

Foraging behaviour of common murres in the Baltic Sea, recorded by simultaneous attachment of GPS and time-depth recorder devices

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ABSTRACT: Global positioning system and time-depth recorders were deployed in combination to investigate the foraging behaviour of common murres *Uria aalge* breeding at Stora Karlsö Island, Baltic Sea, during the chick-rearing period. In the pre-breeding period the main prey species of murres, sprat *Sprattus sprattus*, is targeted by commercial fisheries, likely reducing prey availability during the breeding season. Foraging trips typically consisted of a short flight followed by a period sitting on the sea surface (0.39 ± 0.48 h), followed by several (5.3 ± 3.8) diving bouts interspersed by flights and water surface activity. Following the final diving bout, murres returned directly to the colony. Overnight foraging trips lasted longer than daytime trips, and that result corresponded with greater diving activity and reduced dive depths around dawn and dusk, likely times of high prey accessibility. High outward flight groundspeeds (20.0 ± 2.8 m s⁻¹) were aided by tailwinds, and lower inward flight groundspeeds (15.1 ± 2.5 m s⁻¹) were impeded by headwinds. Flights following the wind direction may reflect a strategy to reduce crosswind drift. Foraging intensity was lower than reported by most other studies of murres, suggesting more abundant or aggregated prey.

KEY WORDS: Foraging behaviour · Diving behaviour · *Uria aalge* · Common murre · Wildlife telemetry · Data loggers · Baltic Sea

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INTRODUCTION

To understand the breeding ecology and behaviour of seabirds it is necessary to study their behaviour both at the breeding colony and at sea. At the colony, detailed visual observations can be made; at-sea visual observation can only provide brief snapshots of behaviour when the individual colony of origin and the breeding status of individuals are unknown (e.g. Scott 1990, Davoren et al. 2002). In recent years, the development of miniaturised electronic devices has allowed recording of detailed behaviour at sea (reviewed by Burger & Shaffer 2008). Studies on alcids have been conducted with regard to both spatial (e.g. Benvenuti et al. 1998, Thaxter et al. 2009)

and diving behaviour (e.g. Tremblay et al. 2003, Paredes et al. 2008). In the present study we describe how 2 commercially available devices were used simultaneously to record both diving activity and spatial activity in a large alcid, the common murre *Uria aalge*.

As single prey loaders, chick-rearing adult murres return from foraging trips with 1 fish held lengthways in its beak to feed to the chick (Bradstreet & Brown 1985), limiting the foraging range when chicks are fed several times a day. This may lead to local depletion of fish populations near the colony and puts pressure on birds to travel further to forage at larger colonies, termed 'Storer-Ashmole's halo' (Ashmole 1963, reviewed in Elliott et al. 2009a, Gas-

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ton et al. 2007). By combining global positioning system (GPS) and time-depth recorder (TDR) devices, it is possible to determine the positions of final diving bouts, i.e. where the prey is captured for a chick.

In the Baltic Sea, a large-scale shift has occurred from a cod *Gadus morhua* dominated to a sprat *Sprattus sprattus* dominated ecosystem. This may have occurred due to a combination of anthropogenic drivers, such as fishing pressure and eutrophication, and climate change, with sprat numbers increasing following reduced predation by cod (MacKenzie et al. 2002, Casini et al. 2009, 2011, Möllmann et al. 2009). Common murres in the Baltic Sea are heavily dependent on sprat (Lyngs & Durinck 1998). Thus, this change in the dominant species means a strong increase in prey abundance, but also a reduction in prey condition and weight, resulting in a reduction in prey quality (Österblom et al. 2006, Casini et al. 2011). In recent years, when the cod fishery was reduced, cod numbers started to recover. At the same time, fishing pressure on sprat increased, resulting in a decrease in biomass of ca. 30% since a peak in the late 1990s (ICES 2010). However, on the scale of the Baltic Sea, sprat abundance is still high in comparison with that in the 1970s and 1980s, when numbers were at approximately one-third of the 2009 levels (ICES 2010). The sprat fishery near Stora Karlsö practically ceases from June to August, so it is not in direct competition with murres during the breeding season. However, if fish numbers are sufficiently depleted by the beginning of the breeding season, murres may be faced with high foraging effort, due to a rapid depletion of fish close to the island. Alternatively sprat disperse after spawning, and this reduced aggregation may influence murres, causing them to use a large area of sea to forage. Anecdotal evidence (e.g. observations by fishermen) suggests that foraging murres from the Karlsö islands use a wide area and concentrate off the northern tip of Öland and south of Gotland at the Hoburgs Bank (Fig. 1).

In the present study, we describe the foraging behaviour of chick-rearing common murres using simultaneous GPS device (GPSD) and TDR deployments. The study aimed to gain a better understanding of the foraging activity at Stora Karlsö by recording foraging locations, temporal patterns, and foraging strategies. The detailed data allow a fine-scale analysis of the activity during foraging trips, the behaviour at the start of a trip, as well as the number of foraging sites used during a trip. The GPS data allow foraging flights to be analysed, including how these may be affected by wind. We hypothesise that foraging routes

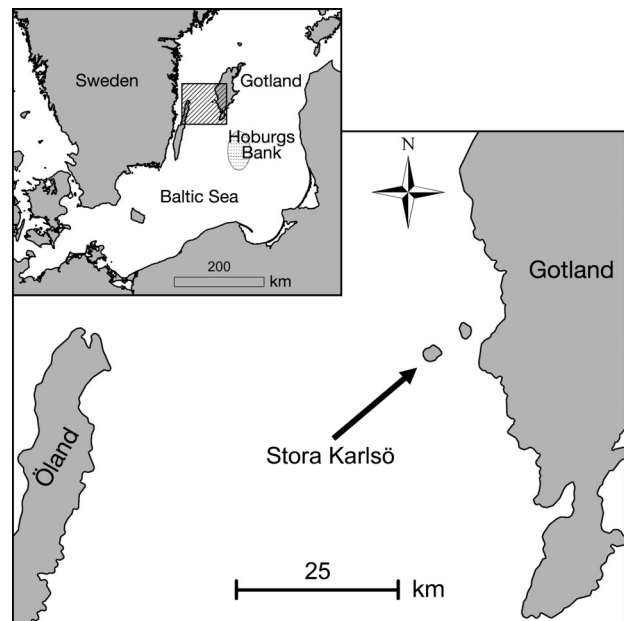


Fig. 1. Location of the study colony at the Stora Karlsö Island, Sweden, to the west of Gotland, in the south-eastern Baltic Sea. The main map is an expansion of the hatched area in the inset map

and locations are affected by wind speed and direction. We predict that foraging activity will be concentrated around dusk and dawn, as has been determined at several other locations (e.g. Regular et al. 2010). The population in our study area has shown a relatively high reproductive output (e.g. fledging success of 0.88 to 0.97 chicks per year in the years prior to our study) and a stable or increasing population size (Kadin et al. 2012, authors' unpubl. data); therefore, we expect that foraging and diving effort will be equivalent to or lower than in other murre colonies. This is the first study describing the foraging strategies and spatial distribution of foraging events of common murres in the Baltic Sea.

MATERIALS AND METHODS

Study site and species

The study took place at Stora Karlsö Island, Sweden (57° 17' N, 17° 58' E), in the south-eastern Baltic Sea (Fig. 1). Approximately 8000 pairs (Österblom et al. 2002) of common murres *Uria aalge* Pontoppidan, 1763 breed here, somewhat more than at the neighbouring island of Lilla Karlsö (Lyngs 1993). Field work took place from 9 to 20 June 2009, with devices deployed from 9 to 15 June 2009. Common murres

are present at the breeding colony during late winter, with daily presence from mid-April, when the breeding period begins. Experienced birds typically show both high site and mate fidelity (Moody et al. 2004). In mid-April mating occurs; ca. 15 d later a single egg is laid (Hatchwell & Pellatt 1990). After hatching, both parents provision the chick (Kadin et al. 2012), with ca. 3 to 5 feeds d^{-1} (Österblom & Olsson 2002, Thaxter et al. 2009). At 15 to 30 d of age, the still flightless chick leaves the colony accompanied by the male parent, on whom it continues to depend for over a month (Scott 1990). We caught breeding adults at the same natural rock ledge situated directly beneath an artificial breeding cliff structure described by Hentati-Sundberg et al. (2012). At the base of this structure was a trapdoor in the floor, through which we caught the birds by using a noose pole.

Bird-borne data loggers

We used 2 different devices together: a back-mounted GPSD (Model GT-120 by Mobile Action Technology) and a leg-mounted TDR (Model LAT 1500 by Lotek Wireless) to record the foraging movements and diving behaviour (detailed description in Fig. S1 in Supplement 1 at www.int-res.com/articles/suppl/m475p277_supp.pdf). Eight GPSD were deployed, half were set to record every 90 s, the others every 60 s, all but 2 were set to turn off from 23:00 to 03:00 h local time (time is central European standard time [CEST] unless otherwise stated), to save power at a time when activity was expected to be low (e.g. Regular et al. 2010). Two versions of the TDR were used, with either 50 (n = 3) or 500 m (n = 8) depth limits. All GPSD deployments included a TDR, but 3 TDRs were deployed without a GPSD, resulting in 8 GPSD with TDR deployments and 3 TDR only deployments. We attached an identification ring to the right leg of each bird, following the Swedish Bird Ringing Centre scheme (Naturhistoriska riksmuseet, Stockholm). The TDR was then mounted on an aluminium leg ring. The GPS was attached to the back feathers using several strips of black Tesa marine tape (Product 4651, Tesa SE). The total weight of the bird-borne instrumentation (including identification ring, attachments, and devices) was ca. 29 g, equivalent to ca. 3% (range: 2.9 to 3.8%) of the bird's body weight.

Owing to some deployments with both GPSD and TDR and others with only TDR, it was necessary to use different parts of the data-set depending on the analysis. Thus, sample sizes differed depending on

the factor of interest. We recovered devices from 7 common murre tracked during the breeding period: 6 with a GPSD and TDR and 1 with a TDR only; the remaining 4 birds were not recaptured, so devices could not be recovered. However, these birds were observed on the breeding ledge apparently continuing to provision their chicks. There were three 60 s and three 90 s interval GPSDs. One 60 s device and one 90 s device failed for unknown reasons after 4 and 12 h, respectively. The remaining 4 devices recorded, on average, for 53 h (60 s device) and 58 h (90 s device). In total, 27 foraging trips were tracked, of which 18 were complete; 22 included at least the start and end of the trips, and the remaining 5 missed the start or end positions (for detailed sample sizes see Supplement 1).

Data treatment and statistics

TDR data were analysed with MultiTrace-Dive (Jensen Software Systems) to recognise and parameterize each dive and sequence of dives, i.e. a dive bout. An activity was classified as a dive when it reached a maximum depth of at least 3 m (after Paredes et al. 2008); the start and end of a dive was set when 5% of the maximum dive depth was exceeded or reached, respectively. The bottom phase of the dive, which roughly represents the portion of the dive spent actively foraging, was defined as the time at which >75% of the maximum dive depth was reached (Tremblay et al. 2003, Halsey et al. 2007). We calculated various measures for each dive, including dive duration, maximum dive depth, and vertical ascent and descent rates.

To investigate the minimal recovery period following dives, data were pooled, and minimum post-dive interval (PDI) values taken for each dive duration at 1 s resolution were plotted against dive duration (see Fig. 8A). Dive efficiency was calculated as (Camphuysen 2005):

$$\text{Dive efficiency} = \text{bottom time} / (\text{dive duration} + \text{PDI})$$

Dive bouts, 'periods of sustained diving activity' (Thaxter et al. 2010), are a sequence of dives with only brief PDIs. Definitions of dive bouts differ, generally using either a fixed criterion, or varying, for example using both differences in dive depths and PDI (e.g. Mori et al. 2001). Here the method of Sibly et al. (1990) was applied to calculate a fixed maximum PDI providing a bout-ending criterion (Paredes et al. 2008, Hedd et al. 2009) and plotting log(frequency) against PDI using the R statistical environ-

ment (R Development Core Team 2010) with the package 'HyperbolicDist' (Scott 2009). A natural cut-off indicating the end of a bout was 250 s. Various measures were calculated for dive bouts, e.g. number of dives and mean maximum dive depths.

We analysed foraging trips using a combination of GPSD and TDR data, which allowed trip start and end times to be determined. We classified behaviour during trips into 4 categories: (1) diving bouts, (2) splashdown, (3) surface resting, and (4) flight (see Supplement 1). 'Splashdown' periods were recognised as the first uninterrupted (i.e. with no flight or diving) period of water surface activity (Burger 1997, Davoren & Montevecchi 2003).

Data from the GPSDs were mapped in ArcMap (9.3 and 10.0, Environmental Systems Research Institute), with which all map figures were produced.

To compare the distance from the colony of final dive bouts with the rest of the dive bouts (non-final dive bouts) occurring during each foraging trip, we calculated the ratio of the distance from the breeding ledge for a dive bout to the maximum distance reached during a trip. To compare final bouts with non-final bouts, the mean ratio was calculated for non-final dive bouts for each foraging trip, producing an index and allowing comparison irrespective of actual distances. In a paired *t*-test these 2 values were compared with all foraging trips pooled.

To examine how trip duration relates to activity on foraging trips, we looked at (1) the maximum distance from the colony reached, (2) the number of dives, and (3) the number of bouts per foraging trip. Although time of day is likely to affect activity (e.g. see Fig. 5), this was not included in our models because of the small sample size. We developed linear mixed-effects models (LMMs) with individual as a random effect. Model selection and validation followed those outlined by Zuur et al. (2009), using the 'nlme' package (Pinheiro et al. 2011) in R.

Flight segments were separated from GPS data (see Supplement 1) to analyse flight activity. Amongst other parameters we calculated ground speed, the speed of the bird relative to the ground (as opposed to 'air speed'), and the speed travelled relative to the air mass. We classified flights into 3 groups. (1) Outward flight included flights between breeding ledge departure and the first diving bout (this included the flight both before and after a splashdown). (2) Foraging flights were any flights during a trip that occurred after the first dive bout and before the final dive bout. (3) Inward flights took place from the final dive bout to arrival at the breeding ledge. Wind data from a nearby weather station (70 km from the study

site at the north point of the island of Öland; Fig. 1) gave the median wind direction in 10° bins and the mean wind speed at 1 m s⁻¹ resolution, both in 3 h blocks.

We looked at possible device effects on the study birds, through weight change and breeding success (in Supplement 2 at www.int-res.com/articles/suppl/m475p277_supp.pdf).

Figures were generated and statistical analyses were performed with R (R Development Core Team 2010), except for the maps which were produced in ArcGIS. Some circular statistics and Fig. 7A,C,E were generated with Oriana (Kovach Computing Services).

RESULTS

Foraging trips and time activity budget

Foraging trips of *Uria aalge* usually started with a short flight to a splashdown period, before the birds either dove or flew to a foraging site and then dove (see Figs. 2 & 3). Dives occurred in short sequences, bouts, with short PDIs. Several dive bouts occurred per trip, sometimes with short flights between these. After the final dive, birds usually flew directly to the breeding ledge, presumably to feed their chick, although this was not systematically observed. This final dive bout generally occurred close to the maximum distance from the breeding ledge (Fig. 3, see also Fig. 6D).

During foraging trips a high proportion of time was spent on the sea surface (>40%), with slightly less time actively foraging in dive bouts (<40%). The remaining time (<20%) (Table 1) was dedicated to flight. During dive bouts, approximately a quarter of the time was spent recovering during PDIs. Trip durations were variable (Fig. 4A), with a median value of 3.1 h, somewhat less than the mean value (Table 1), suggesting many shorter trips with few longer trips. Trips with evening departures were typically longer in duration than daytime trips (Fig. 5A). Four out of 5 trips occurring after 19:00 h were >6 h, and no trip >6 h started between midnight and 19:00 h. The longer the duration of a foraging trip, the greater the maximum distance reached from the breeding colony (Fig. 6A). This relationship did not appear to differ among individuals. LMMs included individual as a random effect, with random intercept and slope or random intercept only both were less parsimonious (higher Akaike's information criterion [AIC] values).

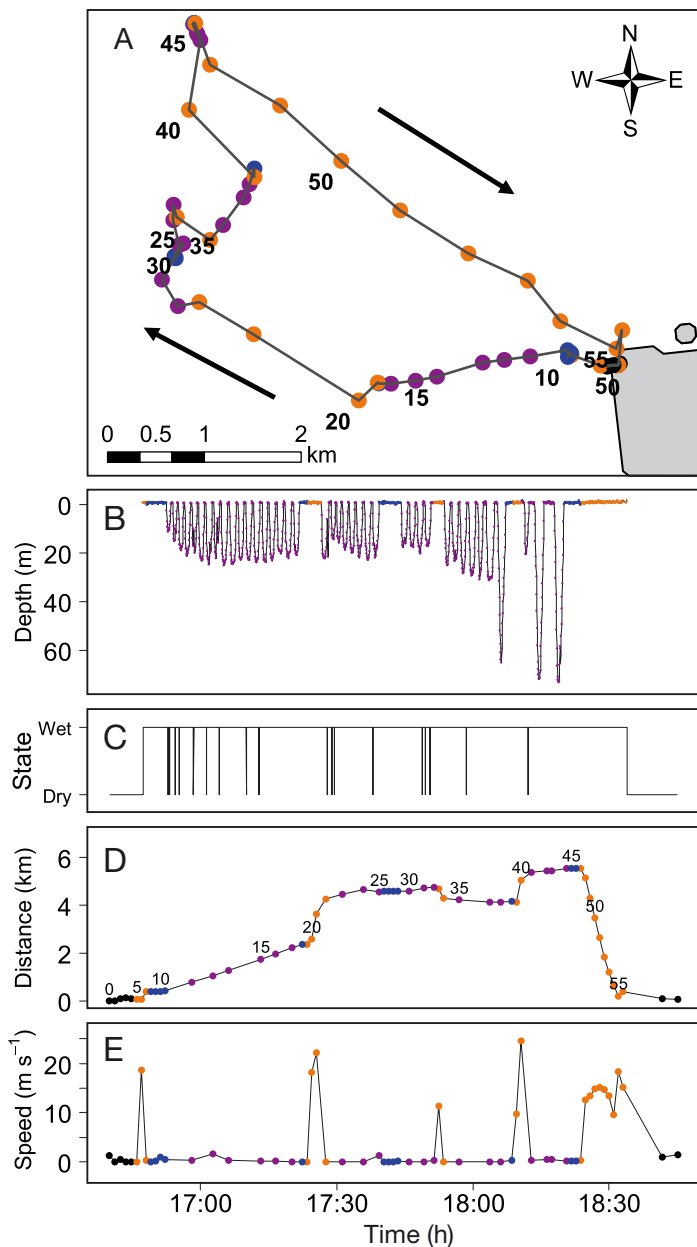


Fig. 2. *Uria aalge*. Example of a common murre foraging trip. (A) Global positioning system (GPS) locations (circles, numbered) and travel direction (arrows). (B to E) Various temperature-depth recorder (TDR) and GPS parameters. Behaviour classification is indicated by colour throughout: flight (orange), diving bout (purple), water surface activity (blue), and colony (black). (B) Depth readings from the TDR device, with dives visible as downward spikes. (C) The wet-dry sensor had a lag phase; shortly before 18:30 h the bird begins flying (E), but the sensor continues to show a 'wet' reading; only likely with a transition from wet to dry (not dry to wet). (D) Distance from the island. Numbers are GPS positions in Panel A. (E) Instantaneous GPS recorded speed. Between ca. 16:50 and 17:20 h movement occurs (displacement from the breeding colony increases, Panel D), but this movement occurs during a diving bout, so it is not reflected in the surface GPS records (Panel E)

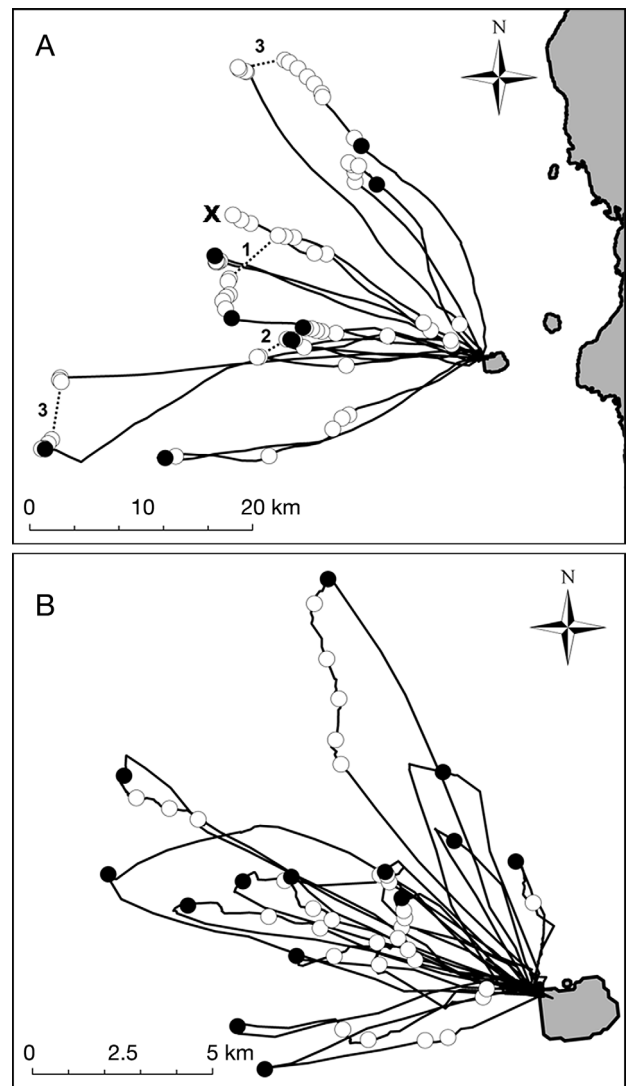


Fig. 3. *Uria aalge*. All foraging trips of common murre tracked via GPS, split into (A) long (maximum distance from breeding ledge > 15 km) and (B) short trips (maximum distance from breeding ledge < 15 km). Dive bouts (O) and the final bout of a trip (●) are indicated. For 4 overnight trips (all long trips), there was a period (between 23:00 and 03:00 h CEST) when the GPS devices were not recording a dotted line is displayed for this period, with a number indicating the number of diving bouts occurring during that time. One trip is truncated, due to depletion of the GPS battery (x in Panel A)

Diving activity increased with trip duration, both the number of dives (Fig. 6B) and the number of dive bouts (Fig. 6C). For both factors, the most parsimonious model did not include individual (selected by AIC), suggesting that little variation was explained by individual. Trip duration (Fig. 4A) and the maximum distance from the breeding ledge reached during trips (Fig. 4B) showed great variation, though distance was more uniform in distribution. The total

Table 1. *Uria aalge*. Characteristics of foraging trips recorded by GPS loggers for common murre breeding at Stora Karlsö, Sweden, in 2009. PDI: post-dive interval

Overall characteristics of trips	Mean	SD	No. ind.; no. trips
Trip duration (h)	4.20	3.50	4;22
Distance from breeding ledge (km)			
Greatest	11.77	7.36	3;18
Mean (whole trip)	7.78	5.34	3;18
Total horizontal distance travelled (km)	26.19	15.81	3;18
Splashdown			
Present (proportion of trips) (%)		73	6;26
Duration (h)	0.39	0.48	6;19
Distance from nest at start (m)	320.6	146.3	6;19
Diving			
Number of bouts	5.27	3.84	4;22
Number of dives (whole trip)	34.77	24.26	4;22
Distance of bout from breeding ledge (km)	9.71	6.29	3;18
Total duration of bouts (h)	1.19	0.74	4;22
Total dive duration (h)	0.83	0.47	4;22
Total PDI duration (h)	0.35	0.27	4;22
Surface time (excluding PDI)			
Duration excluding splashdown (h)	2.53	2.84	4;22
Duration including splashdown (h)	2.54	2.92	4;22
Flight			
Number	3.00	1.15	3;18
Duration (h)	0.39	0.26	3;18
Trip time-activity budget (%)			
Bouts, including diving and PDI	37.33	26.82	3;18
Diving	27.28	19.47	3;18
PDI	10.05	7.72	3;18
Splashdown period (when present)	12.56	15.19	4;16
Surface time (including splashdown, but not PDI)	42.33	36.49	3;18
Surface time (excluding splashdown and PDI)	35.80	40.67	3;18
Flight	16.21	10.33	3;18

distance travelled (Table 1) was only slightly more than double the maximum distance reached (mean ratio: 2.26 ± 0.20), indicating that routes followed were direct (Fig. 3), with straight flights too (Table 2).

Flight behaviour

Flights were of intermediate distance, being several kilometres and generally <500 s long (Table 2). Flight ground speeds recorded by the GPSD were very variable, ranging from ca. 5 up to 32 m s^{-1} (Fig. S1 in Supplement 1) and reflecting (1) the variation in air speed, (2) wind conditions (Fig. 7E,F), or (3) a combination of these. Outward flights mostly occurred over a fairly narrow sector to the north-west of the island (Fig. 7A). The mean ground speed during outward flights was greater than during inward flights (Fig. 7B,D), with outward flights typically having a tailwind component and inward flight a headwind.

Diving behaviour

Dive depths followed a bimodal distribution (Fig. 8C), but dive duration (Fig. 8B) showed a unimodal distribution. Dive parameters are summa-

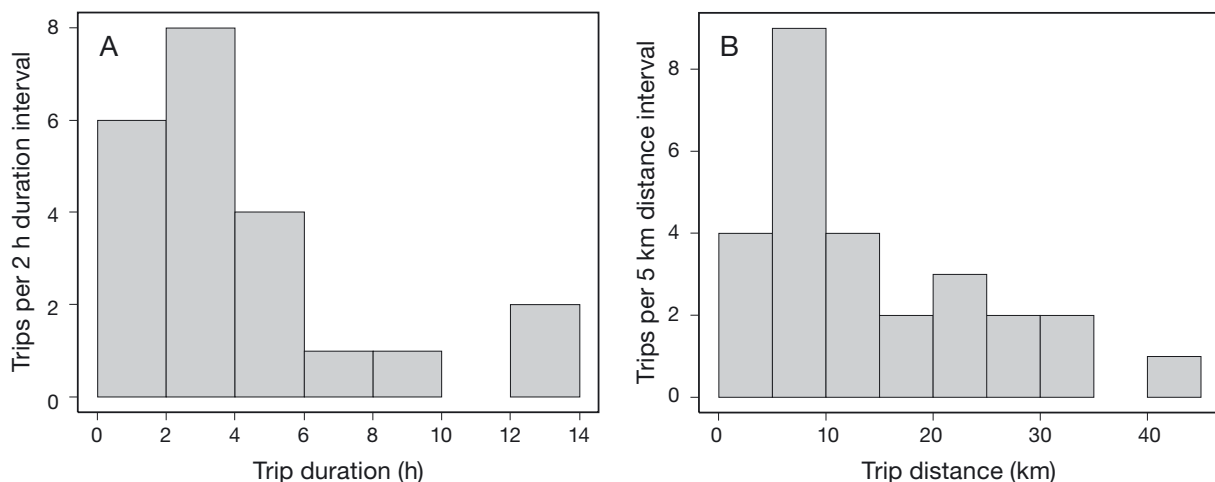


Fig. 4. *Uria aalge*. Frequency of common murre (A) foraging trip duration (n = 22) and (B) maximum distance (n = 27) from the breeding ledge

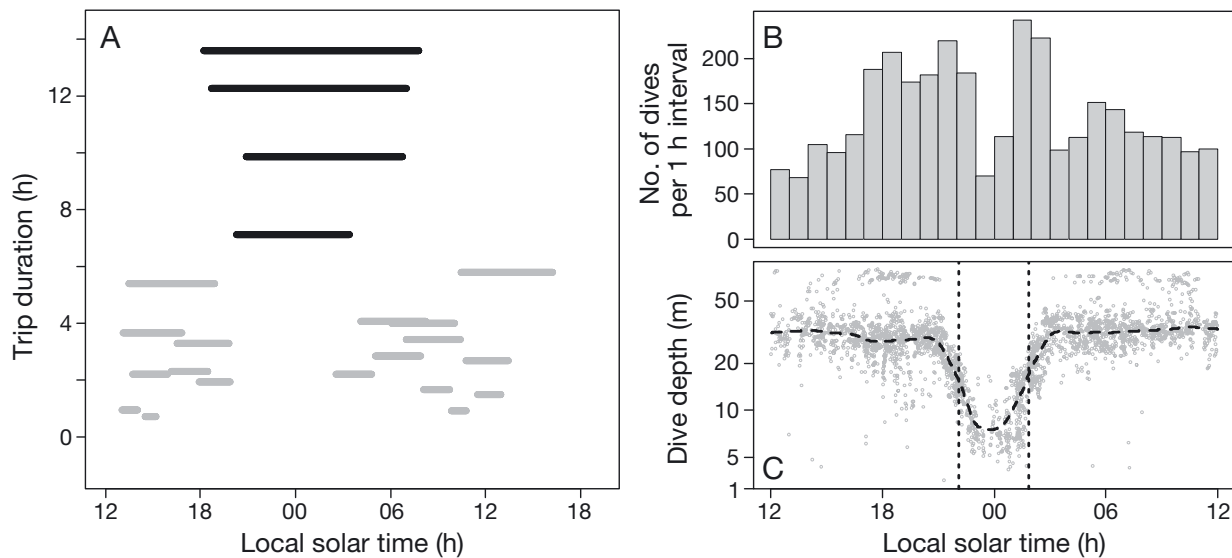


Fig. 5. *Uria aalge*. Foraging activity in common murre by time of day. (A) Trip durations in common murre by trip start time ($n = 22$), with overnight trips (black) and diurnal trips (grey) indicated. (B) Frequency of dives in 1 h bins and (C) depth (log axis) of dives (all individual dives shown by small grey circles) with a smooth line fitted (LOWESS function in R, using 1 h span). Local solar time (GMT + 1:10 h) is displayed, with sunset and sunrise indicated by vertical dashed lines

rised (Table 3). The majority of dives were U-shaped, with a broadness index of mostly >0.015 (the V-shaped threshold; Halsey et al. 2007) (Fig. 8D). Therefore, dive shapes were not analysed further. The minimum surface recovery period, the PDI value, increased with dive duration, with a steep increase beyond 150 s (Fig. 8A). On average, the dive time was slightly more than double the PDI (Table 3). Diving frequency was greatest in the evening (Fig. 5B), from 17:00 to 23:00 h (local solar time) and around dawn (01:00 to 03:00 h). Mean dive depths were nearly constant from 03:00 to 21:00 h, but were then reduced from 21:00 to 03:00 h, reaching a minimum around midnight (Fig. 5C).

DISCUSSION

We found that most foraging parameters measured for common murre *Uria aalge* in the Baltic Sea were similar to those recorded at other sites, but some findings indicated good foraging conditions for breeding murre. Furthermore, the murre used a limited foraging area, suggesting that prey was aggregated rather than dispersed. Alternatively, the wind conditions may have influenced the use of foraging areas. However, our study period was limited and thus may not have been representative of the general conditions throughout the season or between years. These detailed insights into foraging behaviour add to our

understanding of murre foraging. We found that murre may have a bimodal foraging strategy, with long overnight trips and shorter daytime trips, a behaviour that would be less apparent in studies relying on TDRs alone.

Splashdowns

Most foraging trips began with a splashdown period in which birds landed on the water surface close to the colony, a pattern similar to that seen in other studies of common and thick-billed murre (Burger 1997, Elliott et al. 2009b). This suggests that splashdowns are important, although their primary function is still debated. They may offer the opportunity to clean plumage (Elliott et al. 2009b), but may also play a role in determining foraging direction as departing birds observe the direction of incoming birds (Burger 1997). Similar behaviour has been observed in breeding colonies of Guanay cormorants *Phalacrocorax bougainvillii* (Weimerskirch et al. 2010).

Foraging distance and duration

The duration and maximum distance of foraging trips observed at Stora Karlsö were comparable to those measured in other studies (e.g. Tremblay et al.

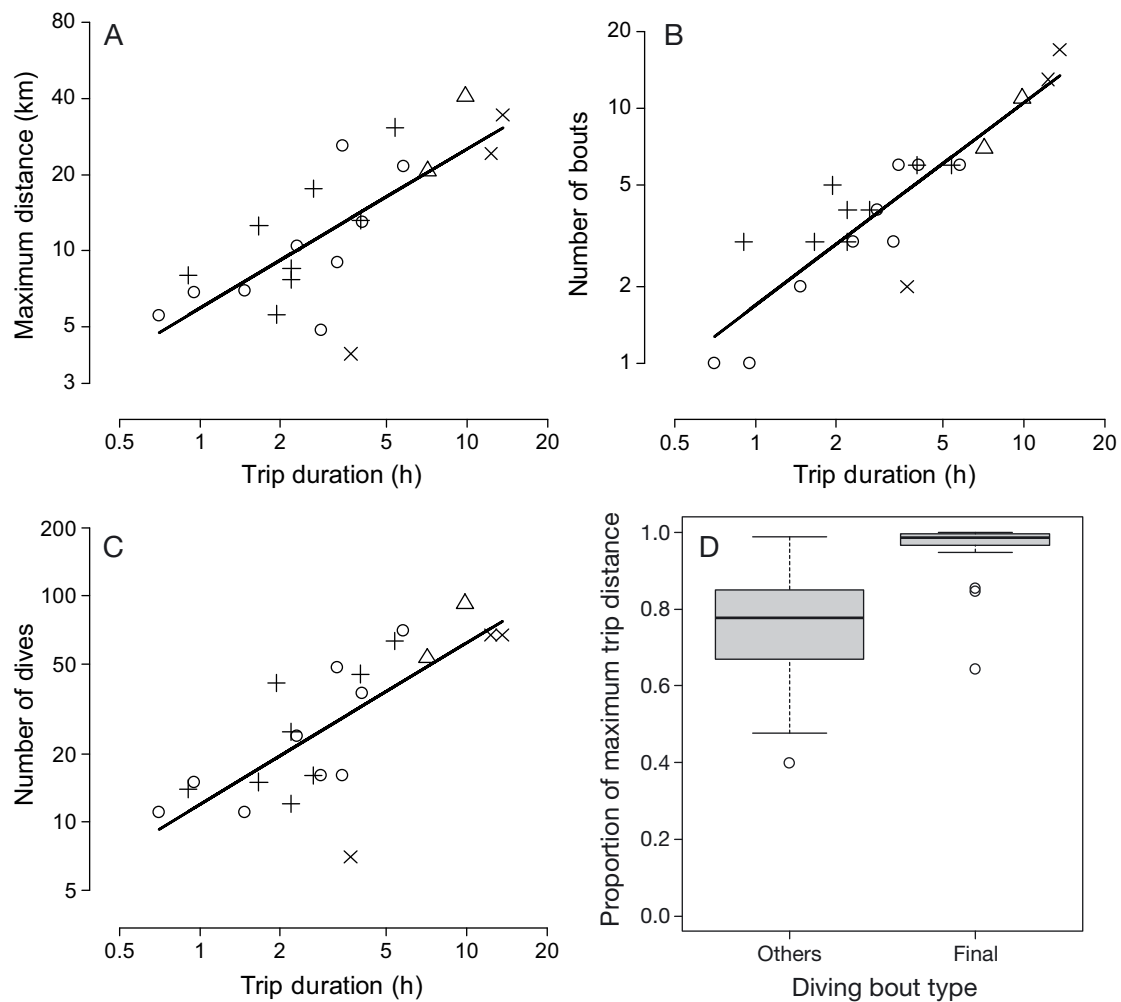


Fig. 6. *Uria aalge*. Foraging trips of common murre. (A to C) Relationships between foraging trip duration and activities ($n = 22$): (A) maximum distance from the breeding ledge (linear regression, $t_{22} = 4.94$, $p < 0.0001$), (B) number of dives (linear regression $t_{22} = 2.74$, $p < 0.0001$), and (C) number of dive bouts (linear regression $t_{22} = 5.60$, $p < 0.0001$). Individuals are indicated by different symbols, linear regression lines (continuous line) for log-transformed data, displayed with log axis. (D) Box-and-whisker plot comparing distance of final diving bouts to non-final dive bouts, using the within-trip ratio of dive bout distance to maximum distance from nest reached during trip. The ends of whiskers represent the least and greatest values within 1.5 times the lowest or highest quartile (shown by box), with open circles for outliers and medians at the centre line. Final dives occur at significantly greater distances than earlier non-final dives (paired t -test: $t = 4.47$, $n = 20$, $p < 0.001$)

Table 2. *Uria aalge*. Summary statistics for all flights (105 from 36 trips by 6 birds) during foraging trips of common murre at Stora Karlsö, Sweden (see Fig. 7 for comparison of outward and inward flight directions and speeds)

Flight characteristics	Mean	SD
Straight line distance (km)	6.31	7.39
Total distance travelled (km)	6.47	7.56
Straightness (total/straight)	1.07	0.24
Speed (m s^{-1})	16.87	4.28
Duration (s)	440.8	446.4
GPS fix number	5.57	5.78

2003, Thaxter et al. 2010), though trip duration was short in 2009 (Kadin et al. 2012). Stora Karlsö is a relatively small colony compared to those at other sites, where tens of thousands of pairs are not uncommon; thus, competition may be relatively low there. With few large colonies nearby, less intra-specific competition may also be found at Stora Karlsö, compared to other colonies; however, inter-specific competition with razorbills is possible, since they occur in similar numbers to murre at Stora Karlsö (Hedgren & Kolehmainen 2006) and with smaller populations on the neighbouring island of Lilla Karlsö (Lyngs 1993).

Flight behaviour and wind

Murre foraging flights largely occurred along the same axis as winds: outward flight with tailwinds and inward flight into headwinds. This could represent a strategy to reduce crosswind drift over the sea, where a fixed frame of reference thought necessary to assess drift is unavailable (Åkesson & Hedenström 2007). However partial compensation for wind drift may be possible through the following methods. (1) Maintaining optical flow (the time taken for an object to pass across the retina) by selecting flight altitude, as used by some insects over land and water (Riley et al. 1999, Srygley & Dudley 2008). (2) Using the 'wave landscape', the pattern of waves over the sea as a fixed reference, which could allow for partial compensation as the wave patterns would change more slowly than wind speeds (Alerstam & Pettersson 1976). (3) Using the coastline as a fixed reference (e.g. Åkesson 1993). Alcids observed at sea have shown a preference for headwinds (Spear & Ainley 1997). Avoidance of crosswind conditions will reduce wind drift. However, by flying into the wind, flight will be more costly per unit distance travelled. As murres have high airspeeds that are associated with their high wingloading, this increased cost of flight in windy conditions is less than for other birds, though still potentially high (Furness & Bryant 1996).

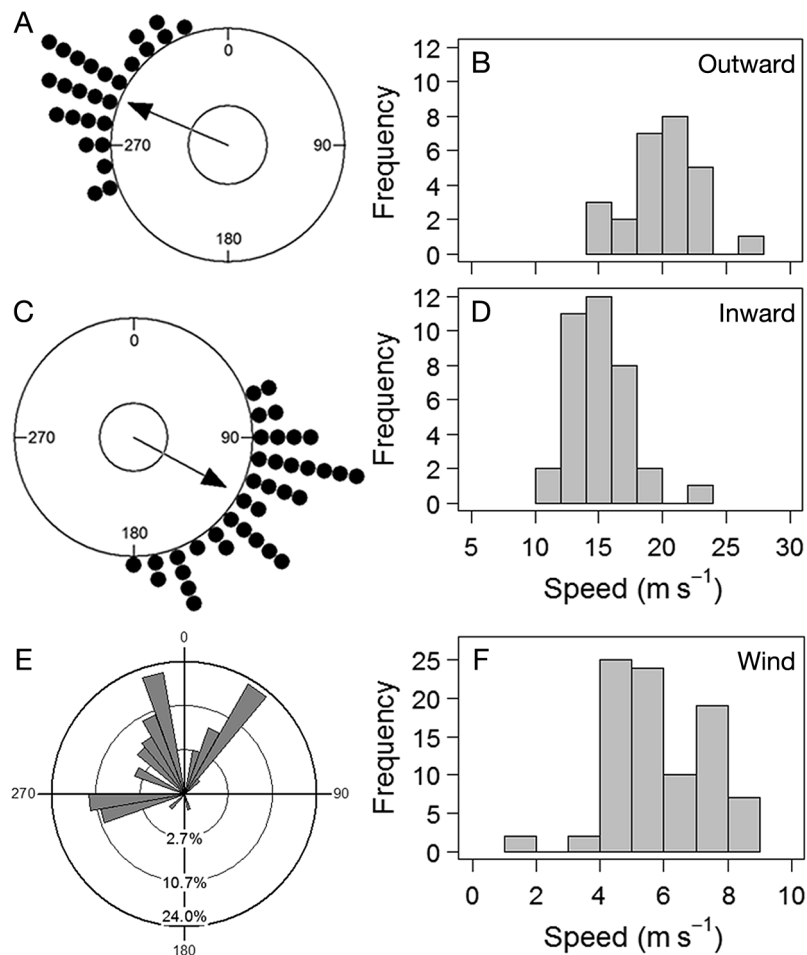


Fig. 7. *Uria aalge*. Summary of resultant vector directions for common murre flights (A,C). The flights are split into outward (A,B) and inward (C,D) movements from the colony (see 'Materials and methods' for definitions), with mean flight vector directions in 10° segments for each flight, mean vector shown (A: $\theta = 298.1^\circ$, $r = 0.92$, $z = 22.13$, $p < 0.001$, $N = 26$; C: $\theta = 124.2^\circ$, $r = 0.88$, $z = 27.82$, $p < 0.001$, $N = 36$). Flight speeds for (B) outward flight (mean $20.0 \pm 2.8 \text{ m s}^{-1}$) were greater than for (D) inward flight (mean $15.1 \pm 2.5 \text{ m s}^{-1}$; paired t -test: $t = 3.14$, $df = 20$, $p = 0.005$). (E) Circular plot showing wind heading direction in 10° bins. (F) Wind speed (mean $6.3 \pm 1.6 \text{ m s}^{-1}$)

Dive activity

The mean maximum dive depths of common murres at Stora Karlsö (20 to 50 m) were similar to those recorded at other colonies (e.g. Camphuysen 2005, Hedd et al. 2009, Thaxter et al. 2009), as were dive efficiency values (Hedd et al. 2009, Thaxter et al. 2010). A steep increase in PDI for dive durations >150 s adds support to the proposition that common murres show a 'behavioural aerobic dive limit' at this point (Tremblay et al. 2003; see also Fig. 4B in Thaxter et al. 2010) as was also found in thick-billed murres (Croll et al. 1992); this may represent the actual aerobic dive limit (Hansen & Ricklefs 2004).

Daily activity patterns

We found a strong diel activity pattern, which was in agreement with many other studies of alcids and with observational studies of chick provisioning at this colony (Österblom & Olsson 2002). Like razorbills *Alca torda* in the southern Baltic Sea (Benvenuti et al. 2001), the common murres at Stora Karlsö followed a bimodal foraging strategy, with overnight trips of a longer duration and shorter daytime trips. This likely reflects the most profitable foraging times (around dusk and dawn), when diving activity was greatest and diving depths were rather shallow. This pattern was also found in several other studies of breeding

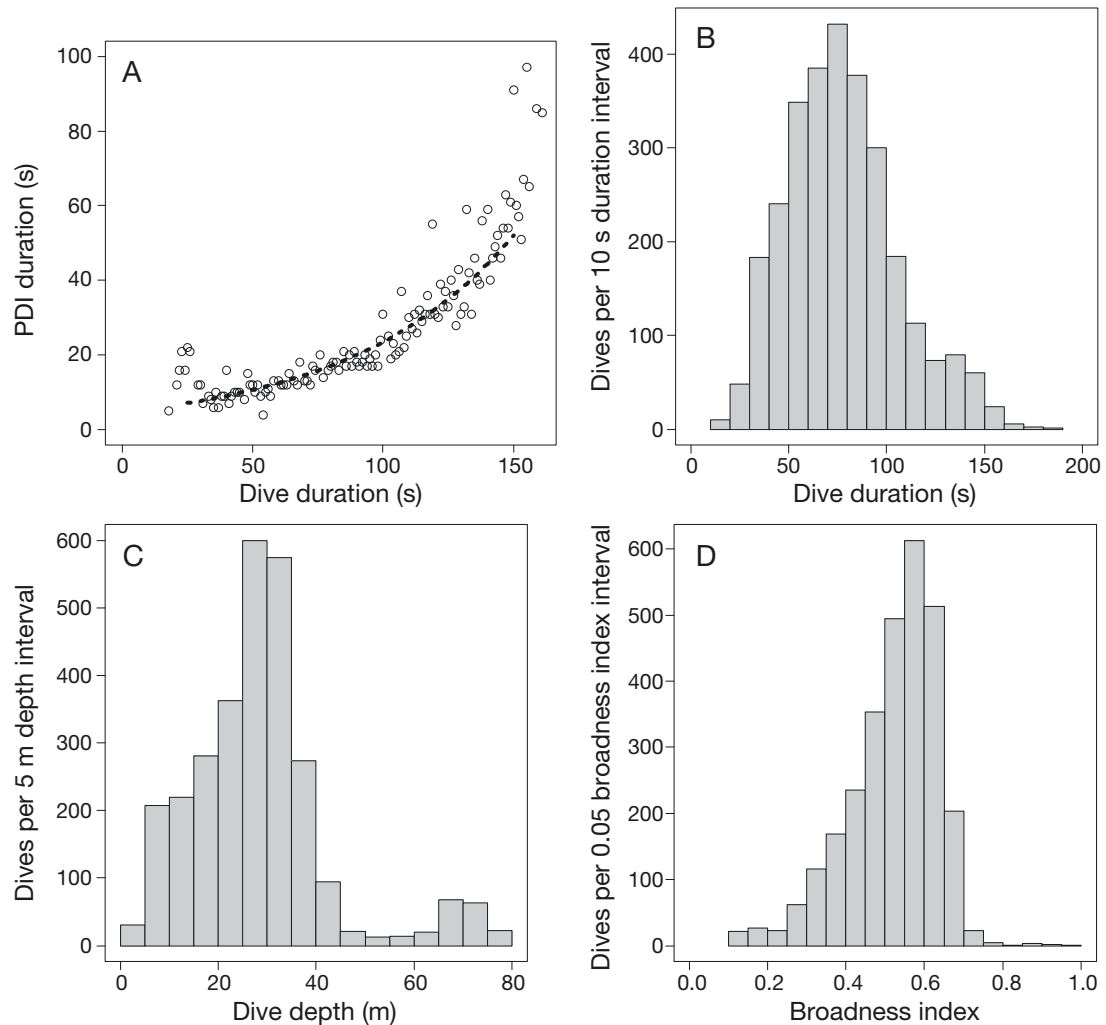


Fig. 8. *Uria aalge*. (A) Relationship between post-dive interval (PDI) duration and dive duration in foraging common murres, with minimum PDIs for dive durations at 1 s intervals. At <150 s the relationship can be described by the regression line: $\log_e(\text{PDI}) = 0.015 (\text{dive duration}) + 1.68$. (B) Dive duration showed a nearly normal distribution, with a slight positive skew towards longer dives. (C) Dive depths. (D) Proportion of time spent at depth is indicated by the broadness index

(Camphuysen 2005, Regular et al. 2010) and post-breeding murres (Nevins 2004). This behaviour likely reflects a balance between prey being accessible near the water surface and the time when sufficient light is available for visual foraging (Regular et al. 2010, 2011). The primary prey species (sprat) for murres at Stora Karlsö, sprat, is known to perform diel migration (Cardinale et al. 2003), moving to surface waters at night.

Foraging conditions

The use of longer trips in addition to short trips, the radial pattern of trip paths, and the presence of diving towards the most distant part of these trips support the proposition that prey closer to the colony could be

depleted, favouring more distant foraging sites. However, the use of a limited sector of the sea suggests that prey may not be widely dispersed but aggregated. However, this may also reflect a preference for flights in headwinds and tailwinds (see above). Murres at Stora Karlsö performed slightly fewer dives per dive bout and per foraging trip, suggesting higher prey availability. This may indicate little competition between fisheries and murres in this part of the Baltic Sea in 2009. It may also explain the stable or growing population at this breeding colony (Kadin et al. 2012), in contrast to other colonies of the species, e.g. around the North (JNCC 2011) and Norwegian Seas (Barrett et al. 2006), which have been decreasing in size. Further information about other sprat-dependent species is necessary to fully understand the interactions between seabirds and the sprat fishery.

Table 3. *Uria aalge*. Summary of dives and dive bout characteristics for chick-rearing common murre at Stora Karlsö, Sweden, in 2009. Post-dive interval (PDI) based calculations use PDIs < 200 s only

Dive characteristics	Mean	SD	No. dives; no. ind.
Dive bouts			
Dive depth maximum (m)	28.46	14.38	2866;6
Duration (s)	803.38	712.08	408 ^a ;6
Number of dives	6.99	5.74	408 ^a ;6
Dives			
Duration (s)	77.64	28.62	3326;7
Mean of individual maximum recorded depths (m)	62.57	17.67	2866;6
Bottom time duration (s)	41.56	18.86	2866;6
Bottom time/dive duration	0.52	0.11	2866;6
Vertical descent rate (m s ⁻¹)	1.10	0.25	2866;6
Vertical ascent rate (m s ⁻¹)	1.13	0.35	2866;6
PDI (s)	42.9	30.0	3326;7
PDI/dive duration ratio	2.30	1.11	3326;7
PDI/(dive duration + PDI)	0.34	0.12	3326;7
Dive efficiency [bottom time/(dive duration + PDI)]	0.35	0.11	2866;6
^a Dive bouts			

CONCLUSIONS

The combined use of separate GPS and TDR devices provides detailed behavioural data, which contribute novel information on individual alcid foraging decisions. The foraging trips for chick-rearing common murre breeding at Stora Karlsö typically started with a short splashdown period followed by several, often spatially separated, diving bouts. These diving bouts were interspersed with periods of surface activity and short flights. After the final diving bout, which typically occurred at the greatest distance from the breeding colony, birds usually returned directly to the breeding ledge. During the study period, outward flights were significantly faster than inward flights, probably due to tailwind assistance. The murre appeared to select either headwinds or tailwinds, avoiding crosswinds, possibly affecting the foraging locations chosen. However, to confirm these observations, studies under more variable wind conditions are required. There was a strong temporal pattern in foraging activity, with an apparent bimodal foraging strategy of long overnight trips and short daytime trips. Diving frequency was greatest in the evening and at dawn, when diving depths were most shallow. The present study illustrates how detailed information about foraging behaviour can be used to assess locations and activities where the interests of humans

and birds overlap. Additionally, the use of a relatively small marine area could be of interest, with a view to setting up a marine protected area in order to protect the population from potential future fishing conflicts and commercial shipping operations nearby.

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