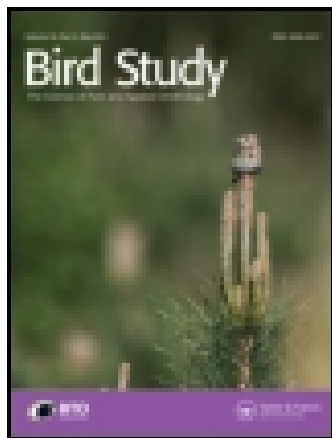


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## Diving behaviour of benthic feeding Black Guillemots

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**Capsule** Dive behaviour in Black Guillemots *Cephus grylle* was close to that predicted for a benthic forager by allometry based on body mass.

**Aims** To report the diving behaviour of Black Guillemots in Northern Ireland.

**Methods** A time-depth-recorders and GPS logger were deployed on four chick-rearing breeding Black Guillemots.

**Results** Dive shape implied most dives were benthic with a small number at the start of each bout associated with searching. Diving only occurred during daylight hours, but dive depth was unrelated to light availability outside of the twilight periods. Dive durations (max = 90 s; mean = 54 s) were shorter and dive depths (max = 15 m; mean = 9 m) were shallower than recorded for guillemots elsewhere. The birds dived a maximum of 1.8 km from the colony.

**Conclusions** Black Guillemots' dive duration was similar to the value predicted from allometry, and is therefore likely representative of this species. Bathymetry likely influences the dive behaviour of this benthic-feeding species because most dives were U-shaped and dive depths were shallow, which is typical for the relatively shallow water where the birds were observed foraging.

In diving animals, oxygen stores are generally believed to increase with body mass<sup>1.0</sup> while basal oxygen consumption rate scales to roughly body mass<sup>0.7</sup> (Lasiewski & Calder 1971, Hudson & Jones 1986, Birt-Friesen *et al.* 1989, Kooyman 1989, Halsey *et al.* 2006b). Therefore, body mass determines much of a species' capacity to make long breath-hold dives (Kooyman & Kooyman 1995), and dive duration across species scales to body mass with an exponent of about 0.3 (mass/mass<sup>0.7</sup>; Halsey *et al.* 2006b). Therefore, small breath-hold divers are particularly constrained in their dive abilities by oxygen availability. Auks, which are some of the smallest marine breath-hold divers, are therefore expected to be strongly selected for optimal dive behaviour so as to extend dive duration as long as possible (Watanuki & Burger 1999, Elliott *et al.* 2010).

The Black Guillemot *Cephus grylle* is widely distributed in Arctic and northern Atlantic waters (Gaston & Jones 1998). This species is an inshore

feeder during breeding and forages mainly on benthic prey, diving typically shallower than 30 m (Cairns 1992), making them potentially susceptible to tidal energy developments (Furness *et al.* 2012, Masden *et al.* 2013). Nevertheless, the dive behaviour of *Cephus* guillemots has only been recorded in detail using electronic recorders by a single study site reporting data from two individual birds (Masden *et al.* 2013). In this study, we deployed time-depth-recorders (TDRs) to study the foraging behaviour of chick-rearing Black Guillemots breeding at Bangor Harbour and Lighthouse Island (Copeland Bird Observatory) in Northern Ireland. In this area, guillemots mainly feed their young with butterfish *Pholis gunnellus* (Ewins 1986; Shoji, pers. obs.). Quantifying dive profiles of marine top predators is essential to understand their potential role in the marine ecosystems, and to conserve and manage those ecosystems (Ashmole 1971, Hunt & Schneider 1987), and there is a need for more data for these species since they have not been well studied to date (Phalan *et al.* 2007).

Our goal was to describe the diving behaviour of Black Guillemots at this site in detail. Mori *et al.* (2002)

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developed a method to estimate the Index of Patch Quality (based on the assumption that individuals will only extend bottom time at an accelerating penalty to overall dive cycle time if patch quality is high; details of calculation is available in Mori *et al.* 2002) to provide insight into the foraging behaviour of another auk species (*Uria lomvia*). The Index of Patch Quality during a dive bout correlates with energy content of the fish captured during that dive bout (Elliott *et al.* 2010). We used the Index of Patch Quality to understand the dive profiles of Black Guillemots. Additionally, we identified dive shapes for all identified dives because U-shaped dives are usually associated with benthic foraging. Thus, it allows us to assess whether Black Guillemots feed only on benthic fish as is generally assumed (Gaston & Jones 1998). We then calculated average dive duration for Black Guillemots at our study site and compared that value with the predicted value based on allometric relationships.

## METHODS

Our observations were made at Black Guillemot colonies at Bangor Harbour (54.66°N, 5.67°W) and on Lighthouse Island (54.67°N, 5.52°W), Northern Ireland during the chick-rearing period in 2013. Bangor Harbour supported 38 pairs of nesting Black Guillemots in 2013 (Greenwood 2014) and Lighthouse Island supported approximately 55–60 pairs of nesting Black Guillemots. Our study birds were nesting in either concrete holes (Bangor Harbour) or artificial nest boxes that were installed in 2000 by Copeland Bird Observatory (Lighthouse Island).

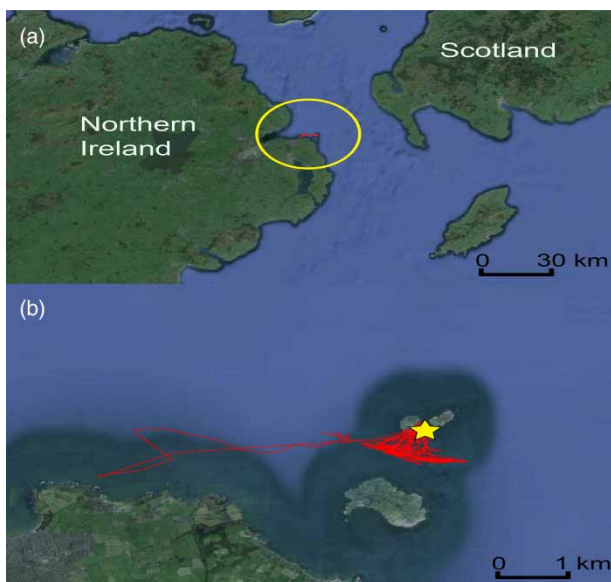
At Lighthouse Island, we stayed in a hide in the colony and we captured Black Guillemot adults by closing the nest entrance when they returned to the nest. At Bangor Harbour, as Black Guillemots nest in an access duct at the Harbour underneath the road (Greenwood 2014), we monitored birds visiting their nest and closed the duct entrance with a butterfly net on their return. Eight chick-rearing adult Black Guillemots (six from Lighthouse Island and two from Bangor Harbour) were captured. TDRs (Lotek 1900 TDRs, Lotek Wireless Inc, St. John's, Canada) were attached to a Darvic leg ring. TDRs recorded pressure every 3 s and temperature every 15 s for roughly one day (mass = 2.0 g; dimension = 17 mm × 9 mm × 16 mm). Seven of the birds also carried a GPS logger (unpacked IgotU GT-120: Mobile Action, Taiwan, mass = 13 g including attachment materials,

dimensions = 43 mm × 24 mm × 9 mm). GPS units were sealed in heat-shrink plastic (Finishrink CLR-20/50) and attached dorsally using Tesa marine cloth tape (Tesa UK Ltd) underlying a small number of contour feathers (Shoji *et al.* 2014). Because we used only cloth tape, the GPS units fell off within three weeks as a failsafe (Shoji *et al.* 2014). Although our devices were near or just over the 3% limit (always <3.5% of Black Guillemots body mass, recommended by Phillips *et al.* 2003), we did not observe any direct negative impact on reproductive success during the study period.

All calculations and statistics were carried out in R 1.5.2 (R Development Core Team 2014). We extracted dive depth, dive duration and surface interval duration for each dive, after accounting for device drift, using the diveMove package in R (Luque & Fried 2011). We used the sequential differences method to subdivide dives into bouts to identify patches using periods at the surface (difference criterion to identify patches: 66 s: Mori *et al.* 2001). We classified dive shapes into V-shape, U-shape and W-shape based on the criterion provided by Elliott *et al.* (2008). As previous studies had examined patch quality (as assessed by Index of Patch Quality) on birds that primarily fed on schooling prey (Mori *et al.* 2002, Elliott *et al.* 2010, Shoji *et al.* 2014), where patch quality is clear because it represents a school of high-quality prey, we were interested in examining patch quality for birds that primarily fed on non-schooling, benthic prey. We tested whether birds remained at high-quality patches when foraging on non-schooling prey. Specifically, we used linear mixed models (LMMs) with individual as a random factor to examine how mean Index of Patch Quality per patch is related to the number of dives per patch. We tested for normality and homoscedasticity, and variables were long-transformed when necessary. Model selection was based on Akaike's information criterion (AIC) and we calculated  $\Delta AIC$  relative to the null model (intercept-only). Lowest AIC models were considered the most parsimonious. Unless otherwise stated, means  $\pm$  1 sd are presented.

## RESULTS

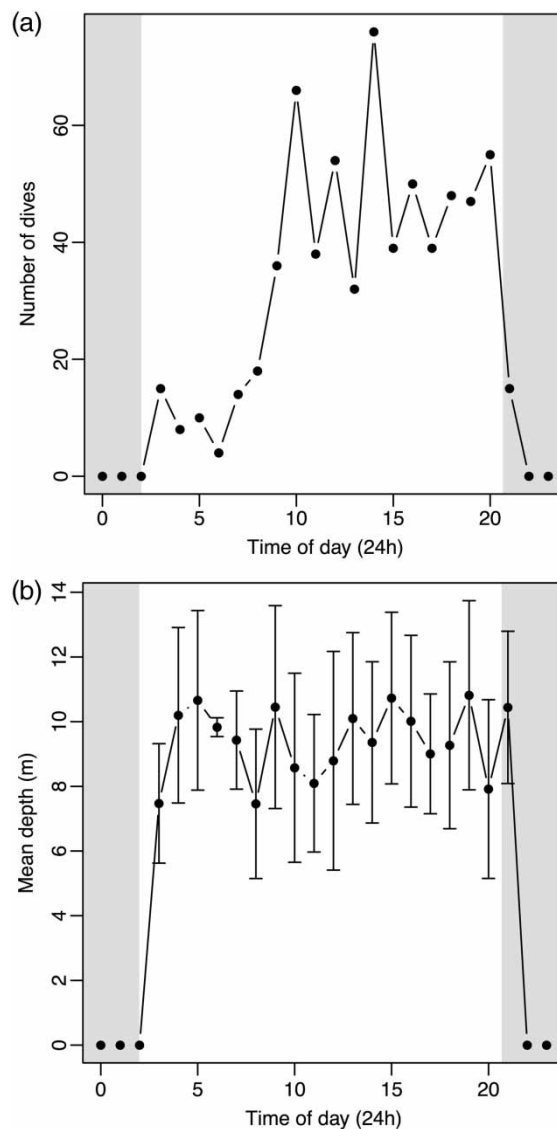
We retrieved TDRs from one adult at Bangor Harbour and three adults at Lighthouse Island. All other birds returned to the colony and continued to breed normally, but we failed to recapture them. Only one of the six GPS loggers was successfully



**Figure 1.** (a) Position of study colonies in Northern Ireland (within the yellow circle) and foraging trip of a breeding black guillemot recorded by a single GPS logger. The red line indicates the GPS trajectory. (b) Detail of the foraging trajectory from the Copeland Bird Observatory colony (red lines) and the yellow star indicates the position of the colony.

retrieved and the data were downloaded. Of the remaining five birds, the GPS logger had fallen off before recapture. All study birds raised young successfully. During the recording period, we observed 21 deliveries from TDR carrying birds at Lighthouse Island and all were butterfish (>20 cm). Total flight time was 1.66 h/day (assuming a speed threshold of 10 km/h) and the furthest distance from dived locations to colony was 1.8 km, as measured by the GPS logger (Fig. 1).

In total, we recorded 664 dives from chick-rearing Black Guillemots ( $n = 4$  birds). Guillemot dives were constrained to daylight hours (Fig. 2a). Mean number of dives per day was  $186 \pm 79$  dives (Fig. 2a), average time spent submerged per day was  $2.13 \pm 0.50$  h, mean dive depth was  $9.3 \pm 2.8$  m (Fig. 2b) and mean dive duration was  $53.6 \pm 21.4$  s. Maximum dive depth averaged  $14.7 \pm 4.0$  m across individuals, with one individual reaching 18.7 m, while maximum dive duration averaged  $89.5 \pm 8.5$  s with two individuals reaching 96 s. Maximum and average dive durations (max = 90 s; mean = 54 s) were shorter and maximum and average dive depths (max = 15 m; mean = 9 m) were shallower than recorded for Black Guillemots elsewhere (Table 1). Dive duration increased with dive depth ( $\Delta\text{AIC} = -335$ , Estimate =  $5.47 \pm 0.26$ ;



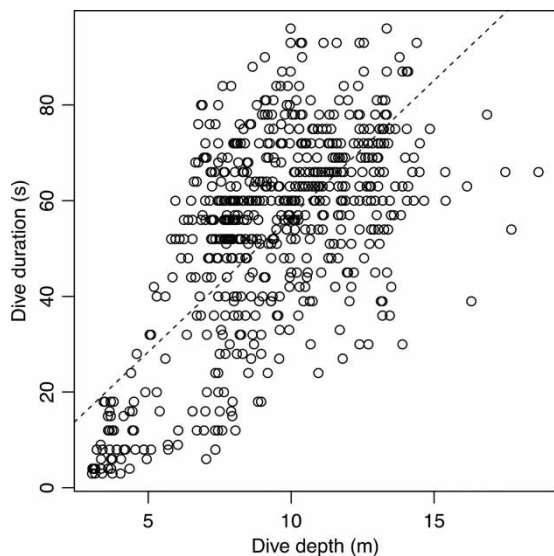
**Figure 2.** (a) Number of dives per hour relative to time of day ( $n = 4$  birds). (b) Mean  $\pm 1$  sd of dive depth per hour relative to time of day ( $n = 4$  birds). The grey box outlines the sunrise/set time.

$P < 0.0001$ ; LMM with individual identity as random effect: Fig. 3). Overall, W-shaped dives were most common (52%), followed by U-shaped dives (32%) and then V-shaped dives (16%). Thirty-one per cent of V-shaped dives were first dives of each dive bout and 22% were second dives. Mean number of dives per patch was  $2.62 \pm 2.28$  dives. In addition, most recorded V-shaped dives were shallower than the subsequent dives. Mean patch Index of Patch Quality was independent of number of dives per patch ( $\Delta\text{AIC} = 11$ , Estimate =  $0.005 \pm 0.003$ ,  $P = 0.77$ ; LMM with individual identity as random effect).

**Table 1.** Summary of dive parameters for *Cephus* species.

Study site	Species	Mean dive duration (s)	Max. dive duration (s)	Mean depth (m)	Method	Source
Southern Vancouver Island, BC	<i>colomba</i>	87	144	10–45	Visual Obs.	Clowater & Burger (1994)
Prince William Sound, Alaska, Benthic foraging	<i>columba</i>	86	–	–	Visual Obs.	Kuletz (1983)
Prince William Sound, Alaska, Pelagic foraging	<i>columba</i>	47	–	–	Visual Obs.	Kuletz (1983)
Rosario Head, Washington	<i>columba</i>	67	105	–	Visual Obs.	Thoresen (1989)
Farallon Islands, California	<i>columba</i>	75	110	20	Visual Obs.	Ainley <i>et al.</i> (1990)
Yaquina Head, Oregon	<i>columba</i>	36	69	–	Visual Obs.	Scott (1973)
Olympic Peninsula, Washington	<i>columba</i>	41	–	–	Visual Obs.	Cody (1973)
Lancaster Sound of the Canadian Archipelago	<i>grylle</i>	67	146	–	Visual Obs.	Bradstreet (1982)
Newfoundland, Canada	<i>grylle</i>	–	112	14 <sup>a</sup>	Visual Obs.	Piatt & Nettleship (1985)
Northeastern Hudson Bay	<i>grylle</i>	70.8	–	4–48	Visual Obs.	Cairns (1992)
Holm of Papa Westray, Orkney	<i>grylle</i>	59	–	–	Radio	Walton <i>et al.</i> (1998)
Stroma Island, Caithness	<i>grylle</i>	95	131	32	TDR	Masden <i>et al.</i> (2013)
Lighthouse Island, Northern Ireland	<i>grylle</i>	54	90	9	TDR	This study

<sup>a</sup>Median values of provided depth ranges were used to calculate the mean depth (m). Methods: Visual Obs. = visual observation; Radio = radio tracking and TDR = time-depth-recorders.



**Figure 3.** Relationship between dive duration (s) and dive depth (m);  $n = 664$  dives,  $n = 4$  birds ( $\Delta AIC = -335$ , Estimate =  $5.47 \pm 0.26$ ;  $P < 0.0001$ ; LMM with individual identity as random effect).

## DISCUSSION

The dive behaviour of Black Guillemots was similar to other small auks; all dives were shallower than 20 m and dive shape was highly variable among individuals. In general, V- and W-shaped dives are associated with capturing prey in mid-water in other auks, while U-shaped dives are associated with benthic feeding

along the seafloor (Elliott *et al.* 2008). The V-shaped dives occurred almost exclusively as the first or second dive of dive bouts, and tended to be substantially shallower than the remaining dives in each dive bout, suggesting that they were associated with probing the water column for prey availability and depth. For instance, birds regulate the degree of hyperventilation for the subsequent dive duration (anticipatory surface intervals) and to do that effectively they must know how deep to dive (Jodice & Collopy 1999, Wilson *et al.* 2003, Elliott *et al.* 2010). Although Black Guillemots fed their offspring almost exclusively on benthic butterfish, and guillemots are usually considered benthic foragers (Cairns 1992), the majority of dives were W-shaped, which is typical of mid-water feeding. Either guillemots fed themselves on alternative, mid-water prey, water column or the bottom topography or prey chases involved undulations in dive profiles. Dive depth was similar between individuals regardless of the proportion of dive shapes, suggesting that they foraged at the similar locations (or at least they foraged at locations with similar bathymetries, which is necessarily true given that guillemots forage close to the colony).

Diving behaviour was constrained by daylight (Fig. 2) because no dive was recorded between 22:00 and 03:00 GMT. While number of dives per hour peaked at midday (Fig. 2a), dive depth within the daylight hours was apparently constrained by bathymetry and, hence, the depth of prey availability rather than visibility, because

dive depth within daylight hours was not affected by time of day (Fig. 2b). At Lighthouse Island, fish delivery frequency is usually high in the morning and evening (Shoji, pers. obs.). Likewise, fish delivery rate peaks at dawn for Black Guillemots in Shetland (Ewins 1986). In contrast, the number of dives was low in the morning and evening in this study and dive rate peaked at midday. Presumably, adults dived to feed themselves at midday and fed their chicks early or late in the day when dive rate would be lower due to the need to return to the offspring to deliver food. At Lighthouse Island, Black Guillemots exclusively brought large butterfish (>20 cm) as a single load to their offspring in this study. We were unable to observe what adults forage for themselves in our study, but Ewins (1986) reported a difference in diet between chicks and adults in Shetland, as is often the case in other auks (Gaston *et al.* 1983, Davoren & Burger 1999, Wilson *et al.* 2004). We speculate that the discrepancy between the daily dive pattern and the provisioning pattern reflects a foraging strategy by Black Guillemots to target different prey items for offspring than for adults, which would also help explain the large number of W-shaped dives.

Patch quality was independent of number of dives per patch. This seems likely to be because Black Guillemots were capturing benthic prey that do not occur in schools. This contrasts with birds chasing schooling fish, and which extend dive duration when a school is present, even if this extends the duration of the post-dive interval (Ydenberg & Clark 1989).

Black Guillemots usually forage close to the colony and the typical travel distance is within 1 km (Ewins 1986). Our retrieved GPS ( $n = 1$ ) confirmed that this was also the case here. Dive depth and duration in our study were shallower (mean depth = 9 m) and shorter (mean duration = 57 s) than individuals at the Stroma islands in Scotland (median depth = 32 m, median duration = 95 s; Masden *et al.* 2013). The Black Guillemots in Scotland could not have dived deeper because they were larger, because the Northern Irish population was actually heavier than Scottish population ( $386 \pm 8$  g,  $359 \pm 19$  g, respectively). Rather, local variation in bathymetry and prey selection may have caused the difference (Halsey *et al.* 2006a). Regardless, our values were more similar to that predicted by the allometric relationship reported by Halsey *et al.* (2006a) and therefore are likely representative of the performance of most Black Guillemots.

In conclusion, dive duration of Black Guillemots foraging in Northern Ireland was similar to the value predicted from allometry, but shorter than those measured in Scotland. Bathymetry likely influences the dive behaviour of this benthic-feeding species because light availability strongly limited dive rate, most dives were U-shaped and shallow dive depths typical of the relatively shallow seas near our study site. Black Guillemots are extreme coastal feeders utilizing shallow water to feed, and based on our data they are likely to be affected by marine energy resources such as tidal stream turbine activities, which will be increasingly installed within UK waters (Department of Energy and Climate Change 2004). To assess the potential impacts of tidal developments on the conservation of Black Guillemots, further study is urgently required that incorporates both diving behaviour and horizontal movement with a larger sample size.

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