Unconventional ventral attachment of time–depth recorders as a new method for investigating time budget and diving behaviour of seabirds

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Summary

We tested the use of commercially available electronic time–depth recorders (TDRs) to quantify activities and thus total time budgets of seabirds. This new method involved first fitting TDRs onto the birds' bellies (not on their backs), and, secondly, analysing continuous recordings of temperature, light and pressure to differentiate activities on land and at sea. The birds studied were 12 common guillemots *Uria aalge* rearing chicks at Hornøya, in northern Norway. The method successfully recorded five different activities: at the colony, flying, diving, and resting or active at the sea surface. Overall, common guillemots spent 68% of their time at the colony and 32% at sea. While at sea, the birds spent the majority (77%) of their time at the surface, during which they were active 64% of the time, and rested only 13%. Birds engaged in the costly behaviours of flying and diving for shorter times (11% and 12% of their time at sea, respectively). The method allowed us to differentiate between two types of trips to sea based on the presence (foraging trips: 77% of the total number of trips) or absence (non-foraging trips: 23%) of dives. On average, foraging trips lasted 3.2 h, but most trips were shorter (<1 h), during which the mean estimated travel distance from the colony was 11 km. Diving occurred in bouts of 7.7±6.6 dives (mean ± S.D.). The mean maximum dive depth was 10.2±7.6 m (deepest dive: 37 m), and the mean dive duration and post-dive intervals were 38.7±21.3 s (longest dive: 119 s) and 20±12 s, respectively. Direct and indirect evidence suggests that common guillemots had no difficulty in finding food during the study period, and that the TDRs had minimal effects on the birds' behaviour and physiology. The method is easy to use in the field and is applicable to many other flying seabird species; it is therefore an efficient way of collecting information on time budgets and diving behaviour in the context of various ecological and monitoring studies.

Key words: alcid, Barents Sea, common guillemot, *Uria aalge*, foraging behaviour.

Introduction

Understanding the role and operation of top predators, such as seabirds, in marine systems requires investigation of their diet and feeding ecology. Knowledge of foraging patterns is essential when responding to many practical and theoretical questions related to marine ecology, behavioural ecology, ecophysiology and the management and conservation of marine ecosystems (Ashmole, 1971; Croxall, 1987; Hunt and Schneider, 1987; Monaghan, 1996; Ricklefs, 1983). However, excluding direct observation (by definition limited in time and space), recording the activity at sea of animals foraging offshore, from a few to thousands of kilometres away from their breeding colony, is challenging. During recent years, the study of seabirds' foraging behaviours has been facilitated by the development of new technologies resulting from electronic miniaturisation. Determining the location of individuals at sea is now possible using satellite tags (Jouventin and Weimerskirch, 1990; Weimerskirch et al., 2002) or light

sensors (Wilson et al., 1995a). It is also of primary importance, however, to distinguish the bird's different activities at sea (flying, diving and resting), but to date quantification of their time budget has remained somewhat problematic, especially for medium and small-sized species such as larids and alcids.

The activities of seabirds have been investigated through the use of specialist electronic loggers that record a few activities only, depending on the type of sensor that they carry, i.e. pressure, conductivity, acceleration and temperature sensors, and propellers (Mohus, 1987; Wilson et al., 1992, 1995b; Afanasyev and Prince, 1993; Wilson, 1995; Yoda et al., 1999; Ropert-Coudert et al., 2002). However, the specialisation of those devices has not permitted simultaneous recording of both time budget and diving behaviour in flying–diving seabirds. To overcome this problem, new devices storing data from wingbeat (microphone membrane

movements) and depth sensors have recently been developed to record the events that characterize a foraging trip and therefore the overall time-budget at sea (Falk et al., 2000; Benvenuti et al., 2001). The main limitations of the technique are that (1) unlike alcids, many seabirds alternate gliding with wing beats while flying, and (2) the devices are not available commercially. In the past, surface swimming activity of little penguins has been recorded using ventrally attached speed meters (Gales et al., 1990), thus overcoming the need for the bird to dive in order to record its swimming speed using a dorsally attached speed meter (Ropert-Coudert et al., 2002).

The goal of this present study was to test the use of commercially available time-depth recorders (TDRs) to quantify activities, and thus time budget, of seabirds. Such bird-borne data loggers have three different sensors recording external pressure, temperature and light. We used TDRs in two unconventional ways. First, we fitted the loggers on the bird's belly, not on its lower back as is usually done (Wanless et al., 1988a,b; Tremblay and Cherel, 1999, 2000; Benvenuti et al., 1998; Watanuki et al., 2001), and secondly, we recorded the three parameters at a high sampling rate and analysed the data in order to differentiate activities at sea and on land, through time changes in water and air temperature, light levels and depth. This method theoretically permits the recording of time budget and diving behaviour simultaneously. We used the common guillemot *Uria aalge* as a study model, which enabled comparison of our various results with the time budget estimated by different methods at different localities and in different environmental conditions (Cairns et al., 1987, 1990; Monaghan et al., 1994). The limited flying and thus carrying capacities of alcids also suggest that, if successful for guillemots, the method will be applicable to a wide range of flying and diving seabirds. Finally, the study is the first, to our knowledge, to investigate the diving behaviour of this abundant seabird species of the Northern Hemisphere using electronic TDRs.

Materials and methods
Study site and birds

We conducted the fieldwork between 25 June and 1 July, 1999, at Hornøya (70°22′N, 31°10′E), northern Norway. Adult common guillemots *Uria aalge* Pont. were studied during the chick-rearing period, when both parents alternate foraging trips at sea and brooding periods at the colony. Only one mate per pair was used, in order to minimize disturbances. Birds were captured at their nest with a noose at the end of a 6 m fishing pole, before departure to sea after the brooding shift. Prey delivered by adults to their chicks was investigated by collecting food from 38 unequipped parent birds carrying a single prey item in their bill. Preys were kept frozen for future analysis in the laboratory.
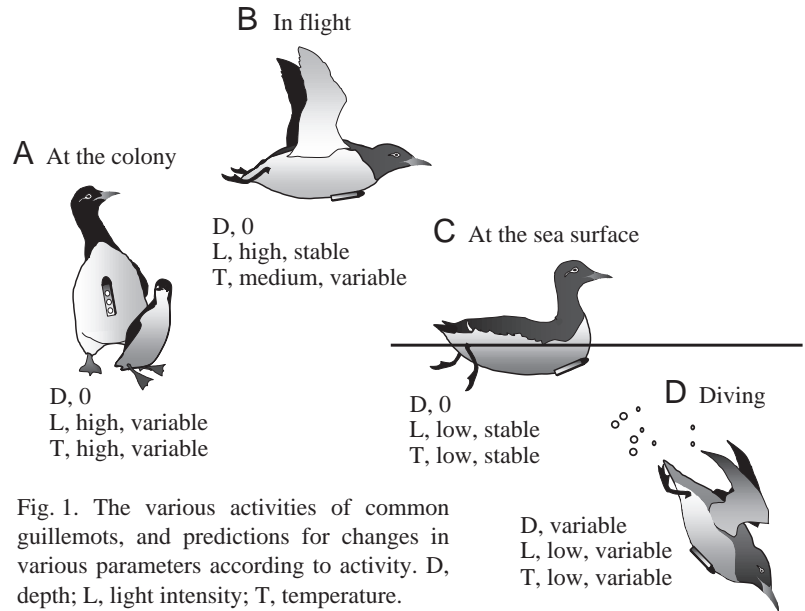

Fig. 1. The various activities of common guillemots, and predictions for changes in various parameters according to activity. D, depth; L, light intensity; T, temperature.

Experimental birds

A time-depth recorder (TDR) was attached ventrally on each of 12 guillemots using cyanoacrylate glue (Loctite 401) and plastic ties (underneath glued feathers), and birds were immediately released. After 1–4 min, birds returned to their nest. After 2–3 days, birds were recaptured and the TDR was removed by carefully separating the feathers from the device, thus avoiding cutting the feathers. The first and second handling times never exceeded 2 and 5 min, respectively. Birds were dyed on their breasts for quick identification in the field.

Electronic TDRs (MK7, Wildlife Computers, Woodinville, Washington, USA) were 8.6 cm long × 2.0 cm wide × 1.1 cm high, and weighed 27 g in air, corresponding to approximately 3% of the bird's body mass. The cross-sectional area (2.2 cm^2) was <5% of the estimated frontal section of a common guillemot, and the tip of the device was streamlined to minimise any effect on the birds' behaviour (Croll et al., 1992). The TDRs were programmed to sample depth and light every second and external temperature every 5 s, because depth and light sensors react immediately to changes in the environment, whereas temperature sensors have a greater time lag. The TDRs contained a 2.03 MB memory. Depth and temperature resolutions were ±1 m and ±0.1°C, respectively. Illumination (on an arbitrary scale) was linearly related to log$_{10}$lux (Wanless et al., 1999). Depth data were analysed using software provided by Wildlife Computers. A dive was deemed to have occurred when the maximum depth was ≥2 m (Falk et al., 2000). Bottom time was defined as the time between the first and last readings that were ≥75% of the dive's maximum depth. Diving bouts were easily determined visually, because common guillemots performed clusters of dives interspersed with other activities (see Results).

We hypothesised that data recorded using three distinct sensors (pressure, light and temperature) from TDRs attached ventrally would allow us to distinguish the different activities

of guillemots (Fig. 1). (1) At the colony, birds mainly brood their single chick, but do also move and interact with other adults. We thus expected changes in the intensity of light, but at high levels, along with relatively higher, variable external temperatures (Fig. 1A). (2) When a guillemot is at the sea surface, the ventrally attached TDR is underwater. Thus under these conditions, we expected that temperature would be relatively stable at a low level and that light intensity would be lower than in air (Fig. 1C). (3) When in flight, the light levels would be high and relatively stable, while the temperature would be lower than in the colony (wind chilling until logger temperature = air temperature in a dry logger or until evaporation was complete in a wet logger) but probably higher than at the sea surface (Fig. 1B). (4) Finally, when the bird dives, the depth sensor would record an increasing hydrostatic pressure, the temperature sensor a variable sea temperature, and the light sensor a decreasing light intensity with depth (Fig. 1D).

In summary, except for diving behaviour, identification of the various activities requires the combination of both light and temperature data. The analysis was performed visually on graphical charts (estimated accuracy ±1–10 s; Fig. 2).

Potential impacts of the time-depth recorders

To investigate possible detrimental effects of carrying a TDR, we compared the duration, number of foraging trips, body mass and hormone levels of the experimental birds with those of a control group. Control birds were fitted with VHF

radio transmitters. VHF transmitters were small, with no external aerials, and were thus unlikely to affect site attendance (Wanless et al., 1988a). VHF transmitters were attached with Tesa tape to the leg ring of 15 birds. The transmitters were approximately 1.5 cm long × 1.0 cm wide × 1.0 cm high. Their L-like shape fitted well around the metal ring, and weighed approximately 3 g in air (Biotrack, UK), corresponding to <0.5% of the bird's body mass. Each transmitter had an internal antenna emitting about 55 pulses min⁻¹. Presence and absence at the colony was assessed continuously during the study period using an automatic recording station, including a receiver, a data logger (R4000 and DCCII, respectively; ATS, Isanti, Minnesota, USA) and a multi-directional antenna. A 12 V battery powered the automatic recording station. Each frequency was scanned for a period of 10 s, providing at least one pulse was detected in the first 5 s. If no pulse was detected in the first 5 s, the logger switched to the next frequency. This procedure optimised the scanning process, so that depending on the number of birds present at the colony, each frequency was scanned every 3–6 min. Data were regularly downloaded from the station to a laptop computer. According to Furness and Barrett (1985), we defined a trip at sea as a period longer than 15 min away from the colony.

Blood sampling and hormone assays

At the end of the study period, both control and experimental birds were weighed and a blood sample collected to determine gender and to measure plasma
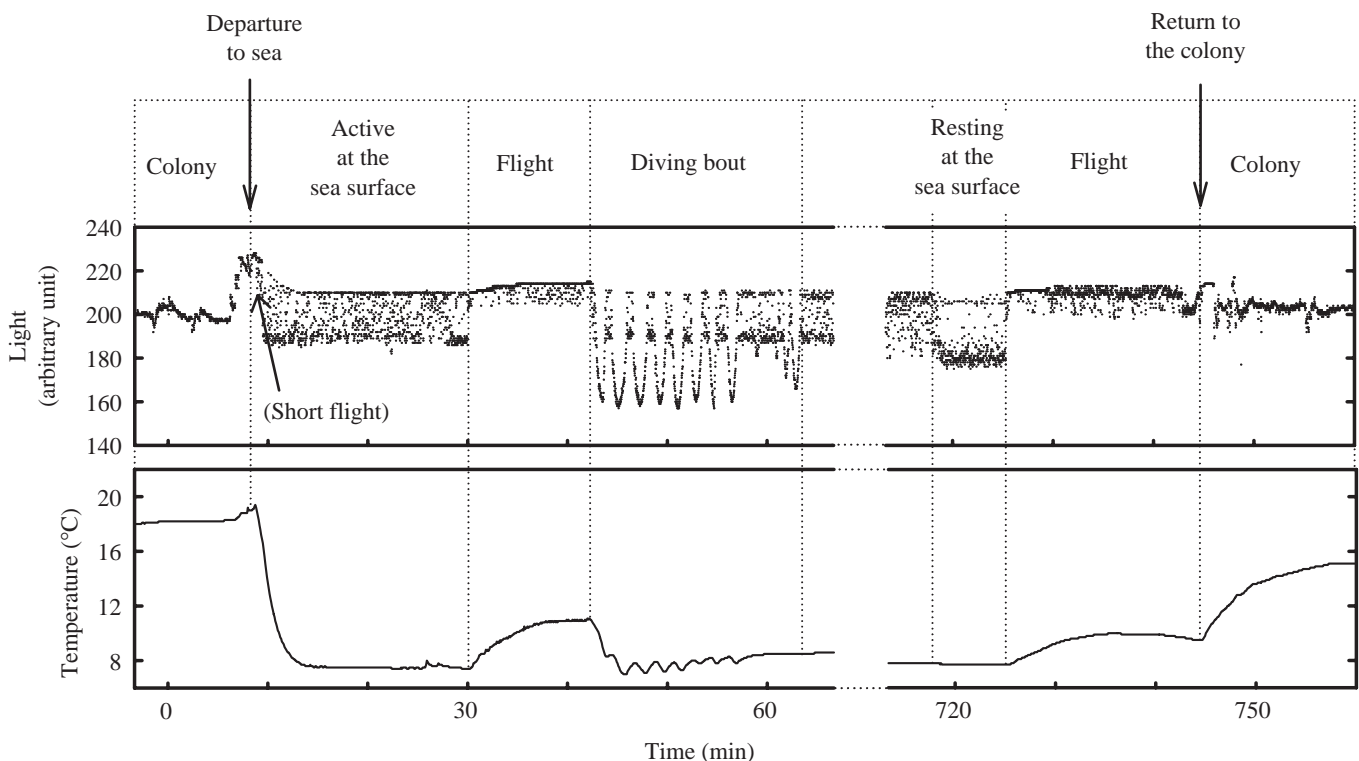

Fig. 2. Light and temperature recordings selected to illustrate various activities of common guillemots fitted with a ventrally attached time-depth recorder

concentrations of baseline corticosterone (the main stress hormone in birds) and prolactin (the main hormone involved in parental care in birds).

Blood samples ($\cong$1 ml) were collected from the alar vein with a 1 ml heparinised syringe. Blood sampling was performed as soon as possible after capture (range: 1–4 min) in order to avoid a stress-linked increase in corticosterone levels (Wingfield, 1994). Blood samples were cooled on ice, centrifuged, and blood cells and plasma stored at –20°C. Molecular sexing was carried out using DNA prepared from blood cells according to the method of Fridolfson and Ellengren (1999). Radioimmunoassays using the procedures of Cherel et al. (1994) and Lormée et al. (in press) were used to determine plasma concentrations of prolactin and corticosterone, respectively. Pooled plasma samples of common guillemots produced a dose–response curve that paralleled that of chicken prolactin standard curves (source: Dr Parlow, N.H.P.P. Harbor-UCLA Medical Center, USA). There was no significant relationship between time after capture and corticosterone levels measured during the initial bleeding (experimental birds, P=0.49, N=12; control birds, P=0.73,

N=15). Thus, blood samples reflected baseline levels of corticosterone. Only one assay was performed, the intra-assay coefficient of variation being 2.2% for prolactin and 2.8% for corticosterone (N=4 duplicates for each assay).

Statistics

Data were analysed statistically using SYSTAT 7.0. When some individual birds represented more than one record in a data set (for example, several foraging trips by the same bird), a nested-ANOVA was performed, and the F-test of the comparison of groups was constructed with the mean square of birds nested within groups as the error term. Data were $\log_{10}$ transformed when their distribution was skewed. Values are means $\pm$ S.D., significance at the $P<0.05$ level.

Results

Data were obtained from all the 12 common guillemots equipped with a TDR. No devices were lost, and no study bird ceased their rearing tasks. Overall, 29 bird-days were recorded, including a total of 2613 dives (43–541 dives per bird)
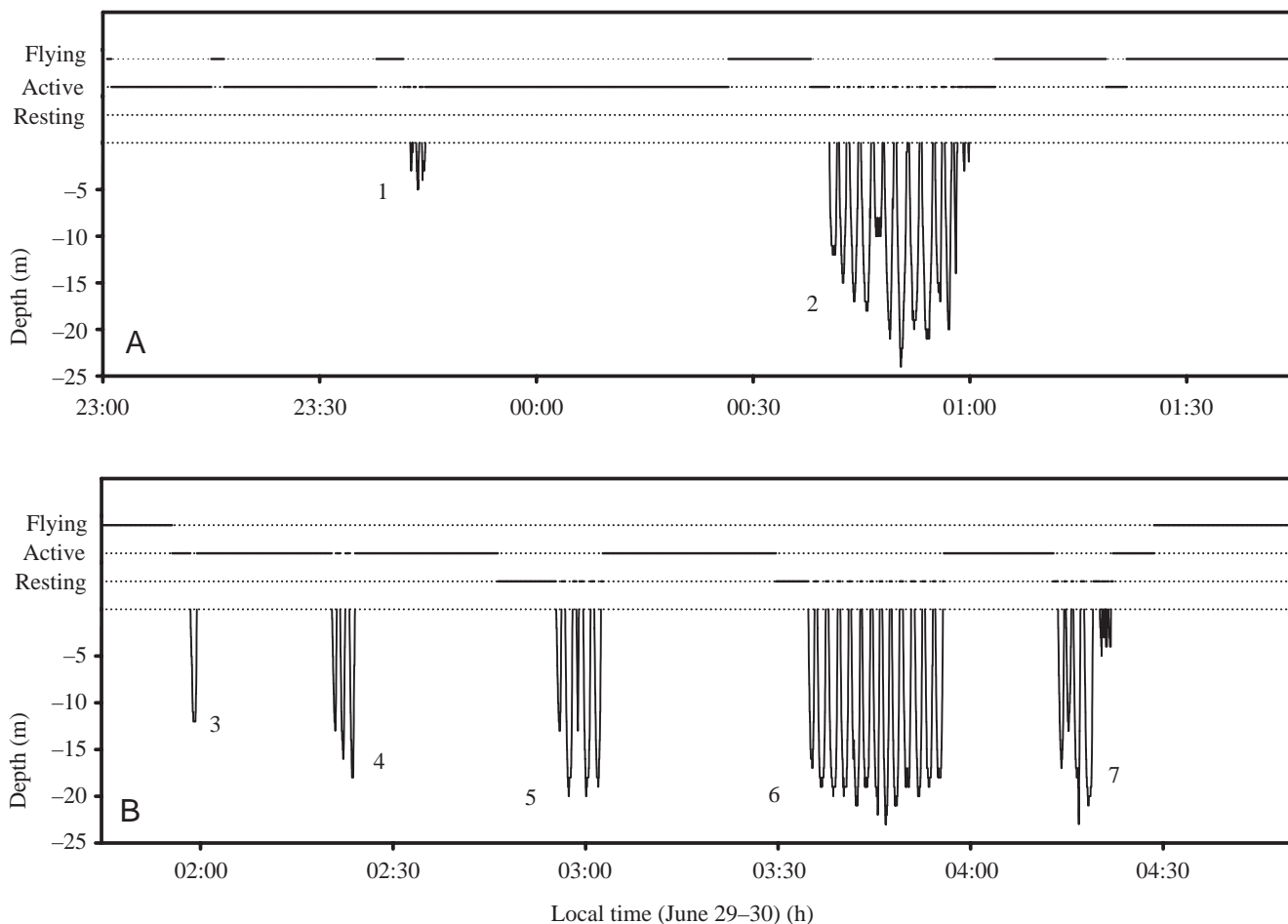

Fig. 3. Foraging behaviour of one common guillemot during one complete foraging trip. (A) The first and (B) the second halves of the trip. The lines indicate the recorded activity of the bird, and its diving depth. Note (i) that the bird did not fly during the time elapsed from diving bout 3 to diving bout 7, and (ii) that it was either active (bouts 1, 2 and 4) or resting (bouts 5, 6 and 7) at the sea surface during dive intervals within diving bouts.

performed during 340 diving bouts in 91 trips at sea (4–16 trips per bird).

Among the 12 common guillemots equipped with TDRs, 7 were males and 5 were females. Since no statistical gender differences were found in the time budget and diving behaviour of the birds, data from males and females were pooled for subsequent analysis.

Reliability of the method

In accordance with our predictions, the simultaneous analysis of light, temperature and depth records permitted identification of the different activities of adult guillemots rearing chicks (Fig. 2). When a guillemot departed to sea, the external temperature dropped steeply and increased again when the bird returned to the colony. Thus, the overall data set was easily split into several at-sea and at-the-colony periods by analysing the temperature record alone. The results were, moreover, confirmed by our visual observations of the behaviour (presence/absence) of given individuals in the colony during the study period.

After handling, all released birds initiated a flight. This allowed us to characterise flight periods in our records. Flights were marked by a high, constant light level together with an asymptotic increase in the external temperature when birds took off from water (Fig. 2). Conversely, when birds were at the sea surface, the temperature was low and constant. Interestingly, light measurements revealed two different behaviours while guillemots were at the sea surface. Light was both relatively low and constant (suggesting that birds were resting), or more variable (suggesting that birds were active). During these two phases, birds were probably either resting,

recovering quietly from a dive at the surface or moving all the time, such as during preening, swimming and interactions with congeners, respectively (see below). Finally, diving was characterised not only by changes in depth (Fig. 3), but also by marked decreases in light intensity and small decreases in temperature (Fig. 2).

By examining the data collected on light, temperature and depth, we could divide the total activity of adult guillemots into five distinct behaviours: at the colony, in flight, resting or active at the sea surface, and diving (Figs 2, 3). It is noticeable that various activities appeared easily detectable by eye and similar from one guillemot to another. However, with less clearcut data sets, it is possible that mathematical analysis could be used to distinguish the activities.

Time budget and foraging pattern

Overall, common guillemots spent 32% of their time at sea and 68% at the colony (Fig. 4). Consequently, depending on the synchronisation between males and females, both parents were present together at the colony 36–68% of the time. While at sea, the major behaviour of the birds was to stay at the sea surface (77%), during which they were mainly active (64%), resting time being much shorter (13%). Guillemots were in flight and dived during 11% and 12% of their total time at sea, respectively (Fig. 4). Note that the total recovery time (time spent at the sea surface between dives) represented only 7% of the time spent at the surface (77%). Inter-individual variations in time budget were found; however, all the birds save one spent much more time at the colony. When at sea they all spent less time in the more energy-intensive behaviours of flying and diving (Fig. 4).
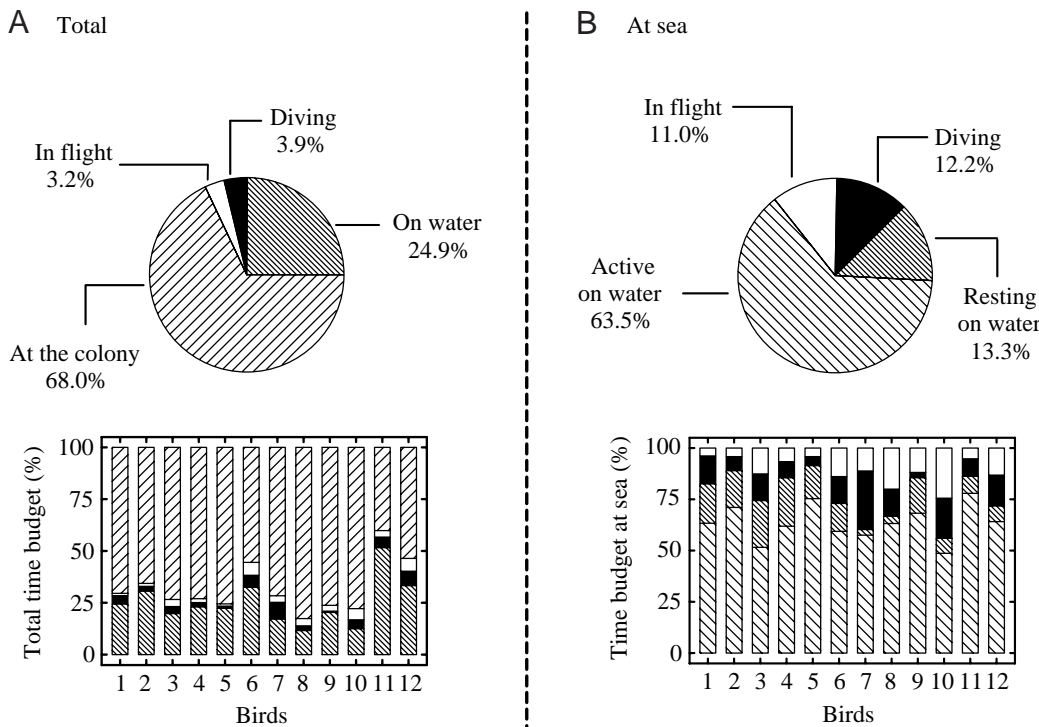

Fig. 4. Overall time budget (A) and time budget at sea (B) of common guillemots rearing chicks. Pie charts (top) include pooled data from all birds, whereas bar charts (bottom) illustrate time allocation for each of the 12 experimental birds.
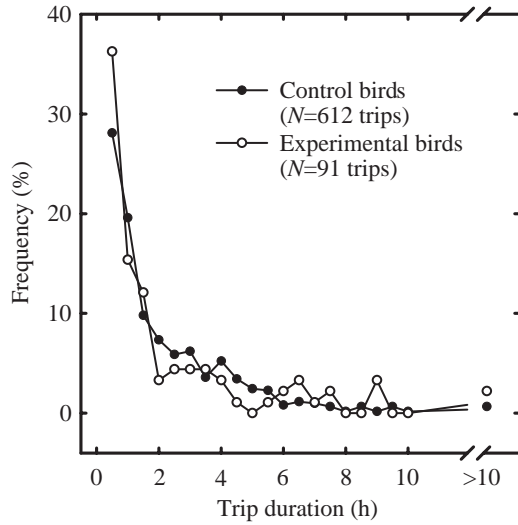
Fig. 5. Frequency distribution of the duration of trips to sea by experimental (open circles; birds fitted with time-depth recorders) and control (filled circles; birds fitted with VHF radio transmitters) common guillemots.

Fig. 6. Number of diving bouts (A) and dives (B), and total flying time (C) relative to trip duration in common guillemots.

The foraging pattern of common guillemots during the brooding period was marked by short trips at sea, 52% of them lasting <1 h, and 76% <3 h (Fig. 5). Birds performed on average 3.2±1.4 trips per day, and departed to sea more often during the flood tide than during the ebb tide (N=69 and 22, respectively; χ^2=24.3, d.f.=1, P<0.0001). Birds did not dive during 23% (N=21) of the 91 trips, which were therefore called non-foraging trips. Non-foraging trips were generally shorter than foraging trips (trips including at least one dive, N=70) (0.4±0.4 h and 3.2±3.9 h, respectively; nested ANOVA: $F_{1,19}$=5.55, P=0.029). Resting time at the surface occurred in 47 of all the trips. During these trips, active time at the surface was positively related to resting time [$\log_{10}$(active time)=2.09+0.55×$\log_{10}$(resting time), r^2=0.47, P<0.0001].

Common guillemots performed 3.5±2.6 flights per trip (range: 2–17, N=91), lasting 4.6±6.2 min (range: 0.1–47.8 min). Total flying time increased significantly with trip duration [$\log_{10}$(flying time)=0.90+0.50×$\log_{10}$(trip duration); Fig. 6], and was shorter during non-foraging trips than during foraging trips (4.98±4.32 and 18.91±20.22 min, respectively; nested ANOVA after $\log_{10}$ transformation: $F_{1,19}$=7.72, P=0.012), but the proportion of flying time was not different (nested ANOVA after arcsine transformation: $F_{1,19}$=2.02, P=0.172).

The maximum horizontal distance travelled from the colony was estimated assuming that birds flew in a straight line for half of the total flying time at a constant travelling speed of 69 km h^{-1} (Pennycuick, 1987). The distance was shorter during non-foraging trips than during foraging trips (2.9±2.5 and 10.9±11.6 km, respectively; nested ANOVA after log10 transformation: $F_{1,19}$=7.72, P=0.0120). When considering all the trips, the inward journey was longer than outward journey in 87% of them (paired t-test: t=6.31, P=0.0008). During foraging trips, the difference between outward and inward
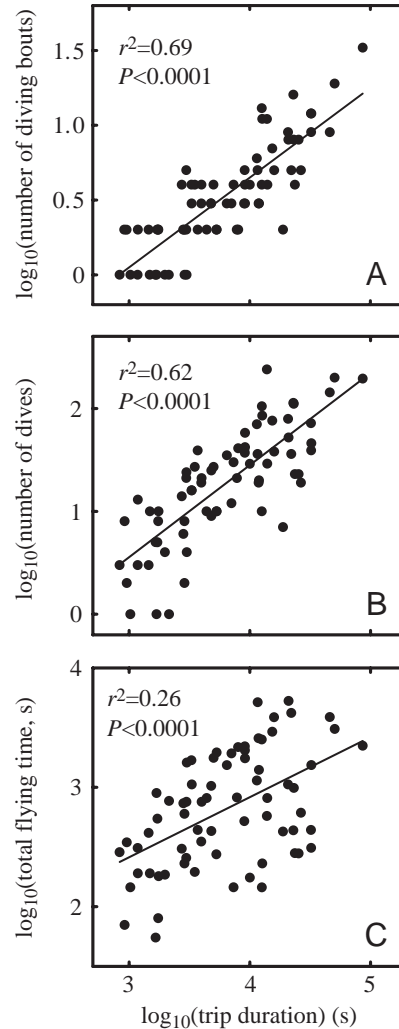
journeys was 5.8±8.0 min, suggesting that birds flew away while foraging at sea at a mean distance of 6.7±9.2 km (up to 42 km).

Diving behaviour

Common guillemots performed 37±48 dives per foraging trip (range: 1–239), with a frequency of 14±11 dives per hour spent at sea (range: 1–62). Diving occurred in bouts of 7.7±6.6 dives (range: 1–140). Both the numbers of diving bouts and dives increased with foraging trip duration [$\log_{10}$(number of diving bouts)=–0.75+0.60×$\log_{10}$(trip duration) and $\log_{10}$(number of dives)=–2.13+0.90×$\log_{10}$(trip duration)] (Fig. 6). Mean total vertical travel distance (VTD; sum of all maximum dive depths×2) was 0.7±1.0 km per foraging trip and 242±218 m h^{-1} at sea. Birds spent 8.1±5.9 min underwater per hour spent at sea and dived significantly more during the flood tide than during the ebb tide (N=1721 and N=892 dives, respectively; χ^2=1984, d.f.=1, P<0.0001).

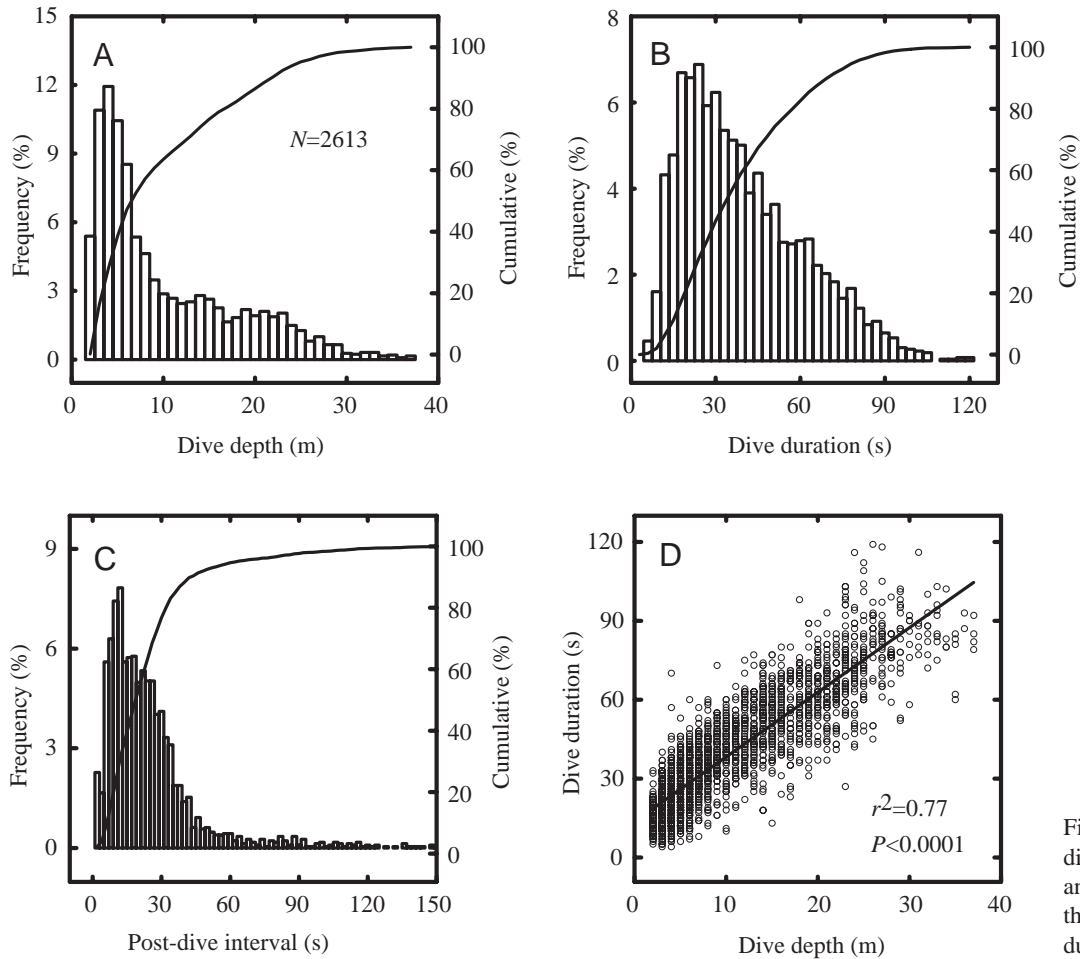Four dive types were characterised, according to their

Fig. 7. Frequency distribution of dive depth (A), dive duration (B) and post-dive interval (C), and the relationship between dive duration and dive depth (D).

profiles: 67% of the total number of dives were U-shaped, 24% were asymmetrical, 5% were W-shaped and 4% were V-shaped. Of the 2123 recorded dives, the deepest reached 37 m and the longest lasted 119 s. The mean maximum dive depth was 10.2 ± 7.6 m, 50% of dives being ≤ 6 m and 90% ≤ 22 m (Fig. 7). Mean dive duration was 38.7 ± 21.3 s, 50% of dives being ≤ 33 s and 90% ≤ 69 s long. Dive duration related positively and linearly to dive depth (dive duration=$2.45 \times$dive depth+13.78; Fig. 7). Post-dive intervals (PDI) included long periods (>60 s) corresponding to intervals between two consecutive bouts. Excluding them, mean PDI (N=2166) was 20 ± 12 s and was related positively to dive duration (PDI=$12.55+0.18 \times$dive duration, r^2=0.87, P<0.0001). The mean ratio of dive duration/PDI was 2.7 ± 2.9. It increased steeply for dive duration between 10 and 40 s, and the positive relationship had a lower slope for longer dives (Fig. 8).

Bottom time of dives, during which predators presumably feed, lasted 19 ± 12 s and was both positively and linearly related to dive duration (bottom time=$-0.34 \times$dive duration, r^2=0.84, P<0.0001). Mean diving efficiency, i.e. the proportion of bottom time over a complete dive cycle (dive duration+PDI; Ydenberg and Clark, 1989), was 0.28 ± 0.15, and its frequency distribution was unimodal with a strong mode at 0.39 (data not shown). Dive depth had no influence on diving efficiency,
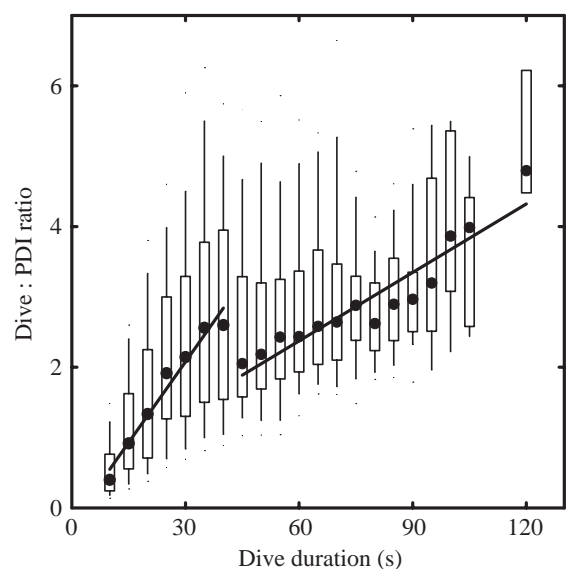

Fig. 8. Relationship between the median dive:PDI ratio and the dive duration. Boxes and bars illustrate the 25/75 and the 10/90 percentiles, respectively.

Table 1. *Body mass, plasma levels of baseline corticosterone and prolactin, and foraging patterns of experimental and control common guillemots*

	Experimental birds (N=12)	Control birds (N=15)	Statistics	
			t	P
Body mass (g)	993±62	1026±72	1.24	0.228
Corticosterone (ng ml^{-1})	6.3±6.0	4.0±3.0	0.90	0.374
Prolactin (ng ml^{-1})	30.3±8.5	35.0±8.8	1.37	0.182
Trip duration[1,2] (h)	3.2±2.8	2.2±0.8	0.93	0.362
Number of trips per day[2]	3.2±1.4	4.8±1.3	3.07	0.005
Time spent at sea per day[1] (h)	7.7±2.9	9.7±2.0	2.55	0.017

[1]Data were log$_{10}$ transformed before statistical analysis.
[2]Foraging and non-foraging trips pooled together.

but dives lasting longer than 25 s had higher efficiency (>0.30).

Mean descent rate was lower than mean ascent rate (0.80±0.47 and 0.97±0.50 m s^{-1}, respectively; paired *t*-test: t=14.78, P<0.0001). Both descent and ascent rates increased with increasing dive depth (descent rate=0.64+0.01×dive depth, r^2=0.84, P<0.0001; and ascent rate=0.78+0.01×dive depth, r^2=0.55, P<0.0001).

Comparison with control birds

No differences were found in body mass and plasma corticosterone and prolactin levels when comparing experimental and control birds at the end of the study period (Table 1). Frequency distribution of trips (Kolmogorov–Smirnov, D=0.238, r^2=0.546; Fig. 5) and trip duration were also identical among the two groups. Experimental birds, however, performed fewer trips per day, and, consequently, spent less time at sea than control guillemots (Table 1).

Diet

All the 38 prey items were fish belonging to three different taxa: 13 were capelin *Mallotus villosus* (34.2%), 13 sandlance *Ammodytes* sp. (34.2%) and 12 herring *Clupea harengus* (31.6%). 11 of the 13 capelins were gravid females, and two had just spawned (some eggs still remained in the cloacas). The standard lengths of capelin (*N*=12), sandlance (*N*=12) and herring (*N*=11) were 118±11, 109±7 and 94±11 mm, and they weighed 12.1±3.7 g, 4.8±0.9 g and 9.5±3.3 g, respectively. When pooling the three taxa, mean fish size was 107±14 mm and 8.8±4.2 g.

Discussion

Unconventional ventral attachment of TDRs was successful in differentiating behaviours of common guillemots through the analysis of continuous recordings of light, temperature and hydrostatic pressure at a high sampling rate. The method thus allows us to simultaneously quantify the birds' time budget and their diving behaviour. The initial purposes of using light and temperature sensors on TDRs were to estimate the latitude and longitude (geolocation), and to correct for temperature effects in pressure transducers and measure water temperature, respectively. Their use in concert appears to provide a means of identifying precisely when the birds are in the colony or are foraging at sea. In addition when at sea, individual behaviours, such as flying and diving, and different surface activities can be identified (Fig. 2). In the same unconventional way, light sensors have recently been used to quantify activity at depths of penguins during pelagic and benthic dives (Tremblay and Cherel, 2000).

Until now, devices allowing the quantification of both time budget and diving behaviour of seabirds were experimental ones built by the scientists themselves (Falk et al., 2000; Dall' Antonia et al., 2001). Instead, we used commercial devices that are readily available on the market. Our method can potentially be applied to many flying seabirds. The main limitations are (1) the ratio between the size of the devices and that of the animals (as for other animal-borne data loggers) and (2) the discrimination between different activities using light and temperature data if birds forage at night and/or if air and water temperatures are similar.

Validity of the method

The use of electronic devices has considerably enhanced our understanding of the behavioural ecology of marine animals in the last decade. However, the question of whether results obtained from equipped individuals represent the natural behaviour of the species remains a concern, especially in seabirds like alcids, which have limited flying, and thus carrying, ability (Nettleship, 1996). Common guillemots are known to be sensitive to disturbance, and some individuals deserted their nest after being externally fitted with devices, including electronic recorders (Benvenuti et al., 1998) and radio transmitters (Wanless et al., 1988a). Moreover, the behaviour of birds that do not desert may be affected by the devices in comparison to control individuals (Wanless et al., 1988a). In the present study, handling time was minimized as much as possible and streamlined TDRs were used to minimize the device-induced turbulence. It is noteworthy that none of the

Table 2. *Time budget of alcids during the chick rearing period at various localities*

Species	Total time budget (%)				Time budget at sea (%)			Locality	Method	References
	Colony	Flying	Surface	Diving	Flying	Surface	Diving			
Common guillemot *Uria aalge*	51.1	4.7	37.6	6.6	10.5	75.3	16.8	Newfoundland	Activity recorders	1
	30.3	7.7	57.5	8.1	8.5–9.4	77.3–79.1	12.5–13.4	Newfoundland	Activity recorders	2
	51.1–71.0*	0.8-3.3*	25.0–29.2*	4.6-16.7	2.7–6.9	58.9–81.9	15.4–34.2	Scotland	VHF transmitters	3
	68.0	3.2	24.9	3.9	11.0	76.8	12.2	Norway	TDR	4
Brünnich guillemot *Uria lomvia*	50.9	7.1	25.4	16.6	14.5	51.7	33.8	Greenland	Activity recorders	5
Razorbill *Alca torda*	50				7.0–11.9	74.3–80.5	12.5–13.8	Baltic Sea	Activity recorders	6
					11–15	53–69	20–32	Iceland	Activity recorders	7

*Estimated graphically.

[1]Cairns et al., 1987; [2]Cairns et al., 1990; [3]Monaghan et al., 1994; [4]Present study; [5]Falk et al., 2000; [6]Benvenuti et al., 2001; [7]Dall'Antonia et al., 2001.

12 common guillemots in the present study deserted, and all of them apparently behaved normally. At the beginning of deployment, birds typically preened and pecked the device, but this behaviour stopped quickly and birds paid little attention to it at the nest afterwards, as previously reported for Brünnich's guillemots (Croll et al., 1992). Some equipped birds were subsequently observed several times carrying prey in their bill and feeding their chick.

There were no significant deleterious effects of the devices detected in terms of body mass and plasma prolactin and corticosterone levels, suggesting that equipped guillemots were not physiologically stressed in comparison to control birds. However, equipped birds initiated fewer trips per day and consequently spent more time at the colony than control. This response contrasts with previous results showing that guillemots spent less time in the colony when fitted with radiotransmitters with an external *versus* internal aerial (Wanless et al., 1988a), and when they have to work harder due to poor environmental conditions (Monaghan et al., 1994). We, however, found no differences in trip duration between our equipped birds and control individuals. This is probably a key point, because foraging trip duration in common guillemots is sensitive to prey availability (Birkhead and Nettleship, 1987; Monaghan et al., 1994; Monaghan, 1996), and is therefore likely to reflect any significant deleterious energetic and behavioural effects encountered by the birds while foraging. Bulkier devices were previously deployed on common guillemots (Cairns et al., 1987) and razorbills (Dall'Antonia et al., 2001) with no apparent deleterious effects on the birds. In conclusion, we cannot assume that the recorders had no negative effects on guillemots, but we are confident that, if there were any, their influence on the birds' foraging behaviour was slight and difficult to detect.

Time budget

On average, common guillemots from Hornøya spent 68% of their total time at the colony. This value is one of the highest recorded for alcids (Table 2), and is close to that calculated by Monaghan et al. (1994) for Scottish birds. The time during which both parents were present together at the colony was estimated to be between 36% and 68%, which includes the value (53%) reported for Brünnich's guillemots at the same site (Furness and Barrett, 1985). When looking at the time budget at sea, our data are again in general agreement with most previous results obtained on common guillemots and razorbills (Table 2). Overall, alcids spent most of their time at the sea surface and much less time in the costly activities of diving and flying. However, their time budget varied according to food availability, with more time spent flying and diving, and less time spent at the surface, during poor food years (Monaghan et al., 1994; Uttley et al., 1994; Dall' Antonia et al., 2001). For example, the foraging effort of Brünnich's guillemots in Greenland was quite high, since they spent only 52% of their time at the surface, flew for 14% of the time and, importantly, dived during the remaining 34% (Falk et al., 2000). When compared to other studies, both total time budget and time budget at sea suggest that 1999 was a good food year for common guillemots at Hornøya (see below). This is also an indirect indication that equipped birds were not working harder due to the presence of TDR on their belly.

Guillemots adjust the time spend on the surface in response to foraging conditions, and surface time can thus represent a reserve available to increase foraging effort (Cairns et al., 1987; Monaghan et al., 1994). Surface time, however, is made of different activities. One of these activities is easy to quantify; the between-dive intervals used to recover from the previous dive and anticipate the following one (7% in the present study). Beyond this recovery period we do not know what time was used in other activities (Burger and Piatt, 1990). Our method gives a new insight in surface-time partitioning since, to our knowledge, we report and quantify here for the first time two different behaviours: resting and active on the surface (Fig. 2). During resting periods, recorded light levels were low and stable, indicating that the birds' chest was always underwater, and that guillemots remained quietly at the surface. During active periods, light levels were highly variable, indicating physical activity, such as preening, swimming, wing flapping, and also diverse social-oriented behavioural sequences (Forssgren and Sjölander, 1978). Active periods could also be related to thermoregulation, because

guillemots meet a thermal challenge in cold waters, so periods of activity may be used to maintain body temperature (Croll and McLaren, 1993). The significant positive relationship between resting and active time at surface during foraging trips supports this hypothesis. However, much more information is required for a better understanding of the adaptive value of active and resting times, particularly when birds face contrasting levels of food availability.

The mean trip duration of common guillemots at Hornøya (153 min) is within the range of that previously found using various methods and sample sizes (Birkhead and Nettleship, 1987; Uttley et al., 1994; Zador and Piatt, 1999). The frequency distribution was, however, heavily skewed toward shorter trips (Fig. 5). Our method allowed us to define two kinds of trips, based on the presence/absence of dives (foraging and non-foraging trips, respectively). Non-foraging trips were generally shorter than foraging trips, but both kinds of trips overlapped in duration. The existence of non-foraging trips is an explanation for birds returning back to the colony without any prey for their chicks. As such, it is noteworthy that the proportion of foraging trips (77%) found in the present study is similar to the frequency with which adults returned with a fish observed for both common (77–89%; Wanless et al., 1988a; Uttley et al., 1994) and Brünnich's (66%; Watanuki et al., 2001) guillemots. The previously reported arrivals at the colony with no fish were thus more likely to have been a result of non-foraging behaviour at sea than of unsuccessful foraging trips.

Diving and foraging behaviour

To our knowledge, this study is the first to investigate the diving behaviour of common guillemots using time-depth recorders. Using maximum depth gauges that only record the deepest dive reached during the deployment period, it was previously found that the species reached on average 36–49 m, up to 138 m (Burger and Simpson, 1986; Harris et al., 1990; Barrett and Furness, 1990). The deepest dive recorded in the present study (37 m) lies within that range, but the use of TDRs showed that common guillemots at Hornøya routinely dived at much shallower depths (mean 10 m). When compared with other alcids equipped with electronic TDRs, common guillemots forage at similar water depths to the lighter razorbills (Benvenuti et al., 2001; Dall' Antonia et al., 2001), but at shallower depths than the similar-sized Brünnich's guillemots (Croll et al., 1992; Falk et al., 2000; Mehlum et al., 2001).

Unlike dive depth, much detailed information is available on dive duration of common guillemots. Birds carrying VHF transmitters in Scotland dived on average between 58–123 s (maximum 202 s) (Wanless et al., 1988b; Monaghan et al., 1994), these durations being by far higher than those reported at Hornøya (mean: 39 s; maximum: 119 s). The closely related Brünnich's guillemot equipped with TDRs also dived longer, with a high inter-site variability in dive characteristics (Croll et al., 1992; Falk et al., 2000; Mehlum et al., 2001). Data from the two species therefore indicate behavioural plasticity linked

to the marine environment, and they suggest that inter-species differences are more likely to result from differences in local feeding conditions than from differences in diving ability.

Dive duration increased linearly with dive depth (Fig. 7), as did bottom-time plotted against dive depth and dive duration, and PDI plotted against dive duration, with no inflection for longer dives (data not shown). Altogether, these data suggest that common guillemots dive well within their behavioural aerobic dive limit (ADL; Kooyman and Kooyman, 1995). The results thus support a behavioural ADL at 150 s rather than the calculated ADL at 48 s for guillemots (Croll et al., 1992), and are in agreement with aerobic biochemical adaptations described in guillemot muscles (Davis and Guderley, 1990). The discrepancy between behavioural and calculated ADL is common among diving seabirds and suggests that the diving metabolic rate is likely to be lower than expected, possibly due to diving hypothermia (Butler, 2001). A peak in the dive:PDI ratio plotted against dive duration was observed in different seabird species, including common guillemots (Wanless et al., 1988b; Walton et al., 1998). The peak is interpreted as a time limit for the use of oxygen stores from the respiratory tract. The use of additional oxygen stores from blood and muscle is induced when dive duration exceeds this time limit. Birds from Hornøya did not show a peak in the dive:PDI ratio at approximately 70 s; instead, the ratio increased for increasing dive duration up to 120 s. Moreover, there was a break in the slope of the linear relationship at approximately 40 s, implying that birds diving for longer duration needed additional time at the sea surface to recover (Fig. 8). The physiological interpretation of this two-step relationship is unclear, but it suggests that the model of Walton et al. (1998) on the sequential use of different oxygen stores during diving requires further investigation.

Most dives performed by common guillemots were U-shaped, which is in agreement with the diving profiles exhibited by Brünnich's guillemots (Croll et al., 1992), but contrasted with the V-shape dives of razorbills (Benvenuti et al., 2001; Dall' Antonia 2001). Unlike penguins (Wilson et al., 1995a; Cherel et al., 1999) but as recently described for another alcid, the razorbill (Benvenuti et al., 2001), common guillemots had lower descent rates than ascent rates. Like penguins and razorbills, however, guillemots descended and ascended more quickly as dive depth increased, indicating that birds anticipated the depth they intended to reach, and thus maximised bottom (presumably feeding) time at the expense of travel time (Wilson, 1995). By so doing, common guillemots maintained a constant proportion of bottom time to dive cycle (i.e. diving efficiency) irrespective of dive depth. On average, birds thus managed their diving time in order to feed at all depths of the water column with the same efficiency, suggesting that the average probability of encountering prey was similar throughout the depth range (0–37 m).

In summer 1999, common guillemots fed on ovid female capelin, sandlance and juvenile herring, which is in agreement with the dietary habits of the species at Hornøya (Barrett et al., 1997; Barrett, 2002). Diving behaviour and estimated foraging

ranges indicate that birds fed on fish schools at shallow depths in the vicinity of the colony, which is again in agreement with common guillemots feeding on mature capelin in the upper water masses close to Hornøya (Furness and Barrett, 1985; Erikstad and Vader, 1989). Time-budget and diving behaviour strongly suggest that common guillemots had no difficulties in obtaining food and thus that 1999 was a good food year. Accordingly, an oceanographic survey indicated that 1999 was a normal year for capelin stocks in the Barents Sea (Barrett, 2002), and previous studies have emphasized that the seabird community has a good food supply at Hornøya in most years (Furness and Barrett, 1985; Vader et al., 1990; Barrett et al., 1997; Barrett, 2002).

In addition to a favourable trophic marine environment, common guillemots from Hornøya take advantage of the permanent daylight of the Arctic summer by having a pattern in feeding activity independent from the day/night cycle (Barrett et al., 1997; authors' unpublished data). This contrasts with the behaviour of birds breeding at more southerly latitudes, because, unlike Brünnich's guillemots (Croll et al., 1992), common guillemots do not forage during hours of darkness (Wanless et al., 1988a). Guillemots from Hornøya, however, initiated more dives and more trips at sea during the flood tide, suggesting that prey availability increased at that time.

In conclusion, ventral attachment of TDRs together with analysis of simultaneous records of light, temperature and depth were successful in differentiating the activities of common guillemots, thus allowing a precise quantification of the time budget of individuals during the chick-rearing period. The method is easy to use in the field and applicable to many other seabird species. The next step is to quantify energy expenditure of equipped animals whilst recording their time, activity and energy budget. This can be done using the doubly labelled water method in conjunction with the use of animal-borne data logger recording heart rate.

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