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ORIGINAL PAPER

# Going deep: common murres dive into frigid water for aggregated, persistent and slow-moving capelin

**April Hedd · P. M. Regular · W. A. Montevecchi · A. D. Buren · C. M. Burke · D. A. Fifield**

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**Abstract** Owing to the necessity of delivering food to offspring at colonies, breeding seabirds are highly constrained in their foraging options. To minimize constraints imposed by central-place foraging and to optimize foraging behavior, many species exhibit flexible foraging tactics. Here we document the behavioral flexibility of pursuit-diving common murres *Uria aalge* when foraging on female capelin *Mallotus villosus* in the northwest Atlantic. Quite unexpectedly, being visual foragers, we found that common murres dived throughout the day and night. Twenty-one percent of recorded dives ($n = 272$ of 1,308 dives) were deep ($\geq 50$ m; maximum depth = 152 m, maximum duration = 212 s), bringing murres into sub-0°C water in the Cold Intermediate Layer (CIL; 40–180 m) of the Labrador Current. Deep dives occurred almost exclusively during the day when murres would have encountered spatially predictable aggregations of capelin between 100 and 150 m in the water column. Temperatures within the CIL shaped trophic interactions and involved trade-offs for both predators and prey. Sub-0°C temperatures limit a fish's ability to escape from endothermic predators by reducing burst/escape speeds and also lengthening the time needed to recover from burst-type activity. Thus, while deep diving may be energetically costly, it likely increases certainty of prey capture. Decreased murre foraging efficiency at night (indicated by an increase in the number of dives per bout) reflects both lower light conditions and changing prey behavior, as capelin migrate to warmer surface waters at night where their potential to escape from avian predators could increase.

## Introduction

Biophysical variability in dynamic marine environments affects the performance, behavioral ecology and distribution of both predators and prey (Domenici et al. 2007). During breeding, the demands of central-place foraging greatly restrict the foraging options and provisioning opportunities of seabirds (Orians and Pearson 1979), often challenging their behavioral and physiological capabilities (Weimerskirch et al. 2003; Jodice et al. 2006; Elliott et al. 2008a). Seabirds may consequently employ flexible foraging tactics in an effort to minimize constraints and effectively cope with breeding demands.

Seabird species that fly and dive are compromised in both forms of locomotion (Burger 1991). Pursuit-diving alcids have taken these adaptations to extremes and exhibit considerable performance capability and agility—"flying" underwater to capture prey (Tremblay et al. 2003). Common murres *Uria aalge*, the deepest diving species among birds that fly (Piatt and Nettleship 1985; Burger 1991), have been shown to make major adjustments in foraging behavior and effort in response to fluctuating prey conditions during chick-rearing (Burger and Piatt 1990; Davoren et al. 2003a; Harding et al. 2007).

Off Newfoundland, in the northwest Atlantic, breeding common murres specialize on capelin *Mallotus villosus*, preferentially feeding themselves and their chicks on mature females (Piatt 1990; Davoren and Montevecchi

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A. Hedd (✉) · P. M. Regular · W. A. Montevecchi ·
A. D. Buren · C. M. Burke · D. A. Fifield
Cognitive and Behavioural Ecology Program,
Psychology Department, Memorial University,
St John's, NF A1B 3X9, Canada
e-mail: ahedd@mun.ca

2003a; Burke and Montevecchi 2008). During spring and early summer, capelin migrate from over-wintering areas near the edge of the continental shelf to the coastal waters of Newfoundland to spawn (Nakashima 1992). Suitable habitat for demersal spawning and staging along the northeast coast of Newfoundland creates persistent aggregations of capelin (Davoren et al. 2006) which, in turn, provide predictable foraging areas for the massive concentration of murres breeding at the nearby Funk Island Seabird Ecological Reserve (Davoren and Montevecchi 2003a, Davoren and Montevecchi 2003b). Spatially persistent demersal spawning sites (<38 m) and staging areas (100–150 m) for capelin have been documented between Funk Island and the northeast coast of Newfoundland (see Davoren et al. 2006 for locations).

Prior to spawning, mixed-sex shoals of maturing capelin stage deep in the water column, remaining within or below the Cold Intermediate Layer (CIL; <0°C) of the Labrador Current during the day and migrating to warmer (~9–13°C) surface waters at night (Davoren et al. 2006). The CIL is a band of sub-0°C water (approximately 50–240 m) that is a prominent oceanographic feature of the Newfoundland Shelf area through much of the year (Petrie et al. 1988, Davoren et al. 2006). When capelin mature, they move inshore to spawn on beaches and at demersal sites located near the coast (Davoren et al. 2006). Capelin that survive spawning may return to deep water staging areas to forage and replenish fat reserves before the onset of winter (Winters 1970).

In this paper, we examine diurnal patterning and physiological efficiency of diving by parental common murres, and focus on deep (≥50 m) dives for capelin located within the CIL. Because the probability of an endothermic avian predator capturing ectothermic prey is at least partially mediated by temperature effects on the fish's ability to perform and recover from burst-type exercise (Kieffer 2000; Cairns et al. 2008), we hypothesize that capelin located within the CIL will be slow-moving and relatively easy for murres to catch. On this premise, if murres are successful at capturing prey during a diving bout (Camphuysen 2005), we predict that they will perform fewer dives per bout as the average depth of dives within the bout increases. Also, if the time spent foraging within a patch (i.e., dive bottom time) relates to pursuit time for prey, we predict that dive bottom times will be shorter in colder waters. Lastly, as the foraging efficiency of penguins and cormorants has been shown to vary with light conditions (Wilson et al. 1993, Wanless et al. 1999), we predict that murres will perform more dives per bout as light availability declines. We consider how the physical environment has shaped interactions between murres and capelin within the Newfoundland Shelf ecosystem.

## Materials and methods

### Study sites

Research was conducted between 14 July and 6 August 2007 at Gull Island (47°16′N, 52°46′W; ~1,632 breeding pairs of common murres; Robertson et al. 2004), Witless Bay, and between 25 July and 4 August 2007 at Funk Island (49°45′N, 53°11′W, ~400,000 pairs, Chardine et al. 2003), Newfoundland, Canada, at a time when most murres were rearing chicks (Fig. 1).

### Oceanographic setting

Temperature data collected at hydrographic Station 27 (Fig. 1; 47°31′50″N, 52°35′10″W; Fisheries and Oceans Canada Oceanographic database, http://www.mar.dfo-mpo.gc.ca/science/ocean/database/data_query.html) on 4 days between 13 and 31 July 2007 were used to describe the thermal profile of the water column (5–165 m), and to delineate the position of the CIL. Temperatures were available at 10 m intervals between the surface and 50 m, then subsequently at 75, 100, 150, and 165 m. Station 27 is located within the Avalon Channel branch of the Labrador Current and provides a robust index of oceanographic

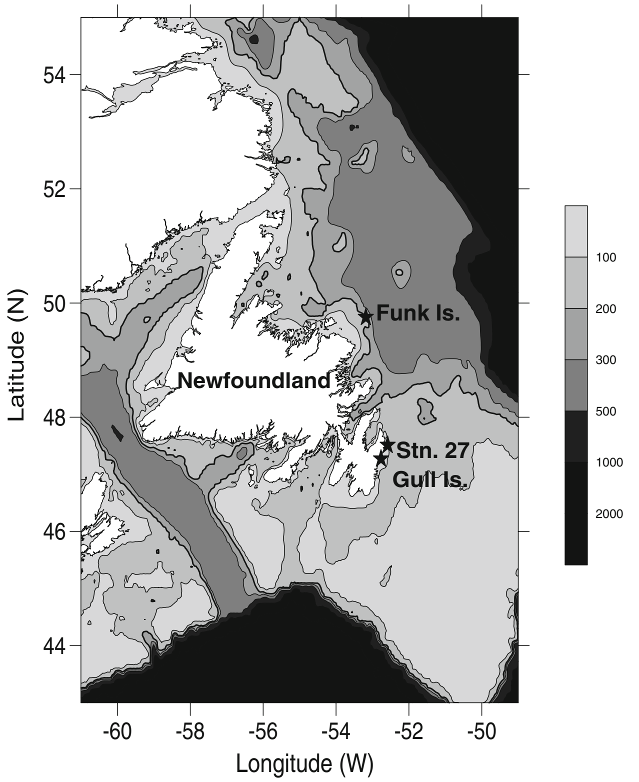


**Fig. 1** Map of the study area indicating the location of seabird colonies and other places noted in the text. *Shaded* depth contours are indicated in the legend

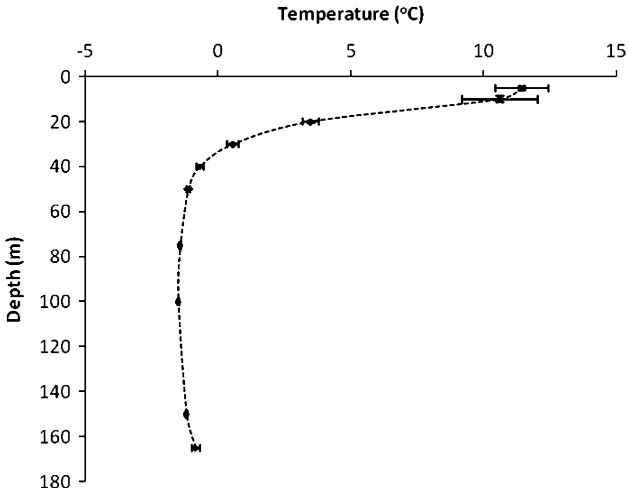


**Fig. 2** Mean ± SE temperature profile of the water column using data collected at hydrographic Station 27 on 4 days between 13 and 31 July 2007

conditions over the Newfoundland and Labrador Shelf (Petrie et al. 1988; Drinkwater 1996).

## Field protocol: devices and procedures

Adults attending chicks ($n = 6$ at Gull Island from 14 to 24 July, and $n = 15$ at Funk Island from 25–30 July) were caught with a 6 m telescoping noose pole and equipped with a Lotek LTD 1110 logger (5 g, 32 × 11 mm; 128 Kb memory) on the left leg and a Canadian Wildlife Service metal band on the right leg. Loggers were secured to plastic leg bands (Pro-Touch Engraving, Saskatoon, Saskatchewan) using cable ties. These loggers recorded pressure (depth resolution ± 0.49 m when maximum depth < 125 m, and ±0.98 m when maximum depth 125–250 m) and temperature (±0.3°C) every 2 s for 36 consecutive hour until their memory filled. Devices remained on the birds for the full 36 h, capturing information across successive foraging trips for each bird. Upon recapture, loggers were removed and murres were weighed with a Pesola® 1 or 1.5 kg spring balance, and 0.5 ml of blood was collected from the brachial vein to determine sex using W-chromosome analysis (Fridolfsson and Ellegren 1999). Birds were held with eyes covered for ∼4 and ∼6 min during logger deployment and recapture, respectively. Nine of the 15 loggers were recovered from murres on Funk Island as were four of the six deployed on Gull Island (60% overall recovery rate). Of the loggers recovered, data were lost from one (Funk Island) and data from two others (Gull Island) were distorted and unrecoverable.

Throughout logger deployments, dawn to dusk observations (05:00–21:00 h Newfoundland Daylight Savings time) were conducted at Gull Island, and equipped birds were observed at Funk Island when work time allowed. Arrival and departure times and prey items delivered to chicks were noted for equipped birds. When observational data were not available, colony arrival and departure times were estimated using continuous temperature and depth records obtained from the data loggers (Tremblay et al. 2003; Elliott et al. 2008a).

At Funk Island, food samples were collected throughout the period of logger deployment using dip-nets on long poles to catch prey-carrying murres as they returned to the colony. Fish were weighed (using an 100 g Pesola® scale), measured (total length ± 1 mm using a ruler), identified,

**Table 1** Number of complete (and partial) foraging trips (FTs), dives and dive bout characteristics for individual chick-rearing common murres along with frequency and occurrence of shallow (<50 m) and deep (≥50 m) dives during the day and night

| Bird | No. FTs | Total dives (bouts) | Mean dives/bout (range) | Day | | | Night | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | | Shallow dives *n* (%) | Deep dives *n* (%) | Mean dives/ bout (*n*) | Shallow dives *n* (%) | Deep dives *n* (%) | Mean dives/ bout (*n*) |
| Funk Island | | | | | | | | | |
| 84650436 | 4 | 94 (36) | 2.6 (1–16) | 42 (45%) | 32 (34%) | 2.3 (32) | 20 (21%) | 0 (–) | 4.8 (4) |
| 84650437 | 3 (1) | 310 (27) | 11.5 (1–92) | 143 (46%) | 27 (9%) | 4.7 (18) | 140 (45%) | 0 (–) | 10.9 (9) |
| 84650438 | 2 (1) | 197 (47) | 3.9 (1–41) | 45 (23%) | 60 (31%) | 2.6 (40) | 83 (41%) | 9 (5%) | 8.1 (7) |
| 84650442[a] | 1 | 38 (14) | 2.7 (1–8) | 12 (32%) | 26 (68%) | 2.7 (14) | 0 (–) | 0 (–) | – |
| 84650445[a] | 1 (1) | 66 (24) | 2.7 (1–6) | 39 (59%) | 27 (41%) | 2.7 (24) | 0 (–) | 0 (–) | – |
| 84650447 | 2 (1) | 121(28) | 3.7 (1–17) | 61 (50%) | 21 (17%) | 3.0 (26) | 39 (32%) | 0 (–) | 10 (2) |
| 84650478[a] | 3 (1) | 409 (33) | 12.2 (1–37) | 355 (87%) | 54 (13%) | 12.2 (33) | 0 (–) | 0 (–) | – |
| Gull Island | | | | | | | | | |
| 99685172 | 3 | 68 (22) | 3.1 (1–27) | 50 (74%) | 14 (21%) | 3.1 (22) | 4 (6%) | 0 (–) | – |
| 99685173 | 1 | 5 (2) | 2.5 (1–4) | 3 (60%) | 2 (40%) | 2.5 (2) | 0 (–) | 0 (–) | – |
| Total or Mean | 20 (5) | 1,308 (233) | 5.0 | 750 (57%) | 263 (20%) | 4.0 | 286 (22%) | 9 (<1%) | 8.4 |

[a] Logger temperature records indicate that birds spent the night at the colony (i.e., there was no nighttime sampling at sea)

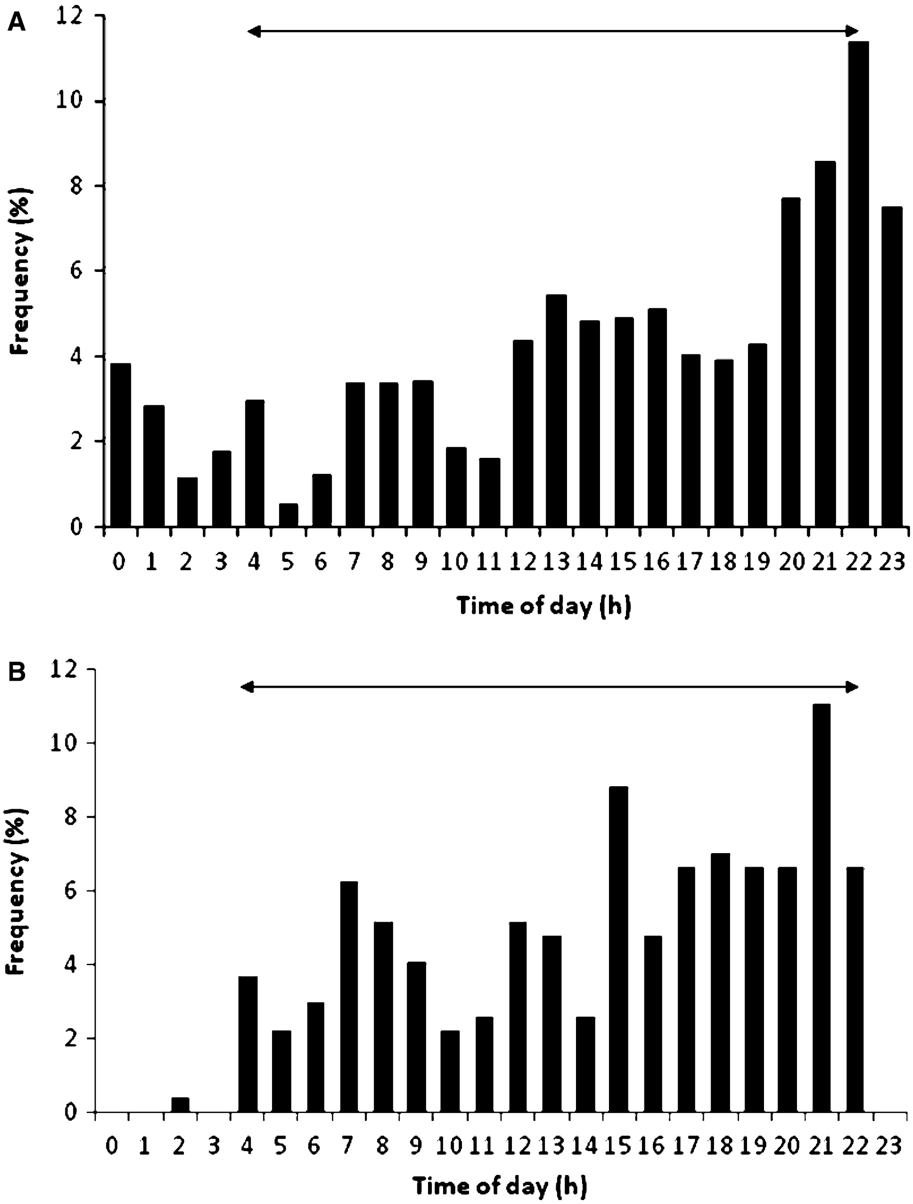


**Fig. 3** Frequency distributions of the time of diving by common murres during chick-rearing, July 2007: **a** all dives, $n = 1{,}308$, **b** deep ($\geq 50$ m) dives only, $n = 272$. *Double headed arrows* indicate the daylight period

sexed and classed as gravid or spent (which may have included a few immature fish).

## Data analysis

As drift in the LTD 0-level exceeded ±1 m in some cases, we defined dives as submersions $\geq 2$ m. Start and end times for each dive were determined, along with the following descriptive parameters: dive duration, maximum depth, minimum temperature, dive bottom time, surface interval duration, and dive and bottom efficiencies. Dive bottom time (generally assumed to represent the time available for foraging) was defined as the time elapsing from the first and last instant when vertical velocity (calculated between successive records) fell below 0.5 $\mathrm{ms}^{-1}$ (e.g., Halsey et al. 2007). Dive efficiency was defined as the ratio of the duration of the dive to the duration of the dive + the subsequent surface time, and bottom efficiency was the ratio of bottom time to the dive + the subsequent surface time (Camphuysen 2005). V-shaped dives ($n = 165$, 12.6%) had no bottom time, and hence had a bottom efficiency of zero. Bouts of diving were identified using a surface interval criterion (e.g., Huin and Prince 1997). A frequency distribution of post-dive surface intervals showed a rapid decline to 220 s after which they remained relatively constant. A bout of diving was therefore defined as a single dive or as a series of dives in which each dive started $\leq$ 220 s after the previous dive had ended.

Dives were classified as either “shallow” (<50 m) or “deep” ($\geq$50 m). We chose 50 m as the criterion to define a

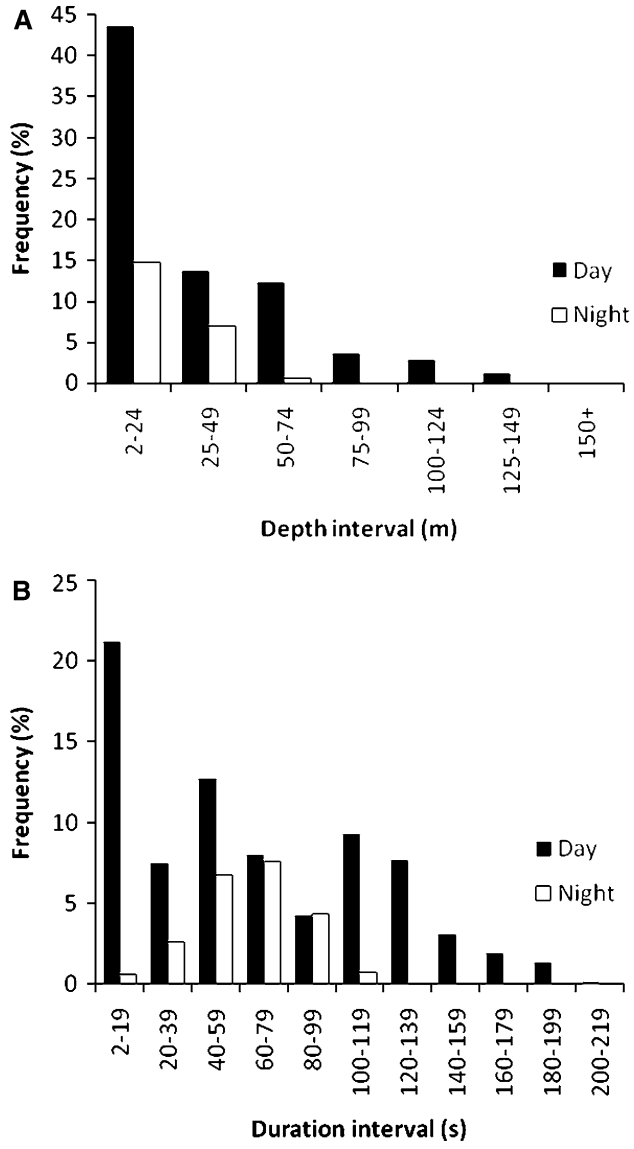


**Fig. 4** Frequency distributions of **a** diving depth (m) and **b** diving duration (s) during the day and night for chick-rearing common murres, July 2007

deep dive, as this depth ensured that birds had reached, and were presumably foraging within the CIL (see "Results"). We plotted frequency distributions of the time of diving (by hour), examining both overall patterns and those for deep dives separately. We used Chi-square tests for independence to determine whether frequency distributions of diving depth and duration were dependent on time of day (day vs. night). Daytime commenced with nautical twilight in the morning (the instant when the rising sun is 12° below the horizon) and continued until nautical twilight in the evening (the instant when the setting sun is 12° below the horizon); nighttime was the intervening period (RASC 2007).

We also assessed whether dive depth varied as a function of time of day by fitting a generalized linear model with a gamma error distribution and inverse links using SAS 9.1 PROC GENMOD (SAS Institute 2005). Data are presented as mean ± SE, and an alpha level ($\alpha$) of 0.05 was used to assess statistical significance.

## Results

### Oceanographic setting and parental prey deliveries

During July 2007, the CIL or band of sub-0°C water across the Newfoundland and Labrador Shelf extended from 40 m to below 165 m (Fig. 2). Hence when below 40 m in the water column, murres and capelin were in <0°C water. Temperature profiles collected by the dive loggers confirmed that murres reached the CIL on all deep dives.

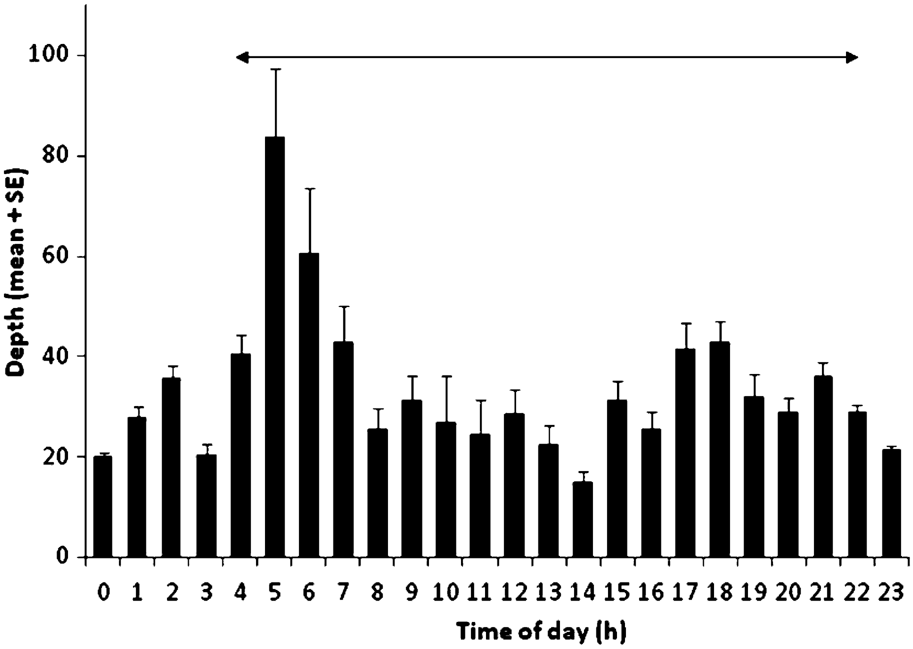
Coincident with the diving records, parental prey deliveries ($n = 86$) by unequipped murres at Funk Island consisted of 100% female capelin; 23% were gravid, 65% were spent, 2% were immature and for the remaining 10% the maturity status was unknown. Concurrent hydro-acoustic surveys detected no capelin at known demersal spawning sites (18–38 m water) within the murre's foraging range from Funk Island when murre diets were collected at the colony (G. K. Davoren and P. Penton, unpublished data).

### Diving performance

Diving profiles were obtained for nine individuals ($n = 7$ from Funk Island, $n = 2$ from Gull Island) during 20 (plus 5 partial) foraging trips, involving a total of 1,308 dives (Table 1). Birds dived throughout the day and night, with a peak in activity near dusk (~21:00–22:00 h; Fig. 3a). Overall, mean ± SE (and maximum) dive depth and duration were 30 ± 0.8 m (152 m) and 64 ± 1.3 s (212 s), respectively. The distribution of both dive depth ($\chi^2_7 = 82.3$, $P < 0.01$) and duration ($\chi^2_{10} = 287.6$, $P < 0.01$) was dependent on time of day (Fig. 4), with long and deep dives occurring almost exclusively during daylight.

By our definition, 21% ($n = 272$) of all dives were deep ($\geq$50 m) and brought murres into the CIL. All murres performed deep dives, and these comprised 9–68% of the dives performed by each individual (Table 1). Most (97%) deep diving occurred during the day, largely from mid-afternoon to dusk, with a smaller peak in early morning (Fig. 3b). Mean dive depth varied with time of day ($\chi^2_{23} = 122.04$, $P < 0.0001$), being significantly deeper in the 2 h after sunrise (05:00–06:59 h) than through the remainder of the day (contrast test: $\chi^2_1 = 29.15$, $P < 0.0001$, Fig. 5). Murres dived frequently at night, but almost exclusively to depths less than 50 m (Figs. 3a, 5; Table 1). Although the number of individuals studied was small, the data suggested a colony difference in the time of

**Fig. 5** Mean (+SE) dive depth by time of day for nine common murres during the chick-rearing period, July 2007. The *double headed arrow* indicates the daylight period



diving, with only Funk Island birds diving at night (Table 1).

Dive efficiency was low for the shallowest dives (2–9 m), and highest for dives between 10 and 29 m (Fig. 6a). Efficiency declined for dives below 30 m and remained relatively constant for deeper depths. Bottom efficiency was also highest for dives between 10 and 29 m, declined progressively between 30 and 79 m, and was extremely low for dives deeper than 80 m (Fig. 6b).

Individual murres performed, on average, 5.0 ± 1.3 dives per bout (range of individual means = 2.5–12.2; Table 1), and as anticipated, they undertook fewer dives per bout as the average depth of dives within the bout increased (Fig. 7). Bouts that consisted of just 1 or 2 dives had average maximum depths $\geq$50 m (Fig. 7). The mean number of dives per bout was also significantly greater during dark conditions at night than during the day (independent $t$-test $= -2.54$, $df = 231$, $P < 0.05$). There was no clear relationship between dive depth and time spent at the bottom of the dive, though the longest bottom times corresponded with the deepest dives. Contrary to our expectations, dive bottom time increased with decreasing temperature (Fig. 8), but the proportion of variance accounted for was small (7%).

## Discussion

This study documents the remarkable behavioral flexibility of common murres. Quite unexpectedly, as murres are considered to be largely visual foragers, birds dived throughout the day and night, and reached depths in excess of 150 m during the day. Our findings exceed depths recorded previously for this species using data loggers (Table 2), but they confirm the impressive diving depths recorded using maximum depth gauges (Burger and Simpson 1986) and inferred through fisheries bycatch data (Piatt and Nettleship 1985) for murres in the region.

A most intriguing feature of this dataset is the incidence of long, deep dives; more than 20% of dives exceeded 50 m, and 8% exceeded 75 m, which is the maximum depth recorded for this species in the eastern Atlantic (Table 2). Deep diving, then, is clearly an important aspect of parental foraging in the western Atlantic where birds specialize on capelin (Piatt 1990; Davoren and Montevecchi 2003a; Davoren 2007; Burke and Montevecchi 2008). Presumably these deep dives would incur high energetic costs as the birds are hunting in frigid (sub-0°C) waters. So why do they perform these deep dives and, when they do, how successful are they at capturing prey?

In all likelihood, murres in the Newfoundland region dive deeply simply because they have to, but we hypothesize that when they do, their prey capture rates are high. The study area near Funk Island has gradually sloping bathymetry from the coast line, with water depth increasing with increasing distance from the coast (see Fig. 1, Davoren et al. 2006). As flapping flight in air is energetically costly for murres, birds may choose to forage close to the colony in deeper water. Murres from Funk Island forage on shoals of capelin located between the colony and the coast (Davoren et al. 2003a, b) that are known to be persistent both in space (at the scale of hundreds of meters) and time (across years; Davoren et al. 2006). These capelin shoals are found deep in the water column, within the CIL, during the day. Temperature can limit fishes' swimming performance (swimming speed

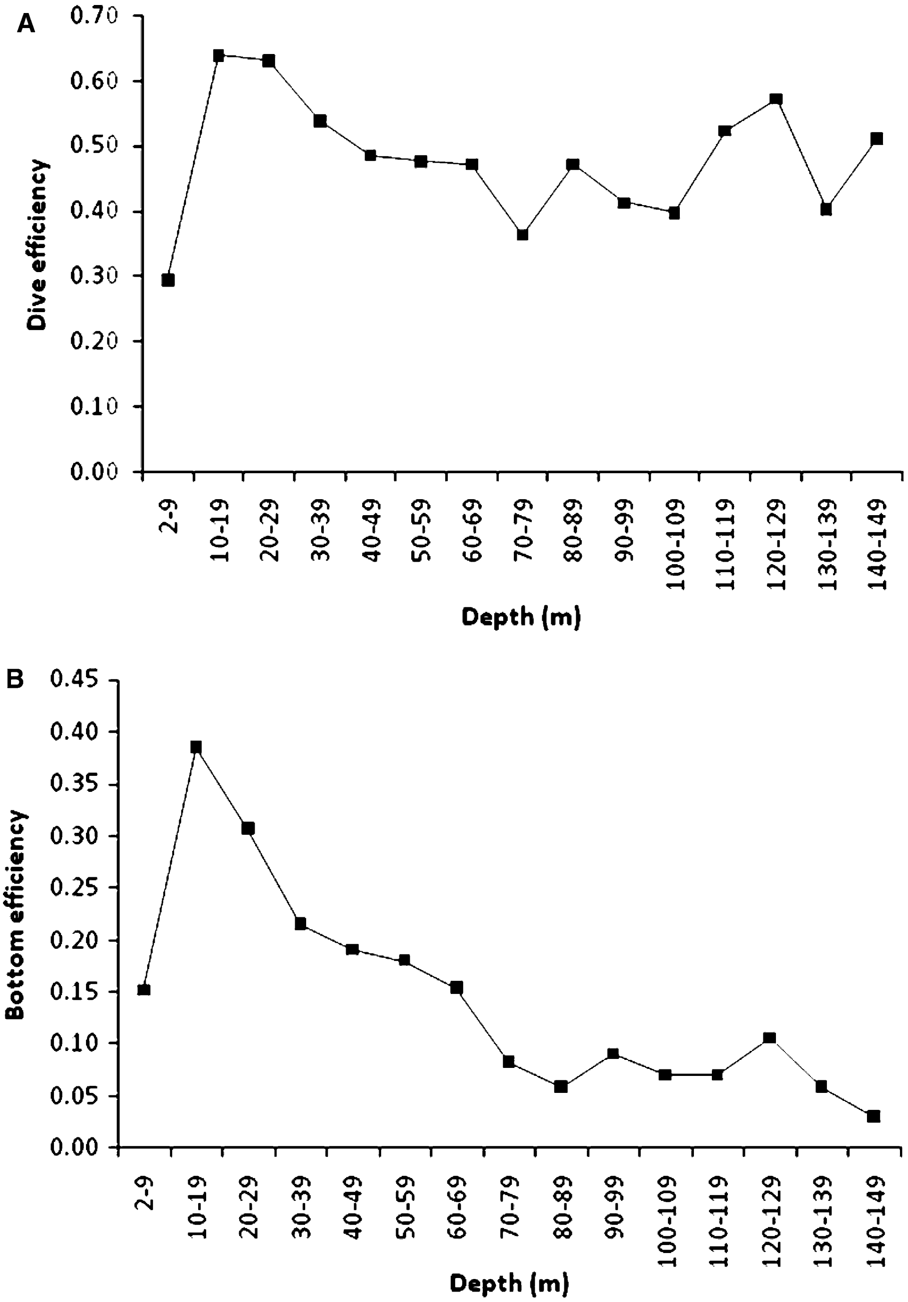
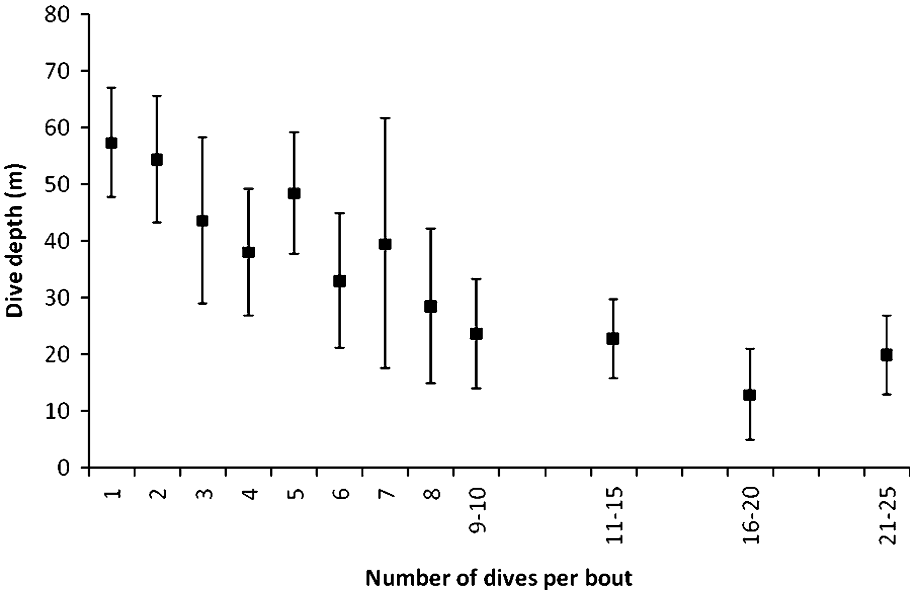


**Fig. 6** Mean **a** dive and **b** bottom efficiency per depth class. Means are plotted only when $n \geq 4$ dives per depth class

halves with every 10°C decrease in water temperature; $Q_{10°C} = 2$; Videler and Wardle 1991), and perhaps more importantly in the context of predator-prey interactions, the cold temperatures would increase the duration of recovery from burst-type exercise (Kieffer 2000). Capelin located in the CIL would therefore have relatively slow escape speeds and would require extended periods of time to recover, which would presumably place them at a disadvantage when facing endothermic predators. So, while deep foraging in the CIL is perhaps energetically demanding, it is also likely an effective tactic, as capelin shoals are easy to find (Davoren et al. 2006) and we hypothesize, the fish are easy to catch.

Murres from Funk Island dived throughout the day and night, and as anticipated from studies of other diving avian predators (Wilson et al. 1993, Wanless et al. 1999), both diving depth and foraging efficiency decreased during dark conditions at night. At night, murres dived frequently to shallow depths (<50 m) and showed decreased foraging efficiency as reflected by an increase in the number of dives per bout. Temporal patterns in murre diving behavior and efficiency reflect diel variation in both light conditions and prey behavior. Capelin shoals occupying deep waters around Funk Island engage in diel vertical migrations (Davoren et al. 2006). During the day, when murres perform deep dives,

**Fig. 7** Mean dive depth (m ± 95% confidence intervals) as a function of the number of dives per bout



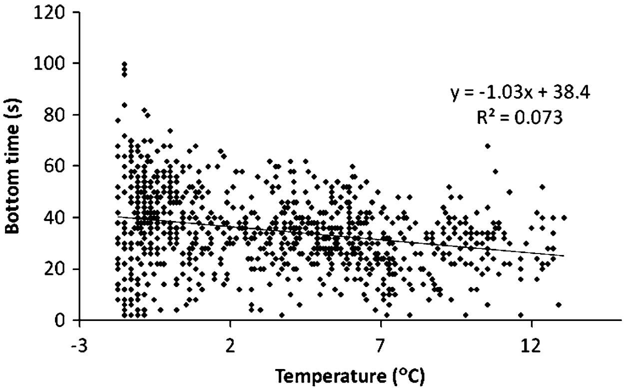


**Fig. 8** Dive bottom time as a function of the minimum temperature attained during a dive. V-dives (with no bottom time) are excluded and to accommodate the lagged response of the temperature sensor, only dives ≥30 s were plotted

capelin occur in discrete shoals within and below the CIL. At dusk, capelin migrate vertically through the CIL to reach the warm surface layer, where they disperse and spend the night (Davoren et al. 2006). At dawn, the pattern is reversed; shoals re-group and migrate down into the CIL and spend the day at depth (Bailey et al. 1977). The murres' deepest dives occurred just after sunrise, when capelin are migrating toward the seabed, perhaps indicating birds were chasing fish to the bottom. Yet, in our study, most diving occurred near sunset, when the capelin are migrating toward the surface. The shoaling behavior and upward movement of capelin at dusk, when light levels are still relatively high, could provide murres with the most favorable foraging conditions.

During the 1990s, capelin shifted deeper in the water column and likely experienced considerable predator–prey tradeoffs (Mowbray 2002). Capelin produce very little anti-freeze protein but can super-cool and have been documented in water temperatures below the freezing point of their bodily fluids (−0.4 to –1.5°C; Raymond and Hassell 2000, Nakshima and Wheeler 2002). It has been hypothesized that capelin shoal in deep, sub-0°C water during the day to reduce predation risk from their primary predator—northern cod *Gadus morhua* that generally occupy waters between −0.5 and 8.5°C (Rose and Leggett 1990; Mowbray 2002). Capelin might also encounter improved feeding conditions at deeper depths during the day when zooplankton biomass is considerably elevated in the lower (>50 m) compared with the upper (<50 m) water column (Mowbray 2002; Davoren et al. 2006). Migrating into warmer surface waters at night likely increases metabolic rates, thereby increasing escape response capabilities (Videler and Wardle 1991) and also accelerates digestion and gonadal development (Winters 1970; Davoren et al. 2006). To summarize, by aggregating at depth in sub-0°C water during the day, capelin are inaccessible to cod and most species of seabirds (Regehr and Montevecchi 1997; Regehr and Rodway 1999) but they remain vulnerable to deep-diving murres. This "cost" for capelin is likely a minor trade-off, as the consumption of capelin by murres pales in comparison to that of cod (Montevecchi 2001).

While we did not find the anticipated relationship between time spent foraging within a patch (i.e., dive bottom time) and water temperature, murres did perform fewer dives per bout as the average depth of dives within the bout increased, supporting our hypothesis that foraging success is high during deep dives. Contrary to our initial rationale, it is possible that bottom time increases in cold (deep) water owing to lower light levels at depth and associated increases in prey handling time. Using stomach temperature loggers, Camphuysen (2005) reported that though foraging success was variable at the level of an individual dive, murres

**Table 2** Common and thick-billed murre approximated mean and maximum (in parentheses) dive characteristics as revealed by electronic data loggers

| Location, year (s) | Dive duration (s) | Dive depth (m) | Method | Sources |
|---|---|---|---|---|
| Common murre | | | | |
| California 2001 | 37 (193) | – | VHF telemetry | Nevins (2004) |
| Newfoundland 2007 | 62 (212) | 30 (152) | TDR | This study |
| Scotland 1986–1987 | 67 (202) | – | VHF telemetry | Wanless et al. (1988) |
| Scotland 1997–1998[a] | 107 (–) | 41 (–) | VHF telemetry | Camphuysen (2005) |
| Scotland 2001–2003[a] | 92 (–) | 34 (~75) | PreciTD loggers | Camphuysen (2005) |
| Norway 1999 | 39 (119) | 10 (37) | TDR | Tremblay et al. (2003) |
| Thick-billed murre | | | | |
| Nunavut 1988–1989 | 55 (224) | 18 (107) | TDR | Croll et al. (1992) |
| Nunavut 1998 | 86 (–) | – | Direction recorders | Falk et al. (2002) |
| Nunavut 2005[b] | 68 (246) | 79 (140) | TDR | Elliott et al. (2007) |
| Labrador 1999 | 100[c] (240) | – | T recorders | Jones et al. (2002) |
| Greenland 1997–1998 | 117[a] (240) | – | Direction recorders | Falk et al. (2000, 2002) |
| Greenland 1998 | 105[d] (–) | –(>70) | Direction recorders | Benvenuti et al. (2002) |
| Norway, 1998 | 97 (196) | 45 (136) | TDR | Mehlum et al. (2001) |

Data are organized by location and arranged west to east

[a] Averaged across years

[b] Non-handicapped birds only

[c] Averaged for males and females

[d] Chick-rearing birds only

successfully captured prey on most diving bouts. If the murres in our study had similar success, fewer deep than shallow dives were needed to catch prey. Standard (physiological) assessment of diving and bout efficiency suggested that the murres deep dives were inefficient, however, these physiological costs need to be integrated with information on catch per unit effort in order to assess overall foraging efficiency. Resolving this will require an understanding of how murres trade-off energetic costs of flying (horizontal movement) and diving (vertical movement) with rates of prey intake in different areas. We are addressing these issues with tracking studies and will attempt to quantify rates of prey capture with stomach thermal (Weimerskirch et al. 2005) and/or beak sensors (Wilson et al. 2002).

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