Diel prey distribution patterns shape predators shared strategies and niche divergence

Astrid Anette Carlsen[1], Claire Saraux[2], Elin Sjöholm[1], Camilla Menestrina[3], Mica Bohacek[1], Natalie Isaksson[4], Sofia Nguyen[5], Joakim Eriksson[5], Michele Casini[3], Samantha Patrick[6], and Jonas Hentati-Sundberg[1]

[1]Swedish University of Agricultural Sciences
[2]IPHC
[3]University of Bologna
[4]Heliaca Naturvårdskonsulting AB
[5]AI Sweden
[6]University of Liverpool

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Abstract

Diel prey distribution patterns drastically alter their availability to predators, but how that affects predator behaviours remain poorly understood due to limited data overlap. Using spatiotemporally concurrent tracking of two sympatric seabird species and their fish prey, we reveal how diel prey distribution patterns influence foraging behaviour. The seabirds invested greater effort during twilight, peaking at dusk, with 25-80% enhanced efficiency. Prey vertical migration increased their abundance near the surface at night with 20%, but number of aggregations showed diel asymmetry, peaking at 140° azimuth before decreasing with 25% in 20°. These dynamics created elevated foraging windows in late afternoons, with extended duration of high efficiency and effort (56–70% of dives). The deep-diving predator Uria aalge followed prey depth linearly, while the comparatively flight-adapted Alca torda was more sensitive to prey depth and aggregations. We provide novel details of diel prey behaviour shaping predator foraging, demonstrating how morphological adaptations drive niche differentiation.

Introduction

Light drives the spatial distribution of lower-trophic organisms, influencing their availability to predators across diel cycles (Hamilton, 1971; Milinski, 1984; Thiebault *et al.* , 2016). Diel variations in distribution patterns occurs across taxa and systems, and are documented in terrestrial vertebrates (Slavenko *et al.* , 2022), invertebrates (Chang and Hanazato, 2004; McMunn and Hernandez, 2018), amphibians (Rocha *et al.* , 2015) and aquatic species (Haney, 1988; Cardinale *et al.* , 2003; Regular, Hedd and Montevecchi, 2011; Mehner, 2012; Isaksson *et al.* , 2019). During twilight transitions, light may still be sufficient for visually oriented predators to exploit temporal windows of enhanced foraging conditions while prey shifts between distribution patterns (Pyke, 1984; Nishimura, 1992; Mella *et al.* , 2018). Thus, diel variations in prey distribution modify their availability within a foraging site, causing the cost of prey capture to vary greatly for predators (Hamilton, 1971; Kacelnik, 1979; Kacelnik and Houston, 1984; Milinski, 1984; Wilson *et al.* , 1993; Benoit-bird and Au, 2003; Sims*et al.* , 2005; Bollens *et al.* , 2011; Regular, Hedd and Montevecchi, 2011; Thiebault *et al.* , 2016). Uncovering predator-prey relationships under natural diel cycles is crucial for understanding how species divide into ecological niches and adapt to environmental constraints. These insights are essential for protecting biodiversity, as they reveal the mechanisms that sustain ecosystem stability and resilience. Small pelagic species are fundamental in aquatic food webs, and often have distinct diel distribution patterns. Many species utilize diel vertical migration by ascending to the surface at night and descending at dawn to spend daylight hours at deeper depths or closer to the seabed (Cardinale *et al.* , 2003; Hays, 2003; Axenrot *et al.* , 2004; Klevjer *et al.* , 2016; Kaartvedt, Christiansen and Titelman, 2023). In addition, many small pelagic species form aggregations e.g. in schools/shoals/swarms (Delcourt and Poncin, 2012) during daylight and disperse to feed at night (Magurran, 1990; Nilsson *et al.* , 2003; Hensor *et al.* , 2005; Bertrand *et al.* , 2006). For prey, aggregation behaviour reduce an individual's chance of being predated through the dilution effect (Hamilton, 1971). For predators, aggregations may be easier to detect than dispersed prey but intimidating and confusing upon approach, leading to reduced efficiency and catch success rate in foraging attempts. Thus many predators have adapted foraging strategies aiming to disrupt aggregations for isolating more easily catchable individual prey (Lett *et al.* , 2014). Interestingly, changes in spatial distribution of prey by depth and aggregation can interact, potentially leading to great impact on predators foraging behaviour (e.g. efficiency, effort, prey type selection and hunting tactics), while light levels must be suitable for prey detection. Thus for predators, identifying times when prey are both abundant and vulnerable is crucial (Waggitt *et al.* , 2018), yet how predators adapt to these fluctuating opportunities remains underexplored due to challenges in collecting high spatiotemporal resolution data on both predator behaviour and prey distributions (Regular *et al.* , 2010; Regular, Hedd and Montevecchi, 2011). We here address this gap using high-resolution hydroacoustic data collected by an autonomous unmanned surface vehicle (USV), matched with the foraging activity (monitored by animal trackers) of two sympatric seabird species reliant on pelagic prey. By capturing the spatiotemporal overlap between prey's diel distributions and predator's foraging patterns, we test how prey distribution and light conditions influence the predators' foraging behaviour. We hypothesize that predators' foraging effort should increase when dive efficiency (i.e. time cost/gain of dives and resting) becomes higher, aligning with shallow depth distributions and low levels of aggregations of prey during twilight. Using two closely related predators that partition their foraging niche based on flight and diving cost efficiencies, *Uria aalge* (common guillemot/murre) and *Alca torda* (razorbill), we illustrate how dive capacity (Carbone and Houston, 1996) and sensitivity to light levels (Smith and Clarke, 2012) shape temporal foraging strategies and adaptations. We investigate diel prey distribution patterns (i.e. depth distribution and number of aggregations; hereby PDPs), to test whether differences in dive ability between the alcids translates to differences in nyctohemeral foraging effort. Finally, we assess how PDPs and light levels influences niche partitioning of the predators through differing behavioural responses (number of dives, bout length, dive depth) and dive efficiency (bottom-dive cycle duration ratio, BDCr). Methods 1 Study system The study was performed in the western part of the central Baltic Sea at and around the island of Stora Karlsö (Appendix A1, Fig. A1), a breeding site for 26,000 pairs of *U. aalge* , and 12,000 pairs of *A. torda* . Both species forage predominantly on *Sprattus sprattus* (Sprat) and *Clupea harengus* (herring) (Kadin *et al.* , 2016; Engwall, Waldenström and Hentati-sundberg, 2022). The role of the rapidly increasing *Gasterosteus aculeatus (* three-spined stickleback) population (Olin *et al.* , 2022) as food source for these seabirds has not yet been evaluated, though it occasionally has been recorded as chick feed (Kadin *et al.* , 2012) and is thus likely to be part of adult diet.

2 Data collection and preparation

All time data was set to Central European Time (CET), excluding daylight saving, to ensure that noon and midnight fell at solar positions of 180° and 0° azimuth, respectively.

2.1 Predator telemetry

2.1.1 Capture and handling

Over 10 years (2010 + 2015-2023), 54 *U. aalge* and 16 *A. torda* were equipped with time depth recorders (TDRs) attached with cable ties to plastic leg rings (Evans *et al.* , 2013; Isaksson*et al.* , 2019). Birds were captured on their nests, both on natural cliffs and on an artificial breeding ledge (Hentati-sundberg*et al.* , 2025), using a noose-pole or by hand. TDRs used were either CEFAS G5 DST (accuracy ±1.5m), mass [?] 3g, log interval 1-12s, or Lotek Wireless LAT1500 (accuracy +-1.0m), mass [?] 5g, log interval 4-12s. Their deployment period varied, ranging from 24h to over-winter data sampling, though only data from May-July was selected for this study. Birds were equipped mainly during chick rearing (late June/early July), except in 2022 when birds were captured during incubation (May/June). For pairs tracked from 2010-2019, the breeding stage was determined at deployment and retrieval (i.e. incubation or chick rearing). For individuals from 2020-2022, breeding stage was assessed every day from surveillance video, and divided into incubation, chick-rearing, post-fledge (after chicks fledged) or non-breeding (individuals that did not lay an egg or lost their egg/chick during the study). One nest was too far from the camera to be identified, upon which the stage was set to the mean of the nearby pairs.

2.1.2 Foraging behaviour and efficiency

All dive sequences were visually checked using the R package diveMove (Luque, 2022) and calibrated with zero offset correction adjusted for each tracking. Dives shallower than 2m or shorter than 3s were excluded (i.e. to remove cleaning dives and inaccurate surface values). Dives were classified as V-shaped when horizontal movements at the bottom lasted less than 2s. V-shaped dives constituted 18% of dives in *A. torda* and 14% dives in *U. aalge* , and were excluded from analysis on foraging efficiency and dive depth due to their lack of horizontal bottom movement generally considered active foraging (See Appendix A1). Post-dive surface durations longer than 300 seconds (Chimienti *et al.* , 2017) were used to distinguish ‘bouts’ (i.e. a set of sequential dives). Foraging behaviour was summarised through 4 parameters: dive depth, bout length, number of dives per 10deg azimuth (See *2.3 Light levels*) and dive efficiency. Dive efficiency represents the proportion of a dive cycle allocated to foraging t , based on the total dive duration T and the surface duration after the dive S , referred to as bottom-dive cycle ratio (BDCr), i.e. $\frac{t}{T+S}$, according to Carbone and Houston(Carbone and Houston, 1996). For efficiency estimations, the last dive of each bout were excluded as it represents activities beyond the recovery from the dive (e.g. flying to a new patch).

2.2 Prey distributions

Prey distribution was assessed from hydroacoustic data collected via a remotely operated unmanned surface vehicle (USV), Sailbuoy (Offshore Sensing AS, Bergen, Norway), equipped with a Simrad Wide Band Transceiver WBT-mini echosounder with an ES-200CDK transducer from Kongsberg Maritime (frequency sweep 185-255 kHz, see Carlsen *et al.* , 2024). Data were collected from April to July in 2019-2023 (42-81 days per year), according to 10 min cycles (7min of recording – 3min pause). This almost entirely covered the seabirds foraging area in space (˜60x80km^2, see Appendix A2). Prey depth was extracted from Echoview Software Pty Ltd v. 13. After the estimation of calibration values, Nautical Area Scattering Coefficients (NASC; m^2 nmi^{-2}) (Simmonds and MacLennan, 2005) were estimated through echo-integration over the 7-minute intervals per 4m-depth layer (Appendix A3 and Carlsen et al. 2024). Prey depth was then extracted as the mean depth of the median layer (i.e. at which the cumulative backscatter accounted for 50% of total) to inform on prey vertical migration and change in prey availability, based on 717,525 NASC values, divided over 36,292 water columns summaries. Prey aggregations (i.e. schools/shoals) were detected through image processing of the raw echograms in Python 3.11 using echoedge which relies on echopype (Lee *et al.* , 2024) 0.8.1 for reading and pre-processing of raw data (See appendix A4). Aggregations were extracted through thresholding methods with a minimum size fixed to 2x2m and excluding aggregations within 1m from the seabed. As drone velocity affected the number of aggregations detected, we (i) removed aggregations observed at extreme speeds (<0.17 or drone velocity as a covariate in all models. The final dataset had 40,570 observations of single aggregations, summarized into 7,089 bins of 10deg azimuth (˜40min time-periods/ 1.3km with average USV speed).

3 Statistical analyses

All statistical analyses were performed in R (version 4.2.2, R Core Team). Some outliers were removed but this never represented information.

3.1 Model variables

Analyses were divided into three groups: light dependent for (i) predators and (ii) prey behaviour (hereby predator~light and prey~light models), and (iii) prey dependent, i.e. predator behaviour based on predictions from light dependent prey behaviour (hereby predator~prey models).

3.1.1 Dependent variables

The predators' behaviour response variables (i.e. efficiency-, number- and depth of dives, and bout length) were selected based on their ability to represent different aspects of foraging behaviour, while being generalizable across species. Number of dives were summed per 10deg azimuth within a day/individual. Bottom-dive-cycle ratio (BDCr) informs on the predators efficiency of presumably foraging dives (Carbone and Houston, 1996). For modelling prey distributions, the response variables were prey depth and number of prey aggregations per 10deg azimuth as they are likely to affect diving predators (see *2.2 Prey distributions*).

3.1.2 Independent variables

Light variables were calculated based on the geographical position of the USV for prey data, and the position of the breeding colony for predators foraging data (Appendix A6). Light dependent models all included the fixed effects 'azimuth', 'zenith', 'week', and interactions between the three. In addition, the prey~light model for aggregations included USV 'velocity' as a covariate to correct for the speed of the drone (see *Prey aggregations* above). Predator~light and prey~light models included the temporal variable 'week', whilst predator~light models in addition included the factor breeding stage ('Stage', i.e. incubation, chick rearing, post-fledging and non-breeding) in interaction with light variables. The PDPs in predator~prey models were based on the 'fish depth' and 'number of aggregations' as predicted from the prey~light models, with interactions between the PDPs, and between those and 'week'. For predator~light and ~prey models where single dives/dive cycles were the unit of observations (i.e. dive efficiency and dive depth), the number of the dive in a bout ('Diven'), and the total number of dives in the bout ('bout length') were included as fixed effects, to reduce temporal autocorrelation. All predator models had fixed effects for 'sex', and random effects of identity of the individual ('BirdID'), logging interval of the TDR ('TDRlogint') and 'Year'. However, we did not include year effects to explain prey aggregation or depth, as those models were used to predict over the entire study period (2010, 2015-2023) even when no prey data were collected. See table 1 for full model structures (i.e. before model selection).

3.2 Distribution families

Model distribution families were gamma (link: log or identity) or Tweedie (power 1.1-1.99), with only natural logarithmic bout length and prey depth fitted with a Gaussian distribution. We visually inspected residual distributions (Appendix A8) to assess assumptions and model fit, and heteroscedasticity was inspected by plotting residuals against model fit.

3.3 Modelling

Generalized additive mixed effect models (Wood, 2024) were used in hypothesis testing (GAMMS; R package mgcv, see Wood, 2017). To account for variance, correlations, and cohort effects within predator and prey behaviours, we performed model selection to prevent overfitting while ensuring biologically meaningful groupings in the data were accounted for. We used backward stepwise selection from full models, based on generalized cross-validation (GCV) and deviance explained (DE), following the principle of parsimony and model simplicity. All parameters were checked for correlation and variance inflation to ensure they could appropriately be included in the same model. See full and final models, including distribution families and smooths in Appendix Table A7. The light dependent behaviour models for both predator and prey allowed for investigation into the effects of light levels independently of prey distribution patterns (Fig 2). All effects mentioned in results and discussion were statistically significant ($p<0.05$) unless otherwise stated. Parameter effects are supported by deviance explained (*DE)* and partial deviance (*pd)* in % figure texts. We here focus solely on the effects of solar azimuth and PDPs, but see model summaries in Appendix A9 and figures of interactions in Appendix A10 and A11. When prey distributions were predicted on the predators movement (i.e. for predator˜prey models), the velocity of the USV was set to the mean of observed velocity, 0.55m/s (See *Prey aggregations* above). Otherwise, the predictions were based on the focal values of predators dives with no modification made to the PDP models before.

Results

Summary statistics of diel activity

We continuously recorded ˜35,000 dives from 54 *U. aalge* individuals and ˜8,000 dives from 16 *A. torda* individuals, ˜36,000 prey depths and bins of 10deg azimuth. Both predators showed higher foraging efficiency during twilight, with a higher peak during dusk compared to dawn (+28% and +17% for *A. torda* and *U. aalge* respectively; Fig 1A), but for *A. torda* the elevated efficiency also lasted much longer during afternoon/dusk (110deg azimuth) than in the morning (60deg azimuth). Both predators concentrated depth of their dives to the depth of the largest abundances of prey (median of prey depth = 16m, *A. torda* depth = 12m and *U. aalge* = 15m; Fig 1B). Still, *U. aalge* , but not *A. torda* , also used deeper depths (˜20% dives at >50m) but only during daylight hours, while prey depth ranged from 4 to 96m both during the day or under low light levels. Both predators had a higher number of dives in light conditions with high foraging efficiency (Fig 1C), however *U. aalge* utilized a much wider range of light levels, both with the highest effort performed in lower light periods and with a higher proportion of dives throughout the day as compared to the *A. torda* . *A. torda* instead concentrated its effort during peak of twilight, with much more dives during dusk than dawn, and a more rapid decline in effort after the dawn peak. The median deg azimuth for dives were 73.7deg for *A. torda* and 68.8deg for *U. aalge* before noon (i.e. 0-180deg azimuth), and 289deg versus 290deg after noon (180-360deg azimuth), respectively. In summary, both predators foraged more in shallower waters, and were more efficient in twilight hours, most marked at dusk compared to dawn, and for *Alca T.* also more throughout the afternoon. Numbers of prey aggregations were highest around dawn and dusk, lowest during the night and at intermediate levels during daylight periods (Fig 1C). There was a distinct difference in prey abundance in the upper 50m of the water column between low-light and daylight periods (Table A3) as a result of vertical fish migration. This led to 22% increase in abundance in the upper 50 m of the water column, and an overall increase of 20% in detected abundance, during low light periods versus daylight (Carlsen et al., 2024).

Light-related activity and distribution patterns

Effort (number of dives) typically started increasing before the efficiency (BDCr) increased in the morning (0-50 versus 30-70 azimuth), and decreased only after the efficiency started decreasing (Fig 2A). Dive depth and bout lengths had opposite relations with solar position for *U. aalge* , where deeper dives coincided with shorter bouts in high light conditions and vice versa in the dark (Fig 2B). For *A. torda* bout lengths were best described as linearly increasing with azimuth. While the raw data previously showed an equal median dive depth across *A. torda* , the models depict a depth trend reflecting the vertical distribution of prey by azimuth similar to the trend in *U. aalge* . The *U. aalge* dives were markedly deeper during the day than night, and with higher peaks during vertical migrations, slightly more so during dawn than dusk (Fig 2B). When investigating the trends in diel PDPs, the depth distribution of prey was symmetrical around noon/midnight (Fig 2C), with inflection points at 73deg and 286deg, and an estimated average depth change of but was not symmetrical around noon/midnight (Fig 2C). The number of aggregations increased before the migration started in the early mornings (0-100deg Azimuth), but already by 160deg aggregations started dissolving and were reduced by ˜25% by early afternoon (Fig 2C) and kept decreasing towards the evening. Notably, while the majority of aggregations, especially in high number, were observed at

Predator activity as a function of prey distribution

When investigating the effect of prey on predators' foraging, we found that foraging efficiency and effort (BDCr, dive depth, dive numbers, bout length) were affected in a complex way for both species, as the interaction between prey depth and prey aggregation was retained in all models and always explained the most partial deviance. *A. torda* were most efficient when prey was at intermediate shallow depths (Fig 3A) and at intermediate aggregation numbers (Fig 3C). Dive efficiency decreased with prey depth in *U. aalge* (halved at deepest prey depth, thought the effect was not statistically significant; Fig 3A) but increased with aggregation numbers up to intermediate levels (1 aggregation/10deg azimuth), after which the steepness of the curve declined (Fig 3C). In both species, the interaction between prey depth and prey aggregation translated into a higher efficiency at deeper depth when prey aggregation numbers were low (Appendix A11), though for both species overall the prey distribution patterns explained very little of the deviance (Fig 3). *A. torda*decreased the number of dives with increasing prey depth (Fig 3B).*U. aalge* kept foraging at deeper distributions, while *A. torda* stopped diving when prey distribution got deeper than 22m. As the numbers of aggregations increased, so did the number of dives with a sigmoid curve for *A. torda* and almost linearly for *U. aalge*. These effects seem to be synergistic as both species performed more dives when there were high numbers of aggregations at shallow depth (Fig A11C&D), though for *U. aalge* high numbers of aggregations and deeper distributions also led to more dives (Fig A11D). Both species dove deeper when prey were deeper (Fig 3E). Dive depth positively increased until 24m prey depth for *U. aalge*, after which the depth stagnated and started decreasing. Interestingly, the same trend was visible in *A. torda* but for much shallower dive depths and a decrease that continued to higher depths. However, the response to increasing number of aggregations alone was negative, with decreasing depth already at lower numbers of aggregations for *A. torda* than*U. aalge* (Fig 3G). Both species also dove extra deep if there were many aggregations and deep distributions (Fig A11E&F).

Both predators had longer bout lengths when prey was shallow, until an optimum of 15m depth. The effect of aggregations alone was weak, both prey depth and aggregations were non-significant in *A. torda* (Fig 3H). However, due to the substantial interaction between prey aggregation and depth, *A. torda* increased bout length if there were many aggregations and shallow depth distributions, but also deep depth distributions with few aggregations (pd=0.38, Fig.A11G). Meanwhile, *U. aalge* had long bouts when aggregations were high except when prey was at its deepest (pd=0.37, Fig A11H).

Discussion

Using a unique detailed concomitant monitoring of both prey and predators, we showed that predators adjusted their foraging behaviour to diel prey distribution patterns (PDPs) and light levels. We found that while the two predators' behavioural response to PDPs followed similar curves, there were interesting differences in response to light levels that could be explained through the PDPs (e.g. the difference in timing of effort, period of elevated efficiency and depth of dives). While*U. aalge* dive behaviour was symmetrical around noon, reflecting the depth distribution of prey, the *A. torda* efforts rather reflected an inverted curve of aggregation numbers, and with next to no dive activity in low light levels despite favourable prey distribution. The predator's niche partitioning is therefore most likely a result of*U. aalge* adaptations to low light conditions (Regular, Hedd and Montevecchi, 2011) which allows them to exploit a wider range of PDPs, both in time and depth, while *A. torda* appear more dependent on high light levels overall. However, *A. torda* ' ability to forage efficiently for an extended period throughout the afternoon and dusk allowed them to meet needs before their efficiency is reduced by late night light conditions. Despite the species differences in response to light, both achieved high efficiency under conditions of shallow prey distributions and intermediate aggregation numbers. Our results highlight shared strategies in adapting to the dynamic prey landscape and niche partitioning in ability to utilize different prey distributions.

1 Predator niche partitioning

Despite their dive capacity (Chimienti *et al.* , 2017), *U. aalge* were most efficient when prey was shallow and/or aggregation numbers were low, particularly under low-light conditions. This may be partially explained by the metabolic constraints of longer, deeper dives, which increase recovery times and thus reduce efficiency of dives (Walton, Ruxton and Monaghan, 1998). *A. torda* , on the other hand, achieved peak efficiency at intermediate prey depths while being more efficient with the deeper of the utilized depth distributions if aggregation numbers were low, indicating that high numbers of aggregations were the main driver for decreased efficiency. This is reflected by their foraging under low azimuth levels, where both species reached peak foraging effort and efficiency well before maximum prey aggregation numbers in the morning, and peaked only after the aggregation numbers had declined in the afternoon. This, along with the dive depth responses suggests that foraging under intermediate and higher number of aggregations during dawn and mornings is likely driven by a trade-off between shallow depths of prey and suitable light levels, rather than by targeting intermediate levels of aggregations. *U. aalge* in addition tended to dive deeper at higher numbers of aggregations suggesting they adapted hunting tactics based on the PDPs. Potentially, *U. aalge* has dive- (Schneider and Piatt, 1986; Ponganis, 2015; Chimienti *et al.* , 2017) and visual (Smith and Clarke, 2012) capacities that allows them to utilize deeper depths with less aggregated prey if needed. Particularly interesting was the finding that in the evenings *A. torda* foraging effort tended to decrease before efficiency had reached its peak, likely reflecting a combination of state-dependent urgency in foraging (Houston and Rosenstrom, 2024), lack of predictability of good foraging patches (Bednekoff and Krebs, 1995; Houston and Rosenstrom, 2024) and the constraints by light availability. Early afternoon foraging efforts could secure resources under suboptimal conditions in anticipation of peak efficiency later in the afternoon, thus avoiding the risk of low-reward, opportunistic foraging after dark (Houston and Rosenstrom, 2024) when site-to-site orientation may be difficult. Despite both species having the dive capacity needed for all available depths in the study area (Piatt and Nettleship, 1985), *A. torda* ceased diving at relatively shallow prey depths as compared to the*U. aalge* and to *A. torda* in other systems (Barrett*et al.* , 1990). This is likely influenced by the poor light conditions and turbidity in the Baltic Sea (Murray *et al.* , 2019), rather than their adaptations regarding pressure at depths (Ponganis, 2015). The predators dove deeper with higher light levels, when prey was highly aggregated and while depth distribution was high. However, if there were more aggregations while prey depth was deep, both species would dive even deeper than before according to the interaction. As aggregations, particularly in high numbers tended to appear at relatively shallow depths, in the period of predator tracking, this response again suggests higher numbers of aggregations were unfavourable to both predator species, leading to strategies specific to aggregations. Much of the deviance in bout length was explained by light levels and prey distributions, where in *A. torda* bout lengths increased when there were many aggregations or distribution was deep, while for *U. aalge* the increase was by large attained high numbers of aggregations. It is however not possible to distinguish whether long bout lengths reflect an increased effort due to favourable foraging conditions or decreased success rate, and the two scenarios may not be mutually exclusive. In summary, *U. aalge* were more flexible in their utilization of prey distribution patterns through exploitation of a broader range of light levels and depths, and may thus be more robust to focal changes within a foraging site or range of colony during breeding.

2 Symmetry and synchrony of PDPs

The twilight bound aggregation peaks observed were likely due to aggregations formed during the vertical migration of clupeids (Zwolinski*et al.* , 2007; Solberg and Kaartvedt, 2017). The differences in numbers of aggregations during the morning versus evening (25% reduction) could be explained by state dependent behaviours (Lima and Dill, 1990) during diel vertical migration. During the morning descent phase (<120deg azimuth) the fish may have foraged all night (Nilsson *et al.* , 2003), and should prioritize energy-saving group swimming (Weihs, 1973), or even anti-predation behaviour by aggregating(Brock and Riffenburgh, 1960). This is perhaps particularly true for planktivores that remains in shallower water during the day after the vertical migration of zooplankton to deeper depths (Bollens*et al.* , 2011). The lower aggregation peak in the afternoon (>250deg azimuth) would then reflect prioritized foraging (Lima and Dill, 1990), an activity which is likely to start already during the ascent (See Appendix A4). The asynchrony between aggregation and depth migration supports this interpretation, since numbers of aggregations started before the descent and decreased as vertical migration was finalized. Interestingly, this asymmetry created a temporal window of elevated foraging conditions in the late afternoon and dusk for predators that perform better with low levels of aggregations and better visual conditions. Increased foraging activity in afternoon/dusk (i.e. vespertine preference) compared to dawn (i.e. matutinal preference), as seen here in *A. torda,* is found in a range of crepuscular taxa (Gupta *et al.* , 2023). Though this has been explained largely by state dependency, cost of movement and risk of starvation, this study identify nuanced spatiotemporal prey behaviour as an underlying mechanism. Previous studies have shown how *U. aalge* , utilises prey distributions at different hierarchical scales, but were unable to determine the dynamics between prey distribution and predator foraging site at fine scale (<3km resolution) (Fauchald, Erikstad and Skarsfjord, 2000). We here present an alternative approach to disentangle such small-scale predator-prey dynamics with high temporal resolution. As prey aggregation patterns were highly variable throughout the study period (Appendix A4), seeing an adaptation to handling a specific level of aggregations would be impractical for the predator unless the pattern impacted fecundity drastically. This may partially explain why aggregations seem to have a higher impact on foraging efficiency, effort and strategy across predator species. It should be noted that the number of aggregations predicted on the birds data were modest compared to the average estimates from the initial prey distribution models, which again was modest compared to some of the aggregation patterns recorded. This is due to most bird tracking being performed later in summer when aggregations activity in prey were lower. It has been unclear whether aggregations serve an advantage (e.g. by prey detectability) or a disadvantage (e.g. reduced prey catchability by confusion effect) to diving predators, and in particular small seabirds with limited dive capacity such as the alcids (Lett *et al.* , 2014; Thiebault*et al.* , 2016). Our study strongly suggest hunting under high aggregation is a focal disadvantage for both species, but our measurement for aggregations here were highly simplistic. Future studies should aim to take more complex aggregation characteristics (i.e. density) and presence-absence into account. Further, as we cannot distinguish the prey species or age/size classes in our prey data, the effects could be prey type related.

3 Conclusion

Light is a major driving factor of the predator niche differentiation, where *U. aalge* have a better ability to hunt in low light conditions as compared to *A. torda* . We were able to explain the higher dive efficiency and effort by predators during dawn and afternoon/dusk through temporal nuances in prey distribution patterns. Both predators performed better under shallow prey distribution with intermediate numbers of aggregations, but with differences in ability to forage under low-light conditions segregating them in timing of foraging and depth in the water column. *U. aalge* showed ability to utilize a wider range of light and prey distribution patterns than *A. torda.* The asymmetry in predator's behaviour around solar angle (i.e. azimuth) was explained by PDPs both directly and indirectly through timing by light. While the deep diving *U. aalge* utilized the light levels during prey's vertical migrations more, the *A. torda* was more affected by dynamics in the numbers of aggregations. The wide range of conditions utilized by *U. aalge* could give them an advantage under changes in PDPs, and perhaps even prey type, by season, or population impacts like fisheries and climate change, buffering them for their limitations in flight adaptation as compared to *A. torda* .

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Literature

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Table 1: Full model structures for each model group (predator~light, prey~light and predator~prey). Brackets [] around variables specific to certain response variables (see main text), parenthesis () for random effects and astrisk * for interactions. See Appendix A7 for full and final (post selection) model structures per response variable, including smooths and k-values, per species.

Model group	Independent variables
Predator ~ light	azimuth + zenith + stage + week + azimuth*zenith + azimuth*stage + zenith*stage + azimuth*week +
Prey ~ light	zenith + azimuth + azimuth*zenith + week+azimuth*week + zenith*week + [velocity]
Predator ~ prey	prey_depth + prey_aggregations + prey_depth*prey_aggregations + [bout length] + [diven] + (year) +(bi

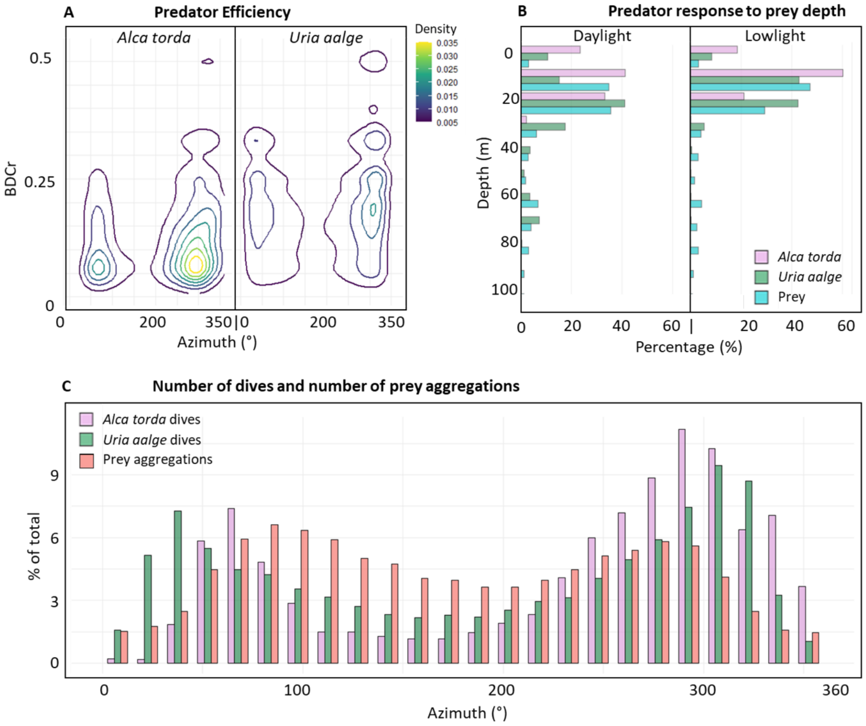

Fig 1: Diel prey distribution patterns and predator responses. **(A)** Predators foraging efficiency as bottom-dive cycle duration ratio (BDCr) per ° azimuth, with colour indicating density of observations. BDCr was scaled across the two predator species by minimum and maximum values. **(B)** Depth of prey (blue) and the corresponding depth of dives (% of total) in *Alca torda* (violet) versus *Uria aalge* (green) under daylight versus low light (I.e. dusk, dawn and night; based on nautical light levels). **(C)** % of total numbers of dives in predators and corresponding numbers of prey aggregations (red) per 15 °s azimuth (binned).

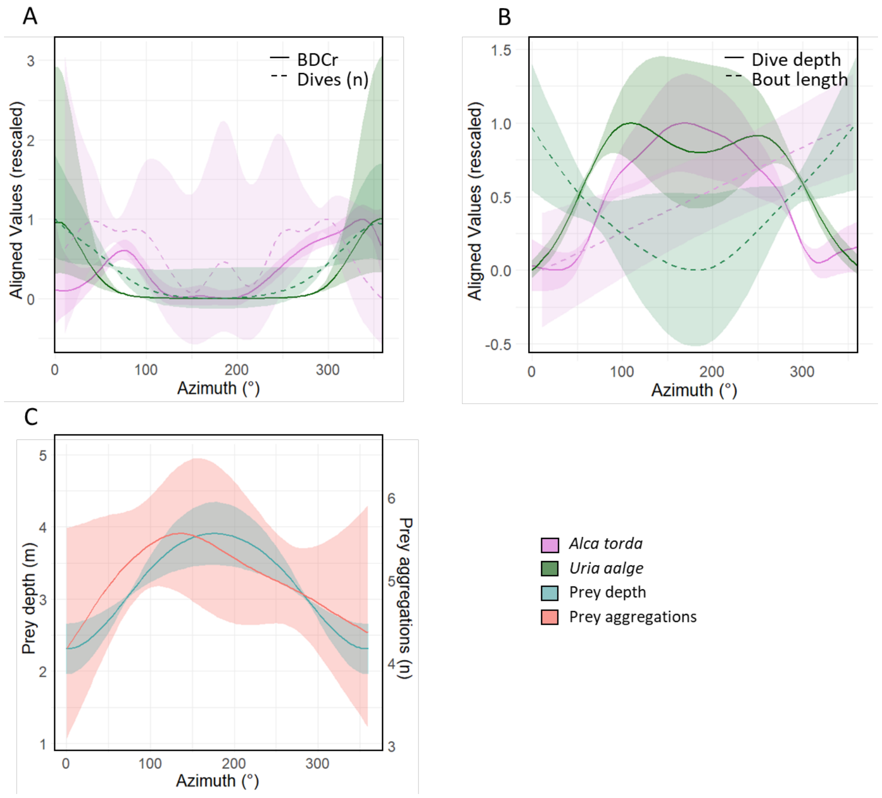

Fig. 2: Scaled predators foraging behaviour and prey distribution patterns by degree (°) azimuth. **(A)** predators' foraging effort by number of dives per 10° Azimuth (DE=17%, pd=68%; *U. aalge* DE= 31%, pd=25%), and efficiency by bottom-dive-cycle ratio (BDCr; *A. torda* DE=21%, pd=5%; *U. aalge* DE=18%, pd=3%). **(B)** Predators foraging depth (depth of dive; *A. torda* DE=14%, pd=23%; *U. aalge* DE=34%, pd=31%) and natural logarithmic bout length (n dives/bout; *A. torda* DE=11%, pd=35%; *U. aalge* DE=9%, pd=24%). **(C)** Depth of prey on natural logarithmic scale (DE=15%, pd=8%) and number of aggregations (DE=25%, pd=6%). *Total deviance explained (DE) and partial deviance (pd) for azimuth, see Appendix A9 for model summary and A10 for interactions.

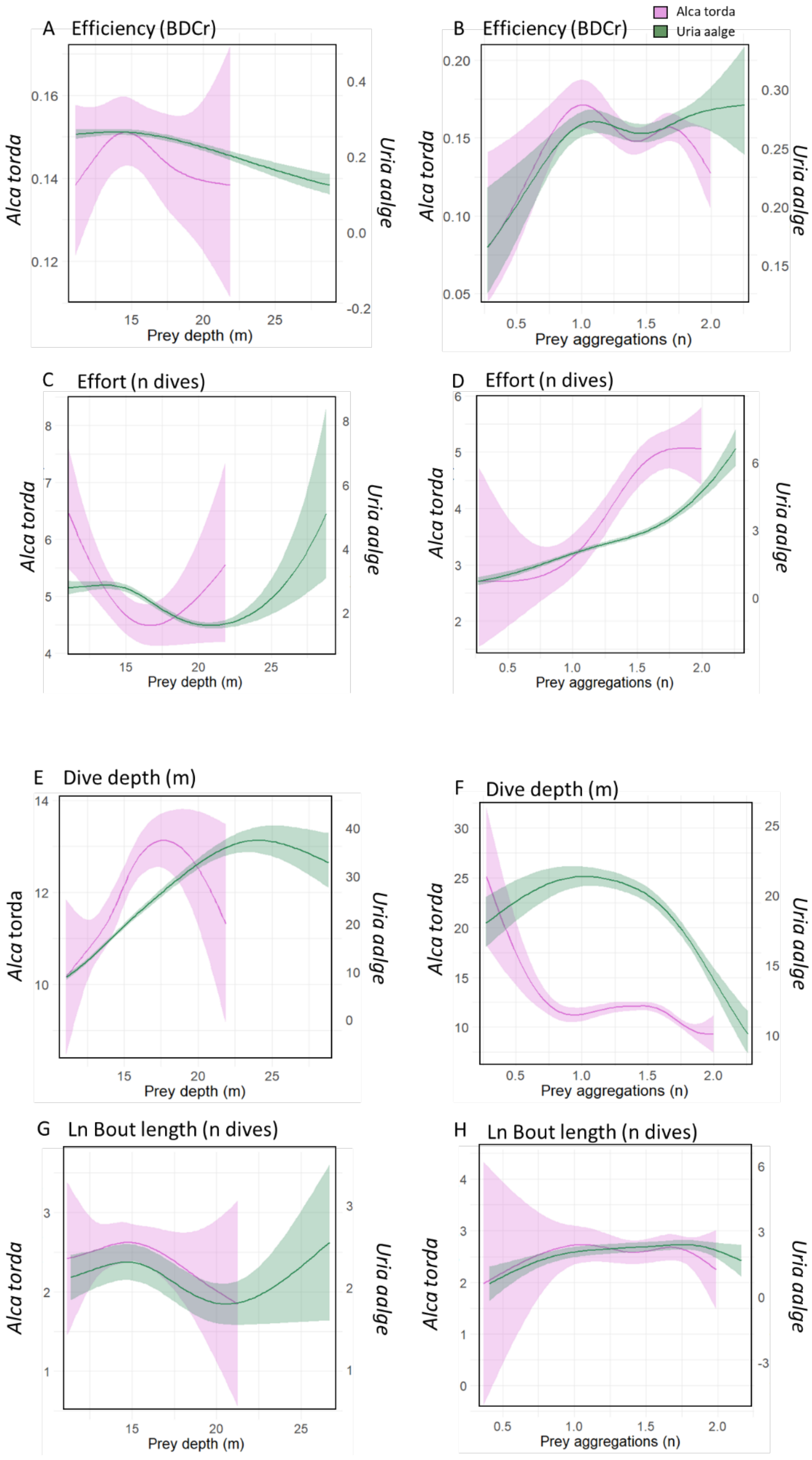

Fig 3a: Predators responses to prey depth distribution and numbers of aggregation. **(A & B)** Dive efficiency by bottom-dive-cycle ratio (BDCr; *A. torda* DE=18%, pd_{depth}=1%, pd_{agg} =2%, pd_{depth}* pd_{agg} =5%; *U.*

aalge DE=16%, pd_{depth} =1%, pd_{agg}=0.5%, pd_{depth}* pd_{agg} =2%). **(C & D)** Number of dives (*A. torda* DE=11%, pd_{depth} =6%, pd_{agg} =8%, pd_{depth} * pd_{agg} =21%; *U. aalge* DE=19%, pd_{depth} =10%, pd_{agg} =20, pd_{depth} * pd_{agg} =32%). **(E&F)** Depth of dives (*A. torda* DE=11%, pd_{depth} =6%, pd_{agg} =8%, pd_{depth} * pd_{agg} =21 *U. aalge* DE=22%, pd_{depth}=17%, pd_{agg} =2%, pd_{depth} * pd_{agg} =29%). And **(G & H)** bout length (n dives; *A. torda* DE=17%, pd_{depth} =2%, pd_{agg} =7%, pd_{depth} * pd_{agg} =38%; *U. aalge* DE= 8%, pd_{depth} =18%, pd_{agg} =13%, pd_{depth} * pd_{agg} =37%). Total deviance explained (DE) and partial deviance (pd) for azimuth, see Appendix A9 for model summary and A11 for interactions.