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Decadal migration phenology of a long-lived Arctic icon keeps pace with climate change

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Animals migrate in response to seasonal environments, to reproduce, to benefit from resource pulses, or to avoid fluctuating hazards. Although climate change is predicted to modify migration, only a few studies to date have demonstrated phenological shifts in marine mammals. In the Arctic, marine mammals are considered among the most sensitive to ongoing climate change due to their narrow habitat preferences and long life spans. Longevity may prove an obstacle for species to evolutionarily respond. For species that exhibit high site fidelity and strong associations with migration routes, adjusting the timing of migration is one of the few recourses available to respond to a changing climate. Here, we demonstrate evidence of significant delays in the timing of narwhal autumn migrations with satellite tracking data spanning 21 y from the Canadian Arctic. Measures of migration phenology varied annually and were explained by sex and climate drivers associated with ice conditions, suggesting that narwhals are adopting strategic migration tactics. Male narwhals were found to lead the migration out of the summering areas, while females, potentially with dependent young, departed later. Narwhals are remaining longer in their summer areas at a rate of 10 d per decade, a similar rate to that observed for climate-driven sea ice loss across the region. The consequences of altered space use and timing have yet to be evaluated but will expose individuals to increasing natural changes and anthropogenic activities on the summering areas.

migration | phenology | climate change | narwhal | satellite telemetry

Migration is a common tactic species adopt to overcome seasonal changes in habitat or resource availability, driving directed movements across both small and large scales (1) coinciding with seasonal shifts in environmental conditions (2), and is often constrained to meet key life history demands (3). Despite the potential for interannual flexibility, directional shifts in migration timing have been reported across global species in response to climate change, with the largest effects seen in long-distance migrants (4). Changes in the predictability of suitable habitat as a result of climate shifts may result in species having to travel farther, leave earlier, and migrate longer (5, 6), thus expending more energy (7). As such, the phenology and life history trade-offs among those species that inhabit extreme environments, such as the Arctic, are expected to rapidly change (8). Assessments of climate change impacts on migration timing have predominantly focused on terrestrial species; however, marine systems are equally impacted, especially at higher latitudes (9, 10). The Arctic, for example, is warming at a rate two to three times higher than that of the global average (11) and as a result, is experiencing a rapid loss of sea ice, with concomitant restructuring of the marine environment (12). It is unclear how declining sea ice and increasing environmental variability are disrupting or modifying and will continue to disrupt or modify the timing and drivers of species' migrations across the region. Within the Arctic marine ecosystem, ice-associated species, which are often long lived, are especially vulnerable as many are niche conservative, have narrow climate envelopes (13), and likely cannot adapt over appropriate evolutionary timescales. Traditionally, the migration dynamics of Arctic marine species were logistically difficult to study, but with the advent of animal biotelemetry, unprecedented monitoring of their behavior and movement is now possible (14).

Meta-analyses suggest that few studies have examined phenological shifts in cetaceans and other marine mammals, presenting a major knowledge gap in the ability to predict responses to future climate scenarios (15, 16). Even in well-studied regions, like the Gulf of Maine, very few studies have directly assessed long-term shifts (17) and have instead focused on establishing baselines in phenology (18). Here, we aimed to determine if the migration phenology of a highly specialized and long-lived Arctic cetacean is being modified by climate change and evaluate the potential drivers. Narwhals (*Monodon monoceros*) provide an ideal model species to investigate climate impacts on migration dynamics given they seasonally migrate across their range from nearshore ice-free environments in the summer months (summering grounds) to regions with

Significance

As narwhal and other Arctic cetaceans can live over 100 y with long generation times, the demonstrated delays in migration phenology suggest that species previously considered inflexible can and are behaviorally responding to the changing dynamics of climate within a single lifetime. Behavioral plasticity would appear to be an important factor driving the observed response to environmental change as many long-lived species are unlikely to exhibit evolutionary responses at the rate necessary to keep pace with climate. Given the longevity of many large-bodied predators, these responses could result in increasing trade-offs and risks for life in the new Arctic.

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>95% ice coverage in the winter (overwintering grounds), where they traverse offshore leads (19, 20). Narwhal migration is considered predictable across its range, with minimal interannual variation reported over short periods of time (20, 21). Evidence demonstrates that stocks with different summer and winter grounds adopt unique migration routes from which they rarely deviate, suggesting limited plasticity (21). Narwhals are one of the longest-lived mammals, reaching ages of >100 y, and form complex social structures (22). Animals that are long lived and exhibit minimal plasticity in migration timing tend to be more vulnerable to environmental change (23). As such, predicting the effects of climate change on long-lived species, such as the narwhal, requires an understanding of a species' behavioral plasticity.

We compared several migration phenology events estimated from telemetry data (Fig. 1) for narwhal in northern Baffin Island relative to time and environmental drivers indicative of local and regional climate cues (*Materials and Methods*). Through access to a long-term telemetry dataset spanning 21 y (1997 to 2018) for 40 individual narwhal tagged in their summering ground, we address two key objectives: 1) to determine if there is evidence for systematic decadal changes in narwhal migration phenology and 2) to quantify the drivers of the onset of narwhal migration in the context of a changing climate. Phenology events included 1) the departure date, estimated using relative changes in move persistence across individual telemetry movement tracks; 2) the dates individuals crossed a passage boundary delineating the exit region from the summering ground (date crossing 75°W); and 3) the transit time, highlighting the difference in time between the departure date and a final passage boundary at 72°W where narwhals are observed to undertake more directed movements to the wintering areas (Fig. 1). Covariates used to evaluate interannual variability of migration phenology included sex, climate oscillation phase (Arctic Oscillation [AO]), ice conditions in the summering area (spring breakup transition week), and a proxy of pan-Arctic climate change (September minimum ice extent).

Results

Decadal Changes in Migration Phenology. Narwhals equipped with satellite telemetry devices in Eclipse Sound were divided into epochs corresponding to 1) 1997 to 1999, 2) 2010 to 2012, and 3) 2016 to 2018 (Table 1). Narwhals were found to delay departure (move persistence) and date crossing the passage boundary at 75°W across epochs (mean day of year: epoch 1: depart = 269.3, cross = 271.6; epoch 2: depart = 274.6, cross = 286.0; epoch 3: depart = 273.5, cross = 289.0). Between the first and last epochs, this translated to delays of 4.2 and 17.4 d of departure and 75°W cross-date, respectively. While there was a trend toward delayed departure dates over time, this was not significant (Kruskal–Wallace rank sum: $\chi^2 = 4.13$, degrees of freedom, $df = 2$, $P = 0.12$). The date narwhals crossed the passage boundary at 75°W, however, was significantly different across the three epochs (cross date 75°W: $\chi^2 = 15.45$, $df = 2$, $P < 0.001$). Yearly mean departure date and yearly mean cross-date at the passage boundary of 75°W were delayed at rates of 2.3 and 9.8 d per decade, respectively (Ordinary least squares, OLS, regression departure date: 0.23 ± 0.19 , $t = 1.17$, $P = 0.24$; OLS cross-date 75°W: 0.981 ± 0.18 , $t = 5.39$, $P < 0.001$). When considering our third metric, transit time, a significant difference was found across epochs (transit time $\chi^2 = 6.98$, $df = 2$, $P = 0.03$), with narwhals spending 4.3 d per decade longer transiting to the 72°W passage boundary (OLS transit time: 0.433 ± 0.16 , $t = 2.66$, $P = 0.011$). The inclusion of sex and the interaction of year and sex was not

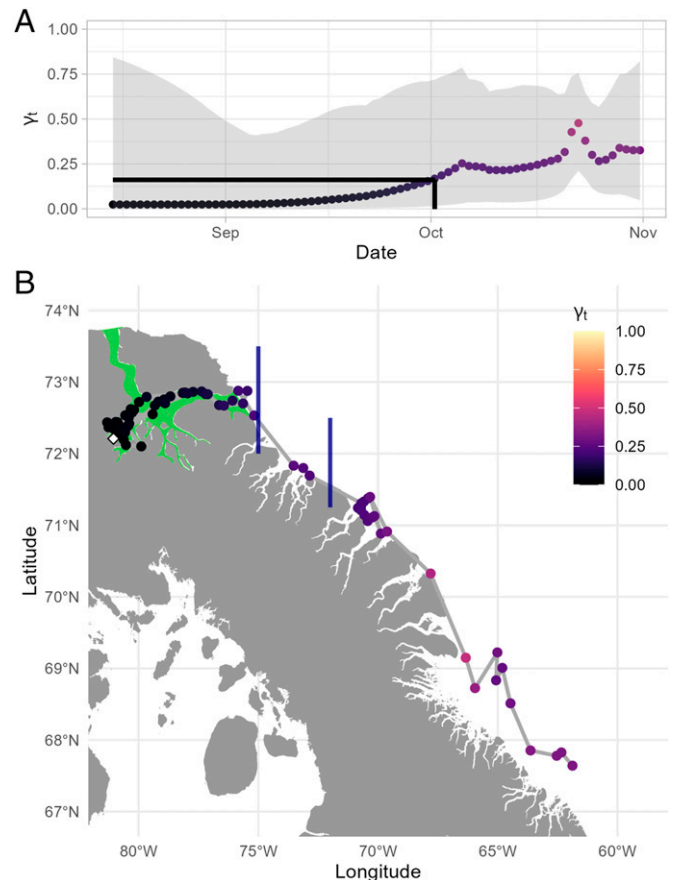


Fig. 1. Phenological events for narwhal migration. (A) Example of move-persistence values estimated for an individual narwhal (female, length = 405 cm) along its movement track from a jointly-fitted move-persistence model. The individual was tagged in Eclipse Sound during the first epoch (1997 to 1999). Thick black lines indicate the threshold value associated with 25% of the difference between minimum and maximum move persistence and the resulting date of departure. (B) The movement track of the 405-cm female is indicated by the gray line, with each 24-h time step colored by its estimated move-persistence (Y_t) value. Vertical blue bars correspond to passage boundaries at 75°W and 72°W longitude, the latter of which was used to assess transit time.

significant in all the models explored, indicating that variable sample sizes of males and females across epochs did not have an effect on the rate of change in migration phenology (*SI Appendix*).

Biological and Climate Modulators of Annual Migration Phenology. Two climatic variables and a biotic variable were significantly associated with the observed change in Eclipse Sound narwhal migration phenology over time. Yearly minimum Arctic Sea ice extent (Fig. 2), a proxy for pan-Arctic climate change, explained the dates narwhals crossed the 75°W passage boundary; a significant delay in cross-date occurred in years when ice extent was lower (Fig. 2). Individuals also spent longer transiting in years when ice extent was lower (*SI Appendix*). A second climatic variable, negative yearly mean AO index, was associated with advances to dates crossing the passage boundary and transit time. When considering the biotic factor, sex, female narwhals were found to cross the 75°W passage boundary 7 d later than males (Fig. 2). For departure date from the summering grounds, sex was also a significant effect, with females departing on average ~6 d later than males (Fig. 3). However, while sex-specific differences were apparent, male and female narwhals were found to delay both departures and passage boundary crossings at a similar rate over the study period (no significant interaction of year and sex)

Table 1. Summary of the narwhal tagging effort

Epoch	Year	n (M, F)	Tag type	Duration (d)	\bar{x} Locs per d	Departure date (\bar{x} d)	Cross-date 75°W (\bar{x} d)	Transit time (\bar{x} d)
1	1997	1 (1, 0)	ST-6	75.3	16.0	263	265	9
1	1998	3 (2, 1)	ST-6, ST-10	90.7 ± 64	19.7 ± 5	274 ± 15.9	266 ± 4.9	6 ± 1.5
1	1999	5 (2, 3)	ST-6, ST-10	104.2 ± 59	23.2 ± 6	268 ± 5.9	276 ± 10.1	15 ± 10.6
2	2010	5 (2, 3)	SPLASH	258.2 ± 99	8.2 ± 2*	271 ± 7.5	278 ± 12.8	12 ± 5.3
2	2011	7 (1, 6)	SPLASH	210.7 ± 75	9.7 ± 2*	275 ± 3.3	290 ± 3.1	20 ± 6.1
2	2012	4 (2, 2)	TDR-10	124.0 ± 4	15.3 ± 1*	278 ± 4.9	288 ± 10.5	20 ± 6.9
3	2016	2 (0, 2)	TDR-10	83.4 ± 5	14.0 ± 1	288 ± 6.3	294 ± 7.8	13 ± 0.7
3	2017	13 (6, 7)	TDR-10; SMRU-CTD	83.1 ± 44	40.7 ± 27	272 ± 9.3	288 ± 3.5	18 ± 7.3
3	2018	1 (0, 1)	SMRU-CTD	78.1	125.0	264	291	28

Each year of the study includes the sample size for individuals with tagging data spanning the migration period with sex ratios as well as the mean duration of location data and the mean number of locations per day (\pm SD). One individual did not have enough tracking data to pass the final passage boundary. Full tagging data can be found in [SI Appendix, Table S1](#). F, female; M, male; Locs, telemetry locations.
*A strict or irregular duty cycling across the migration period.

([SI Appendix](#)). Spring sea ice was also found to be important in top models describing the departure date, but the effect was not significant following model averaging. Moreover, examination of a passage boundary of 72°W along the narwhal’s migration route revealed similar delays in migration timing ([SI Appendix](#)). Fall ice up was ultimately removed as it was found to be highly colinear with AO. Full model-averaged parameter estimates and a condensed model selection table can be found in [SI Appendix](#).

Discussion

Narwhals are considered to be among the most sensitive Arctic marine mammals to the effects of climate change (24). Fidelity and limited plasticity in migration behavior coupled with longevity (i.e., long timescales over which evolutionary adaptation can occur) could indicate that regional narwhal subpopulations have limited capacity to adjust migration timing to meet the time and energy trade-offs therein (23). However, recent theory

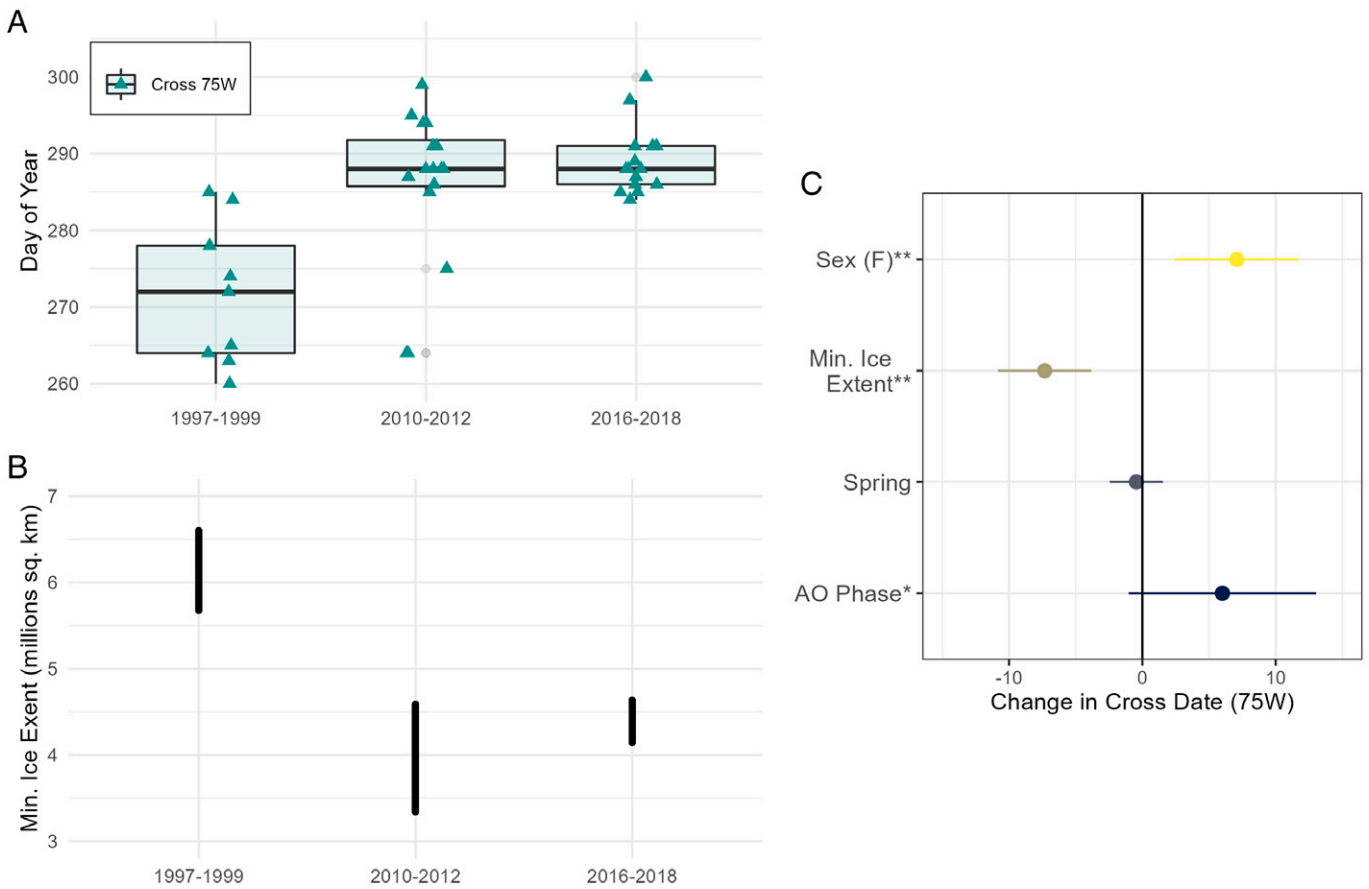


Fig. 2. Decadal phenology shifts in passage boundary crossing of narwhals undertaking migrations. Comparison of dates that narwhals crossed the 75°W longitude passage boundary (A; day of year) across three epochs for narwhal tagged in Eclipse Sound ($n = 40$), highlighting delays in migration timing. (B) Concomitant changes in September minimum ice extent for the Arctic, here represented by the range of minimum ice extent for each of the three epochs considered (86). (C) Forest plot of model-averaged parameter estimates of changes in crossing date of the passage boundary of 75°W longitude. The variable found in the top models that was not significantly different from zero is highlighted with a single asterisk, while variables with significant effects are highlighted with double asterisks. Full model results can be found in [SI Appendix, Table S2](#). F, female.

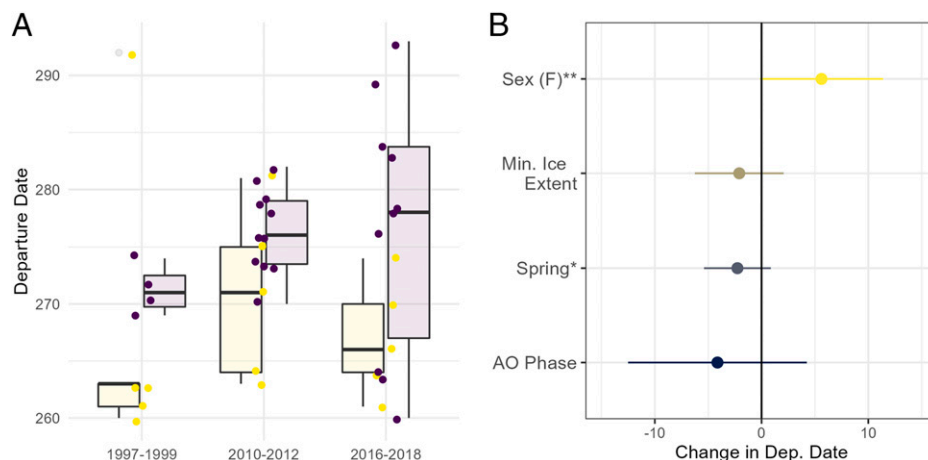


Fig. 3. Decadal phenology shifts in departure timing for narwhals undertaking migrations. (A) Comparison of dates of departure (day of year; determined from move persistence), highlighting the rates of change over three epochs of time for male (yellow bars and points) and female (F; purple bars and points) narwhals tagged in Eclipse Sound. (B) Forest plot of model-averaged parameter estimates of changes in departure date. The variable found in the top models that was not significantly different from zero is highlighted with a single asterisk, while the variable with significant effects is highlighted with a double asterisk. Full model results can be found in [SI Appendix, Table S2](#).

predicts that animals with longer life spans can respond to environmental fluctuations by expressing reversible behavioral plasticity throughout their lifetime (25). Plasticity in long-lived species can help bolster populations against extirpation risks (26) and facilitate tracking of ideal habitats through range expansion (27). However, the speed and limits of plasticity may dictate whether observed changes are adaptive across its range (26, 28). Here, we present evidence that a long-lived Arctic marine mammal has experienced a directional shift in their migration phenology over a 21-y period, adopting a flexible approach to keep pace with larger climate change trajectories across the region.

While previous work found little evidence that narwhal migration was triggered by ice-up dates or environmental cues over a short time period in other regions of the narwhal's range (21), our long-term dataset identified that passage boundary crossing dates were associated with changing sea ice dynamics as a result of climate change. Decreases in basin-scale sea ice minimum were associated with individuals spending more time in their summering grounds. Marginal evidence suggested that spring breakup and yearly AO, which correlates to sea ice in the winter months, also exerted an influence on changes in migration timing, although these were not significant after model averaging. These observed relationships with climatic variables explained the overall directional temporal shift in narwhal migration timing over the 21-y period while still detecting interannual variability due to environmental and biotic factors.

Apparent flexibility to current large-scale climatic shifts indicates that narwhals are adopting a strategic approach to their autumn migration, similar to that reported for other aquatic (29–31) and terrestrial (4, 5, 32) migrants. A strategic migration approach is thought to integrate memory and perception of previous movements, allowing flexibility to shape current behavior (33), and has been shown to forecast and regulate ungulate migrations (34). Similarly, other cetacean species have also been postulated to use long-term memory of past conditions to drive fidelity to predictable foraging areas in order to maintain migration phenology (2, 35). Narwhals may be predicting conditions along their migration corridor and within the wintering grounds through integrating long-term memory and localized cues to dictate phenology associated with departure and crossing the defined passage boundary. While there was limited change in departure dates over our study period, we found notable increases in the amount of time individuals spent transiting. Such broad ranging behavior in

summering areas before heading south could be akin to the scouting behavior that some ungulates use to explore the current environmental conditions to determine migration propensity (36). Narwhals show a preference for cold water, and space use is largely modulated by ice cover and the availability of open water regions (19, 37). As a result, narwhals may be residing in coastal waters within the larger summering areas ([SI Appendix](#)) until ice formation in the autumn and an increasing risk of entrapment force movement over deeper water toward the wintering areas in central Baffin Bay.

We also detected sex-specific differences in departure and passage boundary crossing dates; females departed and crossed the passage boundaries later than males (Fig. 3). These results are in agreement with shore-based observations (38) and local Inuit Qaujimaqatugangit that document males leading the autumn migration (39). While mating in narwhals occurs from May to June and calving typically occurs between June and August (40), interpreting the underlying drivers of sex-specific differences in migration timing is difficult. While detailed demographic data for tagged individuals were unavailable (i.e., females were with or without calves), female narwhals could depart later as a function of slower movements during the initiation of migration to accommodate less-experienced dependent young. Such slow movement of females with calves has been previously observed in cetaceans (41) and may form an important time period to pass knowledge of migratory behavior. Early life experience of migration routes and timing has been shown to be crucial to survival and route fidelity of Caspian terns (*Hydroprogne caspia*) on their first autumn migration (42). Developmental plasticity during the first migration period in black-tailed godwits (*Limosa limosa limosa*) was also found to correlate with greater flexibility in migration later in life, with little evidence of natural selection in this relatively short-lived species (43). While narwhal size could also have influenced migration phenology, we lacked sufficient size variability within each sex to test this. The downstream effects of climate change on different sexes or age classes are an important consideration but remain poorly documented (44). Phenological shifts have been shown to have demographic-specific consequences, such as differential effects on seasonal survival [e.g., yellow-bellied marmots *Marmota flaviventris* (45)], reproductive timing [e.g., Tibetan Plateau fish *Gymnocypris selincuoensis* (46)], and the age structure of a population [e.g., gray seal *Halichoerus grypus* (47)]. For narwhals, remaining

longer in coastal regions may place females and any accompanying young at a disproportionately greater risk of ice entrapment as a result of the increased frequency of extreme events associated with climate change (48), potentially leading to increasing demographic-specific climate change consequences.

The rate of change of narwhal migration phenology measured in the Eclipse Sound population suggests that narwhals are delaying their autumn migration at pace with climate change in the region. Delays to narwhal migration phenology of up to 10 d per decade approximate the rate of change in fall ice-up dates across Baffin Bay and the Canadian Archipelago, a delay in fall ice-up dates of 5.2 d per decade (49). The greatest rate of change in migration timing of Eclipse Sound narwhal was associated with the transition between the first epoch (1997 to 1999) and the later epochs, a delay of 14 to 17 d for crossing the passage boundary of 75°W (Fig. 2). This change tracks ice extent data for Baffin Bay, whereby an 11-d delay in the decadal mean fall ice up occurred between the 1990s and 2000s (49). Beluga populations in the Beaufort and Chukchi Seas were also shown to exhibit decadal shifts in migration phenology as a result of both local environmental drivers and long-term trajectories in climate change (31), resulting in delays to migration timing. Other marine species also appear to have experienced shifts in phenology at pace with climate change, including tiger shark (*Galeocerdo cuvier*) migration and space use in the North Atlantic (50), habitat occupancy of baleen whales in Cape Cod (17), and breeding phenology in Mandt's black guillemot (*Cepphus grille mandtii*) in the Alaskan Arctic (51).

While it is currently unknown if increasing variability in local conditions and associated shifts in migration phenology may place a greater risk on narwhal fitness and survival, we highlight how such changes could be associated with an increase in ice entrapment risk as well as potential positive and negative effects on foraging opportunities and stressors in the environment. First, long-term changes in climate (i.e., prediction) may be a misleading cue to modify the initiation of migration as they do not necessarily signal increases in sudden, extreme shifts in local conditions, which place a greater risk on narwhal entrapment as they migrate southward. Autumn ice-up dates are shifting across the range of narwhal; consequently, localized cues, such as sea surface temperature, may be misleading (52). While studies commonly attribute shifting phenology to changes in thermal environment occupied across plants and animals from both marine and terrestrial environments, temperature-specific correlation to shifts in phenological events may mask true causal mechanisms initiated by multiple cues (53). Given that narwhals are unable to maintain breathing holes, rapidly shifting and increasingly unstable ice cover conditions could result in increased energy expenditure to support movements between available gaps in sea ice (54). In extreme and historically rare cases, ice entrapments, which are associated with unexpected freeze-up events or rapidly shifting ice openings driven by sudden drops in sea surface temperatures or shifts in the prevailing wind direction, can result in mass casualties (48). Increases in the incidence of extreme events as a result of climate change are a concern for other species; extreme icing events over available forage habitat of caribou populations in the Arctic have resulted in catastrophic mortalities (55). It is unclear whether ice entrapments will become more problematic as narwhals remain longer in their summering areas (52).

Temporal and spatial mismatch of consumers and resources is of major concern as a result of irregular phenological shifts across the food web (44). Directional shifts in narwhal

migration phenology could consequently result in complex changes in feeding opportunities. If summer grounds provide a low-resource environment where limited feeding takes place compared with the winter (56), narwhal will be faced with reduced feeding opportunities through remaining resident for longer, a change likely to continue with further loss of ice. Alternatively, if narwhals are foraging in the summer as documented by traditional knowledge (57), they could benefit from longer residency periods on the summering grounds. Greenland halibut (*Reinhardtius hippoglossoides*) migration to the offshore is also timed with ice formation (58), which may suggest that their migration phenology will similarly shift. How Arctic cod (*Boreogadus saida*) in the Eclipse Sound region will respond in the short term to climate shifts is not directly known (59), but a predicted climate-induced increase in cod biomass could result in higher resource availability in the summer. Prey species community composition is also being modified through northward shifts of temperate zooplankton and fish species, which are often of lower caloric value (60). While narwhals have been shown to have a narrow niche breadth (61), evidence of narwhal prey switching associated with declines in sea ice has already been demonstrated both within individuals (62) and across individuals (63). Climate-driven prey switching, however, has been associated with detrimental population effects in other pelagic predators (64). Differing rates and directions of phenology shifts in response to climate change are likely across a food web as a result of variation in motility (e.g., planktonic and benthic vs. nektonic organisms), phenological sensitivity, and life history (15, 18, 44). As a result, interactions among trophic levels may also change, limiting the ability for alternative community-level interactions (e.g., prey switching) to buffer the negative effects of temporally mismatched but preferred interactions, as was previously documented in parasitoid interactions for insects (65). Dietary shifts and potential changes in ingested contaminants tied with diet (66) remain important to monitor, especially when coupled with the increase in physiological burden associated with climate change for many Arctic predators (54, 67).

Increasing natural resource exploitation and an exponential increase in shipping associated with resource exploitation, ice-breaking activities, and tourism in the summer grounds (68) will likely exacerbate any negative effects as a result of these phenological shifts and altered migration cues or counteract potential positive effects. Stress hormones measured in narwhal in Eclipse Sound have increased over the past 20 y, correlated with increasing human activities and climate change (69). If narwhals remain resident longer in the summer grounds (inshore areas) with continued loss of ice, their exposure to human activities will increase, with a greater risk of exposure for females and dependent young that could lead to demographic consequences over long generation times (44). Physical or perceived migratory barriers may also serve to limit plasticity from either natural or anthropogenic fractionation of the landscape (36). The threat of predation from orcas remaining longer in Eclipse Sound (70, 71) also poses a new risk to the population under shifting climate conditions. The cumulative effects of stressors, increasing predation pressure, and other nonconsumptive behavioral effects of climate change (72) may further perturb this species and others, necessitating that effective management adopts a holistic evaluation. The use of tracking data over several decades allowed for the detection of long-term directional shifts in narwhal migration phenology. As such, continued investigation of movement behavior through the use of biotelemetry/biologging devices remains a critical research need in the face of future change (73). Furthermore, incorporating physiological

and energetics measures, such as body condition, will allow for an integrated assessment of narwhal fitness tied with observed migration shifts. These combined data will improve our ability to predict the consequences of continuing climate change in terms of both narwhal life history events as well as food security for Inuit who depend on this species for their culture, economy, and nutrition (74). Many Arctic species have some of the longest life spans documented, and consequently, species' evolutionary responses are unlikely to keep pace with the rate of change in climate. These results demonstrate that behavioral plasticity within long-lived social animals may facilitate species' adjustment of space use and movement behaviors within a single individual's life span. However, given that many Arctic species have narrow environmental preferences, the limits of behavioral plasticity to buffer the negative effects of climate change as the ideal habitat shrinks and shifts still need to be assessed.

Materials and Methods

Study Animals, Tagging Procedures, and Location Data. Narwhals were captured and instrumented with satellite tags over a 21-y period in Eclipse Sound (72°21'N, −81°05'W; 1997 to 1999, 2010 to 2012, 2016 to 2018). Capture and tagging protocols for narwhal are described elsewhere (75, 76). In brief, during each tagging event, the sex and the standard length of each individual narwhal were recorded. Juveniles were considered to be whales <300 cm in length (77, 78). Tag make and model varied over the years (tag data prior to 2012 are published in refs. 20, 21, and 79–81 among others) (*SI Appendix, Table S1*) and were programmed with variable duty cycling schedules depending on the year and study goals. Satellite tags transmitted location data via Service Argos largely using Doppler-shift location estimation with assigned location classes. Argos location data collected before 2008 were fit using a least-squares algorithm, while newer tag data were fit (or reanalyzed; 2010 to 2011) using a Kalman-filtering algorithm via Service Argos (82, 83). In 2017 and 2018, several tags utilized fastloc GPS (global positioning system) technology to obtain more accurate and more frequent location estimates (84–86). These locations were also supplemented by four ground-based Mote systems installed in 2017 and 2018 located around Eclipse Sound [Wildlife Computers (87)]. For the purposes of this study, only individuals with data that span the onset of their autumn migration and subsequent phenology markers (see below) were included in the analysis ($n = 40$). One individual was ultimately removed as it lacked enough data to reach the final passage boundary (see below). A summary of narwhal satellite telemetry data is included in Table 1. Tagging years were blocked into three time periods ("epoch" 1: 1997 to 1999; 2: 2010 to 2012; 3: 2016 to 2018). Full tagging information can be found in *SI Appendix, Table S1*.

Location Filtering and State-Space Modeling. The dataset was first filtered to remove inaccurate or unrealistic locations using a speed filter corresponding to movement velocities exceeding 25 km h^{-1} to eliminate extreme outliers as well as those corresponding to ARGOS location class "Z" using the R package "foieGras" (88). For more recent fastloc GPS data, locations were only included if residuals were less than 35 and more than five satellites were detected (85), and location times were corrected for measured clock drift. Any extended gaps in location data were clipped (often found toward the end of deployments and likely corresponded to depleted batteries or damaged antennae). This filtering resulted in improved state-space model convergence.

To correct for measurement error and estimate regular geolocations, we fitted continuous time state-space models to the filtered location data using the foieGras package in R (88). The package allows for rapid fitting of state-space models by way of maximum likelihood methods and Laplace approximation using the R package "TMB" (88–90), and it is able to handle Argos locations fit via least-squares or Kalman-filtered algorithms as well as fastloc GPS data (91). For all tags/years either with little to no duty cycling across the migration period (1997 to 1999 and 2016 to 2018) or with strict duty cycling (location attempts $\sim 3+$ d) or a split duty cycle schedule during the migration period (e.g., strict duty cycling until the first of October followed by no duty cycling or vice versa) (Table 1), a simple random walk was fit to estimate location data at 24-h time intervals. For

all models, error parameters were fixed using error multiplication factors determined via ref. 92. State-space model fit was assessed via one-step-ahead residuals (93, 94). To assess whether the varying sampling rate affected the results, we also explored changes in migration phenology using only the most highly sampled data (1997 to 1999 and 2016 to 2018) modeled with a 12-h continuous time correlated random walk (details are presented in *SI Appendix*).

Investigating Variation in Narwhal Migration Phenology. Narwhals typically begin their southward migration prior to ice up in their summer grounds, departing between late September and early November (20, 21, 95, 96). Here, we adopted three approaches to quantify the variation in the timing of narwhal migration from northern Baffin Bay summer grounds: 1) identifying a change in the directed movement of individuals using a move-persistence model ("departure date"); 2) delineating the time individuals crossed defined passage boundaries along the migration route (75°W), which delineated the edge of the summering areas to the offshore; and 3) comparing the difference in time between migration initiation (move-persistence departure date) and crossing of a final passage boundary at 72°W, where individuals were all observed to undertake directed movements to the wintering areas to the south ("transit time") (Figs. 1 and 2). In *SI Appendix*, we also compared variation in the timing of narwhal migration associated with a later passage boundary at 72°W longitude separately.

To infer independent changes in movement behavior that characterize the onset of migration (approach 1; departure date), we fitted a state-space model to determine move-persistence values (89, 97). Move persistence (γ_t) measures the serial autocorrelation in subsequent locations corresponding to a continuous scale between area-restricted search (zero; no autocorrelation) and a directed linear movement [one (89)]. The model applies a first-difference correlated random walk to the standardized locations fitted from the previous state-space model (*Location Filtering and State-Space Modeling*) to estimate move-persistence values at each 24-h time step for the duration of tag transmission (97, 98). Move-persistence models were jointly estimated for all individuals within each duty cycle condition (little to no duty cycling vs. strict/inconsistent duty cycling) to better elucidate behavior across the duration of transmitted location data (Fig. 1 and *SI Appendix, Fig. S1*) (99). Here, we defined the onset of migration (departure date) as the first date in which γ_t exceeded 25% of the difference of minimum and maximum γ for each individual between the expected migration period of mid-September and early November.

To examine the time narwhals crossed a defined passage boundary (approach 2), we extracted the dates that tagged individuals crossed 75°W longitude, approximately delineating the edge of the summering grounds for this narwhal stock. This follows the approach previously adopted to examine migration dynamics for other Monodontids in the Arctic (31, 100, 101) and a number of other species exhibiting large-scale migration behaviors (32, 102, 103). In addition, we also quantified the transit time after initiating migration as the difference between departure date and the date individuals crossed 72°W longitude (approach 3; transit time).

To determine if there was evidence for variation in long-term trends in narwhal migration phenology, the migration departure dates, cross-dates, and transit times were compared across the tagging epochs for Eclipse Sound narwhal using Kruskal-Wallis tests, and trends in migration phenology across all years were assessed using ordinary least-squares regression.

Environmental Data. To investigate how local ice conditions within the narwhal summering grounds and larger regional changes in climate may relate to their autumn migration phenology, we examined the effects of several environmental covariates. Weekly ice data were compiled for each year of study as well as the year preceding tagging events (if no tagging occurred in that time frame). Data were extracted from the Canadian Ice Service online archive (<https://ice-glaces.ec.gc.ca/>), which provides conglomerate ice concentration polygons across the region. Weekly total ice cover (percentage; sum of all ice concentration polygons, all stages of development) was extracted for the area approximately encompassing ecologically and biologically significant areas located at the north end of Baffin Island that include the summering grounds (*SI Appendix, Fig. S2*, bounded longitude [−89.98, −60.91] and latitude [67.51, 75.16]) (104). Ice transition periods were defined as the week that ice extent reached 50% of the difference between maximum and minimum ice extent in the region each year for both the

"spring" (spring breakup, week) and "autumn" [fall ice up, week (49, 105)]. We include the spring breakup here as a measure of environmental "memory" (34).

To investigate potential effects of broad changes in climate, we explored two additional climate proxies. First, we included minimum sea ice extent ("minimum ice extent," millions of kilometers squared) in September across the entire Arctic for each tagging year (106). September minimum sea ice extent was considered to be a major component in the composite Arctic Climate Change Index (107), and we include it here as a proxy of Arctic-wide changes in environmental conditions associated with climate change. Second, we explored the influence of the AO index as a yearly mean ("AO phase"), which measures the relative anomaly in the strength of the Arctic polar low (108). Further, we examined the North Atlantic Oscillation (NAO) index (available at <https://www.cpc.ncep.noaa.gov/>), a long-term climate index known to influence migration phenology (5, 32, 109). NAO is an index of decadal-scale oscillations in reference to atmospheric circulation patterns and measures the relative sea surface pressure difference between the subpolar (Icelandic) low and subtropical (Azores) high pressure in the North Atlantic (108, 110). The phases of the NAO index can dictate substantial changes to weather and climate across broad scales and are defined by long-term phase anomalies in the Northern Hemisphere (111, 112). Positive NAO phases are associated with colder winter temperatures and increased sea ice cover in the Baffin Bay/Davis Strait region (110). NAO phase was included as a yearly mean ["NAO phase" (113, 114)]. Both AO and NAO are collinear and could not, therefore, be modeled together; results of models including NAO are included in *SI Appendix, Table S3*.

Modeling Drivers of Annual Migration. To understand the possible factors that initiate migration; individual migration dates, transit times, and dates individuals crossed the passage boundary were examined independently using linear mixed effects models [the "nlme" package in R (115)]. The environmental and climatic covariates explored included the weeks of spring breakup and fall ice up in the region, the AO phase, and minimum ice extent (see above). We also investigated the effect of sex in tagged narwhal as a fixed effect. We did not include age class here as only a single individual was considered to be a juvenile, nor did we include the effect of animal size (standard length) as it could be confounded

with sex (although this is explored in *SI Appendix*). Each tagging year was included as a random effect. If any variables were found to have a variance inflation factor (VIF) greater than or equal to seven, the variable with the highest VIF was removed from the global model (116). Additionally, any variable with collinearity of >0.7 was removed. Any remaining model covariates were included in a global model, and all nested models were ranked based on an Akaike information criterion corrected for small sample size (AICc) and model weight (117, 118). Models with less than or equal to four Δ AICc were deemed to have some credible support. Parameters were model averaged across all models to generate effect sizes and SEs using the "MuMIn" package in R version 4.0.2 (117, 119).

Data, Materials, and Code Availability. All narwhal tracking data used in the study are accessible and available by request through either Fisheries and Oceans Canada (M. Marcoux) or the Greenland Institute for Natural Resources (M.P. Heide-Jørgensen). All other data were derived from the publicly available resources cited in text.

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- H. Dingle, V. A. Drake, What is migration? *Bioscience* **57**, 113–121 (2007).
- B. Abrahms *et al.*, Memory and resource tracking drive blue whale migrations. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 5582–5587 (2019).
- G. W. Cox, The evolution of avian migration systems between temperate and tropical regions of the new world. *Am. Nat.* **126**, 451–474 (1985).
- O. Gordo, Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim. Res.* **35**, 37–58 (2007).
- J. Van Buskirk, R. S. Mulvihill, R. C. Leberman, Variable shifts in spring and autumn migration phenology in North American songbirds associated with climate change. *Glob. Change Biol.* **15**, 760–771 (2009).
- W. T. S. Miles *et al.*, Quantifying full phenological event distributions reveals simultaneous advances, temporal stability and delays in spring and autumn migration timing in long-distance migratory birds. *Glob. Change Biol.* **23**, 1400–1414 (2017).
- C. Howard *et al.*, Flight range, fuel load and the impact of climate change on the journeys of migrant birds. *Proc. Biol. Sci.* **285**, 20172329 (2018).
- P. Wassmann, C. M. Duarte, S. Agustí, M. K. Sejr, Footprints of climate change in the Arctic marine ecosystem. *Glob. Change Biol.* **17**, 1235–1249 (2011).
- M. T. Burrows *et al.*, The pace of shifting climate in marine and terrestrial ecosystems. *Science* **334**, 652–655 (2011).
- O. Hoegh-Guldberg, J. F. Bruno, The impact of climate change on the world's marine ecosystems. *Science* **328**, 1523–1529 (2010).
- Intergovernmental Panel on Climate Change, *Climate Change 2021: The Physical Science Basis. Contribution of the Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, V. Masson-Delmotte *et al.*, Eds. (Cambridge University Press, 2021).
- J. E. Overland, M. Wang, Future regional Arctic sea ice declines. *Geophys. Res. Lett.* **34**, L17705 (2007).
- M. Louis *et al.*, Influence of past climate change on phylogeography and demographic history of narwhals, *Monodon monoceros*. *Proc. Biol. Sci.* **287**, 20192964 (2020).
- N. E. Hussey *et al.*, Aquatic animal telemetry: A panoramic window into the underwater world. *Science* **348**, 1255642 (2015).
- T. K. Lameris *et al.*, Migratory vertebrates shift migration timing and distributions in a warming Arctic. *Anim. Migr.* **8**, 110–131 (2021).
- J. M. Cohen, M. J. Lajeunesse, J. R. Rohr, A global synthesis of animal phenological responses to climate change. *Nat. Clim. Chang.* **8**, 224–228 (2018).
- D. E. Pendleton *et al.*, Decadal-scale phenology and seasonal climate drivers of migratory baleen whales in a rapidly warming marine ecosystem. *Glob. Chang. Biol.* **28**, 4989–5005 (2022).
- M. D. Staudinger *et al.*, It's about time: A synthesis of changing phenology in the Gulf of Maine ecosystem. *Fish. Oceanogr.* **28**, 532–566 (2019).
- K. L. Laird, M. P. Heide-Jørgensen, Life in the lead: Extreme densities of narwhals *Monodon monoceros* in the offshore pack ice. *Mar. Ecol. Prog. Ser.* **423**, 269–278 (2011).
- M. P. Heide-Jørgensen, P. R. Richard, R. Dietz, K. L. Laird, A metapopulation model for Canadian and West Greenland narwhals. *Anim. Conserv.* **16**, 331–343 (2013).
- M. P. Heide-Jørgensen *et al.*, The predictable narwhal: Satellite tracking shows behavioural similarities between isolated subpopulations. *J. Zool. (Lond.)* **297**, 54–65 (2015).
- E. Garde, M. P. Heide-Jørgensen, S. H. Hansen, G. Nachman, M. C. Forchhammer, Age-specific growth and remarkable longevity in narwhals (*Monodon monoceros*) from West Greenland as estimated by aspartic acid racemization. *J. Mammal.* **88**, 49–58 (2007).
- J. J. Anderson, E. Gurarie, C. Bracis, B. J. Burke, K. L. Laird, Modeling climate change impacts on phenology and population dynamics of migratory marine species. *Ecol. Modell.* **264**, 83–97 (2013).
- K. L. Laird *et al.*, Quantifying the sensitivity of Arctic marine mammals to climate-induced habitat change. *Ecol. Appl.* **18** (2 suppl.), S97–S125 (2008).
- I. I. Ratikainen, H. Kokko, The coevolution of lifespan and reversible plasticity. *Nat. Commun.* **10**, 538 (2019).
- S. M. Bisbing *et al.*, Can long-lived species keep pace with climate change? Evidence of local persistence potential in a widespread conifer. *Divers. Distrib.* **27**, 296–312 (2021).
- M. A. Zettlemoyer, M. L. Peterson, Does phenological plasticity help or hinder range shifts under climate change? *Front. Ecol. Evol.* **9**, 689192 (2021).
- E. S. Poloczanska *et al.*, Global imprint of climate change on marine life. *Nat. Clim. Chang.* **3**, 919–925 (2013).
- S. G. Cherry, A. E. Derocher, G. W. Thiemann, N. J. Lunn, Migration phenology and seasonal fidelity of an Arctic marine predator in relation to sea ice dynamics. *J. Anim. Ecol.* **82**, 912–921 (2013).
- J. Otero *et al.*, Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). *Glob. Change Biol.* **20**, 61–75 (2014).
- D. D. W. Hauser *et al.*, Decadal shifts in autumn migration timing by Pacific Arctic beluga whales are related to delayed annual sea ice formation. *Glob. Change Biol.* **23**, 2206–2217 (2017).
- E. Gurarie *et al.*, Tactical departures and strategic arrivals: Divergent effects of climate and weather on caribou spring migrations. *Ecosphere* **10**, e02971 (2019).
- W. F. Fagan *et al.*, Spatial memory and animal movement. *Ecol. Lett.* **16**, 1316–1329 (2013).
- C. Bracis, T. Mueller, Memory, not just perception, plays an important role in terrestrial mammalian migration. *Proc. Biol. Sci.* **284**, 20170449 (2017).
- A. R. Sześciorka *et al.*, Timing is everything: Drivers of interannual variability in blue whale migration. *Sci. Rep.* **10**, 7710 (2020).
- W. Xu *et al.*, The plasticity of ungulate migration in a changing world. *Ecology* **102**, e03293 (2021).
- M. P. Heide-Jørgensen *et al.*, Some like it cold: Temperature-dependent habitat selection by narwhals. *Ecol. Evol.* **10**, 8073–8090 (2020).
- R. G. Greendale, C. Brousseau-Greendale, "Observations of Marine Mammals at Cape Hay, Bylot Island during the Summer of 1976" (Tech. Rep. No. 680, Canada Department of the Environment, Fisheries and Marine Service, Ottawa, ON, Canada, 1976).
- D. B. Stewart, A. Akeagok, R. Amarualik, S. Panipakutsuk, A. Taqtu, "Local Knowledge of Beluga and Narwhal from Four Communities in Arctic Canada" (Canadian Manuscript Rep. of Fisheries and Aquatic Sciences 2065, Ottawa, ON, Canada, 1995).
- M. P. Heide-Jørgensen, E. Garde, Fetal growth of narwhals (*Monodon monoceros*). *Mar. Mamm. Sci.* **27**, 659–664 (2011).

41. B. R. Mate, P. B. Best, B. A. Lagerquist, M. H. Winsor, Coastal, offshore, and migratory movements of South African right whales revealed by satellite telemetry. *Mar. Mamm. Sci.* **27**, 455–476 (2011).
42. P. Byholm, M. Beal, N. Isaksson, U. Lötberg, S. Åkesson, Paternal transmission of migration knowledge in a long-distance bird migrant. *Nat. Commun.* **13**, 1566 (2022).
43. M. A. Verhoeven *et al.*, Age-dependent timing and routes demonstrate developmental plasticity in a long-distance migratory bird. *J. Anim. Ecol.* **91**, 566–579 (2022).
44. A. M. Iler, P. J. Caradonna, J. R. K. Forrest, E. Post, Demographic consequences of phenological shifts in response to climate change. *Annu. Rev. Ecol. Syst.* **52**, 221–245 (2021).
45. L. S. Cordes *et al.*, Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 18119–18126 (2020).
46. J. Tao *et al.*, Strong evidence for changing fish reproductive phenology under climate warming on the Tibetan Plateau. *Glob. Change Biol.* **24**, 2093–2104 (2018).
47. J. C. Bull *et al.*, Climate causes shifts in grey seal phenology by modifying age structure. *Proc. Biol. Sci.* **288**, 20212284 (2021).
48. K. L. Laidre, M. P. Heide-Jørgensen, Arctic sea ice trends and narwhal vulnerability. *Biol. Conserv.* **121**, 509–517 (2005).
49. K. L. Laidre *et al.*, Arctic marine mammal population status, sea ice habitat loss, and conservation recommendations for the 21st century. *Conserv. Biol.* **29**, 724–737 (2015).
50. N. Hammerschlag *et al.*, Ocean warming alters the distributional range, migratory timing, and spatial protections of an apex predator, the tiger shark (*Galeocerdo cuvier*). *Glob. Change Biol.* **28**, 1990–2005 (2022).
51. D. Sauve, G. Divoky, V. L. Friesen, Phenotypic plasticity or evolutionary change? An examination of the phenological response of an arctic seabird to climate change. *Funct. Ecol.* **33**, 2180–2190 (2019).
52. K. Laidre, M. P. Heide-Jørgensen, H. Stern, P. Richard, Unusual narwhal sea ice entrapments and delayed autumn freeze-up trends. *Polar Biol.* **35**, 149–154 (2012).
53. H. E. Chmura *et al.*, The mechanisms of phenology: The patterns and processes of phenological shifts. *Ecol. Monogr.* **89**, 1–22 (2019).
54. A. M. Pagano, T. M. Williams, Physiological consequences of Arctic sea ice loss on large marine carnivores: Unique responses by polar bears and narwhals. *J. Exp. Biol.* **224** (pt suppl. 1), jeb228049 (2021).
55. C. D. Mallory, M. S. Boyce, Observed and predicted effects of climate change on Arctic caribou and reindeer. *Environ. Rev.* **26**, 13–25 (2018).
56. K. L. Laidre, M. P. Heide-Jørgensen, Winter feeding intensity of narwhals (*Monodon monoceros*). *Mar. Mamm. Sci.* **21**, 45–57 (2005).
57. R. A. Remnant, M. L. Thomas, *Inuit Traditional Knowledge of the Distribution and Biology of High Arctic Narwhal and Beluga* (North/South Consultants, Winnipeg, MB, Canada, 1992).
58. A. N. Barkley, A. T. Fisk, K. J. Hedges, M. A. Treble, N. E. Hussey, Transient movements of a deep-water flatfish in coastal waters: Implications of inshore-offshore connectivity for fisheries management. *J. Appl. Ecol.* **55**, 1071–1081 (2018).
59. H. Pettitt-Wade, L. L. Loseto, A. Majewski, N. E. Hussey, Cod movement ecology in a warming world: Circumpolar arctic gadids. *Fish.* **22**, 562–591 (2021).
60. K. R. N. Florko *et al.*, Predicting how climate change threatens the prey base of Arctic marine predators. *Ecol. Lett.* **24**, 2563–2575 (2021).
61. C. A. Watt, M. P. Heide-Jørgensen, S. H. Ferguson, How adaptable are narwhals? A comparison of foraging patterns among the world's three narwhal populations. *Ecosphere* **4**, 1–15 (2013).
62. R. Dietz *et al.*, Analysis of narwhal tusks reveals lifelong feeding ecology and mercury exposure. *Curr. Biol.* **31**, 2012–2019.e2 (2021).
63. C. A. Watt, S. H. Ferguson, Fatty acids and stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) reveal temporal changes in narwhal (*Monodon monoceros*) diet linked to migration patterns. *Mar. Mamm. Sci.* **31**, 21–44 (2015).
64. L. W. Fritz, S. Hinkley, A critical review of the regime shift–“junk food”–nutritional stress hypothesis for the decline of the western stock of Steller sea lion. *Mar. Mamm. Sci.* **21**, 476–518 (2005).
65. N. A. Pardikes *et al.*, Effects of phenological mismatch under warming are modified by community context. *Glob. Chang. Biol.* **28**, 4013–4026 (2022).
66. K. Borgå *et al.*, The influence of global climate change on accumulation and toxicity of persistent organic pollutants and chemicals of emerging concern in Arctic food webs. *Environ. Sci. Process. Impacts*, 10.1039/d1em00469g (2022).
67. T. M. Williams, M. Peter-Heide Jørgensen, A. M. Pagano, C. M. Bryce, Hunters versus hunted: New perspectives on the energetic costs of survival at the top of the food chain. *Funct. Ecol.* **34**, 2015–2029 (2020).
68. Z. Kochanowicz, J. Dawson, O. Mussells, *Shipping Trends in Tallurutiup Imanga (Lancaster Sound), Nunavut from 1990 to 2018* (University of Ottawa, Ottawa, ON, Canada, 2020).
69. C. A. Watt *et al.*, Cortisol levels in narwhal (*Monodon monoceros*) blubber from 2000–2019. *Arch. Sci.* **7**, 690–698 (2021).
70. G. A. Breed *et al.*, Sustained disruption of narwhal habitat use and behavior in the presence of Arctic killer whales. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 2628–2633 (2017).
71. K. L. Laidre, M. P. Heide-Jørgensen, J. R. Orr, Reactions of narwhals, *Monodon monoceros*, to killer whale, *Orcinus orca*, attacks in the eastern Canadian Arctic. *Can. Field Nat.* **120**, 457–465 (2006).
72. E. Pirotta *et al.*, Understanding the population consequences of disturbance. *Ecol. Evol.* **8**, 9934–9946 (2018).
73. H. E. Chmura, T. W. Glass, C. T. Williams, Biologging physiological and ecological responses to climatic variation: New tools for the climate change era. *Front. Ecol. Evol.* **6**, 92 (2018).
74. R. R. Reeves, Recent developments in the commerce in narwhal ivory from the Canadian Arctic. *Arct. Alp. Res.* **24**, 179–187 (1992).
75. J. R. Orr, R. Joe, D. Evic, Capturing and handling of White Whales (*Delphinapterus leucas*) in the Canadian Arctic for instrumentation and release. *Arctic* **54**, 299–304 (2001).
76. C. R. Shuert, M. Marcoux, N. E. Hussey, C. A. Watt, M. Auger-Méthé, Assessing the post-release effects of capture, handling and placement of satellite telemetry devices on narwhal (*Monodon monoceros*) movement behaviour. *Conserv. Physiol.* **9**, a128 (2021).
77. E. Garde *et al.*, Life history parameters of narwhals (*Monodon monoceros*) from Greenland. *J. Mammal.* **96**, 866–879 (2015).
78. K. A. Hay, “The life history of the narwhal (*Monodon monoceros* L.) in the eastern Canadian Arctic,” PhD thesis, McGill University, Montreal, QC, Canada (1984).
79. R. Dietz *et al.*, Movements of narwhals (*Monodon monoceros*) from Admiralty Inlet monitored by satellite telemetry. *Polar Biol.* **31**, 1295–1306 (2008).
80. M. P. Heide-Jørgensen, R. Dietz, K. L. Laidre, P. Richard, Autumn movements, home ranges, and winter density of narwhals (*Monodon monoceros*) tagged in Tremblay Sound, Baffin Island. *Polar Biol.* **25**, 331–341 (2002).
81. M. P. Heide-Jørgensen, N. Hammeken, R. Dietz, J. Orr, P. R. Richard, Surfacing times and dive rates for Narwhals (*Monodon monoceros*) and Belugas (*Delphinapterus leucas*). *Arctic* **54**, 284–298 (2001).
82. A. D. Lowther, C. Lydersen, M. A. Fedak, P. Lovell, K. M. Kovacs, The Argos-CLS Kalman filter: Error structures and state-space modelling relative to Fastloc GPS data. *PLoS One* **10**, e0124754 (2015).
83. T. A. Patterson, B. J. McConnell, M. A. Fedak, M. V. Bravington, M. A. Hindell, Using GPS data to evaluate the accuracy of state-space methods for correction of Argos satellite telemetry error. *Ecology* **91**, 273–285 (2010).
84. E. Bryant, “2D Location Accuracy Statistics for Fastloc® Cores Running Firmware Versions 2.2. & 2.3” (Tech. Rep. No. TR01, Wildtrack Telemetry Systems Ltd., Leeds, United Kingdom, 2007).
85. A. M. Dujon, R. T. Lindstrom, G. C. Hays, The accuracy of Fastloc-GPS locations and implications for animal tracking. *Methods Ecol. Evol.* **5**, 1162–1169 (2014).
86. C. E. Kuhn, D. S. Johnson, R. R. Ream, T. S. Gelatt, Advances in the tracking of marine species: Using GPS locations to evaluate satellite track data and a continuous-time movement model. *Mar. Ecol. Prog. Ser.* **393**, 97–109 (2009).
87. T. Jeannin-du-Dot, K. Holland, G. S. Schorr, D. Vo, Motes enhance data recovery from satellite-relayed biologists and can facilitate collaborative research into marine habitat utilization. *Anim. Biotelem.* **5**, 17 (2017).
88. I. D. Jonsen, T. A. Patterson, foisGras: Fit Continuous-Time State-Space and Latent Variable Models for Filtering Argos Satellite (and Other) Telemetry Data and Estimating Movement Behaviour, R package version 0.6-7. Zenodo. <https://doi.org/10.5281/zenodo.3899972> (2019).
89. M. Auger-Méthé *et al.*, Spatiotemporal modelling of marine movement data using Template Model Builder (TMB). *Mar. Ecol. Prog. Ser.* **565**, 237–249 (2017).
90. K. Kristensen, A. Nielsen, C. W. Berg, H. Skaug, B. M. Bell, TMB: Automatic differentiation and Laplace approximation. *J. Stat. Softw.* **70**, 1–21 (2016).
91. I. D. Jonsen *et al.*, A continuous-time state-space model for rapid quality control of argos locations from animal-borne tags. *Mov. Ecol.* **8**, 31 (2020).
92. D. P. Costa *et al.*, Accuracy of ARGOS locations of Pinnipeds at-sea estimated using Fastloc GPS. *PLoS One* **5**, e8677 (2010).
93. U. H. Thygesen, C. M. Albertsen, C. W. Berg, K. Kristensen, A. Nielsen, Validation of ecological state space models using the Laplace approximation. *Environ. Ecol. Stat.* **24**, 317–339 (2017).
94. M. Auger-Méthé *et al.*, A guide to state-space modeling of ecological time series. *Ecol. Monogr.* **91**, e01470 (2021).
95. H. Frouin-Mouy, K. Kowarski, B. Martin, K. Bröker, Seasonal trends in acoustic detection of marine mammals in Baffin Bay and Melville Bay, Northwest Greenland. *Arctic* **70**, 59–76 (2017).
96. K. A. Kenyon, D. J. Yurkowski, J. Orr, D. Barber, S. H. Ferguson, Baffin Bay narwhal (*Monodon monoceros*) select bathymetry over sea ice during winter. *Polar Biol.* **41**, 2053–2063 (2018).
97. I. D. Jonsen *et al.*, Movement responses to environment: Fast inference of variation among southern elephant seals with a mixed effects model. *Ecology* **100**, e02566 (2019).
98. I. D. Jonsen, J. M. Flemming, R. A. Myers, Robust state-space modeling of animal movement data. *Ecology* **86**, 2874–2880 (2005).
99. I. Jonsen, Joint estimation over multiple individuals improves behavioural state inference from animal movement data. *Sci. Rep.* **6**, 20625 (2016).
100. D. D. W. Hauser, K. L. Laidre, R. S. Suydam, P. R. Richard, Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). *Polar Biol.* **37**, 1171–1183 (2014).
101. R. C. Hobbs *et al.*, Global review of the conservation status of monodontid stocks. *Mar. Fish. Rev.* **81**, 1–53 (2020).
102. W. Cresswell, Migratory connectivity of Palaearctic-African migratory birds and their responses to environmental change: The serial residency hypothesis. *Ibis (Lond. 1859)* **156**, 493–510 (2014).
103. M. Le Corre, C. Dussault, S. D. Côté, Detecting changes in the annual movements of terrestrial migratory species: Using the first-passage time to document the spring migration of caribou. *Mov. Ecol.* **2**, 19 (2014).
104. O. Schimnowski, J. E. Paulic, K. A. Martin, “Information in support of the evaluation of Ecologically and Biologically Significant Areas (EBSA) in the Eastern Arctic Biogeographic Region” (Research Document No. 2017/080, DFO Canadian Science Advisory Secretariat, Ottawa, ON, Canada, 2018).
105. S. H. Ferguson *et al.*, Comparing temporal patterns in body condition of ringed seals living within their core geographic range with those living at the edge. *Ecography* **43**, 1521–1535 (2020).
106. F. Fetterer, K. Knowles, W. N. Meier, M. Savoie, A. K. Windnagel, Sea Ice Index, Version 3. Daily Sea Ice Extent Data Files. Boulder, Colorado USA. National Snow and Ice Data Center, <https://doi.org/10.7265/N5K072F8>.
107. J. E. Overland, M. Wang, J. E. Box, An integrated index of recent pan-Arctic climate change. *Environ. Res. Lett.* **14**, 035006 (2019).
108. J. Zhao, Y. Cao, J. Shi, Core region of Arctic Oscillation and the main atmospheric events impact on the Arctic. *Geophys. Res. Lett.* **33**, L22708 (2006).
109. D. W. Sims, M. J. Genner, A. J. Southward, S. J. Hawkins, Timing of squid migration reflects North Atlantic climate variability. *Proc. Biol. Sci.* **268**, 2607–2611 (2001).
110. B. Wu, R. Huang, D. Gao, Arctic sea ice bordering on the North Atlantic and interannual climate variations. *Chin. Sci. Bull.* **46**, 162–165 (2001).
111. A. G. Barnston, R. E. Livezey, Classification, seasonality and persistence of low-frequency atmospheric circulation patterns. *Mon. Weather Rev.* **115**, 1083–1126 (1987).
112. D. W. J. Thompson, J. M. Wallace, Annular modes in the extratropical circulation. Part I: Month-to-month variability. *J. Clim.* **13**, 1000–1016 (2000).
113. M. P. Heide-Jørgensen, H. Stern, K. L. Laidre, Dynamics of the sea ice edge in Davis Strait. *J. Mar. Syst.* **67**, 170–178 (2007).
114. H. L. Stern, M. P. Heide-Jørgensen, Trends and variability of sea ice in Baffin Bay and Davis Strait, 1953–2001. *Polar Res.* **22**, 11–18 (2003).
115. J. Pinheiro, D. Bates, S. DebRoy, D. Sarkar, RC Team, nlme: Linear and Nonlinear Mixed Effects Models, R package version 3.1-152, <https://CRAN.R-project.org/package=nlme> (2020).
116. G. P. Quinn, M. J. Keough, *Experimental Design and Data Analysis for Biologists* (Cambridge University Press, 2002).
117. K. Barton, MuMIn: Multi-Model Inference, R package version 1.43.17, <https://CRAN.R-project.org/package=MuMIn> (2020).
118. K. P. Burnham, D. R. Anderson, *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach* (Springer-Verlag, ed. 2, 2002).
119. RC Team, R: A Language and Environment for Statistical Computing, version 4.0.2. R Foundation for Statistical Computing, Vienna, Austria, <https://www.R-project.org/> (2020).