Swim speeds and stroke patterns in wing-propelled divers: a comparison among alcids and a penguin

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Summary

In diving birds, the volume and resulting buoyancy of air spaces changes with dive depth, and hydrodynamic drag varies with swim speed. These factors are important in the dive patterns and locomotion of alcids that use their wings both for aerial flight and underwater swimming and of penguins that use their wings only for swimming. Using small data-loggers on free-ranging birds diving to 20–30 m depth, we measured depth at 1 Hz and surge and heave accelerations at 32–64 Hz of four species of alcids (0.6–1.0 kg mass) and the smallest penguin species (1.2 kg). Low- and high-frequency components of the fluctuation of acceleration yielded estimates of body angles and stroke frequencies, respectively. Swim speed was estimated from body angle and rate of depth change. Brünnich's (*Uria lomvia*) and common (*Uria aalge*) guillemots descended almost vertically, whereas descent of razorbills (*Alca torda*), rhinoceros auklets (*Cerorhinca monocerata*) and little penguins (*Eudyptula minor*) was more oblique. For all species, swim speed during descent was within a relatively narrow range. Above depths of 20–30 m, where they were all positively buoyant, all species ascended without wing stroking. During descent, little penguins made forward accelerations on both the upstroke and downstroke regardless of dive depth. By contrast, descending alcids produced forward accelerations on both upstroke and downstroke at depths of <10 m but mainly on the downstroke at greater depths; this change seemed to correspond to the decrease of buoyancy with increasing depth. The magnitude of surge (forward) acceleration during downstrokes was smaller, and that during upstrokes greater, in little penguins than in alcids. This pattern presumably reflected the proportionally greater mass of upstroke muscles in penguins compared with alcids and may allow little penguins to swim at less variable instantaneous speeds.

Key words: acceleration, buoyancy, data-logger, swimming mode, wing stroke.

Introduction

Breath-hold divers are expected to use dive angle and swim speed to regulate transit time to a given foraging depth in order to minimize energy expenditure and maximize time for foraging (Houston and Carbone, 1992; Boyd et al., 1995; Wilson et al., 1996). During dives, endotherms retain much air in their respiratory systems, and birds and many mammals also retain air layers in their plumage or fur (Lovvorn and Jones, 1991; Wilson et al., 1992). As a result, they must work against buoyancy as well as drag under hydrodynamic constraints during descent or ascent (Bannasch, 1995; Williams et al., 2000; Lovvorn, 2001; Sato et al., 2002; Miller et al., 2004). Also, physiological constraints on muscle efficiency and power output may affect swim speeds against varying buoyant resistance (Biewener and Gills, 1999; Lovvorn et al., 2004). A key question is: how are dive angle, swim speed and stroke patterns adjusted as buoyancy changes with depth due to compression of air volumes?

Comparison of diving behaviour among wing-propelled alcids and penguins should help answer this question. First, alcids and penguins exhibit several dive profiles with different body angles, such as U-shaped vertical dives and V-shaped oblique dives (Croll et al., 1992; Wilson et al., 1996; Falk et al., 2000; Benvenuti et al., 2001). Second, being free from the need to fly in air, penguins have developed a number of unique physiological and morphological adaptations for diving,

including high blood haemoglobin and muscle myoglobin and small wings (Mill and Baldwin, 1983; Pennycuick, 1987; Croll et al., 1992). However, after accounting for differences in body mass, alcids dive deeper and for longer periods than penguins (Burger, 1991; Watanuki and Burger, 1999). Differences in wing stroke patterns (Watanuki et al., 2003) might be an important aspect of these different strategies of underwater swimming and should be compared between alcids and penguins of similar size.

Wing stroke patterns have been well studied for captive alcids and penguins swimming horizontally at shallow depths, where they experience large constant buoyancy (Clark and Bemis, 1979; Hui, 1988; Johansson and Aldrin, 2002). However, free-ranging alcids and penguins do not just swim horizontally as they do in shallow tanks; they also dive to depths that may exceed 100 m (Croll et al., 1992; Schreer and Kovacs, 1997), and their buoyancy changes dramatically with depth as their air spaces are compressed (Lovvorn and Jones, 1991; Wilson et al., 1992). Recent development of small data-loggers has allowed studies of the body angles, swim speeds and stroke acceleration patterns of free-ranging seabirds and marine mammals *via* high-frequency sampling of depth change and acceleration (Nowacek et al., 2001; Watanuki et al., 2003). To date, however, stroke patterns and swim speeds of free-ranging birds as measured by standardized methods have not been compared between penguins and alcids.

In this study, we measured body angles, swim speeds and acceleration patterns during dives to depths of 20–30 m by four species of alcids and a single species of penguin. Despite interspecific differences in dive depth, individuals of all five species dived to about 20 m depth, the depth range over which effects of buoyancy are greatest. For these alcid species of a range of body sizes (generally 0.6–1.0 kg), and a penguin whose mass (1.2 kg) is often similar to that of the larger alcids, we determined how body angle, swim speed and wing stroke frequency changed as buoyancy decreased with depth.

Materials and methods
Animals

Study animals included Brünnich's guillemot [BRGU; *Uria lomvia* L.; 0.97±0.06 kg, N=5 (present study)], common guillemot [COGU; *Uria aalge* Pontoppidan; 0.96–0.98 kg (Gaston and Jones, 1998)], razorbill [RAZO; *Alca torda* L.; 0.62–0.73 kg (Gaston and Jones, 1998)], rhinoceros auklet [RHAU; *Cerorhinca monocerata* Pallas; 0.57±0.04 kg, N=7 (present study)] and little penguin [LIPE; *Eudyptula minor* J. R. Forester; 1.21±0.07 kg, N=5 (this study)]. Guillemot species (*Uria* spp.; Alcidae) typically make vertical dives and forage on the bottom or in horizontal prey layers. The other alcids and most penguins usually make oblique dives and forage epipelagically, although penguins sometimes forage benthically (Croll et al., 1992; Wilson et al., 1996; Bethge et al., 1997; Falk et al., 2000; Kuroki et al., 2003). To minimize potential effects of body size on swimming and wing stroke

behaviour (Clark and Bemis, 1979; Pennycuick, 1996), we chose the smallest penguin species that has a similar mass to these alcids.

Buoyancy

Buoyancy was estimated based on the lipid, protein and ash content of each species and equations relating respiratory and plumage air volumes (before diving) to body mass (for details of methods, see Lovvorn et al., 1999). Body composition was determined from birds collected in the field for all species except RAZO, for which values were linearly extrapolated from data for COGU. Specimens included RHAU obtained as chicks in British Columbia and raised in captivity, COGU collected in the Aleutian Islands, Alaska, USA, LIPE collected at the Phillip Island Penguin Reserve, Victoria, Australia, and BRGU collected near the Pribilof Islands, Alaska. For RHAU, we also used data on lipid and water content of wild birds (Oka and Okuyama, 2000). The buoyancy of LIPE might be overestimated, owing to lack of data on plumage air volume and the likelihood that this volume is relatively lower than in the other species (Wilson et al., 1992).

Field studies

Field studies were conducted on BRGU at Ny-Ålesund (78°54′ N, 12°13′ E), Svalvard, Norway in July 2001; COGU and RAZO at the Isle of May (56°11′ N, 2°33′ W), Scotland in June 2003; RHAU at Teuri Island (44°25′ N, 141°19′ E), Japan in June 2001; and LIPE at Oamaru (45°06′ S, 170°58′ E), New Zealand in October 2003, under permits from the Norwegian Animal Authority (#980/01) and Governor of Svalbard, the Environmental Agency and Department of Culture of Japan (#131/2-24~29), the Scottish Natural Heritage (#MON/PRO/60) and the Department of Conservation in New Zealand (#OT-13650-FAU).

Adults with small chicks were captured with a noose-pole or by hand. The data-loggers (15 mm diameter, 60 mm length, 16 g including battery; M190-D2GT; Little Leonardo Ltd, Tokyo, Japan) were attached to the feathers on the centre of the lower back with quickset glue, a plastic net and either cable ties for alcids or Tesa™ tape (Charlotte, NC, USA) for LIPE. The longitudinal axis of the loggers was along the birds' tail-to-head axis, while the vertical axis was along the birds' dorsal-to-ventral axis (Fig. 1) (see Watanuki et al., 2003). The loggers recorded depth with a pressure sensor (±1 m accuracy; FPBS-82A; Fujikura, Tokyo, Japan) every second. Acceleration along the tail-to-head axis (surge) and dorsal-to-ventral axis (heave) was measured with capacitive accelerometers (ADXL202E; Analog Devices, Norwood, MA, USA) at 32 Hz for BRGU and RHAU and at 64 Hz for COGU, RAZO and LIPE.

After deployment of the loggers for 23.5–167.6 h, the birds were recaptured and the loggers removed. All BRGU, RAZO and LIPE were recaptured. Recapture rates were four of five for COGU and five of seven for RHAU. Other individuals of COGU and RHAU did not return during the study periods or else lost their loggers. Of the loggers that were retrieved, two
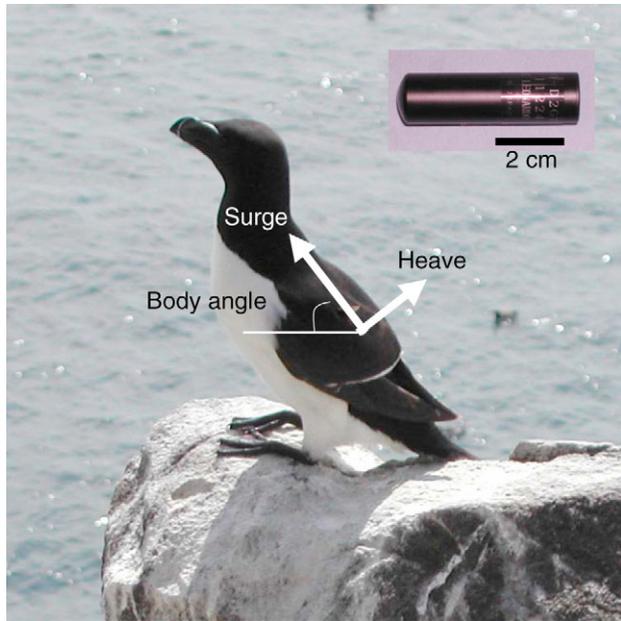
Fig. 1. A razorbill (RAZO) showing the position of the logger attached to the lower back feathers and the two acceleration axes (surge along the longitudinal body axis and heave along the dorso-ventral axis). Photo of the data-logger is inserted.

BRGU, four COGU, four RAZO, three RHAU and five LIPE provided heave and surge data (Table 1). Body mass of BRGU, RHAU and LIPE were measured by a Pesola spring balance (Baar, Switzerland). For LIPE, the circumference of the body trunk just behind the wings was determined with a tape measure. The chicks of instrumented birds remained healthy during deployments. RHAU, which visit the colony less often and only at night, took longer to recapture (6–7 days); consequently, we fed their chicks about 10 g of sand eels (*Ammodytes hexapterus*) per night while the adults were instrumented.

Logger attachment angle, heave, surge, dive angle and swim speed

The attachment angle (α) of a logger was estimated based on heave acceleration when the bird was at the water surface (see Watanuki et al., 2003, 2005) and was –2.1° to +19°. Average heave accelerations recorded when the birds were at the water surface (9.1–9.8 m s^{-2}) were close to the expected accelerations (9.8 m s^{-2} × cosα), indicating that the heave axes of data-loggers fitted on the birds' backs were almost perpendicular to the body axes of the birds. A single LIPE (LIPE/5 in Table 1) had mean heave acceleration of 8.6 m s^{-2} when the bird was at the water surface, indicating that the heave axis was not vertical to the body. Thus, this bird was excluded from analyses.

Along the surge axis of the data-logger, high-frequency components of the fluctuations of surge acceleration should be caused by wing stroking, and low-frequency components by gravity. The low-frequency component was determined by removing the high-frequency component with a two-band low-pass filter (IFDL Igor Pro version 4; Wave Metrics, Portland, OR, USA) (following Watanuki et al., 2003). This filter started at 1 Hz, which was well below the minimum stroke frequency, and ended at 1.5 Hz. This range allowed us to analyze rapid body-angle changes at the start of dives but minimized the risk of misidentifying low-frequency body-angle changes as strokes (Watanuki et al., 2005). The contribution of low-frequency components caused by a change in the mean speed is very small and negligible in this study. For example, if a bird accelerates speed from 1 m s^{-1} to 2 m s^{-1} by 10 s (probably the fastest acceleration observed in this study), the bird is accelerated by 0.1 m s^{-2}. If this bird dives with a body angle of 30° (the shallowest body angle observed), the surge caused by gravity is 4.9 m s^{-2}. In this case, the low-frequency component caused by a change of mean speed was 2% (0.1/4.9) of that caused by gravity. Usually, this value could be smaller. Surge and heave of the data-loggers caused by wing strokes were determined by subtracting the components of gravity from recorded surge and heave accelerations. Heave and surge of a bird's body trunk were corrected for the logger attachment angle (see appendix in Watanuki et al., 2003).

The angle of the bird's body axis relative to horizontal (θ) was determined by adding the logger attachment angle (α) to the logger axis angle (arcsine of the low-frequency component of surge). To smooth variations in body angle presumably caused by wing strokes, we used a 1-s moving average for body angle, corresponding to the sampling interval of the depth. Swim speed was estimated from body angle and the rate of change in depth for each 1-s sample. LIPE (the fastest of our study species) cruise at 1.5–1.7 m s^{-1} and rarely exceed 2.5 m s^{-1} (Barton, 1979; Clark and Bemis, 1979; Bethge et al., 1997). Anomalous swim speeds of >2.5 m s^{-1} or <0 m s^{-1}, possibly resulting from errors in calculating body angle and a very small depth change rate, were excluded from analyses (29% of 1-s samples for BRGU, 17% for COGU, 12% for RAZO, 14% for RHAU and 28% for LIPE).

Wing strokes from filming vs data-loggers

To check the reliability of estimates of wing-stroke patterns and body angles based on accelerations, we video-taped a left-side view of a RHAU using a Sony Hi-8 video camera in an underwater housing at Teuri Island. The bird was fitted with a data-logger and dove to 2–3 m depth along a pier in a harbour. For this experiment, the bird was freely swimming with a 20-m lightweight line attached to its foot. Video-recording and acceleration measurements started at exactly the same time. Displacements of the left eye and the carpal joint of the left wing were plotted from the video image at 0.06-s intervals using PhotoShop (Adobe Systems, Inc., San Jose, CA, USA). We plotted the position of the carpal joint relative to the trajectory of the eye to analyze wing movement.

Definition of upstroke, downstroke and glide

Based on a single dive to 3 m depth by the RHAU that was also video-taped, the body angle (measured from horizontal)

Table 1. *Recording period, number of dives and dive depth*

Species/bird ID	Recording period (h)	No. of dives	Median dive depth* (m)	Mean dive depth[†] (m)	Maximum dive depth (m)	N
BRGU/13	27.2	81	35±53	52±35	120	5
BRGU/17	39.8	173	44±56	43±30	107	3
COGU/2	21.8	359	5±13	15±20	64	2
COGU/3	22.1	135	33±42	37±21	67	6
COGU/4	22.4	154	28±31	35±17	63	3
COGU/5	19.8	353	2±24	29±9	63	3
RAZO/1	19.8	271	6±8	7±5	28	1
RAZO/2	19.7	177	6±13	8±6	31	1
RAZO/3	22.6	55	9±13	11±8	29	4
RAZO/4	20.1	556	3±6	5±5	25	3
RHAU/05	33.8	284	30±7	29±9	60	5
RHAU/06	33.6	393	15±8	14±6	34	5
RHAU/07	33.4	365	20±25	17±12	41	6
LIPE/1	23.5	871	5±5	5±3	17	0
LIPE/2	24	1098	6±8	7±6	21	5
LIPE/3	24	989	5±6	6±5	23	2
LIPE/4	24	1096	7±10	8±6	21	0
LIPE/5	24.5	877	6±10	7±5	21	0

*Values are means ± quantiles.

[†]Values are means ± s.d.

N, number of sample dives used for the analyses. BRGU, Brünnich's guillemot; COGU, common guillemot; RHAU, rhinoceros auklet; RAZO, razorbill; LIPE, little penguin.

determined from surge acceleration (19°) was very close to the angle (around 20°) of the approximate trajectory of the eye in the video sequence (Fig. 2C). Therefore, we assumed that a bird's forward progress is parallel to the axis of the body and that swim speed can be estimated from body angle and the rate of change in depth.

When this RHAU made a downward movement of the carpal joint relative to the trajectory of the eye (downstroke; broken bars in Fig. 2A), positive heave acceleration of the body showed two peaks: strong (5 m s^{-2}) and weak (2 m s^{-2}) (Fig. 2B). No upward movement of the wings was detected between these two peaks and there was no corresponding increase in surge during the second peak of heave acceleration. In free-ranging COGU descending at shallow depths, a small peak of upward heave with no corresponding increase in surge also occurred at the end of the downstroke (Fig. 3).

Based on the above observations, we defined an upstroke as occurring over periods when the body had overall negative heave, and a downstroke over periods when the body had overall positive heave. The upstroke began when heave passed zero during decline to its most negative value. The upstroke ended (downstroke started) when negative heave increased passed zero. The downstroke ended when declining heave passed zero after the second positive peak.

Between the end of descent and the start of ascent ('bottom' in Fig. 3), when swimming was generally horizontal, both heave and surge sometimes stayed at around zero for a period after the downstroke, which we interpreted as a glide (Fig. 3). In such cases, we defined the start of the upstroke as the time

when heave started to decrease steadily (–12.8 m s^{-3} for samples at 64 Hz, and –16.0 m s^{-3} for samples at 32 Hz). All upstrokes and downstrokes were longer than 0.1 s. Since the sampling interval was 0.03125 s for recordings at 32 Hz and 0.015625 s for 64 Hz, glides shorter than 0.1 s could not be discriminated reliably. The durations of upstroke and downstroke and the maximum heave and surge acceleration on upstroke and downstroke were obtained with a macro program in Igor Pro version 4.
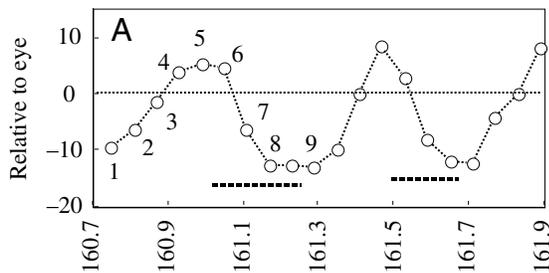
Effects of attached loggers

Externally attached devices sometimes affect the behaviour of alcids and penguins (Wanless et al., 1988; Watanuki et al., 1992; Wilson and Culik, 1992; Paredes et al., 2005). Because of logistic constraints, a formal assessment of device effects was not attempted as part of this research. Loggers of the same size and shape as those in this study did not change the duration of foraging trips by BRGU (Watanuki et al., 2001), but both BRGU and RHAU decreased meal delivery rates to chicks (Watanuki et al., 2001; Kuroki et al., 2003). For all species in this study, the mass of our loggers represented <2% of the mass of adults. Assuming that the density of salt water at 10°C was 1.0269 g ml^{-1}, buoyancy of the logger (16 g mass in the air and 10.6 ml volume) was only –0.05 N, which seems negligible at depths of <20 m where the buoyancy of birds without devices was much larger (0.9–5.0 N).

Because of drag, as the frontal cross-sectional area of attached devices becomes larger relative to that of the birds, birds dive shallower, swim slower and expend more energy
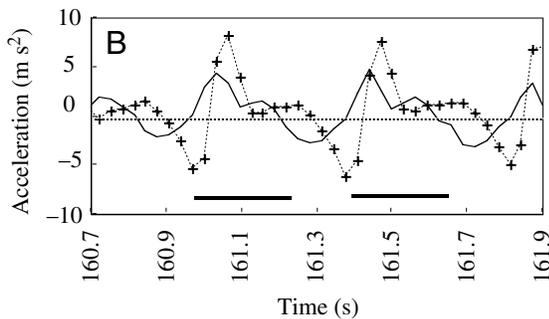
than those without devices (Wilson et al., 1986; Culik and Wilson, 1991; Wilson and Culik, 1992). The cross-sectional area of our loggers (1.77 cm^2) was 3.2% and 6.1% of the maximum cross-sectional area of BRGU (54.77 cm^2) and RHAU (28.99 cm^2) (Osa, 1994). The girth at the base of the wings of LIPE was 39.9±0.6 cm (*N*=5 birds), so the cross-sectional area of the device was 1.4% of that of LIPE

Position of carpal joint

Acceleration measured by data-logger
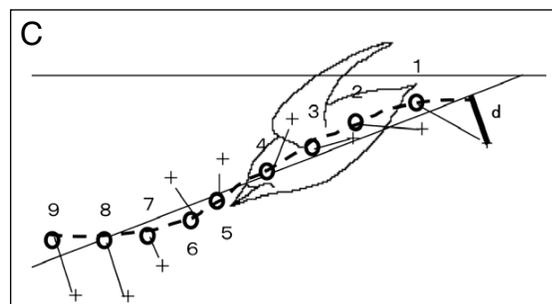
Movement of eye and carpal joint

Fig. 2. Wing stroke and heave and surge acceleration in a videotaped rhinoceros auklet (RHAU) diving to 3 m depth. (A) Position of the carpal joint relative to the eye, (B) heave (solid line) and surge (dotted line) are plotted against time, and (C) diagram showing the positions of the eye (open circles) and carpal joint (crosses). Crosses along the line for surge in B indicate samples at 32 Hz. The positions of the carpal joint of the left wing were sampled at 0.06 s intervals (numbered 1-9) with the video-image. The positions of the carpal joint in A were shown as the distance (*d* in C) between the approximate trajectory of the eye and the carpal joint. The unit of distance was 1/10 of the maximum positive distance recorded. Horizontal broken bars in A indicate the duration of downstroke determined with video-image, and horizontal bars in B indicate the periods when the heave acceleration had a positive value.

(126.69 cm^2). African penguins (*Spheniscus demersus*) are expected to reduce swim speed by 4%, 9% and 18% if they carry devices having cross-sectional areas of 1.4%, 3.2% and 6.1%, respectively, of that of the birds (Wilson et al., 1986). The total wetted surface area and the interaction with the body also affect drag. Even a small structure can have important effects on the flow. Although our devices had a rounded head and we attached them to the lower back of the birds to minimize drag (Fig. 1) (Bannasch et al., 1994), we could not rule out drag effects of loggers in our data for small alcids.

Sample dives and analyses

BRGU and COGU made much deeper dives (maximum individual depths of 107–120 m for BRGU and 63–67 m for COGU) than RAZO (25–31 m), RHAU (34–60 m) and LIPE (17–23 m) (Table 1). Penguins and guillemots adjust dive angle and stroke rate according to the maximum depth of each dive (Wilson et al., 1996; Watanuki et al., 2003). For comparing species, we therefore selected dives to depths of 20–30 m. Our aim was to describe changes in dive angle, swim speed and stroke frequency during steady swimming, so we also selected dives with no abrupt changes of depth during descent and ascent. This protocol minimized the possibility of including dives in which the birds chased prey during these phases. Mean depths (±1 s.d.) of sample dives were 27±1 m for BRGU (*N*=8), 27±1 m for COGU (*N*=14), 25±1 m for RAZO (*N*=9), 24±1 m for RHAU (*N*=16) and 21±0 m for LIPE (*N*=7). Data collected at depths of <1 m were excluded, as they were within the error range of the depth sensor.

Birds descended (descent phase) with a large negative depth change rate, stayed there for a while (bottom phase) with a small depth change rate, and then ascended to the surface (ascent phase) with a large positive depth change rate (Fig. 4). To define the bottom phase, we used the distribution of depth change rate. The distribution of rates of change in vertical depth showed gaps at –0.4 to –1 m s^{-1} and at 0.4 to 1 m s^{-1}. Therefore, birds were defined as descending if their rate of change in depth was lower than –0.6 m s^{-1} and as ascending if it was higher than 0.6 m s^{-1}.

Statistics

To examine effects of species and current depth (depth at a particular moment) on body angle, swim speed, surge and heave, we used mixed general linear models (GLM) with species as a fixed factor and birds as a random factor nested within species (SPSS version 13; SPSS, Inc., Chicago, IL, USA). Current depth was a covariate, yielding an interaction term between species and current depth. Restricted Maximum Likelihood (REML) was used to evaluate fit of the models, and effects of species and depth were examined with Type III tests. We did repeated tests on the same data set, so we used Bonferroni corrections. Bonferroni *post-hoc* tests were used to examine pair-wise species differences. Significance level was α=0.05. We used 1-s samples for analyses of body angle and swim speed, and used each wing stroke (as defined by heave) as the sample unit for analyzing maximum acceleration on
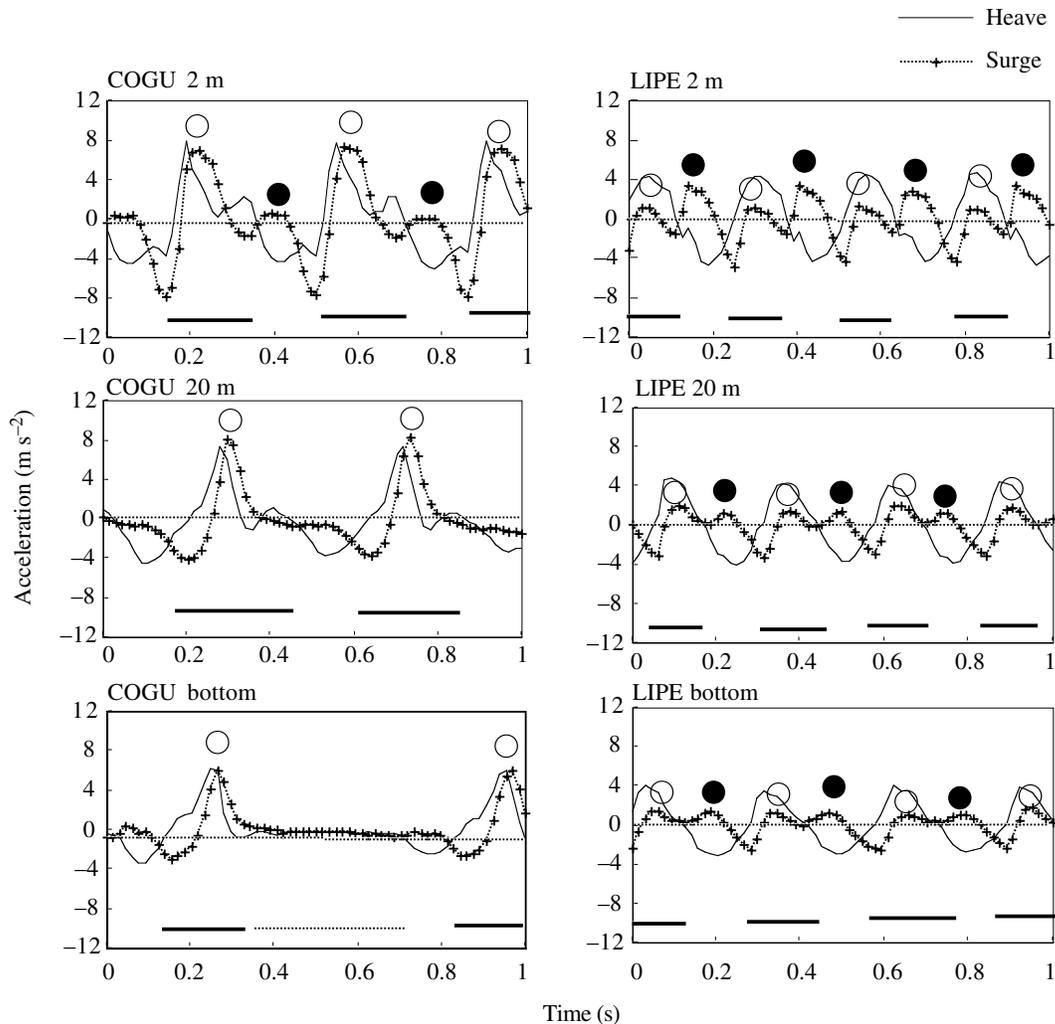
Fig. 3. Typical changes of heave (solid line) and surge (dotted line) acceleration of a common guillemot (COGU) and a little penguin (LIPE) during descent at depths of 2 m and 20 m and during the bottom phase of the dive. Crosses along the line for surge indicate samples at 64 Hz. Downstrokes were assumed to occur during periods of positive heave, as indicated by bold horizontal bars. For COGU, the second small peak of heave was observed at the end of the downstroke at 2 m and 20 m. The horizontal dotted bar in the panel for horizontal swimming during the bottom phase by COGU indicates a glide when there was little heave or surge. Circles show peaks of surge acceleration, indicating forward thrust during upstroke (filled circles) and downstroke (open circles).

upstroke and downstroke, duration of upstrokes and downstrokes, frequency of wing strokes, and peaks of positive surge acceleration during descent and ascent phases of sample dives (to maximum depths of 20–30 m).

Results

Buoyancy

Estimated buoyancies at the water surface were 4.8 N for BRGU, 4.6 N for COGU, 3.9 N for RAZO, 3.6 N for RHAU and 5.0 N for LIPE. Buoyancy decreases rapidly with increasing depth to a depth of about 20 m, after which changes are relatively small and gradual (see Lovvorn et al., 2004). At 20 m depth, all species studied here were positively buoyant: 1.1 N for BRGU, 1.0 N for COGU, 1.0 N for RAZO, 0.9 N for RHAU and 1.2 N for LIPE.

Body angle and swim speed during descent and ascent

Body angle and swim speed during descent differed among species ($P<0.001$ for body angle, $P<0.01$ for swim speed). During descent, the mean body angles of BRGU and COGU were steeper than for RAZO and RHAU, with LIPE having the shallowest body angle (Table 2; Fig. 5). Body angle was affected by current depth and the interaction between species and current depth (in both cases, $P<0.001$). BRGU, COGU, RAZO and RHAU decreased their body angles as they descended, whereas LIPE maintained their shallow body angle within a relatively narrow range (Fig. 5).

During descent, mean swim speed did not differ significantly between LIPE, COGU and RAZO, but that of LIPE was faster than BRGU; RHAU had the slowest swim speed (Table 2). Swim speed was significantly affected by current depth ($P<0.001$) and species × current depth interaction ($P<0.001$).
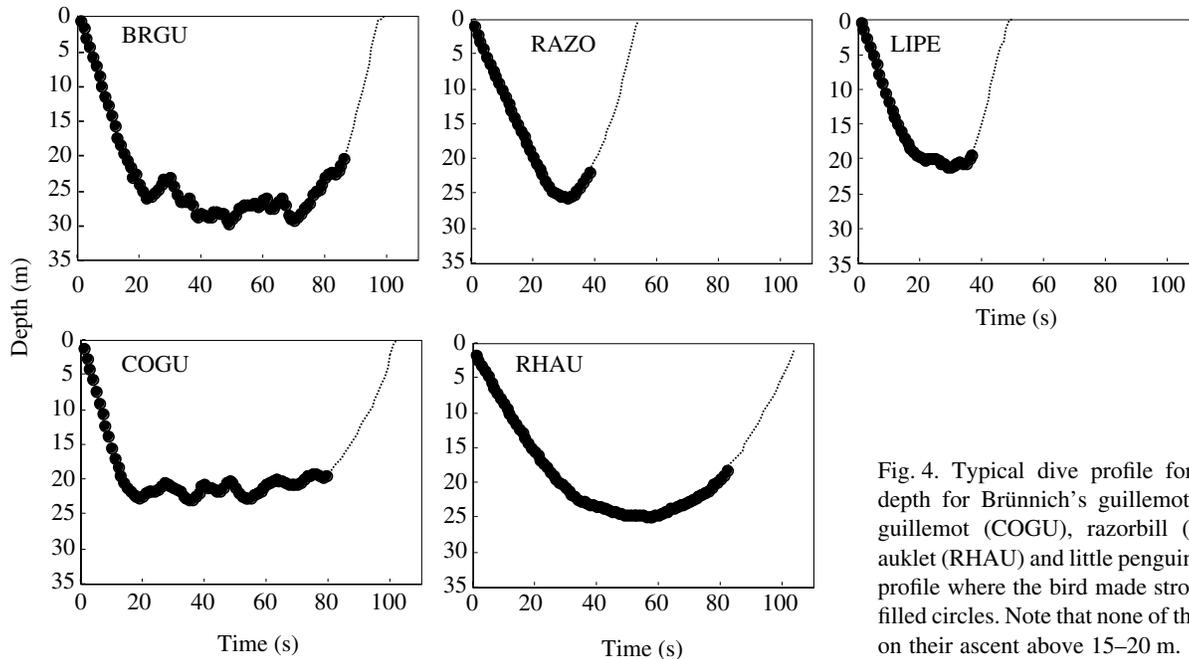
Fig. 4. Typical dive profile for dives to 20–30 m depth for Brünnich's guillemot (BRGU), common guillemot (COGU), razorbill (RAZO), rhinoceros auklet (RHAU) and little penguin (LIPE). Parts of the profile where the bird made strokes are indicated by filled circles. Note that none of the birds made strokes on their ascent above 15–20 m.

BRGU, COGU and RAZO increased swim speed during descent, whereas RHAU and LIPE maintained swim speed within a relatively narrow range (Fig. 5).

During ascent, both body angle and swim speed differed among species ($P<0.05$). Both BRGU and COGU had steeper body angles than RHAU, while no significant difference was found for other pairwise comparisons (Table 2). Body angle was significantly affected by current depth ($P<0.001$) and species × current depth interaction ($P<0.001$). BRGU, COGU, RAZO and RHAU slightly increased body angle, while LIPE decreased body angle, within 15 m of the water surface (Fig. 5).

During ascent, *post-hoc* tests showed no significant pairwise differences in swim speed among species (Table 2). Swim speed was affected by current depth ($P<0.001$) and species × current depth interaction ($P<0.01$): COGU, RAZO and RHAU increased swim speed during ascent, while BRGU and LIPE did not (Fig. 5).

Mean depths (±1 s.e.m.) at which the birds stopped stroking their wings during ascent (see Fig. 4) were 18±1 m ($N=8$ dives) for BRGU, 23±1 m ($N=14$) for COGU, 20±1 m ($N=10$) for RAZO, 19±1 m ($N=16$) for RHAU and 18±1 m ($N=7$) for LIPE (see Fig. 2). Being positively buoyant, birds ascended passively

Table 2. *Differences in body angle and swim speed in descent and ascent phases, and those in stroke duration, frequency of wing stroke and thrusts, heave at upstroke and downstroke, and maximum surges at upstroke and downstroke*

	BRGU (2 birds)	COGU (4 birds)	RAZO (4 birds)	RHAU (3 birds)	LIPE (2 birds)
Descent					
Body angle (deg.)	−78.4±1.3 (106)	−75.6±0.8 (171)	−44.5±0.7 (165)	−43.2±0.5 (380)	−36.5±0.8 (102)
Swim speed (m s^{-1})	1.40±0.02 (106)	1.61±0.01 (171)	1.59±0.02 (164)	1.06±0.01 (380)	1.85±0.02 (93)
Upstroke duration (s)	0.218±0.002 (282)	0.204±0.001 (468)	0.188±0.001 (359)	0.199±0.001 (784)	0.163±0.001 (395)
Downstroke duration (s)	0.211±0.002 (282)	0.180±0.001 (468)	0.172±0.001 (359)	0.194±0.001 (784)	0.132±0.001 (395)
Frequency of wing strokes (n s^{-1})	2.34±0.01 (282)	2.61±0.01 (468)	2.77±0.01 (359)	2.57±0.01 (784)	3.44±0.02 (395)
Frequency of thrusts (n s^{-1})	4.61±0.04 (282)	4.00±0.07 (468)	4.42±0.07 (359)	5.07±0.02 (784)	6.87±0.04 (395)
Min. heave at upstroke (m s^{-2})	−5.94±0.08 (282)	−4.83±0.03 (468)	−5.55±0.04 (359)	−4.28±0.02 (784)	−4.48±0.04 (395)
Max. heave at downstroke (m s^{-2})	7.91±0.12 (282)	7.44±0.04 (468)	8.70±0.06 (359)	6.93±0.05 (784)	4.94±0.05 (395)
Max. surge at upstroke (m s^{-2})	1.83±0.07 (282)	0.33±0.05 (468)	0.42±0.05 (359)	1.45±0.03 (784)	2.36±0.03 (395)
Max. surge at downstroke (m s^{-2})	6.08±0.08 (282)	7.85±0.06 (468)	8.32±0.09 (359)	5.32±0.05 (784)	1.97±0.03 (395)
Ascent					
Body angle (deg.)	56.6±1.6 (112)	56.6±1.1 (172)	45.5±0.9 (153)	26.3±0.5 (350)	50.9±2.0 (85)
Swim speed (m s^{-1})	1.56±0.04 (103)	1.78±0.02 (172)	1.63±0.03 (150)	1.79±0.02 (333)	1.91±0.02 (73)

Means ± 1 s.e.m. are shown, with sample sizes in parentheses. Sample unit is 1-s interval for body angle and swim speed and strokes for others.

BRGU, Brünnich's guillemot; COGU, common guillemot; RHAU, rhinoceros auklet; RAZO, razorbill; LIPE, little penguin.

above 78–87% of maximum dive depths for dives to 20–30 m. Stroke patterns during ascent were not analyzed further.

Duration and frequency of stroke and forward acceleration during descent

During descent, duration of the upstroke did not vary among species (Table 2). Upstroke duration was significantly affected by both current depth and species $\times$ depth interaction ($P<0.001$). BRGU, COGU and RHAU slightly increased upstroke duration during descent, while RAZO and LIPE did not (Fig. 6). Duration of the downstroke did not vary among species and was not affected by current depth, so all species maintained essentially constant downstroke durations while descending. The species $\times$ depth interaction was significant ($P<0.001$), although no obvious patterns were apparent (Fig. 6).

Mean (±1 s.e.m.) duration of glides, when those shorter than 0.1 s were excluded, was 0.441 ± 0.029 s ($N=145$ glides) for BRGU, 0.276 ± 0.020 s ($N=321$) for COGU, 0.289 ± 0.025 s ($N=75$) for RAZO, 0.324 ± 0.010 s ($N=781$) for RHAU and 0.628 ± 0.053 s ($N=45$) for LIPE. Although gliding was common during bottom swimming in alcids (145 of 262 strokes for BRGU, 321 of 555 strokes for COGU, 781 of 1211 strokes for RHAU, 75 of 149 strokes for RAZO but only 45 of 280 strokes for LIPE), glides were rare or absent in all species during descent (two strokes for BRGU, three strokes for RAZO, and no strokes for other species).

The frequency of wing strokes was defined as the inverse of the sum of the durations of upstrokes, downstrokes and glide phases. During descent, the frequency of wing strokes did not vary statistically among species (Table 2). Stroke frequency was affected by current depth ($P<0.001$) and species $\times$ current depth interaction ($P<0.001$). RAZO and LIPE maintained relatively constant stroke frequency during descent, while BRGU, COGU and RHAU slightly decreased stroke frequency as they descended to 20 m depth (Fig. 6).

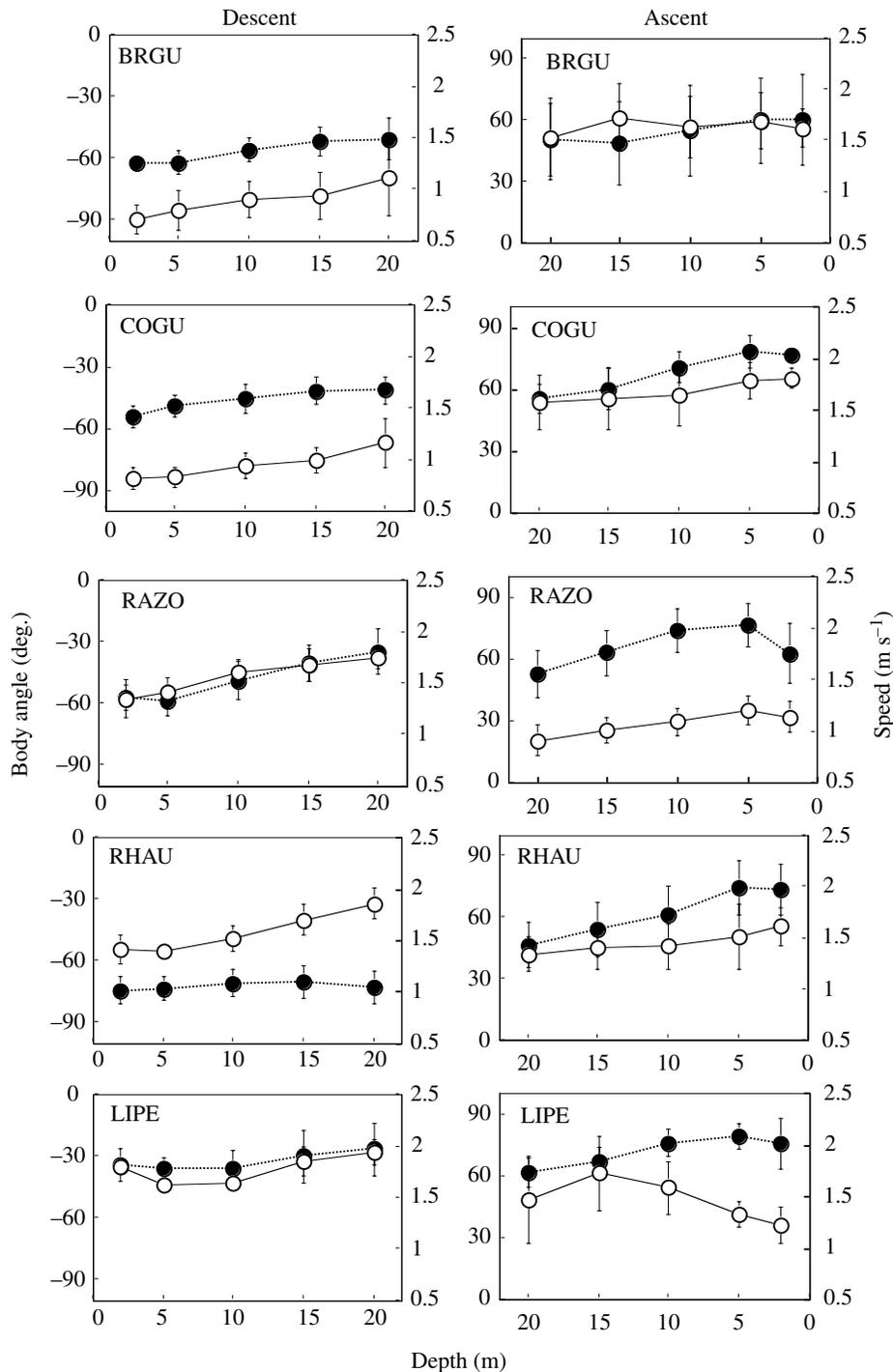Typical changes of heave and surge accelerations of free-ranging COGU

Fig. 5. Changes in body angle (open circles) and speed (filled circles) during descent and ascent, based on eight dives from two Brünnich's guillemots (BRGU), 14 dives from four common guillemots (COGU), nine dives from four razorbills (RAZO), 16 dives from three rhinoceros auklets (RHAU) and seven dives from two little penguins (LIPE). Maximum depths for these sample dives were all between 20 and 30 m. To illustrate the effects of current depth on body angle and swim speed, mean body angle was calculated for each of 1–2 m, 2–5 m, 5–10 m, 10–15 m and 15–20 m depths, and means $\pm$ 1 s.d. (vertical bars) across 1-s samples are shown. Statistical testing was done using all 1-s samples. Note that axes for descent and ascent differ.

and LIPE during descent (Fig. 3) show that COGU had peaks of positive (forward) surge acceleration during both upstroke and downstroke at 2 m depth, but at 20 m had a single peak of positive surge only during the downstroke. LIPE showed peaks of positive surge during both upstroke and downstroke at both 2 and 20 m depth. During descent, the frequency of the peaks of positive surges did not differ among species (Table 2). The frequency of the peaks of positive surges was affected by current depth and species × depth interaction ($P<0.001$). COGU and RAZO decreased the frequency of the peaks of positive surges more quickly as depth increased than did BRGU and RHAU, since these alcids did not show forward surge on upstrokes in deep water. LIPE maintained high

frequency of the peaks of positive surges during descent (Fig. 6), possibly by making thrusts on both upstroke and downstroke over the entire depth range.

Maximum heave and surge during strokes

We also measured the maximum downward and upward heave accelerations recorded on upstroke and downstroke, respectively. Strokes with extreme heave accelerations, presumably because of prey pursuit or rapid depth undulations, were considered outliers and were deleted (3.1% of all strokes for BRGU, 0.6% for COGU, 7.9% for RAZO, 0.8% for RHAU and 1.9% for LIPE).

Maximum downward heave on the upstroke varied among species ($P<0.05$), although *post-hoc* tests showed no significant pairwise differences. Maximum downward heave on the upstroke was not affected by current depth but was affected by species × depth interaction ($P<0.001$). RAZO and BRGU seemed to decrease maximum upstroke heave slightly as depth increased, but the other species did not (Fig. 7). Maximum upward heave on the downstroke did not differ among species (Table 2). Maximum upward heave on the downstroke was affected by current depth and species × depth interaction ($P<0.001$). BRGU, RHAU and RAZO increased maximum upward heave on the downstroke with increasing depth while COGU and LIPE did not (Fig. 7).

Maximum surge acceleration on the upstroke varied among species ($P<0.05$). LIPE and BRGU produced greater acceleration than COGU and RAZO, while that of RHAU did not differ from the others (Table 2). Maximum surge on upstroke was affected by current depth and species × depth interaction ($P<0.001$). Maximum surge on the upstroke decreased during descent, with stronger effects of depth in alcids than LIPE (Fig. 7). On the downstroke also, maximum surge acceleration varied among species ($P<0.001$). RAZO and COGU produced greater surge acceleration on the downstroke than LIPE (Table 2). RHAU and BRGU also produced greater surge acceleration than LIPE, but that of RHAU was smaller than that of COGU. Maximum surge on the downstroke was affected by current depth and
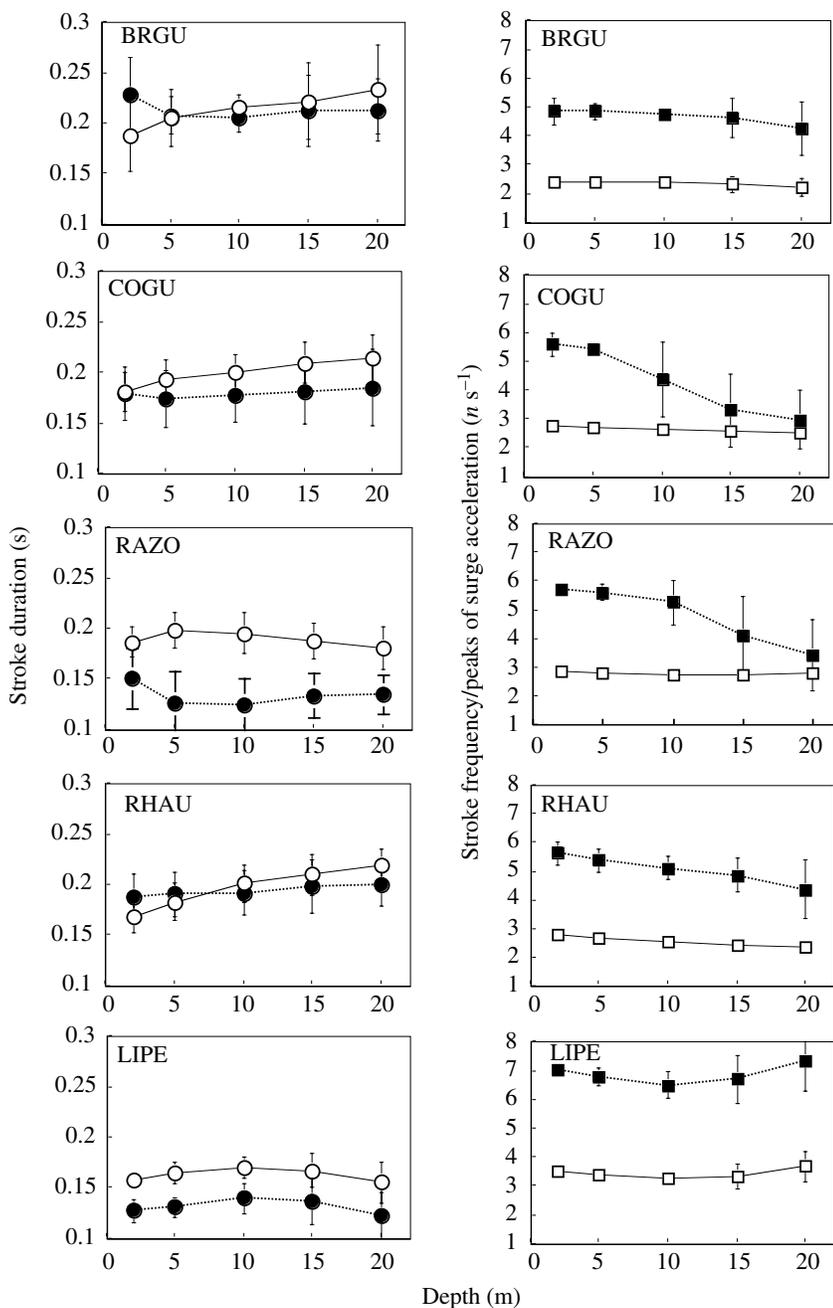

Fig. 6. Changes in the duration of upstroke (open circles) and that of downstroke (closed circles), and the frequency of wing strokes (open squares) and that of peaks of surge acceleration (closed squares) during descent to 20 m depths. See legend of Fig. 5 for abbreviations of species names and further explanation. Statistical testing was done using all wing strokes.

species × depth interaction ($P<0.001$). Maximum surge on the downstroke increased with increasing depth in alcids but decreased with increasing depth in LIPE (Fig. 7).

Discussion

Dive profiles and depths

The dive profiles and depths reported here (Table 1; Fig. 2) were similar to those described previously in other studies. BRGU make mostly U-shaped dives to an average depth of 18 m, with median depth of 49 m and maximum depth of 210 m (Croll et al., 1992; Falk et al., 2000). Typical dive depths of COGU are 20–60 m (Gaston and Jones, 1998; Daunt et al., 2003). RAZO usually make V-shaped dives to mean depths of 8–24 m (Benvenuti et al., 2001). RHAU made V-shaped dives, with median depths of 12–17 m and maximum depths of 35–57 m (Kuroki et al., 2003). LIPE usually make V-shaped dives to mean depths of 1–4 m and maximum depths of 15–50 m (Gales et al., 1990; Bethge et al., 1997).

Deeper-diving species (BRGU and COGU) did not always swim faster, stroke more frequently (Table 2) or stop stroke at deeper depths than shallower divers (RAZO, RHAU, LIPE). However, species-specific dive profiles corresponded to patterns of body angle in our study. Thus, the deeper-diving BRGU and COGU had steep body angles while descending (–76° and –78° on average) and ascending (57° on average). During the 'bottom' (mostly horizontal) phase of dives, BRGU and COGU are believed to feed on epibenthic prey or on epipelagic prey in predictable layers (Coyle et al., 1992; Croll et al., 1992; Bryant and Jones, 1999); thus, they may maximize foraging time by descending and ascending with steeper body angles. COGU on the Isle of May eat mainly 0-year-class lesser sandeels (*Ammodytes marinus)* and feed their chicks either on larger, adult sandeels or sprats (*Sprattus sprattus*) (Wilson et al., 2004). Comparison of dive depths with local hydrography indicates that birds are predominantly feeding below the themocline close to the seabed (Daunt et al., 2006). Among obliquely diving species, LIPE descended with shallower (–37°) and ascended with steeper (51°) body angles, while RHAU descended with steeper (–43°) and ascended with shallower (26°) body angles. RAZO descended (–45°) and ascended (46°) with similar angles. How these interspecific differences in body angle during descent and ascent relate to foraging ecology is currently uncertain.

Buoyancy and regulation of stroke patterns

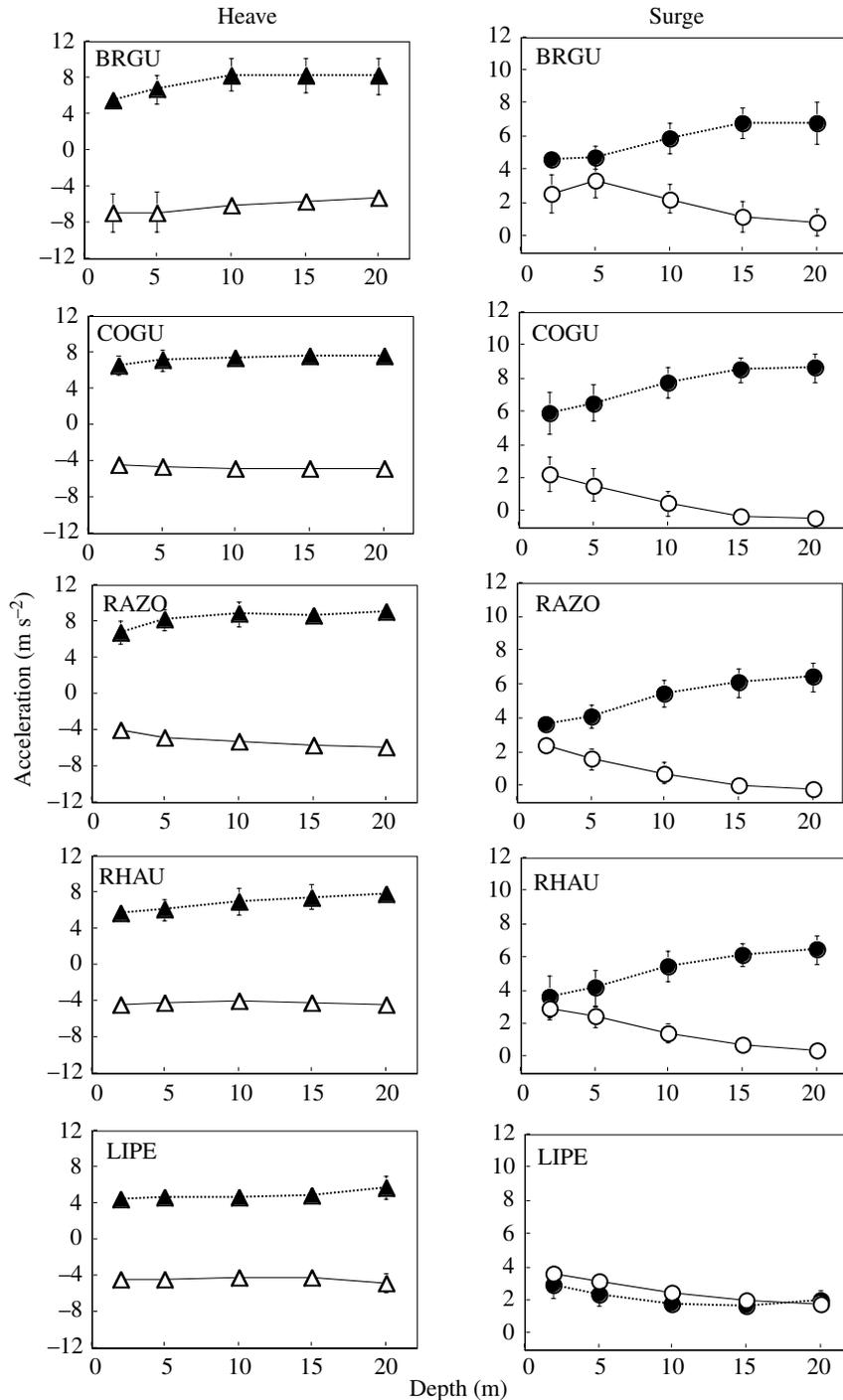The estimated buoyancy of our study species at the water surface ranged from 3.6

Fig. 7. Changes in the maximum upward heave on downstrokes (closed triangle), the maximum downward heave on upstrokes (open triangle), the maximum surge both on upstrokes (open circle) and downstrokes (closed circle). See legend of Fig. 5 for abbreviations of species names and further explanation.

for RHAU to 5.0 N for LIPE. Based on body masses obtained in this study or reported in the literature, mass-specific buoyancy is estimated as greater for RHAU (6.3 N kg^{-1}) and RAZO (5.7 N kg^{-1}) than for BRGU (4.9 N kg^{-1}) and COGU (4.7 N kg^{-1}), and that of LIPE is smallest (<4.1 N kg^{-1}). The buoyancy of tissues does not change with depth; however, owing to compression of air volumes in the respiratory system and plumage, buoyancy decreases rapidly with increasing depth to a depth of about 20 m. Below 20 m, the air spaces are mostly compressed and buoyancy changes only gradually. This pattern of buoyancy change with depth is the same regardless of variations in the magnitude of air volumes in different species (Lovvorn and Jones, 1991; Lovvorn et al., 1999; Lovvorn et al., 2004). Because the buoyancy of birds of all alcid species, and presumably that of LIPE, was positive at 20 m depth and buoyancy increases rapidly above this depth, ascent from 20 m depth could occur passively (without stroking). All species responded to this pattern by ceasing strokes at about 20 m depth during ascent.

During descent, alcids decreased the frequency of peaks of positive surge acceleration (those based on upstroke and downstroke considered as separate) between 5 and 15 m depth (Fig. 6), possibly to reduce thrust as buoyancy decreased (Watanuki et al., 2003; Lovvorn et al., 2004), although the pattern was not so obvious in BRGU. Stroke frequency also decreased with depth in BRGU, COGU and RHAU, but the decrease was small (5–19%) compared with the decrease in frequency of the peaks of positive surge accelerations (49–54%; Fig. 7). RAZO maintained the same stroke frequency as depth increased. Therefore, in alcids, the decrease in the frequency of forward acceleration was achieved mainly by a decrease in surge acceleration on the upstroke as depth approached 20 m (Fig. 7). This pattern also occurred in BRGU diving to 100 m depth (Watanuki et al., 2003). Our present study provides additional evidence that this mechanism is widespread across alcids exhibiting a range of dive profile types and foraging patterns, even for species with relatively shallow dives.

In contrast to alcids, LIPE did not decrease the frequency of peaks of positive surge acceleration as depth increased during descent but instead reduced the amplitude of surge acceleration during both upstroke and downstroke as buoyancy decreased (Fig. 7). An analogous decrease in the amplitude of wing strokes with increasing depth was observed in Magellanic penguins (*Pygoscelis magellanicus*) (Wilson and Liebsch, 2003). Our present study found that LIPE accelerated forward during both upstroke and downstroke throughout descent to 20 m depth, whereas alcids accelerated forward during the upstroke and downstroke at shallow depths and mainly on downstroke at deeper depths.

Similar patterns of acceleration during both upstroke and downstroke have been reported for various species of penguins (Clark and Bemis, 1979; Hui, 1988) and Atlantic puffin, *Fratercula arctica* (Johansson and Aldrin, 2002), swimming horizontality in a tank. Observed surge acceleration results from the sum of forward thrust by the birds and resistance by buoyancy, drag and inertia. At the same mean speed and stroke frequency during descent, shallower dive angles against buoyancy might result in greater acceleration during strokes due to less work against buoyancy (less vertical distance moved against buoyancy during a stroke). However, this effect should not alter one of the major differences we found in comparing alcids and penguins. With increasing depth during descent, alcids generally decreased relative surge acceleration on the upstroke *vs* downstroke, whereas LIPE decreased surge acceleration similarly on upstroke and downstroke. Downstrokes are powered mainly by the pectoral muscles and upstrokes by the supracoracoideus muscles. The mass proportion of pectoral to supracoracoideus muscles is greater in BRGU (3.5), COGU (3.5) and RHAU (3.3) than in LIPE (2.1) (Mill and Baldwin, 1983), emperor penguins (*Aptenodytes forsteri*; 2.3) and king penguins (*A. patagonicus*; 1.8) (values calculated from Osa, 1994). These values suggest that penguins rely more on the upstroke. Relatively large supracoracoideus muscles may allow LIPE to distribute thrust more evenly between upstroke and downstroke (Fig. 7), thereby reducing peak instantaneous speeds and associated higher drag (Lovvorn, 2001).

Wing stroke frequency of 1.2 kg LIPE (3.4 Hz) did not differ significantly from those of 0.6–1.0 kg alcids (2.3 to 2.8 Hz), although the trend was for LIPE to stroke more frequently. This pattern was not expected, given the general observation that larger animals stroke less frequently than smaller ones both in water (Clark and Bemis, 1979) and in air (Pennycuick, 1996). Proportionally greater wing area of alcids than penguins (Pennycuick, 1987; Osa, 1994) might explain this trend, although more data are needed on wing stroke frequency of larger penguins and the wing geometry of penguins and diving alcids.

Despite this difference in stroke patterns between alcids and penguins, duration of the downstroke did not change with depth during descent for either alcids or penguins. During descent, alcids had slightly lower maximum heave on downstroke at depths of 2–5 m, where buoyancy was very high, than at greater depths. By contrast, LIPE showed no change in maximum heave on downstroke with depth. Given that downstroke duration (and thus contraction frequency) did not change with depth, changing heave with depth indicates that the alcids exhibited some variation in power output against load during descent when these shallow depths are included. Guillemots diving to 105 m expended greater work per stroke in the top 5–10 m of dives when overcoming high buoyancy, after which work per stroke became relatively constant (Lovvorn et al., 2004). Muscle is presumed to have maximum efficiency over a relatively narrow range of contraction speeds and loads (Goldspink, 1977; Lovvorn, 2001). The width of this range for load is unknown for the pectoralis muscles of alcids, which must also fly in air at much higher stroke frequencies (~8.7 Hz in air *vs* 1.9–2.8 Hz in water for murres) in a far less dense medium (salt water is 800 times denser than air) (see Lovvorn et al., 1999). The means by which alcids accommodate these widely varying demands on muscle

function, and the extent to which variations in power output affect the efficiency of wing muscles, are intriguing but unclear (cf. Biewener and Gillis, 1999).

Speed change with depth and its regulation

In our study, mean swim speed of LIPE (1.8 m s^{-1}) was within the range of speeds reported in the wild (Bethge et al., 1997). As BRGU dive almost vertically, their swim speed is almost identical to descent and ascent rates. Our values of swim speeds of descending BRGU accorded closely with previously reported descent rates (1.4–1.6 m s^{-1}) (Lovvorn et al., 1999; Lovvorn et al., 2004). During horizontal swimming, guillemot species attain variable speeds ranging from 1.0 m s^{-1} (see appendix in Watanuki et al., 2003) to 2.18 m s^{-1} (Swennen and Duiven, 1991), probably depending on feeding activity. Maximum speeds of RAZO were 1.9 m s^{-1} during descent and 2.5 m s^{-1} during ascent (Benvenuti et al., 2001). Thus, swim speeds during descent in our study were similar to those in previous reports.

For dives to 20 m depth, our study shows that free-ranging alcids often increased swim speed during descent and ascent by 0.2–0.5 m s^{-1}. During passive ascent, COGU, RAZO and RHAU increased their speed as buoyancy rapidly increased above 20 m. BRGU did not increase speed as much, indicating that effects of buoyancy might be smaller for shallow dives by this species. When BRGU approached the surface after diving to 100 m depth, they increased swim speed to 2.3 m s^{-1} without stroking their wings (Watanuki et al., 2003). During descent, BRGU, COGU and RAZO slightly increased swim speed (Fig. 5). RHAU and LIPE maintained a relatively narrow range of speeds while descending. Increase of speed during descent to 20 m (18%, 8%, 10% and 34% for COGU, RAZO, RHAU and LIPE, respectively) seemed to be smaller than increases during ascent (28%, 39%, 30% and 20% for COGU, RAZO, RHAU and LIPE, respectively), although BRGU increased speed by 21% during descent but by only 13% during ascent. Note that these speed changes were over a depth range of rapidly changing buoyancy, whereas speed changes at deeper depths may be far less (Lovvorn et al., 2004).

What determines swim speed as buoyancy changes with depth? At depths greater than 5–10 m, work against buoyancy has declined and work against drag becomes the main mechanical cost of swimming (Lovvorn, 2001; Lovvorn et al., 2004). At depths over 10 m, BRGU diving to over 100 m swam at a narrow range of speeds (1.4–1.8 m s^{-1}) at the upper end of the mostly linear part of the drag curve before major increases in drag occurred (Lovvorn et al., 2004). In the present study, BRGU also kept within this range of speeds during dives to 20–30 m depth (Fig. 5). However, for guillemots, there are no obvious thresholds of the increase in drag with speed that would predict the observed speeds beyond depths at which buoyancy is negligible (Lovvorn et al., 2004). Similarly, the curve of drag vs speed in frozen LIPE (Lovvorn et al., 2001) does not indicate a clear threshold to explain their choice of 1.8–2 m s^{-1} observed in this study (Fig. 5). Lacking clear thresholds in drag, it appears that constraints on power output

or endurance of muscles may be more important than patterns of drag in determining swim speed of these birds, even when drag is the main determinant of the power those muscles must deliver. Data presented here and elsewhere (Lovvorn et al., 2004) suggest that guillemots may exceed optimum work rates at depths less than 5–10 m when overcoming very high buoyancy but reduce work rates to more constant and sustainable levels once they reach deeper depths.

Another possibility is that birds swim at speeds that minimize the cost of transport (COT), or the oxygen consumption required to transport a unit mass a unit distance. Pygoscelid penguins swimming horizontally chose to swim at speeds near their minimum COT (Culik et al., 1991; Culik et al., 1994), whereas spheniscid penguins and cormorants chose to swim at speeds below their minimum COT (Schmid et al., 1995; Luna-Jorquera and Culik, 2000). In LIPE swimming horizontally, COT decreased with increasing speed and seemed to approach a minimum at 1.8 m s^{-1} (Bethge et al., 1997); our LIPE swam at 1.8–1.9 m s^{-1}. At present, there are no respirometry data for alcids swimming at different speeds to indicate how COT changes with speed. Mechanical power required to overcome buoyancy changes substantially with depth (Lovvorn et al., 2004), so the speed that minimizes COT during descent is expected to change with depth and may not be apparent from studies in shallow tanks. Predictions of swim speed based on COT during horizontal swimming may apply better to LIPE with their oblique dive angles and low specific buoyancy (Wilson et al., 1992) than to guillemots with their more vertical dive angles and higher specific air volumes. Aerobic efficiencies (mechanical power output/aerobic power input) and COT may also be affected by thermoregulation costs and the potential for substitution of heat from the inefficiency of exercise to reduce costs of thermogenesis (Schmid et al., 1995; Lovvorn, 2006). Determining if small increases of swim speed in descending alcids can be explained in terms of COT will require detailed respirometry of work rates relative to mechanical costs at relevant water temperatures (Lovvorn, 2006).

In conclusion, as buoyancy declined during descent to 20 m depth, alcids decreased acceleration on the upstroke while LIPE maintained more equal distribution of acceleration between upstroke and downstroke. This pattern in alcids occurred despite variation in dive angle. The range of acceleration during strokes was much smaller for LIPE than alcids, which may reduce nonlinear increases in drag at higher instantaneous speeds (Lovvorn, 2001; Lovvorn and Liggins, 2002). This difference in stroke patterns, which corresponds to a proportionally greater mass of upstroke muscles in penguins than alcids, may result from constraints of aerial flight in alcids.

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