Stroke and glide of wing-propelled divers: deep diving seabirds adjust surge frequency to buoyancy change with depth

Yutaka Watanuki[1*]**, Yasuaki Niizuma**[2]**, Geir Wing Gabrielsen**[3]**, Katsufumi Sato**[4] **and Yasuhiko Naito**[4]

[1]*Laboratory of Animal Ecology, Graduate School of Agriculture, Hokkaido University, Kita-ku, Sapporo 060-8589, Japan*
[2]*Japan Society for Promotion of Science, Hokkaido National Fisheries Research Institute, Kushiro 085-0802, Japan*
[3]*The Norwegian Polar Institute, Hjalmar Johansensgt. 14, N-9296 Trømso, Norway*
[4]*National Institute of Polar Research, 1-9-10 Itabashi-ku, Tokyo 173-8515, Japan*

In order to increase locomotor efficiency, breath-holding divers are expected to adjust their forward thrusts in relation to changes of buoyancy with depth. Wing propulsion during deep diving by Brünnich's guillemots (*Uria lomvia*) was measured in the wild by high-speed (32 Hz) sampling of surge (tail-to-head) and heave (ventral-to-dorsal) accelerations with bird-borne data loggers. At the start of descent, the birds produced frequent surges (3.2 Hz) during both the upstroke and the downstroke against buoyancy to attain a mean speed of 1.2–1.8 m s^{-1} that was close to the expected optimal swim speed. As they descended deeper, the birds decreased the frequency of surges to 2.4 Hz, relaying only on the downstroke. During their ascent, they stopped stroking at 18 m depth, after which the swim speed increased to 2.3 m s^{-1}, possibly because of increasing buoyancy as air volumes expanded. This smooth change of surge frequency was achieved while maintaining a constant stroke duration (0.4–0.5 s), presumably allowing efficient muscle contraction.

Keywords: buoyancy; biomechanics; diving; guillemot; wing stroke

1. INTRODUCTION

Breath-holding divers experience changes in buoyant resistance because of the compression of air in their respiratory system, feathers or hair (Lovvorn & Jones 1991; Wilson *et al.* 1992). Since thrusting by wing or flipper requires more power than gliding or resting (Schmidt-Nielsen 1972; Williams *et al.* 2000), adjusting stroke thrust to the change of buoyant resistance is important for saving energy, and hence for prolonging underwater foraging time (Williams *et al.* 2000; Williams 2001). Muscle is presumed to have a maximum efficiency when contracting within a narrow range of speeds and loads (Goldspink 1977). Therefore, alternating stroking with gliding of variable duration while maintaining a constant contraction speed is the most cost-efficient method (Pennycuick 1996; Lovvorn *et al.* 1999; Lovvorn 2001). This pattern is described qualitatively in large diving mammals that have relatively small buoyancy (Williams *et al.* 2000; Nowacek *et al.* 2001).

Seabirds in the family Alcidae use their wings to fly in both air and water. Alcids experience greater buoyancy in the water since they have a 1.4 times greater air volume per mass than penguins (Wilson *et al.* 1992); hence they should need strong or frequent thrusts to descend in shallow water (Lovvorn *et al.* 1999). Unlike penguins, which swim steadily by producing lift during both upstrokes and downstrokes (Clarke & Bemis 1979; Bannasch 1995), alcids swim unsteadily, mainly by downstrokes (Rayner 1995). Alcids, however, dive longer than penguins and marine mammals relative to body mass (Boyd & Croxall 1996; Watanuki & Burger 1999). How this small (less than 1 kg) seabird adjusts thrust power to changes of buoyancy is key to its energy-saving mechanism (Lovvorn 2001).

Brünnich's guillemots (*Uria lomvia*, Alcidae, 1.0 kg mass) frequently dive deeper than 100 m (Croll *et al.* 1992). Their buoyancy is *ca.* 4.5 N at the water surface, and decreases with depth to zero at *ca.* 62 m as the air space is compressed following Boyle's law (Lovvorn *et al.* 1999). Observations of deep-diving animals are now possible by recording accelerations with data loggers attached to the animals (Nowacek *et al.* 2001; Yoda *et al.* 2001; Sato *et al.* 2002). We measured accelerations parallel (surge) and perpendicular (heave) to the body trunk of guillemots in the wild. We tested the theory that this small seabird adjusts its surge frequency smoothly by regulating stroke and glide in relation to the expected changes of buoyancy, while maintaining a constant stroke speed.

2. MATERIAL AND METHODS

(a) *Field study and data logger*

The study was carried out at Kongsfjorden colony, Ny-Ålesund, Svalbard, Norway, in July 2001. Parents brooding chicks (less than 1 day old) were captured using a 7 m noose pole. The data loggers (15 mm diameter, 60 mm length, 16 g mass (less than 2% of bird mass); M190-D2GT, Little Leonardo Ltd, Tokyo) were fitted on the centre of the lower back of three birds

*Author for correspondence (ywata@res.agr.hokudai.ac.jp).

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with quickset glue and cable ties. They were recaptured after 2–4 days deployment and the loggers were removed. The chicks of the instrumented birds remained healthy during deployment. No significant difference in trip duration was seen between birds with (170 min) and without loggers (128 min), though birds with loggers had a lower probability of returning with meals (24%) than those without loggers (66%; Watanuki *et al.* 2001). The Norwegian Animal Research Authority and Governor of Svalbard approved the field study.

The loggers recorded depth every second by pressure sensor (± 1 m accuracy; FPBS-82A, Fujikura), and acceleration along the perpendicular axes at 32 Hz by piezo accelerometer (ADXL202E, Analog device; see electronic Appendix A available on The Royal Society's Publications Web site). Loggers recorded tail-to-head (surge) and ventral-to-dorsal (heave) accelerations of birds BG13 and BG17 (figure 1*a*), and surge and right-to-left accelerations of bird BG09. The loggers were attached to the lower back of birds at an attachment angle α (figure 1*a*). α was estimated by the accelerations recorded when the birds were at the water surface and hence staid horizontally (see electronic Appendix A). Average heave accelerations recorded when birds were at the water surface were 9.7–9.8 m s^{-2}, indicating that the heave axis of data loggers was vertical to the bird's trunk (figure 1*a*).

A total of 414 dives were sampled. The maximum depth was 125 m, and 35% of the dives exceeded the depth of neutral buoyancy for this species. Our aim was to describe the wing strokes of birds diving to deep waters. Therefore, we sampled 35 dives deeper than 20 m that had clear flat bottom phases and ascent and descent phases with no abrupt changes of depth (10 from BG13, 21 from BG09 and 4 from BG17; figure 1*b*). This would minimize the possibility of including dives where the birds chased prey.

(b) *Dive angle*

The component of the gravity acceleration along the surge axis of the data logger (YaL; figure 1*b*) was given by removing the high-frequency component based on wing strokes from the surge acceleration by the low-pass filter (IFDL IGOR Pro v. 4, Wave Metrics; Tanaka *et al.* (2001); see electronic Appendix A). We added the logger attachment angle (α) to the logger axis angle (arcsine YaL) to give the angle of the bird body trunk to the horizontal (θ), which was defined as the dive angle (figure 1*a*).

Swim speed (v) was estimated from the dive angle (θ) and depth change rate (r) as $v = r/\sin\theta$, assuming that the birds moved ahead as the direction of tail-to-head axis. At the bottom phase, the swim speed could not be estimated because of the small dive angle and small depth change rate. Anomalous swim speeds greater than 2.5 m s^{-1}, possibly resulting from an error in the calculated dive angle (θ), were excluded from the analyses since penguins cruise at 1.7–2.0 m s^{-1} and rarely exceed 2.5 m s^{-1} (Wilson *et al.* 1996; Ropert-Coudert *et al.* 2000).

(c) *Surge and heave*

The Atlantic puffin (*Fratercula arctica*, Alcidae) accelerates the body forward and upward during the downstroke, and downward during the upstroke (Johansson & Aldrin 2002). Thus, wing stroke and thrust can be estimated based on the high-frequency components of heave and surge accelerations of the body, respectively. We inferred that the upstroke of the guillemots started at the middle of the peak and the valley of heave acceleration, and ended at the middle of the valley and the next
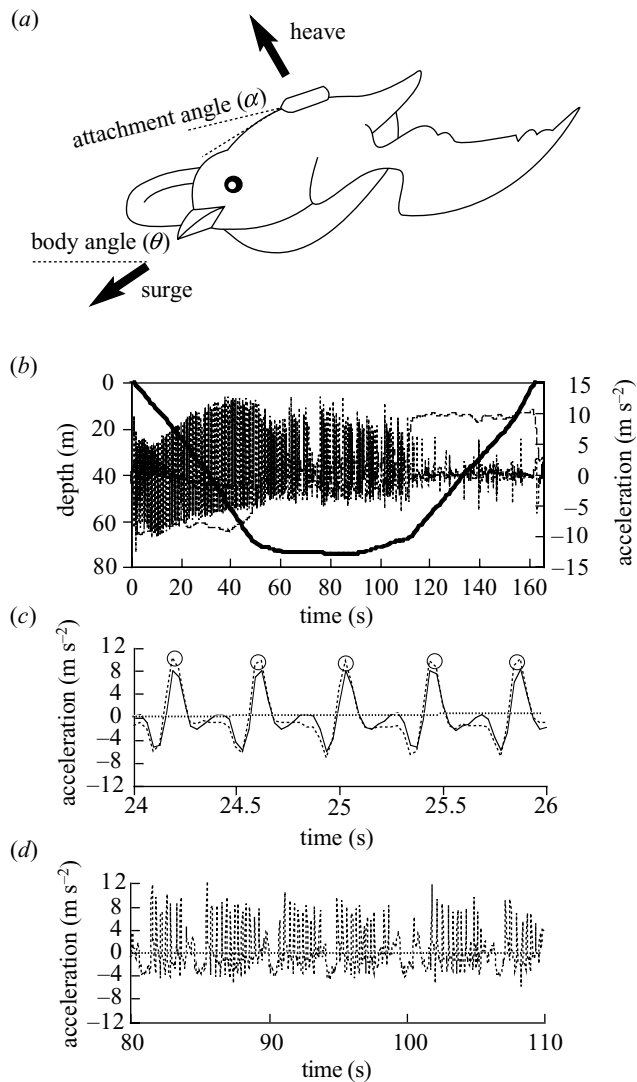
Figure 1. Measurement of accelerations by bird-borne data loggers. (*a*) Tail-to-head (surge) and ventral-to-dorsal (heave) accelerations were sampled at 32 Hz by data loggers. (*b*) Depth (thick line), the gravity-based surge acceleration of the data logger (YaL: thick broken line) where the high-frequency component based on wing strokes was removed, and the high-frequency component of surge acceleration (YaH: thin broken line) where YaL was subtracted, in a sample dive of bird BG13. Dive angle (θ) was given by adding the logger attachment angle (α) to the arcsine of YaL. (*c*) Enlarged wing-stroke-based surge of the data logger (YaH: broken line) and that of the bird's body where the logger attachment angle (α) was corrected (YGH: line). Peaks determined by the IGOR macro are shown by circles. (*d*) Wing-stroke-based surge (YaH) of the data logger in the bottom phase. Clear alternations of the glides and series of surges were observed.

peak as observed in this puffin (figure 2*a–d*). A single stroke includes the pair of an upstroke and a downstroke.

Wing-stroke-based surge (YaH in figure 1) and heave (XaH) of the data loggers were given by subtracting the components of gravity from recorded surge and heave accelerations. Heave (XGH) and surge (YGH) of the birds' body trunk were given by correcting the logger attachment angle (see electronic Appendix A) for 14 dives from BG13 and BG17. YaH explained YGH (figure 1*c*) well in BG13 ($r^2 = 0.88$, $p < 0.001$, YGH = 0.743 × YaH − 0.004). Therefore, to include data from bird BG09, we
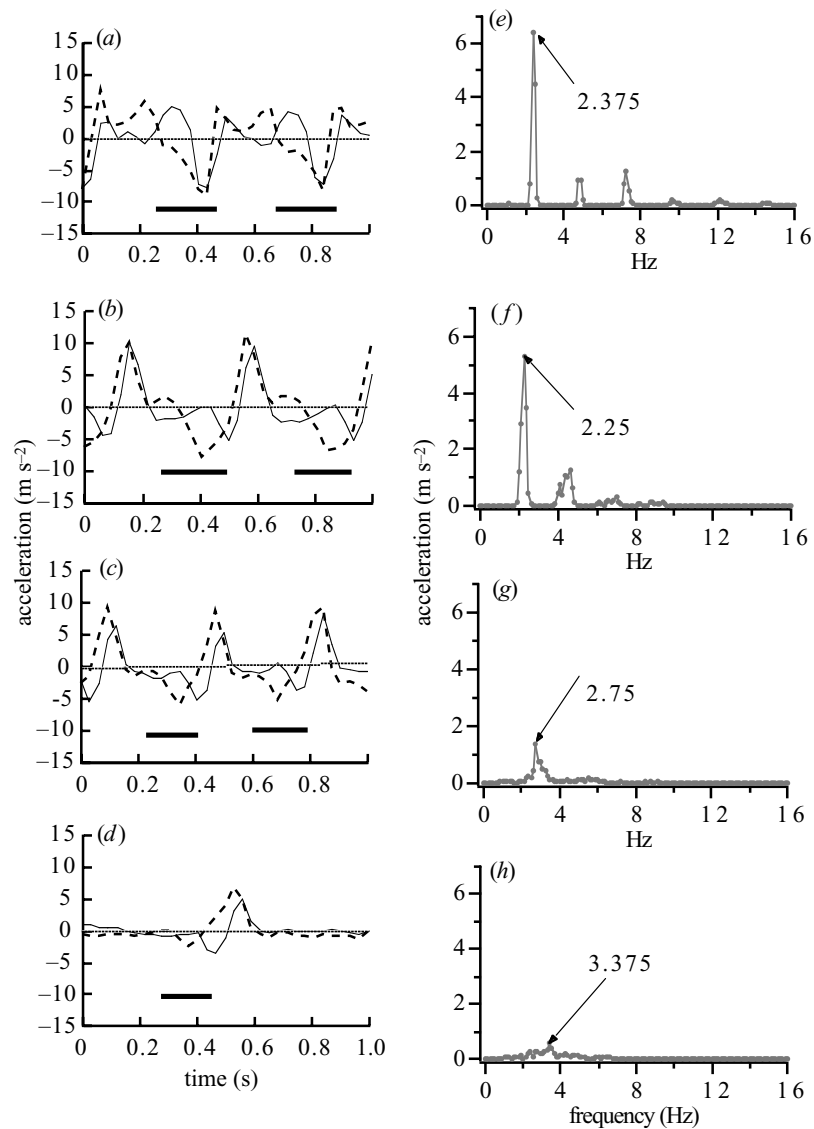
Figure 2. Changes of surge and heave accelerations and frequency of wing stroke given by power spectral density of heave. (*a*–*d*) Examples of the surge (YGH: line) and heave (XGH: broken line) accelerations of the bird's body at each phase of a dive by bird BG13. Data during 20 s intervals were taken from phases of (*a*) shallow descent (descent below 5 m depth, from 6 to 33 m on average); (*b*) deep descent (descent before the start of bottom, from 53 to 84 m on average); (*c*) bottom (early part of bottom, from 85 m to 86 m on average); and (*d*) early part of ascent (from 84 to 61 m on average). A time of 20 s was chosen because it is the minimum time interval during which the power spectral density could be calculated. The horizontal bar indicates the upstroke (see the text). (*e*–*h*) Examples of power spectral density of the heaves in each phase: (*e*) shallow descent; (*f*) deep descent; (*g*) bottom; (*h*) ascent. The numerals indicate the dominant frequencies.

used YaH to estimate surge frequency. The peaks were apparent in surge (YaH), which could be empirically defined if there were more than 0.8 m s^{-2} changes at 1/32 s intervals. The number of peaks per second was counted by the IGOR macro (figure 1*c*) in order to determine surge frequency. As the valley was apparent in heaves (figure 2*a*–*d*), the number of valleys per second was similarly defined as wing stroke frequency during each 20 s interval for shallow descent, deep descent, bottom and ascent (figure 2).

Maximum and minimum heave accelerations were assumed to be maximum accelerations during the downstroke and upstroke, respectively. When the birds change gliding duration after each stroke, stroke duration is overestimated if it is defined as the reciprocal of the wing stroke frequency. Therefore, we defined the stroke duration as the reciprocal of the heave (XGH) frequency giving dominant power spectral density calculated by the PSD macro in IGOR Pro v. 4 (figure 2*e*–*h*).

(d) Statistics

Differences in surge and wing stroke frequencies, maximum stroke acceleration and stroke duration averaged over each phase among the descent, bottom and ascent phases were examined by repeated-measures analysis of variance (ANOVA) where the bird was the factor and phase was the repeated measure. A Bonferroni–Dunn post hoc test was applied if the phase effects were significant. Effects of the bottom depth on dive angle and surge frequency at the bottom were examined using analysis of covariance (ANCOVA) with the bird as the factor and bottom depth as the covariate. If depth effects were significant, Spearman's rank correlation coefficient (r_S) was calculated to investigate the relative magnitude of effects. Differences in frequency values were examined using the χ^2-test. Statistical analyses were carried out using the STAT VIEW program (SAS Institute Inc.). We used $p = 0.05$ as the significant level. All the values are shown as average ± s.d. (sample size), unless otherwise described.
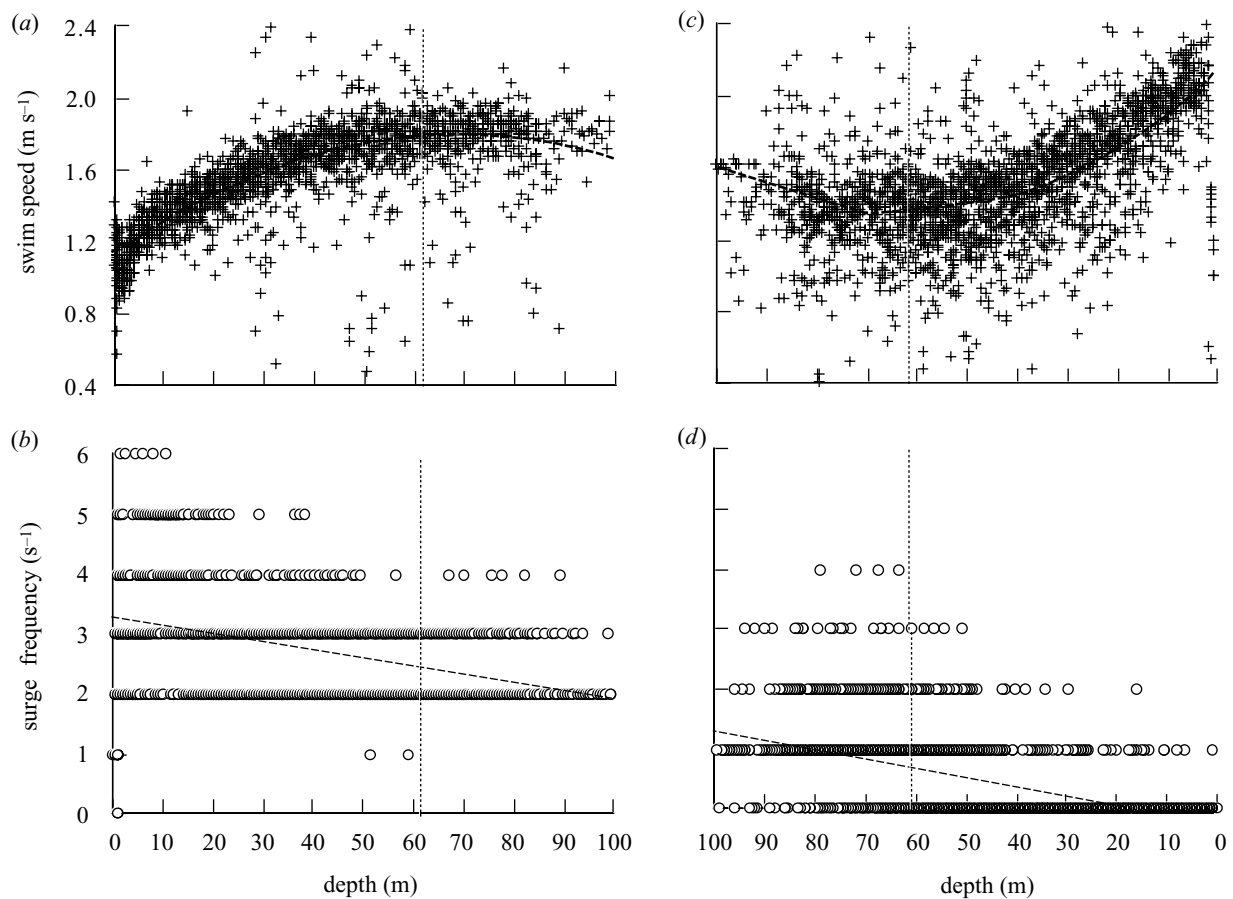
Figure 3. Changes in swim speed and surge frequency with depth during the (a,b) descent and (c,d) ascent phases based on 35 deep and flat-bottomed dives from three birds. Data of 1 s intervals are plotted. Curvilinear regressions of swimming speed (v) versus depth (D) for the descent phase ($r^2 = 0.56$, $p < 0.01$, $v = 1.122 + 0.019 \times D - 1.387 \times 10^{-4} \times D^2$) and the ascent phase ($r^2 = 0.36$, $p < 0.01$, $v = 2.083 - 0.023 \times D + 1.774 \times 10^{-4} \times D^2$) and linear regressions of surge frequency (FF) versus depth (D) for the descent phase ($r^2 = 0.16$, $p < 0.01$, $FF = 3.265 - 0.013 \times D$) and ascent phases ($r^2 = 0.32$, $p < 0.01$, $FF = -0.289 + 0.016 \times D$) were significant. Expected neutral buoyancy depth (Lovvorn *et al.* 1999) is indicated by the broken line.

3. RESULTS

(a) *Surge frequency and swim speed in descent and ascent*

The distribution of depth change rate in 1 s intervals for 35 sample dives showed three clear modes: a descent phase (greater than 0.6 m s^{-1}), a bottom phase (0.4 to -0.4 m s^{-1}) and an ascent phase (less than -0.6 m s^{-1}). The guillemots descended to depths of $81 \pm 15 \text{ m}$ ($n = 35$ dives) at an angle relative to the horizontal of $79 \pm 6°$ and a descent rate of $1.5 \pm 0.1 \text{ m s}^{-1}$. They swam horizontally during the bottom phase. They ascended at an angle of $-56 \pm 7°$ at an ascent rate of 1.2 m s^{-1}. During descent the birds decreased surge frequency linearly with depth but increased swim speed to $1.6–1.8 \text{ m s}^{-1}$ (figure 3). During the early part of the ascent the birds made a few surges and swam at a speed of $1.2–1.5 \text{ m s}^{-1}$ and they decreased surge frequency as they ascended. The linear regression of surge frequency on depth indicated that the birds stopped surging at 18 m while ascending but that they increased their swim speed to 2.3 m s^{-1} near the surface by gliding with the buoyancy (figure 3).

The dive angle ($F_{1,29} = 14.02$, $p < 0.001$, ANCOVA) and descent rate ($F_{1,29} = 16.60$, $p < 0.001$) in the early part of descent (5–15 m depth) depended on the bottom depth. The birds descended at a steeper angle in the early

part of their descent if they were diving to a greater depth ($r_S = 0.35$, $p < 0.05$, $n = 35$ dives); this steeper angle increased the descent rate in relation to bottom depth ($r_S = 0.43$, $p < 0.05$). The effects of bottom depth on swim speed ($F_{1,29} = 3.58$, $p = 0.06$, ANCOVA) and those on stroke frequency ($F_{1,29} = 2.92$, $p = 0.10$) were not significant.

(b) *Surge in the bottom phase*

During the bottom phase, the birds glided for $1.5 \pm 0.9 \text{ s}$ ($n = 56$ interval) between bouts of stroking that lasted $6.2 \pm 4.8 \text{ s}$ ($n = 59$ interval) in some dives (figure 1d). The dives were categorized into the 'continuous-surge' bottom type during which the birds stroked in more than 90% of 1 s intervals, the 'surge/glide' bottom type during which the bird did not stroke in 10–60% of 1 s intervals, and the 'glide' bottom type during which the birds did not stroke in more than 60% of 1 s intervals. The continuous-surge bottom type was more common (19 of 21 dives) when the average bottom depth was more than 80 m ($91 \pm 11 \text{ m}$) than when the average bottom depth was less than 80 m (3 of 14 dives, $67 \pm 6 \text{ m}$; $\chi^2 = 17.18$, d.f. = 1, $p < 0.001$). Average depth of bottom phase affected average surge frequency during the bottom phase ($F_{1,29} = 21.50$, $p < 0.001$), and the average surge

Table 1. Number of forward surges and wing strokes, duration of strokes, and maximum downstroke and upstroke accelerations recorded during 20 s of shallow descent (below 5 m), deep descent (to bottom phase), bottom, and early ascent phases sampled from 14 dives of two guillemots.

(Mean and s.d. are shown. Differences between phases are tested with repeated-measures ANOVA.)

phase	forward surge frequency (Hz)	wing stroke frequency (Hz)	stroke duration (s)[a]	maximum downstroke acceleration (m s^{-2})[a]	maximum upstroke acceleration (m s^{-2})[a]
shallow descent	3.22 ± 0.44	2.50 ± 0.10	0.40 ± 0.01	10.3 ± 1.4	12.8 ± 2.0
deep descent	2.41 ± 0.31	2.25 ± 0.10	0.43 ± 0.03	11.0 ± 1.6	7.3 ± 0.5
bottom	2.02 ± 0.83	2.17 ± 0.65	0.38 ± 0.06	9.5 ± 2.2	6.4 ± 0.8
ascent	0.79 ± 0.42	0.87 ± 0.44	0.46 ± 0.16	8.3 ± 1.0	4.6 ± 1.8
birds	$F = 2.1$, n.s.	$F = 5.0$, $p < 0.05$	$F = 2.4$, n.s.	$F = 45.8$, $p < 0.001$	$F = 6.7$, $p < 0.05$
phase	$F = 75.0$, $p < 0.001$	$F = 73.7$, $p < 0.001$	$F = 1.9$, n.s.	$F = 32.8$, $p < 0.001$	$F = 102.4$, $p < 0.001$

[a] Sample size was reduced to 13 as one bird did not make any wing strokes during ascent in one dive to only 57 m.

frequency was greater for deeper dives ($r_S = 0.63$, $p < 0.001$, $n = 35$ dives).

(c) *Wing stroke and surge*

The surge frequency was higher during the shallow descent phase than during the deep descent and bottom phases, while the stroke frequency was similar among these phases (table 1; post hoc test). This was achieved by surging forward during both the upstroke and downstroke during the shallow descent phase (figure 2a–d). The birds decreased the upstroke-based surge in the deep descent phase, and made surges only during downstrokes in the bottom and early ascent phases. The birds made 33% and 7% more surges than wing strokes in the shallow ($F_{1,12} = 40.2$, $p < 0.001$, repeated-measures ANOVA) and deep descent phases ($F_{1,12} = 25.5$, $p < 0.001$), respectively, while they made 7% and 10% more wing strokes than surges in the bottom ($F_{1,12} = 7.8$, $p < 0.05$) and early ascent phases ($F_{1,12} = 7.6$, $p < 0.05$), respectively.

Maximum upstroke acceleration in the shallow descent phase was greater than that in the deep descent and bottom phases, while maximum downstroke accelerations did not differ among these phases (table 1).

During the early ascent, the birds surged and stroked at the smallest frequency by making the weakest downstrokes and upstrokes (table 1). However, there was no significant difference in the duration of individual strokes among all phases (table 1), indicating that the birds changed glide duration after each stroke.

4. DISCUSSION

The guillemots in the field showed higher surge frequencies during descent in shallow water, in order to overcome the expected high buoyancy, than during descent in deep water and ascent (figure 3). The birds made more downstroke-based surges as they swam horizontally during deep (91 m on average) than shallow (67 m on average) bottom phases. This indicates that they might make frequent upward thrusts to stay in deep water by compensating for a possibly reduced buoyancy, while they might stay easily at depths close to that of neutral buoyancy (62 m; Lovvorn et al. 1999). However, we could not rule out the possibility that the birds might make frequent forward thrusts for chasing prey over deep bottoms.

We also found that this regulation of surge frequency was achieved smoothly while keeping stroke duration nearly constant (table 1), which may allow the muscles to contract at a range of speeds and loads that optimize muscle efficiency (Pennycuick 1996; Lovvorn et al. 1999; Lovvorn 2001). The guillemots changed their surge frequency by changing glide duration after each stroke during the descent and ascent phases (figure 2). During descent, they might have to stroke continuously in order to maintain speed against profile drag and buoyancy (Lovvorn et al. 1999). During the bottom phase of an average of 67 m that is close to their neutral buoyancy depth, the birds alternated gliding with bouts of stroking while swimming horizontally (figure 1d). This pattern is similar to bounding or undulating flight in birds, which is believed to save energy by reducing profile drag while wings are folded against the body, or by generating lift while the wings are outstretched (Rayner 1985; Alexander 1992).

Alcids have been characterized as generating thrust mainly during the downstroke since they have proportionally greater major pectoral muscles than do penguins (Rayner 1995). Recently, the generation of thrust during the upstroke has been noted in horizontally swimming alcids in tanks (Lovvorn 2001; Johansson & Aldrin 2002). The present study showed that the guillemots in the wild surged during both the upstroke and downstroke when they were descending vertically in shallow water (figure 2a; table 1). This could be a mechanism to increase surge frequency against buoyancy in keeping stroke duration constant. The highest upstroke acceleration in the shallow descent phase (table 1) may contribute to the production of forward thrust during the upstroke. Diving guillemots might also change the attack angle of the wings in order to produce more thrust during the upstroke as suggested in other alcids (Lovvorn 2001; Johansson & Aldrin 2002).

The diving behaviour in seabirds is regulated to stay longer at foraging depth by minimizing energy expenditure by keeping optimal swim speed (Lovvorn et al. 1999) and regulating the dive angle (Wilson et al. 1996). The guillemots stopped their wing strokes but increased swimming speed while ascending in shallow water because of increasing buoyancy (less than 18 m, which was close to an expected depth when this species stops wing strokes, 19 m; Lovvorn et al. (1999); figure 3). This passive ascent

could be an energy-saving strategy (Williams *et al.* 2000; Sato *et al.* 2002). Except for this passive ascent, our birds maintained their swimming speed in a range of 1.2–1.8 m s^{-1} (figure 3), which is similar to the speed of 1.2–1.5 m s^{-1} that minimizes the drag coefficient in this species (Lovvorn *et al.* 1999). Presumably, in order to reach this optimal speed quickly, our birds exhibited their highest surge frequencies during the start of descent (table 1). The guillemots also regulated dive angle. They dived at a steeper angle in the early part of their descent when they made deeper dives. This indicates that they anticipated their dive depth before they dived, as in the manner of penguins (Wilson *et al.* 1996; Sato *et al.* 2002), thereby extending the time at the bottom phase relative to the time spent descending for the same dive duration.

In conclusion, Brünnich's guillemots changed their surge frequency with depth, resulting in an expected optimal swim speed. This adjustment was achieved while maintaining a constant stroke duration, presumably allowing efficient muscle contraction.

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