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RESEARCH ARTICLE

Functional Ecology

Empirically testing the influence of light regime on diel activity patterns in a marine predator reveals complex interacting factors shaping behaviour

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Abstract

- Diel cycles in marine predator diving behaviour centre around the lightmediated diel vertical migration (DVM) of prey, and are considered critical for optimizing foraging and limiting competition across global seascapes. Yet, our understanding of predator diel behaviour is based primarily on examining relative depth usage between constant day/night cycles with no formal investigation of how varying light regimes interact with abiotic factors to shape diel activity.
- 2. The extreme seasonal light regimes (midnight sun, polar night, day/night cycle) in the Arctic provide a unique natural experimental setting to empirically investigate the occurrence and intensity of diel behaviour in marine predators relative to changing light levels while concomitantly assessing interacting abiotic factors.
- 3. Depth time series data from satellite-linked tags deployed on six beluga whales (*Delphinapterus leucas*) for up to 12 months were used to quantify diel behaviour by calculating dissimilarity in time-at-depth between periods of low and high solar altitude on each day. Generalized additive mixed effects models were used to examine the influence of hours of daylight across extreme light cycles, coupled with bathymetry and sea ice concentration; focal diel patterns were further examined relative to the thermal structure of the water column.
- 4. As predicted, belugas exhibited cathemerality during the midnight sun, and initiated diel behaviour with the onset of the fall day/night cycle, with a marked increase in its intensity with the progression to equal day/night length. Occurrence of diel patterns, however, was complex; ceasing in regions with seafloor depths <700 m, and occurring with greatest intensity when the water column was thermally homogeneous within the upper 150 m.</p>
- 5. Through empirical investigation, this study demonstrates that the onset of day/ night light cycles and presumably associated prey DVM can modulate predator

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diel dive behaviour under certain circumstances, but highlights how the complex interaction of abiotic factors with light regime shape dynamic spatiotemporal patterns. These findings, building on a body of recent work, emphasize that the traditional view of the ubiquitous occurrence of diel behaviour tied to DVM at the base of the food web oversimplifies vertical predator-prey interactions, identifying the need for more structured investigation.

KEYWORDS

Arctic, Central Arctic Ocean, diel vertical migration, diurnal, dive, natural experiment, nocturnal, whale

1 | INTRODUCTION

Diel cycles in behaviour have evolved throughout the animal kingdom in response to predictable daily changes in light and temperature and represent a fundamental behavioural type that structures food web interactions. Partitioning behavioural modes between day and night enables organisms to balance activity with thermoregulation, avoid predators, exploit niches, and limit competition (Bennie et al., 2014). In marine ecosystems, diel behaviour centres around the diel vertical migration (DVM) of zooplankton, which typically descend deeper during the day to avoid visual predators and ascend at night to feed on productive surface waters (Hays 2003). The multilayered and highly interactive structure of marine food webs complicate this general trend, with the vertical behaviour employed at each trophic level driven by the presence of predators, coined 'landscape of fear' (Urmy & Benoit-Bird 2021). Furthermore, the vertical migration strategies of prey can vary depending on whether their dominant predator uses visual or nonvisual cues to target prev (Ohman 1990), which can lead to exploitation by other predators with greater visual acuity or nonvisual means of targeting prey over a diel cycle.

Marine predators exhibit diel patterns in depth occupancy closely associated with diel changes in insolation, directly linked to foraging and/or thermal physiology (Friedlaender et al. 2013, Papastimatiou et al. 2015). Strategies vary among air-breathing vs. water-breathing, endothermic vs. ectothermic, and visual vs. echolocating predators. But fundamentally, diel behaviour enables foraging to occur when and where prey forms aggregations (Vedor et al., 2021), are energetically cheaper to reach (air-breathing predators) (Friedlaender et al., 2013) or easier to see (visual predators) (Regular et al. 2011), while also balancing the need to maintain a thermal optimum (ectothermic predators) (Papastamatiou et al., 2015). Diel behaviour can further be influenced by competition (Castellote et al., 2015), environmental features (Campagna et al., 2007) and the presence of predators (Baird et al., 2008). While numerous experimental studies have explored the drivers of DVM in zooplankton (Bandara et al., 2021), our understanding of diel behavioural patterns in marine predators has primarily been based on observing differences in dive depth and frequency between day and night in systems where light regimes are relatively constant; determining whether marine predators respond to a switch from 24-h irradiance or darkness to a day/night cycle in light is yet to be formally investigated.

Regions north of the Arctic circle (66.5°N) experience extreme light regimes, with periods of 24-h darkness (polar night), 24-h daylight (midnight sun) and progressive daily light/dark cycles during spring and fall. These unique seasonal light cycles allow testing of hypotheses on organisms' behavioural and physiological responses to diel and seasonal changes in light and temperature (e.g. Grémillet, Kuntz, Woakes, et al., 2005, Grémillet, Kuntz, Gilbert, et al., 2005). Belugas from the Eastern Beaufort Sea (EBS) population represent a highly mobile, endothermic marine predator that experiences all seasonal light regimes, and hence function as a model predator under natural experimental conditions to examine the occurrence and intensity of diel behaviour and the interacting factors that shape its prevalence and form. Furthermore, given belugas target prey throughout the water column (to 1400m, Storrie et al., 2022), dive depths can inform on DVM and habitat use in lower trophic level species (e.g. Arranz et al., 2011). Here, we examine time series depth data from satellite-tagged belugas from the EBS population to test the hypothesis that a mobile, endothermic marine predator initiates diel dive behaviour with the onset of the day/night cycles in light and ceases diel behaviour during 24-h daylight or darkness. We then examine the interacting factors associated with DVM; sea ice concentration, seafloor depth and water column structure, to tease apart light regime vs. other environmental factors driving diel behaviour in a marine predator.

FIGURE 1 (a) Daily locations of belugas derived from a continuous-time correlated random walk (CTCRW) model, with those specified as having presence or absence of diel behaviour identified. Map shows the delineation of regions of the Arctic Basin used in temperature profile analyses (WB = West Basin, NEB = Northeast Basin, SEB = Southeast Basin), and the Central Arctic Ocean (CAO) boundary. Ice contour shows \geq 50% ice concentration for 15 September 2018, during the period when most of the diel behaviour occurred (Figure 2). (b) Tracks of individual belugas with locations colour-coded by month.



2 | MATERIALS AND METHODS

2.1 | Tag deployment

Six male belugas were tagged with SPLASH10-F-238 satellite-linked transmitters (Wildlife Computers Ltd.), from Hendrickson Island (69.50°N, 133.60°W, Figure 1a), Northwest Territories, Canada, in July 2018. Belugas were tagged using a live capture method (Storrie et al., 2022). Belugas often display complex and dynamic social groupings, either as context dependent fission-fusion societies or stable social units that regularly congregate and disperse (O'Corry-Crowe et al., 2020). The belugas in this study were part of a large, loose aggregation of animals that were regularly separated by several hundred kilometres during movements following tagging (Figure 1b); consequently, the social relationships among these individuals were unknown. Tags sampled depth (± 0.5 m) and temperature ($\pm 0.05^{\circ}$ C) at 1 s intervals and transmitted the data as time series in hour-long messages subsampled at 75s intervals. Tags collected Fastloc GPS locations, and estimated Argos locations each time a transmission was made (see Storrie et al., 2022 for details of tag programming). Three of these belugas were also equipped with a MiniPAT (popup archival tag), which archived and then transmitted depth and temperature time series data after release from an animal. MiniPAT data were used to fill in missing depth/temperature data from the SPLASH10-F-238 tags (Table 1). The following approvals were required for whale capture and handling procedures: DFO Licence to Fish for Scientific Purposes (S-18/19-3020-YK), Freshwater Institute Animal Care Committee permit (FWI-ACC-2018-24) and Letters of Support from Inuvialuit Hunters and Trappers Committees.

2.2 | Assigning environmental variables to animal locations

The filtered locations (see details in Storrie et al., 2022) occurred on average 35.1 min apart, with 8.4% of locations occurring >1 h after the previous location, continuous-time correlated random walk (CTCRW) models were consequently used to re-estimate locations at regular 15 min intervals (Johnson et al., 2008). Locations were then assigned associated seafloor depth and sea ice concentration, and dives were isolated and characterized by time and depth metrics (see details in Storrie et al., 2022). The SUNCALC package v0.5.0 (Thieurmel & Elmarhraoui 2019) in R v4.1.2 (R Core Development Team, 2019) was then used to assign the solar altitude relative to the horizon for each CTCRW-modelled location based on latitude, longitude, date and time (UTC). Daylight was defined by solar altitudes $> -0.83^{\circ}$; the angle below the horizon when the sun is still visible due to atmospheric refraction. This altitude was used to assign a seasonal light regime to individual days of data; midnight sun (solar altitude > -0.83° throughout a given day); polar night (solar altitude ≤ -0.83° throughout a given day); 'Fall-' or 'Spring day/night cycle' (days from July-December, and January-June, respectively, when the solar altitude ranged between > −0.83° and ≤ −0.83° on a given

days in which diel behaviour was days in the midnight sun for the three Beluga ID' denotes individuals which were also equipped with a secondary MiniPAT. based on these estimate light regime encountered' is an gives the number of number of extrapolated total 'Diel' seasonal number of days with sufficient depth data to test whether diel patterns occurred. contain the Proportion of the year locations, and parentheses by light regime. Asterisk next to following June. period in the CTCRW light regime based on Details on tag deployments and days with diel behaviour individuals (marked with \dagger) that transmitted their final data during this in parentheses in each total thet the total number of days spent identified, with the proportion of the total gives . analysed' 'Total ; three individuals. 'Total' gives -TABLE

					Seasonal	light regin	ЭС									
		Relitos			Midnight	sun (days)		Fall day/	'night cycle	(days)	Polar ni	ght (days)		Spring d	ay/night cyc	e (days)
Beluga ID	ЪТТ	length (m)	Tag deployment date range	Duration (days)	Total	Total analysed	Diel	Total	Total analysed	Diel	Total	Total analysed	Diel	Total	Total analysed	Diel
LC2018#1*	174965	4.20	03/07/18-02/01/19	184	40	37	0 (0.0%)	122	98	9 (9.2%)	21	14	0 (0.0%)	7	0	NA
$LC2018#2^{\dagger}$	174967	4.70	04/07/18-19/06/19	351	58 (72)	36	2 (5.6%)	159	104	6 (5.8%)	0	AN	NA	134	97	6 (6.2%)
LC2018#3	174962	4.06	06/07/18-15/12/18	163	37	32	0 (0.0%)	119	87	31 (35.6%)	7	1	0 (0.0%)	0	AN	NA
LC2018#4* [†]	174963	4.44	08/07/18-07/06/19	335	64 (94)	48	0 (0.0%)	133	79	15 (19.0%)	80	9	0 (0.0%)	130	103	16 (15.5%)
LC2018#6* [†]	174966	4.40	08/07/18-29/06/19	357	71 (79)	52	0 (0.0%)	151	55	5 (9.1%)	e	0	NA	132	51	2 (3.9%)
LC2018#8	174969	4.25	09/07/18-19/12/18	164	34	27	0 (0.0%)	128	24	10 (41.7%)	2	0	NA	0	NA	NA
Total				1554	304	232	2 (0.9%)	812	447	76 (17.0%)	41	21	0 (0.0%)	397	251	24 (9.6%)
Proportion of t	the year se	easonal lig	ht regime encountered		22.4%			40.5%			1.0%			36.2%		

day). Mean seafloor depth, sea ice concentration and hours of daylight were calculated for each unique day (UTC) for each individual beluga using all CTCRW-modelled locations from that day.

2.3 | Identifying diel patterns in dive behaviour

To identify diel patterns in dive behaviour, we calculated whether the dissimilarity in the proportional time-at-depth (TAD) between phases of low and high solar altitude on a given day was greater than the dissimilarity calculated between phases of equivalent solar altitude on the preceding and following days, based on a split moving window method used to identify discontinuities in depth use (Queiroz et al., 2010). We used low and high solar altitude phases (LowAlt and HighAlt, respectively) rather than a simple night or day designation to enable identification of diel behaviour during the polar night and midnight sun as well as periods with a day/night cycle. This acknowledges that DVM can occur during all these periods (Last et al., 2016, Dmitrenko et al., 2020). Methodological discussion is provided in Supplementary Material 1.

2.3.1 | Calculating TAD by solar altitude phase

For each hour with complete depth time series data, the proportional TAD was calculated in eight depth bins (0-20, 20–50, 50–100, 100–200, 200–300, 300–400, 400–500, >500). Each hour of TAD data was then associated with the solar altitude experienced at the midpoint of each hour (HourAlt) based on the closest timestamp from the CTCRW-modelled location data. The midrange solar altitude (MidAlt) was calculated for each day, and each hour of TAD data was then assigned as LowAlt or HighAlt depending on whether the HourAlt was \leq MidAlt or > MidAlt, respectively for the given day. The mean TAD in each depth bin was then calculated across hours for each given day separately for the LowAlt and HighAlt phase. If a given LowAlt or HighAlt phase in a day had <3h of data, it was deemed data deficient and excluded from analyses.

2.3.2 | Calculating dissimilarity in TAD between daily solar altitude phases

Firstly, Manhattan distances were calculated between the mean LowAlt and HighAlt TAD vectors for each given day. Secondly, Manhattan distances were calculated for equivalent solar altitude phases between a given day and the surrounding days, that is, between the LowAlt TAD vector on day *d* and the LowAlt TAD vectors on d - 1 and d+1, which was then repeated for the HighAlt TAD vectors. If the LowAlt or HighAlt phases on d - 1 or d+1 had <3h of TAD data, the TAD vectors for d - 2 and d+2 were used, respectively. In situations where all surrounding days had insufficient data, this day was deemed data deficient for diel patterns to be identified. Thirdly (for days with sufficient data), the Manhattan distances

calculated between the LowAlt and HighAlt TAD vectors on d were compared with the Manhattan distances calculated between equivalent phases among d with d - 1 and d + 1 (or d - 2 and/or d + 2in the case of insufficient sample sizes). If the Manhattan distance between the LowAlt and HighAlt TAD vector on d was greater than all four of the Manhattan distances calculated between equivalent solar altitude phases on the surrounding days, the day d was categorized as containing possible diel patterns. Finally, to further discriminate among differences in the diel depth occupancy being due to chance or the change in solar altitude, we only considered a day of behaviour to have diel patterns if it was either preceded or followed by a day which was also categorized as containing possible diel patterns. The above process of identifying diel behaviour was conducted separately for each beluga, and each day was assigned a 1 or 0 based on presence or absence of diel patterns in TAD, respectively.

2.4 | Testing environmental drivers of diel behaviour

Binomial generalized additive mixed effects models (GAMMs) with thin plate regression splines and a maximum of five knots were constructed to inform whether the presence of diel behaviour varied as a function of hours of daylight, seafloor depth and sea ice concentration, with individual beluga included as a random effect. GAMMs were used because nonlinear relationships were expected. Separate models were constructed with all possible combinations of the three variables using the MGCV package v1.8–36 (Wood 2021) in R; and the Akaike Information Criteria (AIC) was calculated for each to inform selection of the best model.

2.5 | Examining fine scale diel behaviour in relation to water column thermal structure

Following review of the GAMM results and seasonal frequency of diel activity, we identified that the majority (66/102) of days with diel behaviour occurred over deep waters in the Arctic Basin during fall, with differences in the occurrence and intensity of diel behaviour among regions of this habitat. To further explore how environmental conditions regulate diel behaviour, the Arctic Basin (>1000m, excluding the Beaufort Slope) was divided into west and east at 164°W (Chukchi Plateau, Figure 1a), with the east region further divided into north and south due to heavier ice cover in the north $(n = 3 \text{ regions: West Basin, Northeast Basin, Southeast Basin). Water$ column temperature profiles were reconstructed in each of these regions during this period from the tags' temperature- and depth time series data by calculating the rolling mean and standard deviation of temperature every 10 m (\pm 10 m). For each of these regions, the maximum depths of all individual dives (Storrie et al., 2022) were plotted against the solar altitude at the time of the dive to explore patterns in diel behaviour. Water column thermal structure was not included in the GAMMs as large differences in seafloor depths

(Figure 1a) resulted in incomparable parameters among regions and major features such as the depth and strength of the thermocline were highly correlated with seafloor depth.

3 | RESULTS

3.1 | Occurrence of diel behaviour

Data were transmitted by six male belugas between 03 July 2018 and 29 June 2019 (Table 1, Figure 1b); fall and spring day/night cycles were the most encountered seasonal light regimes, and polar night was the least encountered. Diel dive behaviour was identified on 10.7% of the days that had sufficient data (Table 1). All individuals transmitted data during the midnight sun but only one individual recorded 2 days with diel behaviour during this period. Diel behaviour became most pronounced and frequent during the fall day/night cycle (17.0% of the days during this period, Table 1). No diel patterns were identified during the polar night. Three belugas transmitted data into the spring day/night cycle and exhibited diel behaviour on 9.6% of the days during this period while occupying the Bering Strait/Sea region (Figures 1a and 2, see results and discussion regarding this in Supplementary Material 2).

3.2 | Environmental drivers of diel behaviour

Of the candidate GAMMs, *m*3 (variables = seafloor depth and daylight hours, Table 2) was selected as it had the joint lowest AIC score and the sea ice variable in *m*1 was not significant (p = 0.213). Both environmental variables had significant effects on the presence of diel behaviour (p < 0.001, Figure 3). Diel behaviour rarely occurred on days approaching 0 and 24 h of daylight and increased in frequency towards days with equal phases of daylight and darkness; with peak occurrence under 12 h of daylight (Figure 3a). Diel behaviour had the lowest probability of occurring in regions with seafloor depths <700 m (± 2 SE = 540–850 m, Figure 3b). Individual beluga had a significant effect in the model (p < 0.001); coinciding with differences in fall distribution and seafloor depths encountered (Supplementary Material 3; Table 1; Figure 1b).

Representative data for the influence of the number hours of daylight and seafloor depth on the occurrence of diel behaviour is shown in Figure 4a (beluga LC2018#3). During the period with midnight sun and into the fall day/night cycle (6–24 August), this individual made benthic dives to ~500 m with no evidence of diel behaviour. The beluga entered deeper waters on 24 August and begun to exhibit a degree of diel behaviour between 27 and 30 August (17.50 h of daylight), diving deeper (~750 m) during daylight hours, and shallower (~600 m) during dusk and dawn. Diel behaviour became pronounced between 7 and 19 September (16.25–13.5 h of daylight), and between 25 September and 8 October (12.0–9.5 h of daylight), with the beluga making dives to >600 m and <50 m during daylight hours and dives from 100–300 m during dusk and dawn (Figure 4b). Between 20–24 September, and on 9 October, the beluga entered shallower waters (<750 m) and diel patterns ceased, with behaviour switching to constant dives to the seafloor through all light phases (Figure 4c).

3.3 | The influence of solar altitude and water column thermal structure on diel behaviour

Pronounced patterns in diel behaviour occurred during fall in deep waters (Arctic Basin). During the HighAlt period, when the sun was highest in the sky, belugas spent more time at depths between 0 and 20m, and >500m; whereas, during the LowAlt period, when the sun was low in the sky/below the horizon, depths from 50-200m were occupied more frequently (Figure 5). The most pronounced patterns in diel behaviour occurred in a region that had relatively homogeneous temperatures ($-1.3^{\circ}C \pm 0.4^{\circ}C$) between the surface and 150m deep (West Basin). There were several distinct patterns in the depths targeted associated with the solar altitude and water column thermal structure in this region. Diving was shallow (~50m) during the darkest hours of the night (lower solar altitude), becoming progressively deeper and closer to the base of the inverted thermocline (~300 m, with water temperatures increasing to $1.0^{\circ}C \pm 0.6^{\circ}C$, Figure 6) approaching daylight hours (solar altitude $> -0.83^{\circ}$). During daylight hours, dives targeted the bottom of the thermocline (250-350 m), deeper waters (500-750 m) (except LC2018#1) and shallow depths (0-50m), with no clear relationship evident between solar altitude and dive depth during this time; however, avoidance of the base of the thermocline was observed (350-500m; Figure 6).

Diel patterns were less frequent and pronounced when there was greater thermal stratification in the upper 200m of the water column (Southeast and Northeast Basin regions, Figures 1, 6). Belugas tended to avoid diving to 50-150m, coinciding with the depths of a warmer water layer (-0.5°C) and shallow thermocline (Figure 6). Weak diel patterns in dive behaviour were observed, with belugas diving to the deep thermocline between 200-400m more frequently during the night (Figure 6). In the Southeast Basin, while dives below the deep thermocline (500-800m) occurred during the night and day, deeper diving typically occurred during periods with a higher solar altitude. Belugas in the Southeast Basin avoided diving to the base of the thermocline (400-500m), as observed in the West Basin (Figure 6); however, this trend was not observed in the Northeast Basin. The Northeast Basin was characterized by greater sea ice coverage than the other regions (Figure 1a); only one beluga entered this region, and the deepest dives recorded were generally shallower compared to the other two Arctic Basin regions (400-600m vs 500-800m, Figure 6).

4 | DISCUSSION

Marine predators inhabiting mid to low latitudes frequently exhibit diel patterns in behaviour associated with relatively uniform day/



FIGURE 2 Daily locations of belugas derived from a CTCRW model by month, with symbol denoting presence or absence of diel behaviour. Light regime polygons were calculated based on the 15th day of each month. See Figure 1a for more detailed bathymetry.

night light cycles (e.g. Arranz et al., 2011, Madigan et al., 2021, Shaff & Baird 2021). The present study confirms the hypothesis that initiation of diel patterns in dive behaviour by a marine predator coincides with the switch from 24-hour daylight to a daily light/dark cycle, as would be expected. These diel behavioural patterns became more frequent and pronounced approaching days with equal phases of light and darkness. But despite experiencing a day/night cycle for 76.7% of the year, belugas exhibited diel behaviour on just 10.7% of days, primarily during fall. Seafloor depth played a strong regulatory role in the occurrence of diel behaviour during this period, with individuals terminating diel behaviour in regions with seafloor depths <700m, while the relative intensity of diel behaviour was tied with variation in water column thermal structure. Furthermore, differences in the frequency of diel behaviour were observed among individuals. These data highlight the complex interacting effects shaping diel patterns in behaviour of mobile marine predators, providing an informed understanding of responses to extreme seasonality in light regimes and the relative influence of bathymetry and water column physical structure on diel behaviour.

TABLE 2 Candidate generalized additive mixed effects models for the presence of diel behaviour (as determined by dissimilarity in time-at-depth between solar altitude phases) as a smoothed function of environmental variables. Models are ranked by AIC

Model no.	Variables	AIC
m3	Seafloor depth, daylight hours	403
m1	Seafloor depth, daylight hours, ice concentration	403
m4	Seafloor depth, ice concentration	455
m6	Daylight hours	458
m5	Daylight hours, ice concentration	458
m2	Seafloor depth	471
m7	Ice concentration	587

p-value < 0.001 p-value < 0.001 (a) (b) ო 4 \sim ĉ 2 0 s(2.99) s(3.84) <u>_</u> $\overline{\ }$ Ņ 0 က္ 7 4 $\dot{\gamma}$

0 4 12 24 0 1000 2000 3000 4000 8 16 20 Hours of daylight (hr) Depth (m)

FIGURE 3 Relationship between the estimated probability of occurrence of diel behaviour and environmental covariates, v-axis represents the GAMM smooth function of each term with the effective degrees of freedom (edf) of the smooth term in parentheses. The zero on the y-axis (red line) represents absence of an effect of the covariate on the occurrence of diel behaviour. Dashed lines represent two standard errors. The final model included (a) hours of daylight, and (b) seafloor depth.

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4.1 Initiation of diel behaviour in fall

The marked progression in diel behaviour during fall following cathemeral behaviour during the midnight sun suggests tracking prey that initiates DVM during this period. The pronounced diel patterns west of the Chukchi Plateau (West Basin region) during this period indicate prey remain at the base of the deep thermocline (~350m) during the day and reach progressively shallower depths (up to ~50m) between sunset and the darkest hours of the night. Vertical migration strategies in pelagic prey may be employed principally due to 'fear'; including anticipatory diel migrations to avoid resident predators with limited diving and/or sensory capabilities, and reactive responses to the passage of predators (Urmy & Benoit-Bird 2021). This is the case for adult Arctic cod (Boreogadus saida), the main prey item of EBS belugas in the Beaufort Sea (Choy et al., 2020), which remain near the seafloor during summer and commence DVM with the onset of the fall day/night cycle as a strategy to avoid visual predators such as ringed seals (Benoit et al., 2010, Geoffroy et al., 2016). The fact that transitory male belugas track prey between 50-350m over the diel cycle suggests the presence of other more abundant and/or more resident predators stimulate DVM of prey that then allows exploitation by belugas. As well as ringed seals, diving visual predators such as common guillemots (Uria aalge) (Regular et al., 2011) overlap in diet with belugas and likely cooccur near the Chukchi Plateau during fall (Portenko 1989). Belugas can make deep dives and echolocate prey 300m away (Zahn et al., 2021), enabling foraging throughout the water column in the absence of light. By targeting prey at shallower depths during the night, belugas minimize transiting costs and maximize the time spent foraging (Mori 1998); a pattern often seen in odontocetes (Shaff & Baird 2021, and references therein). Furthermore, their transitory use of this region may represent exploitation of a seasonal pulse in prey distribution shaped by cooccurrence of a broader



FIGURE 4 (a) Dive profiles over a 12-week period between 6 August (midnight sun) and 29 October (fall day/night cycle) 2018, for beluga LC2018#3, showing the progression in occurrence and intensity of diel behaviour, and the cessation of diel behaviour in shallower habitats. (b, c) show 24-hour periods with diel, and no diel patterns, respectively, identified in (a). Periods with no dive profiles shown denote missing depth data. Brown shaded area represents seafloor depth. All dates in UTC.

visual predator assemblage. Deep dives to >500m during daylight hours also suggest profitable/consistent food at depth; the prey assemblage has not been well studied in this region of the Central Arctic Ocean, but circumpolar species which remain at this depth including the squid *Gonatus fabricii* (Snoeijs-Leijonmalm et al., 2021, and references therein) would provide consistent prey.

Greater occupancy of the upper 20m during the day suggests transiting or recovery behaviour (Storrie et al., 2022) after intensive foraging at night (see Figure 4b 20:00 onwards). Diel patterns in resting behaviour have been identified in other marine predators to optimize foraging strategies based on their thermal physiology (Papastamatiou et al., 2015) and prey distribution or detectability (Izadi et al., 2018).

4.2 | Complex interacting drivers of diel behaviour in marine predators

4.2.1 | Cessation of diel behaviour in shallower habitats

The cathemeral targeting of the seafloor in shallower regions (seafloor depths <700 m) irrespective of seasonal or daily light regimes suggests foraging on prey which do not undertake DVM and aggregate at the seafloor over a diel cycle. Predictability and/or high abundance of prey at the seafloor could provide a more valuable resource than pelagic prey, and lack of diel patterns in benthic foraging have been observed in other predators (Campagna et al., 2007, Shearer et al., 2019). The principal prey item of EBS belugas, large Arctic cod, remain near the seafloor during the spring day/night



FIGURE 5 Mean proportional TAD on the days identified as having diel behaviour in the Arctic Basin (seafloor depths >1000 m). Data recorded by five belugas from August-October.

cycle and midnight sun (Geoffroy et al., 2016), and likely present a predictable food source during this period. But with decreasing photoperiod in fall, Arctic cod occupy the pelagic zone and undertake DVM (Geoffroy et al., 2016), consequently the cessation of diel patterns by belugas indicates other benthic prey must be targeted at this time; the dependence on benthic foraging habitats for male EBS belugas has previously been shown (Storrie et al., 2022). Lack of diel patterns in behaviour or spatiotemporal habitat occupancy can also indicate a lack of competition with cooccurring predators which have dietary overlap (e.g. Castellote et al., 2015); particularly ringed seals in the Beaufort Sea (Benoit et al., 2010). Together this suggests that fine-scale spatial partitioning and/or high abundance of benthic prey promote predator coexistence.

4.2.2 | Association between predator diel behaviour and water column thermal structure

Marked differences in depths targeted during fall among deep habitats identify the influence of variable water column thermal structure



FIGURE 6 (Left) Mean water column temperature profiles in each of the three regions of the Arctic Basin (>1000 m seafloor depth, Figure 1a). Temperature calculated as rolling mean every 10 m (\pm 10 m). (Right) Maximum dive depth of pelagic dives plotted against solar altitude, within the respective region of the Arctic Basin specified left. Solar altitudes $\leq -0.83^{\circ}$ denote twilight/night, and > -0.83^{\circ} denote day.

on predator diel behaviour. More pronounced diel patterns in dive behaviour occurred in regions where the water column was thermally homogeneous versus more stratified across the upper 150m. Whilst the range of temperatures observed are unlikely to present a physical barrier to the movements of prey, depths occupied by species undertaking DVM typically depend on their thermal optimum (Berge et al., 2014). The thermocline also structures where migratory organisms settle (Hazen & Johnston 2010); lower trophic level organisms often aggregate around thermoclines, which can attract higher predators such as fish and marine mammals (e.g. Kuhn 2011). Such variation in water column thermal structure, which can be highly dynamic in space and time, can lead to switches in prey distribution over daily and seasonal cycles that regulate predator dive behaviour (Pelletier et al., 2014) and may modify diel dive patterns.

Avoidance of depths immediately below the thermocline by belugas could indicate absence of prey and suggest separation between pelagic biomes. The bathypelagic zone typically starts at the base of the permanent thermocline; and is characterized by lack of diel variation in illumination and relatively constant temperature and salinity (Sutton 2013). Small diel changes in light intensity in the lower mesopelagic, however, may trigger DVM from the bathypelagic zone; in the Mid-Atlantic, bathypelagic biomass increased between 700-1000m and decreased between 1000-1900m at night compared to day (Cook et al., 2013). Weak diel patterns in beluga dives between 500-800m in the Southeast Basin may represent tracking diel movements in bathypelagic prey in response to mesopelagic light intensity.

Several alternative explanations could explain why depths immediately below the thermocline were avoided. Belugas can echolocate prey over large distances (Zahn et al., 2021), however refraction of sound waves at the thermocline boundary (Frosch 1964) could distort received signals; consequently, echolocating predators may optimize depths targeted to maximize success in locating prey. Alternatively, pelagic dives deep below the thermocline in the West Basin could represent searching for navigational cues and/or to locate more consistent foraging habitat. While there is uncertainty around how cetaceans navigate, they may use oceanographic and gravitational cues that result from localized bathymetry and bedrock, respectively (Derville et al., 2020; Horton et al., 2020). Avoidance of certain depths could also represent vertical partitioning among predators with dietary niche overlap, such as with ringed seals which rely more on visual cues to target prey and dive more frequently and to greater depths during daylight hours (Von Duyke et al., 2020).

The causes of weaker diel patterns in the ice-covered region (Northeast Basin) are unclear; diving between 150–600m indicates that prey were likely distributed across these layers, corresponding to the depths of the deep scattering layer identified in nearby icecovered regions during September (Snoeijs-Leijonmalm et al., 2021). Sea ice coverage results in greater attenuation of light than in open water regions, which could explain the shallower maximum depths of dives compared with open water regions if prey are distributed relative to light intensity. Whilst the attenuating property of sea ice can extend DVM of zooplankton into the midnight sun (Dmitrenko et al. 2020), dives to the seafloor by belugas during this period indicate this prey base was not targeted. Dynamic spatiotemporal variation in predator dive behaviour relative to interacting biotic and abiotic factors highlight the need to consider these variables, but may also reveal distinct properties of the ecosystem a predator inhabits.

4.3 | Behavioural flexibility and complexity in diel behaviour among Arctic odontocetes

Animal migrations are often closely synchronized to the phenology of their prey (Dingle & Drake 2007). The westward movements and switch from cathemeral benthic diving to diel pelagic diving with the onset of the fall day/night cycle (Figure 2) could indicate belugas time their migrations preemptively to coincide with the brief open water period (Supplementary Material 4) and the equal daily light/dark cycle west of the Chukchi Plateau. This could enable exploitation of the ephemeral resource of prey undertaking DVM, maximizing resource acquisition which is critical for long-distance migrators to reach their next residency area. Furthermore, one beluga, LC2018#2, did not enter this region and continued cathemeral benthic dive behaviour (Supplementary Material 3). Identifying this level of individual variation in behaviour, which could extend to preferences for prey that undertake DVM or prey that do not, highlights the capacity of beluga whales to acquire knowledge and predatory skills for the exploitation of diverse prey. Such knowledge and behaviours may be acquired de novo which can be highly risky or via social learning, mediated through a complex web of social ties (O'Corry-Crowe et al. 2020), that could develop into cultural traditions (O'Corry-Crowe et al. 2018). Foraging specialization has been observed among social groups within populations of other odontocetes (Daura-Jorge et al., 2012, Herzing et al., 2017). It is not clear whether the patterns in the present study represent individual- or social group level specialization as the social relationships among the tagged belugas were unknown.

Previous studies on diel behaviour in the Arctic odontocetes are limited in their temporal scope and did not explicitly test for the influence of seasonal light regime, but often found inconsistent diel patterns by sex, region, and among and within populations (e.g. Heide-Jørgensen et al., 1998, Martin et al., 1994, 2001, Ngô et al., 2019). For example, female belugas in the Eastern High Arctic exhibited greater diving activity during the night, but this pattern was not observed for males (Heide-Jørgensen et al., 1998), while belugas at lower latitudes in southwest Hudson Bay tended to occupy the surface more at night (Martin et al., 2001), but this pattern was not consistent among all individuals. These studies combined with the EBS beluga behaviour exemplify a high degree of variability in the relationship between light cycles and diel patterns in behaviour within and among populations of the Arctic odontocetes, suggesting flexible and/or cultural behaviour but also highlighting the influence of the dynamic environment they inhabit.

4.4 | Future directions

Extreme latitudes provide a natural experimental setting to test how mobile marine predators respond to a diel day/night light cycle versus 24-h darkness or daylight in combination with interacting abiotic factors. While the diverse and dynamic environments occupied by EBS belugas over an annual cycle make this study correlational to a degree; marked progression in the intensity of diel patterns in dive behaviour coinciding with the progression of the day/night cycle in light provide strong support for a light-mediated switch from cathemeral to diel patterns in dive behaviour. Past tagging studies on Arctic marine predators have been limited in their ability to answer this question due to tag resolution or longevity; additional year-long deployments among these species, and comparisons among populations occupying different latitudes are required to confirm whether this light-mediated switch is ubiquitous. As endothermic echolocators, diel patterns in beluga behaviour are most likely related to energy conservation and prey accessibility; ectothermic and visual predators may exhibit diel behaviour related to thermoregulation and relative ability to see their prey, respectively (Madigan et al., 2021). Further studies on Arctic ectotherms such as Greenland sharks (Somniosus microcephalus) and nonecholocating endotherms such as the Arctic seals are required to test whether light-mediated initiation of diel behaviour is common among mobile predators with disparate requirements of insolation, and can provide insight into the cues used by predators in foraging (Grémillet, Kuntz, Gilbert, et al., 2005). The low sample size and beluga distribution during spring precluded robust conclusions regarding responses to the switch from polar night to the spring day/night cycle (although see Supplementary Material 2 for discussion); further targeted studies on the Arctic odontocetes, in particular the higher latitude narwhal populations, could address this question. Furthermore, the lunar cycle is known to influence diel behaviour in predators, which generally make deeper nighttime dives during a full moon related to prey depth or visibility (Owen et al., 2019, Shaff & Baird 2021). In the Arctic, the rising of the moon can disrupt DVM during late fall; and during the polar night, lunar vertical migration (LVM) of zooplankton can occur over several days centred around the full moon (Last et al., 2016). The lunar cycle was not assessed in the present study as the methods were selected specifically to identify diel behaviour based on diel cycles in solar altitude. While this relationship requires further investigation, we hypothesize that the belugas in the present study are not influenced by the lunar cycle to the same extent as predators which target the pelagic food web due to focused foraging near the seafloor during all times of year except for the day/night cycle in early fall. The potential for individual- or social group level specialization in monodontids proposed in the present study are speculative due to the low sample size and our lack of understanding on beluga social group stability. Targeted studies to tag and biopsy individuals from the same pod and collect photo-id and drone observations will help uncover these relationships and their consequences on behaviour.

5 | CONCLUSIONS

Diel vertical behaviour in mobile marine predators is critical for optimizing foraging and limiting competition, is ubiquitous across species in the marine realm and is largely considered to be driven by insolation and predator-prey interactions. But our understanding of diel behaviour in predators has primarily relied on observing depth usage between relatively constant day/night light cycles. Here we demonstrate that diel behaviour in an Arctic predator inhabiting a unique natural experimental setting, occurs over dynamic spatiotemporal scales, switching from cathemeral dive behaviour during 24-h daylight to distinct diel behaviour during the fall light/dark cycle, and becoming more pronounced with the progression of day/ night. While these data empirically demonstrate the importance of day/night light cycles on predator diel behaviour, they explicitly reveal the complex interactions of insolation, seafloor depth, and water column thermal structure in modulating the occurrence and intensity of diel behaviour in a marine predator. Accurately interpreting diel behavioural patterns in predators is complex depending on the scale of examination and due to disparate requirements of insolation, but can reveal dynamic species interactions, and predator and prey distributions in understudied areas.

AUTHOR CONTRIBUTIONS

Luke Storrie performed all data analyses, wrote the manuscript, and created all figures and tables. Lisa L. Loseto and Shannon A. MacPhee led on program implementation and secured funding and partnerships. Luke Storrie, Lisa L. Loseto, Nigel E. Hussey, Shannon A. MacPhee and Greg O'Corry-Crowe conceptualized the study and collected data. Lisa L. Loseto, Nigel E. Hussey, Shannon A. MacPhee and Greg O'Corry-Crowe planned the field programs. Lisa L. Loseto and Nigel E. Hussey were involved in critical discussions of the manuscript with Luke Storrie throughout the process. Lisa L. Loseto, Nigel E. Hussey, Shannon A. MacPhee, Greg O'Corry-Crowe, John Iacozza and David G. Barber supported early discussions with Luke Storrie regarding objectives and methods and revised the manuscript.

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CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

A subset of the location and dive data is available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.fttdz08wk (Storrie et al., 2022). R code for replicating the methods used for identifying diel patterns in behaviour can be downloaded from a GitHub repository (https://github.com/storriel/Diel_Dive_Behaviour). The datasets presented in this article are available upon reasonable request. Requests should be directed to Lisa L. Loseto (lisa.loseto@ dfo-mpo.gc.ca) and will be reviewed by the Inuvialuit Game Council and Fisheries and Oceans Canada.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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