

# Diel vertical migration of prey and light availability constrain foraging in an Arctic seabird

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**Abstract** Studies of seabird–prey interactions often focus on biotic factors, such as prey abundance, seabird biomechanics and competition. In contrast, we examined the influence of abiotic factors, particularly weather, light and tide, on the diving behaviour of thick-billed murre (*Uria lomvia*) foraging in the Canadian Low Arctic. We found little evidence that tide and weather influenced dive behaviour. As visual predators, light availability limits foraging opportunities; however, prey often surface at night so there may be a trade-off between increased food availability and reduced foraging ability during low-light conditions. Our data lent support to both ideas, as dive depth increased with light availability and the proportion of vertically migrating schooling prey was highest during sunup and sundown. There was no difference in dive depth between sexes outside the period of sundown; males, which forage at night, dove shallower than females in the late afternoon, which we suggest is because they specialize on shallow prey often caught at night. Apparently, adaptation for higher oxygen stores or lower oxygen consumption in deeper-diving females overrode any adaptation for improved vision in night-specialist males. We concluded that light availability

interacted with prey vertical migration to impact underwater foraging abilities of breath-hold divers.

## Introduction

Visual predators that feed near the surface, such as birds, are limited by particular abiotic constraints, such as tides, light and wave action (Boyd et al. 2002; Wilson et al. 2011). Understanding how those limitations interact with the prey field is valuable for interpreting what seabird behaviour tells us about the changing marine environment (Davoren et al. 2003; Montevecchi 2007; Garthe et al. 2007). For example, seabird diet is one of the few existing data sets relevant to ongoing food web changes in Hudson Bay, a region that is logistically challenging to census and holds no large-scale commercial fishery. However, these changes occur against a backdrop of changes in ice and weather patterns (Gaston et al. 2003, 2005; Gaston and Elliott 2014). Better knowledge of how foraging is affected by weather and other abiotic factors can improve our understanding of how diet trends reflect ecosystem changes. Nonetheless, studies of seabird–prey interactions usually focus on biotic factors, such as prey availability, seabird biomechanics and competition (e.g. Piatt et al. 2007; Cook et al. 2007; Elliott et al. 2008a).

Inclement weather can impact the foraging behaviour of birds by altering prey accessibility or activity costs (Grubb 1977; Gilchrist et al. 1998; Robinson et al. 2002). For instance, high wind speeds reduce foraging costs in petrels but increase foraging costs in auks, reflecting their different flight styles (Furness and Bryant 1996). Low water temperatures increase diving and resting costs in endotherms (Croll and McLaren 1993; Enstipp et al. 2007). Not surprisingly, then, storms can reduce adult body mass

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and chick-provisioning rates of piscivorous birds, ultimately lowering reproductive success (Gende et al. 1997; Elliott et al. 2005; Mallory et al. 2009), especially in auks (Birkhead 1976; Hatch 1984; Finney et al. 1999). Storms may impact even diving birds that pursue prey well below the water surface because wave action disrupts cues for locating prey or impacts the costs of resting at the surface (Finney et al. 1999; Shoji et al. 2010).

In contrast to the erratic nature of weather patterns, light availability changes more predictably during diel and lunar cycles, although water clarity and cloud cover can also play a less predictable role (Cannell and Cullen 1998; Regular et al. 2010, 2011; Rubolini et al. 2015). For visual predators, such as most marine birds and mammals, light intensity limits foraging opportunities, and dive depth usually decreases at night (Kooymann 1975; Wilson et al. 1993; Paredes et al. 2008). In common murre (*Uria aalge*), for example, dive depth increases on moonlit nights and decreases on starlit nights (Regular et al. 2011). However, zooplankton approach the surface at night to take advantage of reduced predation by sight-hunting predators and forage on phytoplankton that are abundant near the surface, where solar energy is high (diel vertical migration; Wilson et al. 1993; Regular et al. 2010, 2011). Hence, there may be a trade-off between high food availability and low visibility for avian predators at night (Croll and McLaren 1992; Luque et al. 2007; Riou and Hamer 2008). To maximize foraging efficiency, many marine predators are crepuscular, foraging at dusk and dawn on swarms of zooplankton or their associated predators, such as fish, that are visible and yet no longer below the depth range of marine birds (Hedd et al. 2009; Garthe et al. 2007).

The effect of light availability can influence and be compounded by daily schedules. For instance, murre show strong sex-stereotyped daily schedules, with one sex foraging for 12 h including solar midnight and the other for 12 h including solar noon; the exact schedule varies among colonies (Jones et al. 2002; Paredes et al. 2008; Elliott et al. 2010b). Indeed, when Croll et al. (1992) first studied murre, they concluded that most murre foraged primarily at night, presumably because they equipped mostly males (sex was not determined), which is the sex that forages at night at their study site. Thus, some individuals may consistently spend the night at sea, while others do not, and the birds that spend nights at sea make shallow dives (Thaxter et al. 2009; Elliott et al. 2010b; Harding et al. 2013). The sex that specializes on night diving may have better vision (e.g. Fernández-Juricic et al. 2013), leading to deeper diving at all times of day. Alternatively, if night-foraging birds are specializing on vertically migrating prey, they may continue to follow prey as they descend to darker depths because even if the dives become less profitable, that

may still be more profitable than spending the time and energy to locate a new patch. If birds are specializing on different prey at night, then we would predict a bimodal distribution in flight times for the “night specialists”, but not day specialists, as night specialists spend the nights foraging at a different location, foraging on vertically migrating prey, than during the daytime.

A third abiotic factor, tide, operates primarily at the scale of hours although the amplitude of cycles is tied to lunar cycles, and can influence predator behaviour (Bornemann et al. 1998; Frere et al. 2002). In the intertidal zone, feeding rates often increase as the tide recedes because birds can then access prey left exposed (Watson et al. 1991; Elliott et al. 2003, 2005; Schwemmer and Garthe 2010). Below the intertidal zone, tide can still have a strong effect on prey availability. Tidal currents can also affect seabirds by altering prey abundance (Grigg et al. 1985; Holm and Burger 2002; Tarlow et al. 2003) or profitability (Wilson et al. 2001; Heath and Gilchrist 2010; Cottin et al. 2012). For instance, planktivorous auks increase dive depth, dive frequency and the proportion of euphausiids in the diet during spring tides when advective tidal currents bring swarms of easily captured planktonic euphausiids to the surface (Burger and Powell 1990; Elliott et al. 2010a; Shoji et al. 2010). Likewise, Cairns and Schneider (1990) speculated that thick-billed murre (*Uria lomvia*) congregated at hot spots created by tidal “pumps” between islands in northern Hudson Bay to take advantage of amphipods caught in the current or attracted to the nutrients brought to the surface.

As climate change is expected to increase the severity of summer storms and to bring animals from areas of long nights to areas with no nights (Finney et al. 1999), our paper provides a background for investigating the non-trophic impact of climate change on marine animals. We studied the effects of three abiotic factors: weather, light availability and tide, on the foraging behaviour of Low Arctic thick-billed murre. Diel variation in diving depths and frequency have been documented for murre at low (Nevins 2004; Paredes et al. 2008; Thaxter et al. 2009) but not high (Falk et al. 2000; Mehlum et al. 2001; Tremblay et al. 2003) latitudes, and it is intriguing to study the phenomenon in a situation intermediate between no nights (High Arctic) and long nights (temperate regions). Furthermore, whereas most studies occurred at locations where murre fed predominately on only one or two prey items, prey diversity is much higher in the Low Arctic allowing murre confronted with reducing diving capability due to changing light availability to switch prey. Past studies of the effect of weather on auk foraging tended to only include one, or a few, seasons (Birkhead 1976; Konarzewski and Taylor 1989; Finney et al. 1999; Harter 2007), so that a few poor weather days in a row coincident with poor food

availability could have created spurious relationships. To avoid issues of autocorrelation, we included data covering many years and providing strong mechanistic linkages between different temporal scales. We predicted that wind, via wave action, light availability and tide would impact the dive behaviour of murres, with high wind speed decreasing dive frequency, light availability reducing dive depth and duration, and tide height increasing dive depth. We have previously demonstrated that light availability and wind impact flying and provisioning rates of murres, but that adults buffer the effect of wind over the scale of days so that offspring growth rates are not affected (Elliott et al. 2008b, 2014). Given that males are “night specialists” at our study site (Elliott et al. 2010b), we predicted that males would dive deeper at any time of day than females, and would show a bimodal distribution in flight times.

## Materials and methods

We studied murres at the west colony on Coats Island, Nunavut (62°57'N, 82°00'W), during the chick-rearing period (July 15–August 15) 1998–2011. As part of a long-term monitoring study (Gaston et al. 2003, 2009), we completed at least three continuous 24-h feeding watches during each season (44 total watches). During the watches, we estimated visually the species and length of all fish delivered to offspring at ~30 breeding sites and used species-specific relationships between total energy and fish length to determine energy delivery rates (Gaston et al. 2003; Elliott and Gaston 2008; Elliott et al. 2009). We only included birds with chicks 3–15 days old because feeding rates are constant for murres with chicks within that age range (Elliott et al. 2009). All birds were sexed using a combination of genetic markers, behavioural observations (position during copulation) and partner history (Elliott et al. 2010b). Night (sundown to sunup) duration at our study site stretched from 4 h and 17 min on 15 July to 7 h and 34 min on 15 August and never reached astronomical twilight during that period. On 15 July, there was also no nautical twilight, while by 15 August, there were 5 h and 25 min of civil twilight and 2 h and 9 min of nautical twilight.

We attached Lotek LTD1100 (5 g; 2004–2007,  $N = 140$ ), LAT1400 (5 g; 2008,  $N = 20$ ) and LAT1500 (3 g; 2009,  $N = 50$ ) time-depth recorders to the legs of breeding murres and extracted dive behaviour (frequency, depth and duration) from the pressure log and flights from the temperature log (Elliott et al. 2008b, 2009). The leg-mounted time-depth recorders do not measurably impact murre behaviour (Elliott et al. 2008). All raw dive files are archived alongside Elliott et al. (2015).

The vast majority of chick-rearing birds at the Coats Island west colony forage within 100 km to the west of the colony (Elliott et al. 2008). Therefore, the core foraging area is bounded by the colony and the community of Coral Harbour (145 km distant). We downloaded average daily weather recorded at Coral Harbour airport (temperature, pressure, rainfall, wind speed and direction obtained from [www.weatheroffice.gc.ca](http://www.weatheroffice.gc.ca)). We recorded weather daily (18 h 00 min) at a fixed point near the Coats Island cabin, immediately adjacent to the murre colony, using a hand-held anemometer (wind speed and direction), a rain gauge (rainfall), barometer (pressure) and electronic thermometer (maximum and minimum temperatures). We used daily average weather values for the Coral Harbour data. Variables recorded at Coral Harbour and Coats Island were correlated, and we used a principal component analysis to remove correlations between similar variables (Finney et al. 1999). Hourly tide height was obtained from [www.tides.gc.ca](http://www.tides.gc.ca).

## Statistical analyses

For each diving and feeding watch variables (hourly bins), we constructed a general linear model using tide height in metres, time of day (circularly transformed), calendar date, device type and PC1–PC4 of the daily weather variables as independent variables (PC1–PC4 were constant across all hourly bins within a given day). To examine behaviour in detail, we computed a general linear mixed model with individual (for diving) or site (for feeding watches) as a random effect, dive depth, dive duration and dive frequency as dependent variables, and either light availability as the independent variable. We calculated light availability using the *R* script validated by Regular et al. (2011) based on calculated absolute solar irradiance and sun angle, calculated moon angle, phase and absolute irradiance, and cloud cover. Light intensity at the water's surface was calculated after correcting for extinction, time of absolute irradiance from day and date. We also accounted for the earth's atmosphere and cloud cover by assuming that global solar irradiance was 60, 50 and 20 % same set of absolute solar irradiance during clear, partially cloudy and cloudy periods (Regular et al. 2011). Light intensity estimates were calculated by applying appropriate extinction values, according to analyses with cloud cover, date and moon phase (days from or until new moon) as covariates instead of inferred light availability to local cloud cover, to absolute solar and lunar irradiance (Regular et al. 2011). Active radiation was approximated by multiplying total global irradiance by 50 % (Regular et al. 2011) to examine what component of variation in light availability was most important. We completed all statistical analyses in R 2.14.2.

**Table 1** Loadings of weather variables on the first four axes of a principal components analysis (PCA) that included all weather variables

	Axis 1	Axis 2	Axis 3	Axis 4
(%) Variation explained	28	14	10	10
Maximum temperature (°C)	<b>0.362</b>	0.186	0.038	-0.197
Minimum temperature (°C)	0.294	<b>0.349</b>	0.096	-0.097
Rainfall (mm)	-0.231	<b>0.289</b>	-0.028	0.053
Barometric pressure (mmHg)	0.216	<b>-0.402</b>	0.054	0.195
Wind speed (ms <sup>-1</sup> )	-0.070	<b>0.258</b>	-0.200	-0.029
Northerly winds (ms <sup>-1</sup> )	-0.070	0.118	-0.307	<b>0.362</b>
Easterly winds (ms <sup>-1</sup> )	-0.099	0.034	<b>0.543</b>	0.419
<i>Maximum temperature</i> (°C)	<b>0.419</b>	0.085	-0.147	0.153
<i>Minimum temperature</i> (°C)	0.298	<b>0.387</b>	0.019	0.220
<i>Average temperature</i> (°C)	<b>0.424</b>	0.213	-0.101	0.198
<i>Rainfall</i> (mm)	-0.216	0.343	0.230	-0.157
<i>Barometric pressure</i> (mmHg)	0.285	-0.299	<b>0.305</b>	0.202
<i>Wind speed</i> (ms <sup>-1</sup> )	-0.256	<b>0.257</b>	-0.252	0.319
<i>Northerly winds</i> (ms <sup>-1</sup> )	-0.105	0.041	-0.372	<b>0.452</b>
<i>Easterly winds</i> (ms <sup>-1</sup> )	-0.118	0.224	<b>0.477</b>	0.348

Weather associated with dominant axes are shown in bold

Variables measured at the Coats Island colony are non-italicized, and variables measured at Coral Harbour are italicized. To remove seasonal trends, all variables represent residuals for each day on the average value for that date across all years. Strongest associations (>0.25) between variables and principal components 1–4 are shown

## Results

Daily maximum ( $R = 0.59$ ,  $P < 0.0001$ ) and minimum ( $R = 0.57$ ,  $P < 0.0001$ ) temperatures, rainfall ( $R = 0.41$ ,  $P < 0.0001$ ), pressure ( $R = 0.42$ ,  $P < 0.0001$ ), wind speed ( $R = 0.30$ ,  $P < 0.0001$ ) and magnitude of wind in a particular direction ( $R = 0.46$ ,  $P < 0.0001$ ) were all correlated between Coral Harbour and Coats Island camp, showing that weather was correlated across the spatial scale of our study. The first four axes of a principal components analysis explained 62 % of the variation in weather variables (Table 1), with temperature positively loaded on the first axis (“temperature axis”) and wind and rainfall positively and pressure negatively loaded on the second axis (“storm axis”, Fig. 1; Table 1). Easterly winds (the component of wind in the easterly direction: wind speed multiplied by the sine of wind direction) positively loaded on the third axis and northerly winds (the component of wind in the northerly direction: wind speed multiplied by the cosine of wind direction) positively loaded on the fourth axis (Table 1; Fig. 1).

Energy delivered in the form of amphipods depended on time of day (sine term,  $t_{251} = -2.48$ ,  $P < 0.0001$ , Fig. 1), date ( $t_{251} = 4.22$ ,  $P < 0.0001$ ) and weather PC1 ( $t_{251} = -4.33$ ,

$P < 0.0001$ ) and PC2 ( $t_{251} = -4.31$ ,  $P < 0.0001$ ). Energy delivered in the form of capelin depended on date ( $t_{251} = 5.91$ ,  $P < 0.0001$ ) and weather PC1 ( $t_{251} = -5.35$ ,  $P < 0.0001$ ) and PC4 ( $t_{251} = 4.77$ ,  $P < 0.0001$ ). Energy delivered in the form of two schooling fish, cod and sand lance, depended on date (cod:  $t_{251} = -2.93$ ,  $P < 0.0001$ ; sand lance:  $t_{251} = 2.88$ ,  $P < 0.0001$ ), weather PC2 (cod:  $t_{251} = 4.55$ ,  $P < 0.0001$ ; sand lance:  $t_{251} = 3.43$ ,  $P < 0.0001$ ) and PC4 (cod:  $t_{251} = 3.87$ ,  $P < 0.0001$ ; sand lance:  $t_{251} = 4.01$ ,  $P < 0.0001$ ) and, for sand lance alone, time of day (sine term:  $t_{251} = 3.11$ ,  $P < 0.0001$ , Fig. 2). Energy delivered in the form of three benthic fish, snakeblenny (*Eumesogrammus praecisus*), fish doctor (*Gymnelus viridis*) and daubed shanny (*Leptoclinus maculatus*), depended on time of day (cosine term, snakeblenny:  $t_{251} = 4.75$ ,  $P < 0.0001$ ; fish doctor:  $t_{251} = 3.24$ ,  $P < 0.0001$ ; daubed shanny:  $t_{251} = 3.00$ ,  $P < 0.0001$ , Fig. 1) and, for daubed shanny alone, date ( $t_{251} = -7.34$ ,  $P < 0.0001$ ). No other relationships were significant (Table 2).

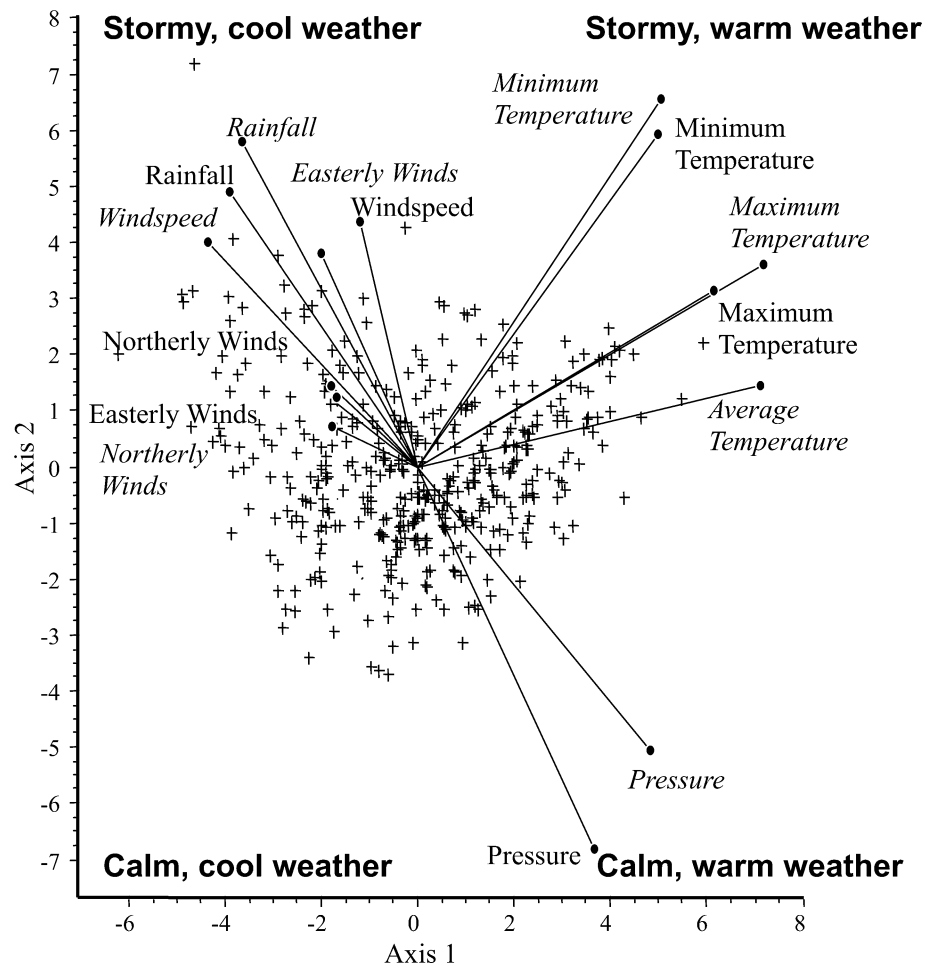
Dive depth depended heavily on time of day, with individuals making more, shallower dives when light was low (Fig. 3). Specifically, when included in a general linear mixed model with individual as a random effect, dive frequency ( $t_{207} = -43.1$ ,  $P < 0.0001$ ), dive depth ( $t_{207} = -231$ ,  $P < 0.0001$ ) and dive duration ( $t_{207} = -165$ ,  $P < 0.0001$ ) all depended on light availability. At a given time of day, there is no apparent difference in dive depth between males and females, except in the late afternoon (Fig. 3), when females dive deeper than males. Males, but not females, showed a bimodal distribution in return flight times (Fig. 4). When we restricted analyses to the darkest time of day ( $\pm 1.5$  h from solar midnight), dive frequency ( $t_{101} = -7.56$ ,  $P < 0.0001$ ) and depth ( $t_{101} = -9.34$ ,  $P < 0.0001$ ) decreased with date. However, cloud cover and moonlight had no effect on any of those parameters (all  $P > 0.05$ ).

## Discussion

Light availability constrained dive behaviour in Low Arctic thick-billed murres, whereas tide and weather did not have a strong effect. A strong impact of light availability on foraging behaviour has been found previously in fish (e.g. McMahon and Holanov 1995; Fraser and Metcalfe 1997), marine mammals (e.g. Kooyman 1975; Horning and Trillmich 1999) and both terrestrial (Jetz et al. 2003) and marine birds (Wilson et al. 1993; White et al. 2007; Zimmer et al. 2008). In our study, murres made fewer, but longer and deeper, dives when light intensity was higher.

Our results mirror closely those described for murres equipped with light sensors; murres forage at very low

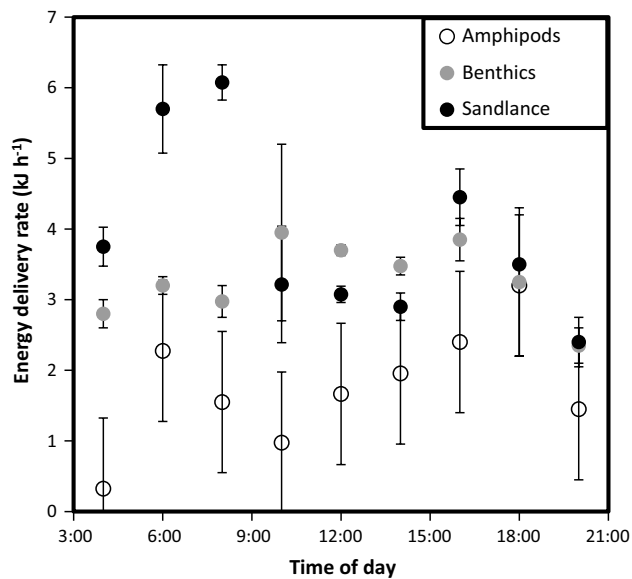
**Fig. 1** Axes 1 and 2 of a principal component analysis (PCA) which included all weather variables and their effect on the foraging behaviour of thick-billed murres (*Uria lomvia*). Variables measured at the Coats Island colony are *non-italicized*, and variables measured at Coral Harbour are *italicized*. In **bold**, the main environmental patterns interpreted from the PCA results. To remove seasonal trends, all variables represent residuals for each day on the average value for that date across all years



light intensities, and dive depth at night is determined by light availability (Paredes et al. 2008; Regular et al. 2011). Indeed, time of day factored into most of our models for dive and flight behaviour (murres seldom fly at night; Elliott et al. 2008b), but dive depths at night tended to be shallower than those described for murres elsewhere, despite the higher latitude and shorter nights (presumably meaning more light available) at our study site; common murres regularly dove to ~30 m at night (Regular et al. 2010, 2011). The most likely difference is prey type, as common murres fed primarily on capelin schools, whereas thick-billed murres likely fed on amphipods; stable isotopes and stomach contents of males, which dive primarily at night, imply that they feed to a greater degree on amphipods than females, which dive primarily during the day (Elliott et al. 2010b). Whereas moonlight played a strong role in modulating light availability, and therefore dive behaviour, in Newfoundland, moonlight and cloud cover played no measurable role at our study site where true darkness was extremely brief. There is no night in the Far North, and so light availability changes little if at all during the breeding season and presumably does not affect foraging.

At lower latitudes, twilight is relatively brief and the effect of moonlight is strong (Regular et al. 2011). At our study site, where virtually all of “night” consists of civil twilight, the dominant effect is one of date with its concomitant effect on night length and the duration and deepness of civil twilight leading to individuals diving less often and shallower (Fig. 5).

Diet composition was also influenced by light availability, with energy delivery rates for sand lance increasing and amphipods decreasing with a sine term for time of day, meaning that sand lance were delivered primarily in the morning (~06:00) and amphipods in the evening (~18:00). Amphipods and sand lance are the two prey groups that would be most likely to complete daily vertical migration in search of plankton at the surface. We suggest that the diurnal trends reflect diel vertical migration, with planktivorous prey following diel cycles such that predators can only access them during crepuscular feeding; many marine animals show peak foraging rates at dawn and dusk when prey are still within the reach of birds but when there is still sufficient light to forage (Piersma et al. 1988; Wilson et al. 1993; Zimmer et al. 2008). Meanwhile, energy



**Fig. 2** Energy delivery rate ( $\text{kJ h}^{-1}$ ) relative to time of day (h) for thick-billed murres at Coats Island 1998–2011. Shown are the three prey groups that showed a significant relationship, and averages were calculated excluding periods of darkness when delivery rates were low (21:00–04:00; Elliott et al. 2008b). The cosine term was significant for benthic prey, indicating that energy delivery rate was highest at 12:00, while the sine term was significant for sand lance and amphipods, indicating that energy delivery rate was highest near 6:00 and 18:00

delivery rates for benthic prey items decreased at night (the cosine term for time of day), showing that they were delivered primarily during the middle of the day. Presumably, deep, benthic prey items would be inaccessible for visible predators at night. In addition, schooling fish were delivered less frequently during stormy weather, when murres switched to more predictable prey (Elliott et al. 2014), and during late breeding (calendar date) as high-quality items (cod/benthics) were depleted over the course of the season (Elliott et al. 2009).

Diel variation in foraging behaviour had a strong impact on average dive parameters for each sex, as males forage primarily at night and females during the day (Elliott et al. 2010b). Indeed, when Croll et al. (1992) first

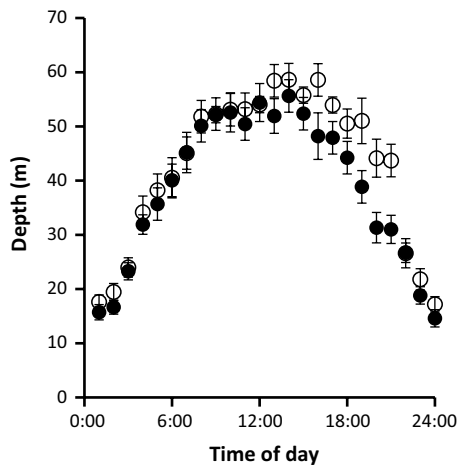
studied murres at our study site, they concluded that most murres foraged primarily at night, presumably because they equipped mostly males. For the most part, there was no intrinsic difference in dive depth for males versus females, except that males tended to forage shallower than females during the late afternoon—contradicting the notion that they are specialized visually for darker water. Rather, we suggest that this is a consequence of females specializing on deep water prey and males specializing on vertically migrating amphipods (Elliott et al. 2010b). The females may have continued to forage on deep water prey as light deteriorated because they were already present at a location where deep water prey occurred, while males, which would have been beginning their foraging trip at that time, may have moved to locations where amphipods, sand lance and other vertically migrating prey were beginning to appear. The bimodal distribution of return flights in males likely reflected alternations between long, overnight trips for self-feeding (murres rarely deliver food at night; Elliott et al. 2008b) and shorter trips during daylight for chick-provisioning. A similar pattern has been observed in many seabirds (Weimerskirch et al. 1994; Gray and Hamer 2001; Ropert-Coudert et al. 2004), even without the forced self-feeding overnight period associated with 12-h shifts in the sub-Arctic (Welcker et al. 2009).

Many weather variables correlated with one another, and weather could largely be divided into two components: a temperature component (warm vs. cold days) and a storm component (low pressure, high wind speed/rainfall vs. high pressure, low wind speed/rainfall). We previously showed that the storm component, and especially wind speed and direction, strongly impacted flight behaviour (Elliott et al. 2014), and we now show that it had little impact on underwater behaviour. In contrast, wind impacted diving behaviour and chick growth rates in shallow-diving auks (Konarzewski and Taylor 1989; Shoji et al. 2010), but not deep-diving auks (Finney et al. 1999), and feeding rates were impacted in other auks (Birkhead 1976; Finney et al. 1999; Harter 2007). There was no effect of weather on attendance patterns of murres in Newfoundland (Piatt and McLagan 1987).

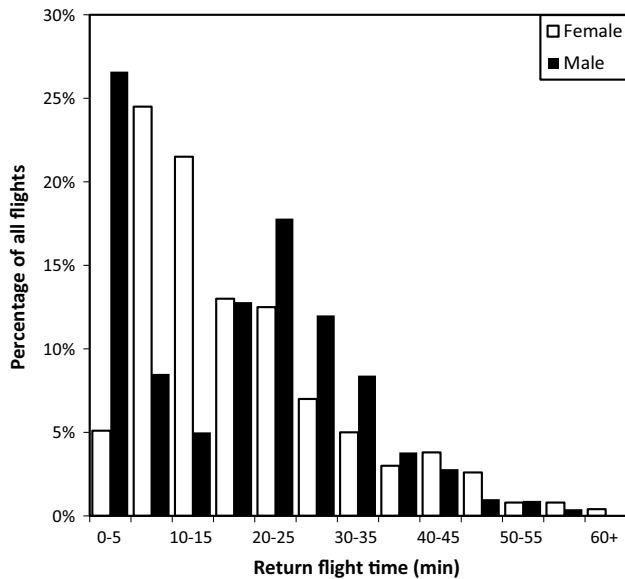
**Table 2** *F* values (*P* values in parentheses) from general linear mixed models (GLMMs), with individual as a random factor, between four measures of diving behaviour and seven abiotic environmental variables

	PC1	PC2	PC3	PC4	Tide	Time	Year
Dive duration	0.15 (0.70)	1.38 (0.24)	0.07 (0.80)	2.15 (0.14)	1.48 (0.22)	<b>612 (&lt;0.0001)</b>	<b>15.8 (&lt;0.0001)</b>
Dive depth	2.56 (0.11)	0.94 (0.33)	0.39 (0.53)	1.66 (0.20)	0.11 (0.74)	<b>677 (&lt;0.0001)</b>	<b>7.15 (&lt;0.0001)</b>
Dive frequency	5.04 (0.02)	1.30 (0.26)	0.22 (0.64)	4.82 (0.03)	0.08 (0.78)	<b>289 (&lt;0.0001)</b>	<b>8.2 (&lt;0.0001)</b>
Index of patch quality	7.09 (0.008)	0.06 (0.81)	1.22 (0.27)	0.00 (0.99)	2.68 (0.10)	<b>21.2 (&lt;0.0001)</b>	<b>14.4 (&lt;0.0001)</b>

Values in bold are statistically significant at the sequential Bonferroni-corrected value of  $P < 0.003$

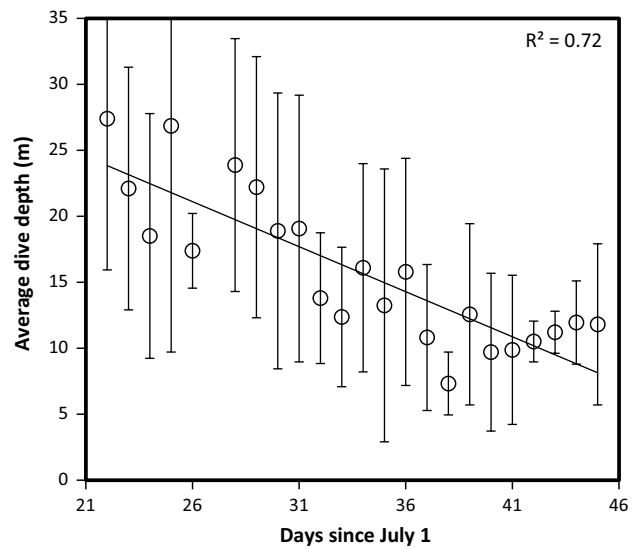


**Fig. 3** Average dive depth ( $\pm$ SE) relative to time of day (GMT-5.5) for 56 male and 48 female thick-billed murrelets at Coats Island between 2004 and 2009. Average dive depth was calculated for each 1-h bin for each individual and then averaged across individuals



**Fig. 4** Frequency distribution (%) of return flight times for male (filled bars) and female (empty bars) thick-billed murrelets at Coats Island between 2004 and 2009 showed a bimodal distribution for males and a unimodal distribution for females

Tide did not factor into any of our models and did not appear to play a strong role in murre foraging behaviour. In contrast, Piatt and McLagan (1987) found a relationship between tide and murre attendance patterns. Strong tidal currents are created between islands (Cairns and Schneider 1990; Holm and Burger 2002; Heath et al. 2006) or along inlets (Wilson et al. 2001), especially where tidal amplitude is large. However, foraging at Coats Island is mostly offshore



**Fig. 5** Relationship between the average dive depth ( $\pm$ 1.5 h from solar midnight) of thick-billed murrelets at Coats Island and days since July 1. Coefficient of determination ( $R^2$ ) shown

(Elliott et al. 2008a), and tidal amplitudes in nearby waters are low. Consequently it is probably not surprising that tide played less of a role in murre foraging behaviour at Coats Island than at the Nuvuk Islands, 300 km to the west (Cairns and Schneider 1990), or strongly tidal regions of the Bering Sea (Haney and Schauer 1994). Likewise, unlike benthic-feeding cormorants (Gandini et al. 2005; Zeenath and Zacharias 2010), tide had little impact on benthic foraging in our study. It appears that tide plays a strong role in the nearshore foraging behaviour of benthic specialists (Zeenath and Zacharias 2010), in the offshore foraging behaviour of planktivorous feeders (Burger and Powell 1990; Elliott et al. 2010a; Shoji et al. 2010), and where topography creates strong tidal currents (Wilson et al. 1993; Heath et al. 2010). However, the offshore, pelagic foraging behaviour of piscivorous birds is generally not affected (but see Tarlow et al. 2003 for a possible exception).

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