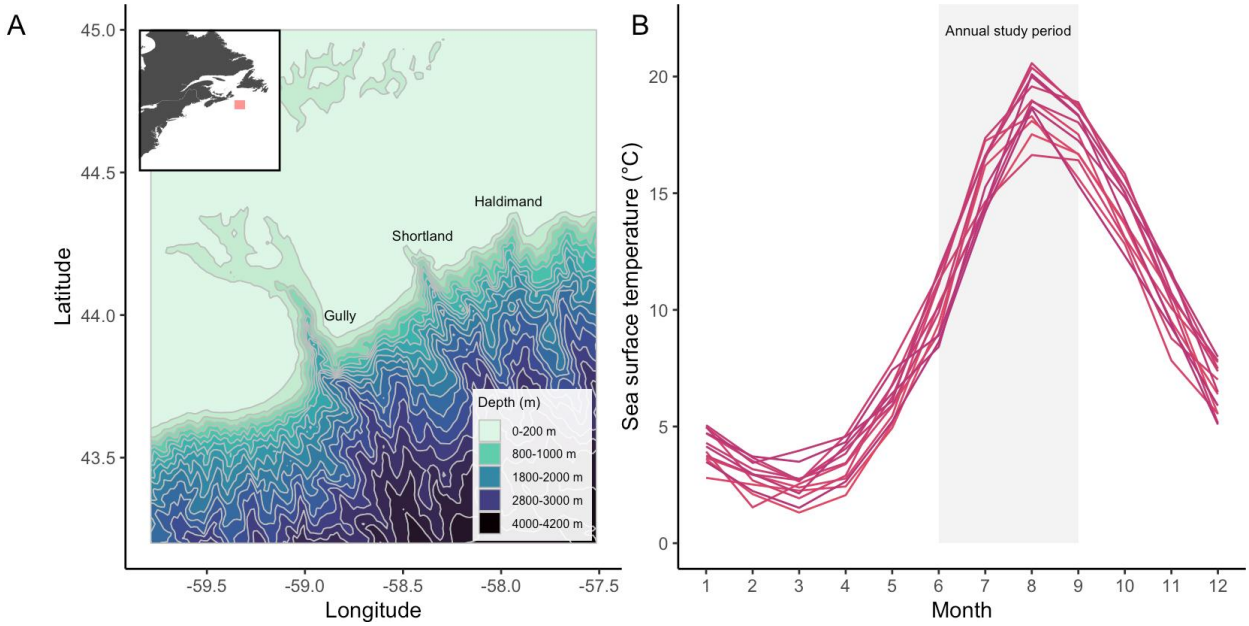

Figure 1 | (A) Map showing the Gully and surrounding canyons with depth. (B) Annual changes of sea surface temperature (ºC) in the Gully with annual study period shaded. Lines represent different years between 2007 and 2019.

Table 1 | Counts of all diatom coverage values from 2007 to 2019.

Diatom Coverage (%)	**Count**
0-20	1532
20-40	56
40-60	26
60-80	15
80-100	9
Not discernable	137

3.2 | Effect of sea surface temperature on diatom coverage

The main GLMM testing for a relationship between SST and diatom coverage indicated that SST has a significant negative effect on diatom cover (coefficient $\beta = -0.105$, $p < 2 \times 10^{-16}$, AIC = -4289.7, Figure 2). The effect of SST on diatom cover was similarly negative and significant in GLMMs controlling for the effects of sex and minimum age (Table S3; Table S4). 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 non-linear (for Model 2: effective degrees of freedom (e.d.f.) = 2.96, $p < 2 \times 10^{-16}$, AIC = -4277.45, Figure 2).

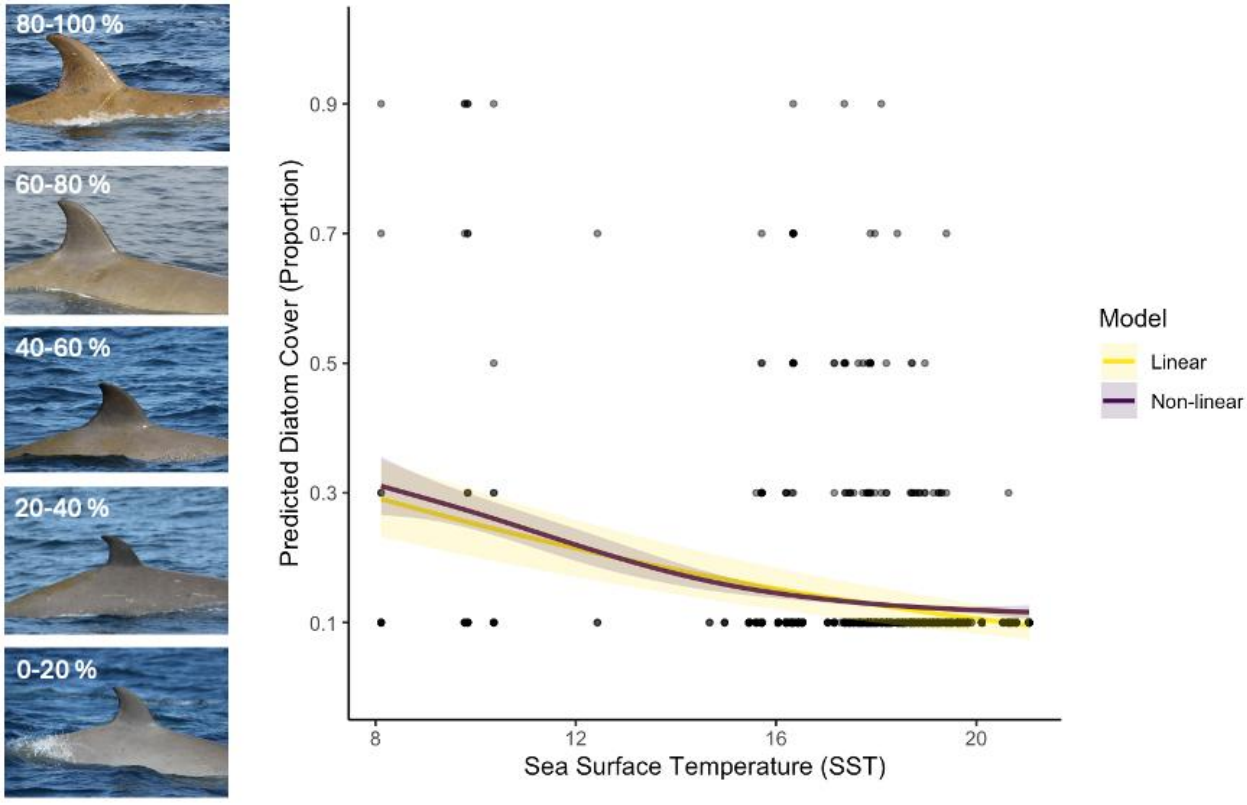

Figure 2 | Examples of different levels of diatom coverage (left). Predicted effects of sea surface temperature on diatom coverage from linear (GLMM – yellow) and non-linear (GAMM – purple) mixed models with shaded areas representing the 95% CI (right).

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

The random effect of individual-specific variation in the GLMM indicated some variability across individuals baseline diatom coverage, however, this effect did not appear to have a major contribution to variation in diatom cover (variance = 0.05). The GLMM and GAMM models observing the sex-specific variation included a total of 1,066 observations from 222 individuals. Both models indicate that males had lower diatom cover compared to females (GLMM: $\beta = -0.098$, $p = .059$; GAMM: $\beta = -0.09$, $p = .005$)

The GLMM investigating age-specific variation identified an uncertain but positive relationship between minimum age and diatom cover, though the effect was not significant ($\beta = 0.0027$, $p = 0.376$). However, the GAMM investigating age-specific variation revealed a significant non-linear effect on diatom cover ($\beta = 0.008$, $p = 0.021$; Figure 3). The resulting relationship was not especially complex, however, indicating a small positive link between minimum age and diatom cover (Figure 3).

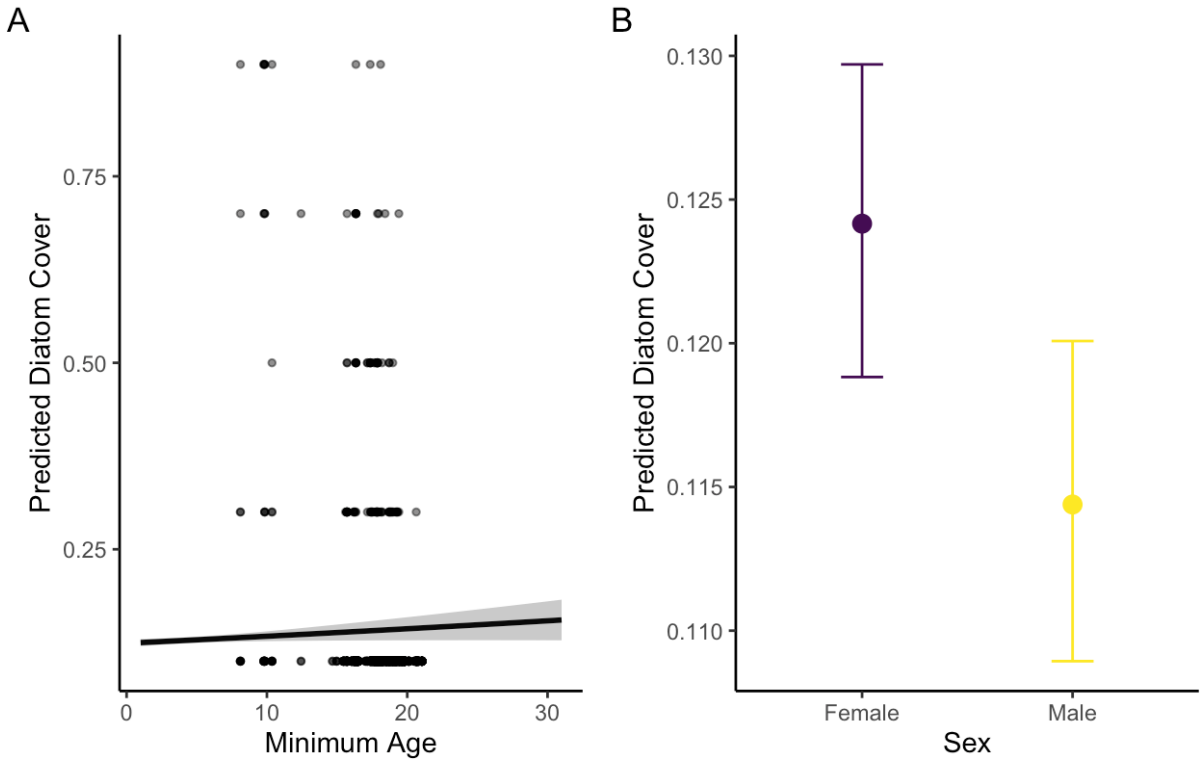

Figure 3 | (A) Linear relationship between minimum age and diatom cover (Model 6). The black trend line shows the prediction while the shaded band represents the 95% CI. (B) Predicted probabilities of diatom coverage as a function of sex, with error bars representing 95% CIs.

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, this study contributes to a growing body of evidence that migration in cetaceans is also used for physiological maintenance. 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, consistent with what an individual would experience when migrating from sub-polar waters to temperate waters (Durban & Pitman, 2012; Lefort et al., 2025; Wensveen et al. 2025). Although it's 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. The observed link between higher SST and reduced diatom coverage strengthens support for the physiological maintenance hypothesis.

Our findings add to growing evidence that sea surface temperature influences diatom coverage on cetaceans. Previous studies have linked this relationship to migratory behaviour in northern bottlenose whales. Lefort et al. (2025) and Wensveen et al. (2025) tracked six individual northern bottlenose whales. These individuals travelled south from the Davis Strait, Iceland and Jan Mayen (~ 4ºC) towards warmer waters (~23ºC). These trips were brief, involved shallow areas, and were not associated with breeding or foraging behaviour, suggesting a role in epidermal shedding. Similar patterns have been documented in orcas, which undertake long-distance migrations from polar Antarctic waters to warmer regions for physiological maintenance (Durban & Pitman, 2012; Hooper et al., 2019). In contrast, the Scotian Shelf population of northern bottlenose whales has not been observed making such migratory trips, raising the possibility that local temperature changes may be sufficient to support physiological maintenance, at least on a seasonal basis.

We found that diatom coverage varied between sexes, with males showing less diatom coverage than females. Similar patterns have been identified in other cetaceans. For example, female bottlenose dolphins (*Tursiops truncatus*) were found to have higher levels of 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., 2018). These differences could affect the rate at which diatoms are removed during physical interactions with conspecifics or their environment.

Our results provide support for our prediction about the effects of age, suggesting that older individuals have higher diatom coverage, though the effect was relatively weak (Figure 3). It is also important to note here that our proxy for age (minimum age based on re-sightings) is imperfect and may result in down-biased estimates of age-related changes in diatom coverage. We expect that this pattern of age-related increases in diatom levels may be due to a reduced immune system which would decrease the rate of epidermal shedding (Leone et al., 2019). Different effects may be expected for very young cetaceans. For example, "orange on grey lesions" from aggregations of epidermal diatoms were most prevalent in orca calves (0-1 years old), possibly due to calves having a thicker stratum corneum layer which may allow more diatoms to adhere to the epithelium (Gaydos et al., 2023). Additionally, bottlenose dolphin calves experience a greater level of orange lesions than adult or sub-adults (Wilson et al., 1997). However, from our observations in the field, northern bottlenose whale calves tend to not show significantly greater diatom coverage compared to older individuals.

These results underlie the importance of epidermal shedding in cetaceans for physiological and health maintenance as diatoms are more prevalent on individuals whose immune system may be compromised. Failure to undergo epidermal shedding can result in an increase of epidermal diseases (Gaydos et al., 2023; Hooper et al., 2019; Wilson et al., 1999). 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 were found on whales with damaged epidermal tissue due to epidermal lesions in comparison to healthy individuals (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 temperatures in their habitat vary dramatically between July and August. This may mean that they do not have to expend energy migrating to warmer waters during this time of year, or maybe any time, if only

one warm temperature event per year is sufficient, as implied by Wensveen et al.'s (2025) report that all five northeastern Atlantic bottlenose whales made the migration to the Azores in summer, as did the tracked whale from the northwestern Atlantic (Lefort et al. 2025).

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, seasonal migrations have the benefit of reducing health risks (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 promote epidermal shedding, a process critical for skin and individual health. In regions where seasonal temperature variation is limited, whales may need to undertake short-term migrations to warmer waters to facilitate epidermal shedding and maintain healthy skin. 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; Wensveen 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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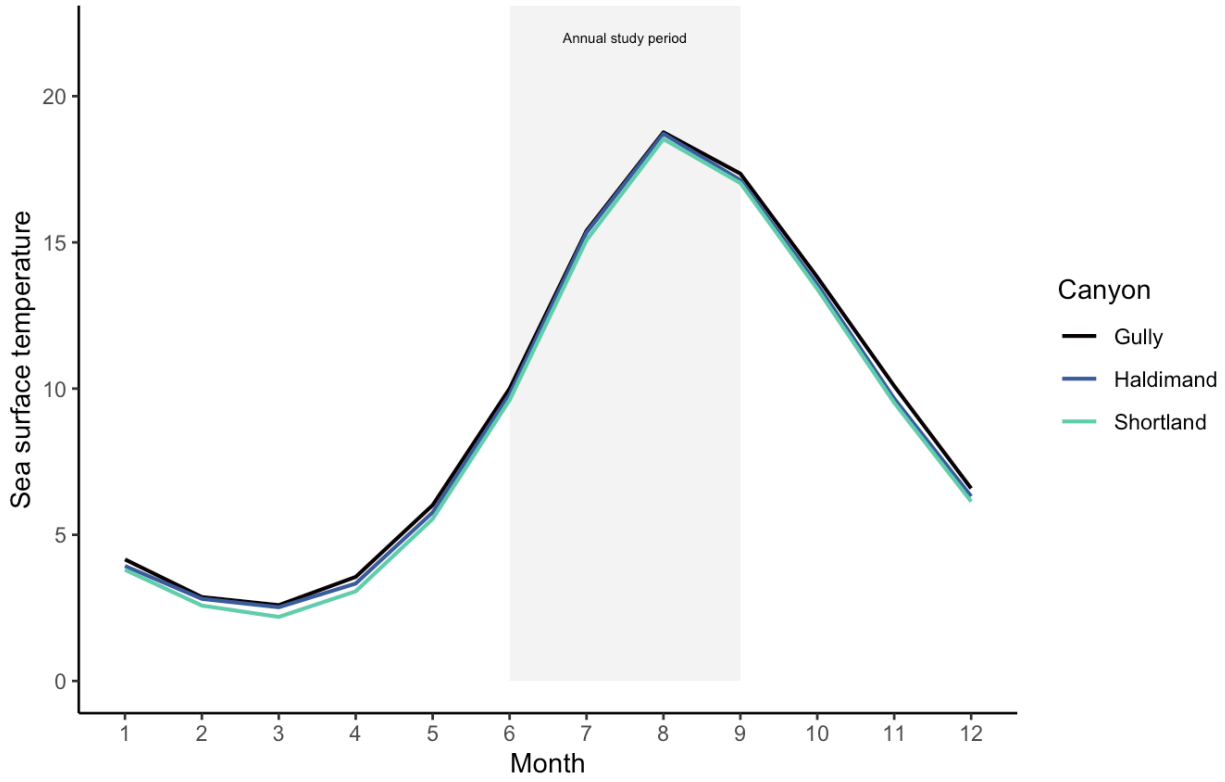
386 **Supplementary Material**



387

388 **Figure S1** | Sea surface temperatures (SST) from all three canyons where observations took place.

389 Temperatures were very similar across canyons.

Table S1 | 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	-0.015	0.124	0.912
Sea surface temperature	-0.105	0.007	$< 2 \times 10^{-16}$
Random effect variance (Individual): 0.062			

Table S2 | 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	-1.897	0.015	$< 2 \times 10^{-16}$
Sea surface temperature	e.d.f = 2.96	--	$< 2 \times 10^{-16}$
Individual	e.d.f = 0.002	--	0.554

Table S3 | Summary of GLMM explaining diatom coverage on northern bottlenose whales as a function of sea surface temperature and sex (Model 3).

Coefficient	**Estimate**	**Std. Error**	***p***
Intercept	0.023	0.144	0.875
Sea surface temperature	-0.108	0.008	$< 2 \times 10^{-16}$
Sex	-0.098	0.052	0.059
Random effect variance (Individual): 0.064			

Table S4 | Summary of GLMM explaining diatom coverage on northern bottlenose whales as a function of sea surface temperature and (minimum) age (Model 4).

Coefficient	**Estimate**	**Std. Error**	***p***

Intercept	-0.028	0.124	0.820
Sea surface temperature	-0.104	0.007	$< 2 \times 10^{-16}$
(minimum) Age	0.003	0.003	0.376
Random effect variance (Individual): 0.062			

401

402 **Table S5** | Summary of GAMM explaining diatom coverage on northern bottlenose whales as a non-
403 linear function of sea surface temperature and sex (Model 5).

Coefficient	**Estimate**	**Std. Error**	***p***
Intercept	-1.883	0.042	$< 2 \times 10^{-16}$
Sea surface temperature	e.d.f = 3.417	--	$< 2 \times 10^{-16}$
Individual	e.d.f = 0.590	--	0.120
Sex	-0.093	0.033	0.005

404

405 **Table S6** | Summary of GAMM explaining diatom coverage on northern bottlenose whales as a non-
406 linear function of sea surface temperature and (minimum) age (Model 6).

Coefficient	**Estimate**	**Std. Error**	***p***
Intercept	-2.062	0.071	$< 2 \times 10^{-16}$
Sea surface temperature	e.d.f. = 2.882	--	$< 2 \times 10^{-16}$
Individual	e.d.f. = 0.850	--	0.009
(minimum) Age	0.008	0.003	0.021

407