Regulation of stroke and glide in a foot-propelled avian diver

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Summary

Bottom-feeding, breath-hold divers would be expected to minimize transit time between the surface and foraging depth, thus maximizing the opportunities for prey capture during the bottom phase of the dive. To achieve this they can potentially adjust a variety of dive parameters, including dive angle and swim speed. However, because of predictable changes in buoyancy with depth, individuals would also be expected to adjust dive behavior according to dive depth. To test these predictions we deployed miniature, dorsally attached data-loggers that recorded surge and heave accelerations at 64 Hz to obtain the first detailed measurements of a foot-propelled diving bird, the European shag *Phalacrocorax aristotelis*, in the wild. The results were used to investigate biomechanical changes during the descent, ascent and bottom phases for dives varying between 7 m and 43 m deep. Shags descended and ascended almost vertically (60–90° relative to the sea surface). During descent, swim speed varied between 1.2–1.8 m s^{-1} and the frequency of the foot stroke used for propulsion decreased significantly with depth, mainly due to a fivefold increase in the duration of the glide between strokes. Birds appeared to maintain the duration and the maximum strength of power stroke and thus optimize muscle contraction efficiency.

Key words: buoyancy, foot-stroke, dive, shag, *Phalacrocorax aristotelis*, data-logger, biomechanics.

Introduction

In addition to the loss of heat to cold water and the limitation of oxygen stores, diving seabirds are faced with a number of other physical difficulties (Kooyman, 1987; Butler and Jones, 1997; Lovvorn, 2001). Firstly, they experience a large buoyant resistance due to the presence of air trapped in the plumage and air passages, which decreases markedly as birds descend deeper because the air is compressed (Lovvorn et al., 1991a; Wilson et al., 1992a); secondly, they have to expend mechanical power to compensate for the drag as they travel through the water (Lovvorn, 2001); and thirdly, muscle is assumed to operate at maximum efficiency when contracting over a narrow range of speeds and loads (Goldspink, 1977). Understanding how buoyant species such as seabirds dive under these conditions is a key question for ecophysiologists (e.g. Wilson et al., 1992a; Butler and Jones, 1997; Lovvorn, 2001). Theoretical and laboratory studies predict that birds should adjust the frequency of stroke to compensate for changes in resistance due to changes in buoyancy with depth, but that swim speed and the duration or amplitude of the power stroke should remain constant (Pennycuick, 1996; Lovvorn et al., 1999; Lovvorn, 2001; Taylor et al., 2003). However, there

are few empirical data from free-ranging birds diving under natural conditions available to test these predictions.

With the exception of penguins that swim by producing lift during both upstrokes and downstrokes (Bannasch, 1995), diving seabirds generate forward thrust mainly by the contraction of major muscles in order to make a propulsive downstroke with their wings or push their webbed feet backwards (hereafter referred to as the power stroke; Alexander, 1992; Rayner, 1995; Riback et al., 2004). Birds decelerate (hereafter glide) either during the upstroke of the wings or during the forward movement of the feet. By alternating the power stroke and the glide, seabirds have been shown to swim within a range of speeds (Lovvorn, 2001). However, most previous studies have been carried out using birds swimming horizontally in shallow experimental tanks, where they experience constant and high buoyancy. To understand fully the regulation of power stroke and glide, it is essential to collect data on birds diving vertically to depths over which they will experience large changes in buoyancy. The recent development of micro data-loggers has enabled wing propulsion of small seabirds to be measured in the wild

using high frequency sampling of acceleration of the body (Watanuki et al., 2003). To date, however, similar measurements have not been made for foot-propelled divers.

Shags and cormorants (Phalacrocoracidae) are foot-propelled divers. Typically they descend directly (descent phase) to a given depth (from 10 m to >100 m), where they remain foraging (bottom phase) before ascending directly (ascent phase) to the surface (Croxall et al., 1991; Watanuki et al., 1996; Grémillet et al., 1998). To maximize feeding time, bottom-feeders should minimize transit time, and hence descend and ascend vertically (Houston and Carbone, 1992; Hansen and Ricklefs, 2004). Although shags and cormorants are less buoyant than many other diving birds, in general, they are positively buoyant over the range of depths used for foraging (Wilson et al., 1992a; Husler, 1992; Riback et al., 2004). Shags and cormorants make forward thrusts by pushing both of their webbed feet backwards simultaneously, i.e. a power stroke (Schmid et al., 1995). Hence, they are expected to make a forward thrust only during a power stroke.

To further understand how power stroke and glide are regulated to achieve efficient diving in foot-propelled divers, we deployed bird-borne miniaturised data-loggers on free-ranging European shags *Phalacrocorax aristotelis* (hereafter referred to as shags). The loggers enabled us to determine the body angle and the characteristics of foot strokes by recording heave (ventral-to-dorsal) and surge (tail-to-head) accelerations of the bird's body at 64 Hz. We used these data to test three hypotheses: (1) shags descend vertically; (2) shags use a range of swim speeds during descent; and (3) during dive descent shags decrease the frequency of the power stroke by increasing the duration of the glide. We also describe the body angle and the stroke pattern during the bottom and ascent phases.

Materials and methods

Study site and species

Fieldwork was carried out on the Isle of May, off the coast of southeast Scotland, between 9 and 22 June 2003. During the breeding season shags at this colony typically forage benthically at depths of between 20 and 40 m (Wanless et al., 1991a,b). Fourteen birds, with broods of three small- to medium-sized chicks, were caught at the nest using a hook attached to a 5 m bamboo pole. The birds were weighed using a pesola spring balance to the nearest 5 g and sexed from vocalization (males are vocal, females are mute) and size (males are significantly larger and heavier than females; Snow, 1963).

A data-logger (16 mm in diameter, 60 mm long, mass in air 16 g; M190-D2GT, Little Leonardo Ltd, Tokyo, Japan) was attached in the middle of the lower back of each bird (Fig. 1). To keep the longitudinal axis of the logger parallel to the bird's head-to-tail axis, loggers were attached using two plastic cable ties and waterproof adhesive tape to a piece of plastic netting (3 cm×5 cm) glued among the feathers with a fast-setting glue (Loctite 401). The attachment process took less than 10 min, after which birds were released; 12 returned directly to the nest,
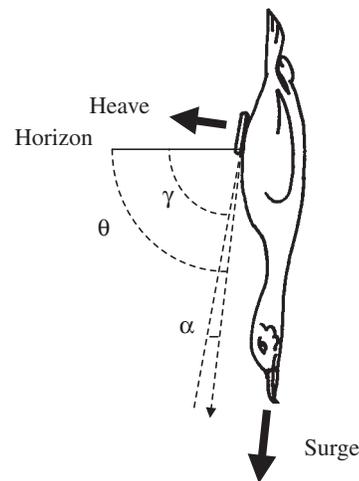

Fig. 1. Attachment of data-logger on bird's back. Diagram shows angle of Y (surge) axis of logger to horizon (γ), that of body axis to horizon (θ) defined as body angle (negative as the bird descends) and logger attachment angle (α).

two initially went onto the sea to wash and preen but were still back on the nest within 10 min. The nests of birds with loggers were checked each morning and evening and attendance of the pair and the brood size recorded on each visit. Birds were recaptured within 3 days of logger deployment and the devices removed.

Data-logger

The loggers had a 16 MB EEPROM memory and recorded depth with a pressure sensor (±1 m accuracy, FPBS-82A, Fujikura, Tokyo, Japan) every second, and acceleration along the perpendicular axes with a capacitive accelerometer (ADXL202E, Analog device, Norwood, MA, USA) at 64 Hz for approximately 24 h.

To calibrate the recorded acceleration values, gravity accelerations (9.8 m s^{-2}) were recorded by each logger set at angles of 90°, 0° and –90°, respectively, to the horizon at room temperature. Temperature effects of between 7–20° are <4% and do not require corrections (Watanuki et al., 2003). To measure the attachment angles of each logger along the bird's body axis (α, Fig. 1), we arbitrarily selected ten samples of 4 s duration of surge acceleration when the bird was on the surface between dives and the body axis should have been horizontal (see appendix in Watanuki et al., 2003). The average over 4 s was within 96–102% of the overall average for each bird, indicating that the attachment angle was stable during the deployment. The estimated attachment angle (α) varied between –7° and 9° (Table 1).

Body angle, swim speed and stroke

For ten of the shags data-loggers were used to record surge and heave by aligning the vertical axis of the logger parallel to the bird's ventral-to-dorsal axis (Table 1). The remaining four birds were used to check for evidence of sway (right–left) acceleration by aligning the vertical axis of the data-loggers

Table 1. *Sex of sample birds, body mass at capture, direction of* x-*axis of loggers to bird's back, attachment angle of loggers (α) and angle of* x-*axis to horizontal axis of the body (β) and dive depth and duration for each bird*

Bird sex	Body mass (g)	*x* axis	α (degrees)	β (degrees)	Number of dives	Median depth (m)	Median duration (s)	Maximum depth (m)	Maximum duration (s)
Sg1M	1730	Heave	8	90	50	40.1	97	43.4	150
Sg2F	1520	Heave	1	90	91	30.0	71	37.3	93
Sg2M	1840	Heave	0	90	102	26.9	64	32.4	103
Sg3F	1500	Heave	9	48	141	32.0	69	35.8	89
Sg4F	1550	Heave	6	90	118	22.7	61	30.9	99
Sg5M	1820	Sway	−7	11	59	40.6	81	49.7	103
Sg6M	1910	Heave	4	90	160	10.2	43	41.8	98
Sg7F	1600	Sway	0	−18	120	25.0	62	30.4	86
Sg7M	1860	Sway	0	33	88	18.9	60	48.2	117
Sg8F	1780	Heave	7	68	66	43.3	93	47.8	114
Sg9F	1750	Heave	5	75	119	32.3	78	42.6	101
Sg9M	2050	Sway	5	8	85	39.9	86	48.3	112
Sg10F	1690	Heave	5	63	86	32.5	77	51.2	110
Sg10M	2060	Heave	2	66	122	24.5	60	46.9	100

F, female; M, male.

parallel to the bird's left–right axis (Yoda et al., 2001). There was no evidence of any significant change in sway acceleration during descent or ascent, indicating that birds did not produce accelerations around the yaw or roll axes. Total acceleration recorded by the loggers could therefore be separated into that due to gravity and that due to body movement. The high frequency component (YH, Fig. 2C) of total surge acceleration (YG, thin line in Fig. 2A) is caused by the foot stroke while the low frequency component (YL, thick line in Fig. 2B) is the gravity component along the surge axis of the data-logger. Hence YL can be converted to the angle of the data-logger relative to the horizon (γ). YL was obtained by removing the high frequency component with a filter.

To select an appropriate filter band, we filtered the total surge (YG) or total heave (XG) by the two-band low-pass filter where the end of the first band and the start of the second band were 0.1 and 0.5 Hz, 1 and 1.5 Hz and 2 and 3 Hz, respectively. The first band is a pass band and the second band is a stop band. Thus the filter passes frequencies smaller than the first band, allowing transition band between the first and second band (IFDL Igor Pro, WaveMetrics 1998, Portland, OR, USA; see also Tanaka et al., 2001). Foot-stroke based surge (YH) and heave (XH) of the data-loggers were obtained by subtracting the components of gravity (YL or XL) from recorded total surge (YG) and heave (XG) accelerations, respectively (Fig. 2). High frequency components of surge and heave obtained using the 1/1.5 Hz and 2/3 Hz two-band low-pass filters were almost identical during the start of the descent and bottom phases (Fig. 3A,C). With a 0.1/0.5 Hz filter, the very rapid change of body angle, which occurred at the start of dives, could be confounded by surge and not detected (Fig. 3A). In the middle of descent, the strokes were confounded as body angle changes with a 2/3 Hz filter (Fig. 3B). Therefore, we used a 1/1.5 Hz two-band low-pass filter that allowed us to analyze the rapid body angle change at the start of dives but minimized the risk of misidentifying the

low-frequency body angle change as stroke. During the passive ascent phase, where no power strokes or rapid body angle changes were observed, recorded surge was almost identical to 1/1.5 Hz low-pass filtered surge, also indicating that this filter was appropriate for estimating body angle.

The angle of the logger axis relative to the horizon (γ) was the arcsine YL (Fig. 1). Logger attachment angle (α) was added to the logger axis angle (γ) to give the angle of the bird's body axis to the horizon (θ), defined as the body angle (Sato et al., 2003). Our aim was to estimate the angle of dives (angle of incidence) based on body angle. To further minimize the effects of stroke on body angle, we used a 1 s average (average of 64 samples of body angle between 0.5 s before and after each second where the depth was sampled) as an estimate of body angle for each second. We then assumed that dive angle approximated to body angle.

Swim speed (V in m s^{-1}) was estimated as $V=R/\sin\theta$ for each second, where R was vertical depth change rate (m s^{-1}) and θ was body angle. Thus, we could not estimate instantaneous swim speed but rather the average value over a 1 s interval. Swim speed was not estimated during the bottom phase because of the small depth change rate and shallow body angle. Swim speeds previously estimated for a variety of seabird species indicate that individuals typically cruise at between 1.5 and 2.0 m s^{-1} and rarely exceed 2.5 m s^{-1} (e.g. Schmid et al., 1995; Wilson et al., 1996; Ropert-Coudert et al., 2000). Thus, in our analyses we assumed that swim speeds greater than 2.5 m s^{-1} (N=113 records, 3% of cases excluding those in the bottom phase) were due to errors in calculating body angle, and such records were excluded from the dataset.

Heave and surge of the bird's body were given by correcting the logger attachment angle (α) as follows:

$$\text{Heave} = XH\cos\alpha + YH\sin\alpha ,$$

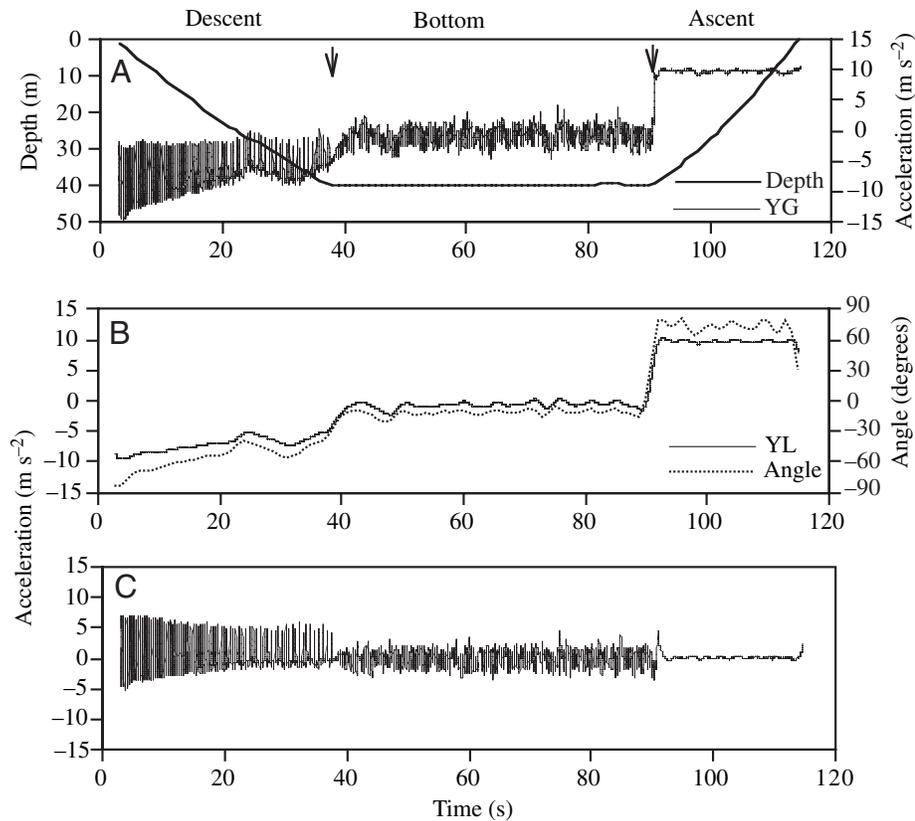$$\text{Surge} = YH\cos\alpha - XH\sin\alpha ,$$

Fig. 2. Data from a male bird dive. (A) Diving behavior and total surge acceleration (YG), (B) the low frequency component of surge (YL) that was given by filtering total surge (YG) using a two-band low-pass filter, and the body angle (θ=arcsineYL+logger attachment angle α) and (C) the high frequency component of surge (YH) that was given by subtracting the low frequency component of surge (YL) from total surge (YG).

where XH and YH are the high frequency components of heave and surge, respectively.

In cormorant species the power stroke is generated by sweeping the webbed feet backwards and upward to make drag- and lift-based forward thrust (Johansson and Norberg, 2003). In great cormorants *Phalacrocorax carbo* swimming horizontally in shallow water, the body is accelerated downward and forward during the power stroke of the feet and decelerated during the glide or recovery phase (Riback et al., 2004). For shags we also found that when the body accelerated downwards, it simultaneously accelerated forwards (Fig. 3A,B). Hence, we classified power stroke and glide as, respectively, negative and positive heave acceleration of the body (Fig. 3). Peaks were apparent in surge, which could be empirically defined if there were more than 0.16 m s^{-2} changes at 1/64 s intervals (see Watanuki et al., 2003) (Fig. 3A,B). The number of peaks of surge per second, counted by a Macro program on Igor (Tanaka et al., 1999) was defined as the frequency of thrust.

Sample dives and analyses

Data from nine of the 14 birds could be used to measure acceleration. Data from six individuals (three males and three

females) carrying data-loggers attached so as to record the heave-axis gave surge and heave acceleration directly since the loggers were almost vertical (>75°; Table 1) to the body axis of the birds. For the other three individuals (including two for which sway rather than heave was measured), we could only estimate uncorrected surge acceleration since the attachment angle (α) (see Fig. 1) was <2° and the heave or sway axis of the loggers was not vertical to the body axis (Table 1). From these nine birds, we sampled 100 dives between 7 and 43 m deep that showed a clearly defined bottom phase and no rapid changes of body angle or acceleration during descent and ascent.

We ran separate statistical analyses on the descent, ascent and bottom phases. For the descent and ascent phases, we carried out separate Restricted Maximum Likelihood (REML; Patterson and Thompson, 1971) analyses on body angle, frequency of thrust and swim speed, with the exception of frequency of thrust during ascent, since negligible thrust takes place during this phase and so no analyses were necessary (see Results). For each analysis, we included individual as a random effect, and instantaneous (i.e. current) depth (referred to in the results as 'depth') as a covariate. Previous studies have shown that diving seabirds may change body angle and swim speed according to the bottom or maximum depth to which an individual dives (Wilson et al., 1996; Sato et al., 2002; Watanuki et al., 2003). We therefore also included mean bottom depth as a covariate in the analyses. An interaction term between current depth and mean bottom depth was also included. For the bottom phase, we carried out analyses on body angle and frequency of thrust only. Since instantaneous depth and mean bottom depth are almost identical during the bottom phase, only the former was included in the analyses. In addition, there were consistent differences in bottom depth between individuals, resulting in the REML analyses not producing robust results. Therefore, we pooled data for all individuals and used linear regression analyses with ANOVA. In total, three analyses were carried out on the descent phase, two on the ascent phase and two on the bottom phase.

To analyze the stroke pattern during descent further, we sampled 17 'deep dives' (>40 m) from three birds for which surge and heave were measured. We sampled heave and surge acceleration over 1 s intervals at depths of 1 m, 2 m, 5 m, 10 m, and at 5 m intervals thereafter to 35 m. In each 1 s sample, there were between one and three strokes from which we selected one at random. The duration of the power stroke and glide, and maximum positive heave and surge acceleration
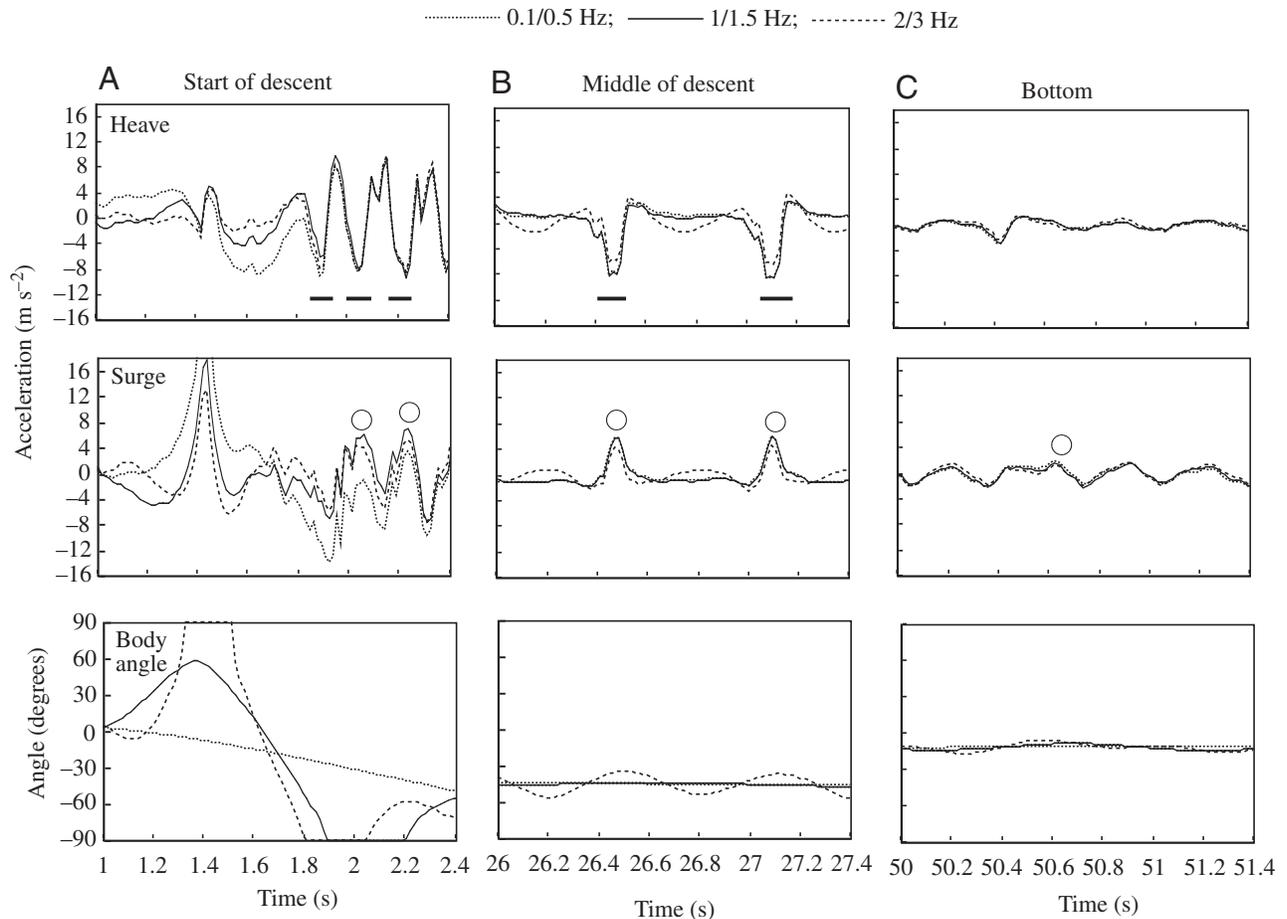
Fig. 3. Enlarged records of acceleration and body angle during phases of the same dive as in Fig. 1. (A) High frequency component of heave (XH: foot stroke), that of surge (YH: forward thrust) and body angle at the start (0–1 m depth) and, (B) middle of descent phase (28–30 m depth) and (C) those at the bottom phase (40 m depth). The high frequency components were obtained using the three types of low-pass filter, where the end of the first band/the start of the second band were 0.1/0.5 Hz, 1/1.5 Hz and 2/3 Hz, and shown by different types of lines. Thick horizontal bars in heave show power strokes. Circles in the figures for high frequency component of surge indicate forward thrusts (see the text for definition).

were measured on the print out of the data. The sum of the duration of the power stroke (the period when the heave was negative) and the duration of the glide (the period when the heave was positive) was defined as the stroke cycle (Fig. 3A,B), and the reciprocal of the stroke cycle as the frequency of the power stroke. Effects of current depth on the frequency of power stroke, power stroke duration, glide duration, maximum heave acceleration and maximum surge acceleration were examined using five separate REML analyses, each with individual as a random effect and current depth as a covariate. In all REML analyses, significance of variables and interaction terms was determined by comparing Wald statistics with percentiles of χ^2 distributions (Elston et al., 2001).

Results

Diving behavior

A total of 1407 dives (>1 m) were recorded. Median dive depth and dive duration of individuals varied between 10.2 and 43.3 m and 43 and 97 s, respectively (Table 1). Mean body mass was significantly greater in males (1896±113 g, mean ± s.d.) than females (1627±105 g) (Mann–Whitney U-test, $U=2$, $P<0.01$). However, there were no significant sex differences in median dive depth ($U=21$, $P=0.65$), maximum dive depth ($U=21$, $P=0.65$), median dive duration ($U=21$, $P=0.65$) and maximum dive duration ($U=12$, $P=0.11$).

For the subset of 100 dives from the nine birds where surge and body angle were measured, the distribution of depth change rate showed a trimodal pattern with gaps between –0.6 to 0.3 m s^{-1} and +0.3 to 1.0 m s^{-1}. Accordingly the descent and ascent phases were defined as depth change rates below –0.6 m s^{-1} and above 1 m s^{-1}, respectively. Birds were classified as being in the bottom phase of the dive if they had a narrow range of depth change rates between –0.3 m s^{-1} and +0.3 m s^{-1}. 113 (1.4%) of records could not be classified into these categories and were therefore excluded from subsequent analyses.
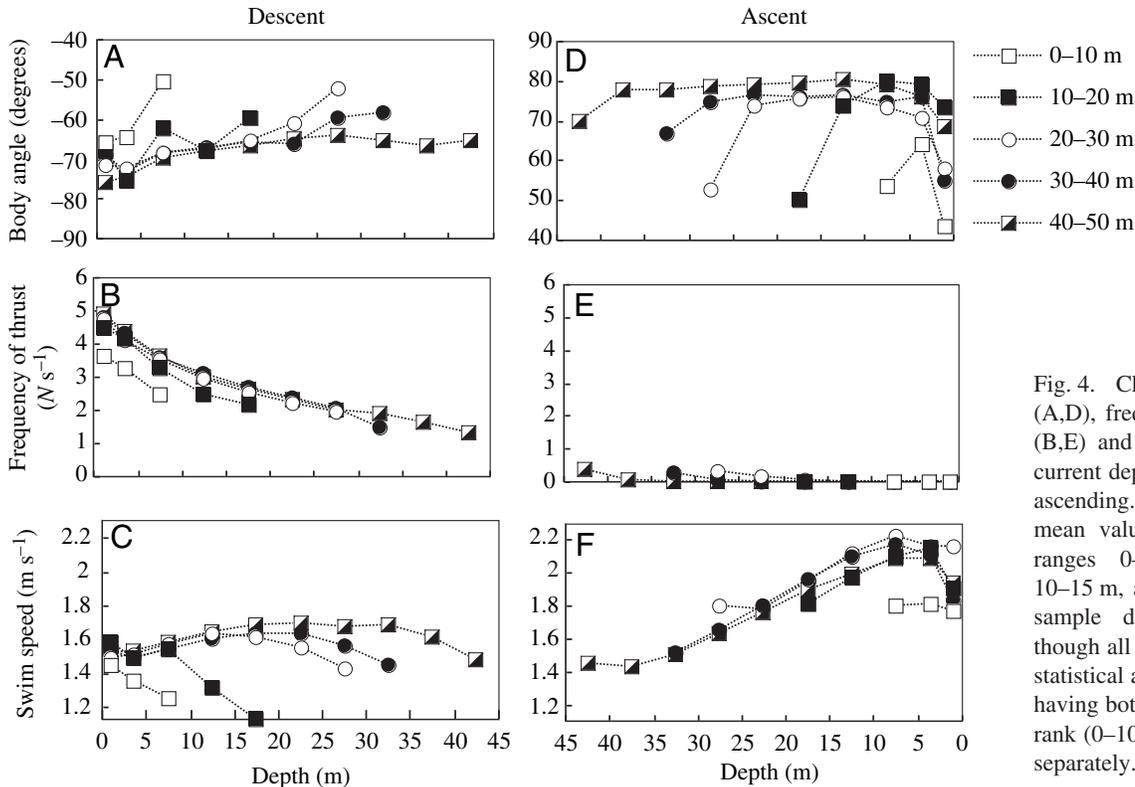
Fig. 4. Changes of body angle (A,D), frequency of forward thrust (B,E) and swim speed (C,F) with current depth while descending and ascending. To show the trends, only mean values are indicated in the ranges 0–2 m, 2–5 m, 5–10 m, 10–15 m, and so on, based on 100 sample dives from nine birds, though all the data were used in the statistical analyses. Data from dives having bottom depths of each depth rank (0–10 m and so on) are shown separately.

Behavior during descent

Within 0.5 s of the start of a dive, shags made a >15 m s^{-2} forward thrust accompanied by a rapid change in body angle from +60 to –90° (Fig. 3A). The mean of the maximum surge acceleration at the start of a dive varied between 18.1±2.0 m s^{-2} and 23.5±2.0 m s^{-2} among individuals.

At the start of the descent, body angle was almost vertical (–80°) but became significantly shallower (–70 to –60°) by the time a bird reached a depth of 5–10 m depth (Fig. 4A, Table 2). There was a significant effect of mean bottom depth on body angle during descent, with body angle remaining closer to vertical on deeper dives. There was a significant interaction between depth and mean bottom depth such that for a given depth, body angle was steeper on deeper dives (Fig. 4A, Table 2). The frequency of thrust decreased with increasing depth and increased with mean bottom depth (Fig. 4B, Table 2). The interaction between depth and mean bottom depth was significant with the frequency of thrust decreasing less rapidly on deeper dives (Fig. 4B, Table 2). Swim speed did not vary with depth but was significantly higher for dives with greater mean bottom depth (Fig. 4C, Table 2). The interaction between depth and mean bottom depth was not significant.

There was a highly significant decrease in the frequency of the power stroke with depth (Fig. 5A, Table 2) due to a fivefold increase in glide duration and a 1.2-fold increase in power stroke duration (Fig. 5B, Table 2). Maximum heave acceleration recorded during a power stroke declined significantly with depth, but there was no effect of depth on maximum forward surge during a power stroke (Fig. 5C, Table 2).

Behavior during ascent

At the start of the ascent, there was a gradual shift in body orientation from a negative angle during the bottom phase to a positive body angle. Initially body angle was relatively steep (>70°; Fig. 4D), but as the bird approached the surface, orientation became slightly but significantly shallower (Fig. 4C, Table 2). Body angle was steeper during ascent from deeper dives but there was no significant interaction between depth and mean bottom depth (Fig. 4D, Table 2). The frequency of thrust during ascent was infrequent and was not related to dive depth (Fig. 4E). Birds stopped stroking for at least 3 s at 90–100% (94.2±4.7%) of the mean bottom depths and ascended passively for the remainder of the ascent. There was a highly significant increase in swim speed as the bird ascended (Fig. 4F, Table 2). Swim speed on the ascent was not related to mean bottom depth, but the interaction between depth and mean bottom depth was significant with a greater increase in swim speed in birds ascending from deeper depths (Fig. 4F, Table 2).

Behavior during the bottom phase of the dive

There was no evidence of a cyclic surge during the bottom phase (Fig. 3C), indicating that shags did not swim horizontally using a cyclic power stroke. Mean body angle of individuals during the bottom phase of the dive was negative and varied between –10 and –69° (overall mean for all individuals –35°) for 100 dives. We found a positive and significant effect of depth on body angle such that body angle increased from –42±20° at 20–25 m depth to –33±14° at 40–45 m depth (Table 2). Depth did not affect the frequency of thrusts.

Table 2. *Results of the REML analyses carried out on the descent and ascent phases and regression analyses carried out on the bottom phase*

Phase	Dependent variable	Fixed effect	Number of birds	Number of dives	Number of records	Wald	P
Descent	Body angle	Depth	9	100	2064	563.29	<0.001
		Mean bottom depth	9	100	2064	301.51	<0.001
		Interaction term	9	100	2064	164.43	<0.001
	Thrust frequency	Depth	9	100	2064	4529.69	<0.001
		Mean bottom depth	9	100	2064	287.62	<0.001
		Interaction term	9	100	2064	112.21	<0.001
	Swim speed	Depth	9	100	2061	0.40	0.53
		Mean bottom depth	9	100	2061	91.64	<0.001
		Interaction term	9	100	2061	0.07	0.79
	Foot stroke frequency	Depth	3	17	153	1109.38	<0.001
	Power stroke duration	Depth	3	17	153	847.62	<0.001
	Glide duration	Depth	3	17	153	1732.51	<0.001
	Max. heave acceleration	Depth	3	17	153	9.73	<0.001
	Max. surge acceleration	Depth	3	17	153	0.06	0.81
Ascent	Body angle	Depth	9	100	1761	12.00	<0.001
		Mean bottom Depth	9	100	1761	41.65	<0.001
		Interaction term	9	100	1761	1.45	0.23
	Swim speed	Depth	9	100	1713	2463.14	<0.001
		Mean bottom depth	9	100	1713	2.94	0.09
		Interaction term	9	100	1713	7.46	<0.01

Phase	Dependent variable	Fixed effort	Number of birds	Number of dives	Number of records	ANOVA F	P
Bottom	Body angle	Depth	9	100	4016	175.37	<0.001
	Frequency of thrust	Depth	9	100	4016	0.42	0.52

REML, restricted maximum likelihood. All statistically significant results were retained after sequential Bonferroni adjustment.

Discussion

Effects of devices and potential error

It was impossible to estimate trip durations of birds without loggers during the study in order to make a direct comparison of attendance patterns of birds with and without loggers. However, there was no obvious sign that the data-loggers disrupted the attendance behavior of any of the shags since none of the study birds lost young while they were carrying a logger. The device mass was <1% of shag body mass; radio transmitters of this size deployed in a similar manner did not appear to disrupt behavior or breeding success of European shags (Wanless et al., 1991a) or Japanese cormorants *P. filamentosus* (Watanuki et al., 2004). We therefore assumed that our data-loggers, which were only deployed for a short period (<2 days), did not adversely affect behavior, although we could not rule out possible effects on swimming behavior and energetics as suggested by Croll et al. (1991) and Culik and Wilson (1991).

We also assumed that the angle of dives was the same as the body angle. Great cormorants swimming horizontally in shallow (<1 m) water have a negative tilt (angle of body axis against swimming direction) of 6–15°, which gives negative lift, presumably to compensate high buoyancy (Riback et al., 2004). When the shags have a body angle of –70° during descent, the maximum error of estimated speed is 15% allowing 15° of tilt. In our study we did not measure tilt directly but as shags descended almost vertically they might not require tilt to compensate buoyancy. Clearly it would be advantageous to collect information on body angle and tilt for shags but until such data are available we believe that the assumption that the angle of dive is equivalent to the body angle is reasonable.

Regulation of stroke

Buoyancy in cormorant species of similar mass to European shags has previously been estimated to be between 2.2 and 8 N at the surface, to have decreased markedly by 20–40 m, and to remain positive down to depths of at least 100 m (Lovvorn et al., 1991b; Wilson et al., 1992a; Riback et al., 2004). In our study, in which shags did not dive deeper than 40 m, birds ascended passively from this depth, indicating that they had positive buoyancy down to at least 40 m.

During descent shags maintained an approximately constant swim speed and apparently responded to decreasing buoyancy by reducing the frequency of thrust by decreasing the rate of power strokes (Figs 4A, 5A). A decrease in the frequency of forward thrusts during descent has also been described in Brünnich's guillemots *Uria lomvia*, a wing-propelled diving seabird (Watanuki et al., 2003).
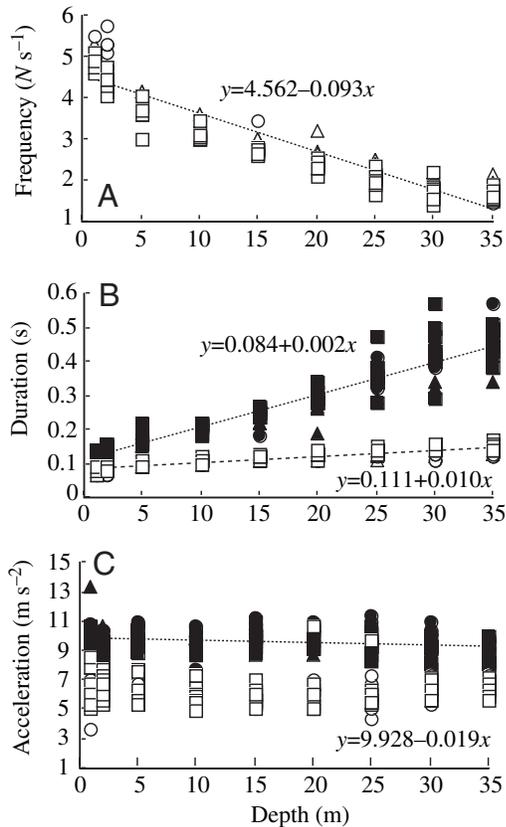
Fig. 5. Changes of (A) the foot stroke frequency, (B) the duration of power stroke (open symbols) and glide (closed symbols) and (C) the maximum acceleration of surges (open symbols) and heaves (closed symbols) during descent phase for 17 deep (>40 m) dives from three birds. Different symbols indicate different birds. Effects of depth on the frequency of strokes, duration of power stroke and glide, maximum heave acceleration were significant. To demonstrate these effects, linear regression lines are also given.

Fig. 6. Effects of bottom depth on the mean frequency of forward thrust while descending for each dive. The regression line was significant ($r=0.72$, $F_{(1,98)}=107.41$, $P<0.001$; frequency= $3.61-0.02\times$depth in m). Different symbols are data from different birds.

Shags did not alter the maximum forward thrust acceleration in a power stroke during descent (Fig. 5C). They decreased the maximum heave acceleration, but the decrease was small (<5%). Therefore, a decrease in the frequency of forward thrusts, rather than a change in strength, was the main mechanism used to adjust average forward thrust. This decrease in the frequency of stroke was not achieved by varying the duration of the power stroke, which showed only a slight (1.2-fold) increase with depth; rather, shags adjusted the duration of the glide (fivefold variation; Fig. 5B). Our findings therefore support the general idea that seabirds keep within a range of high physiological efficiency of contracting muscle (Goldspink, 1977; Pennycuick, 1996; Lovvorn et al., 1999; Lovvorn, 2001). However, in zebra finch *Taenopygia guttata* flying in a wind tunnel, contractile velocity in the pectoralis muscle changes with flight speed (Tobalske et al., 1999). The regulation of strokes in air and water therefore needs to be compared using consistent technique.

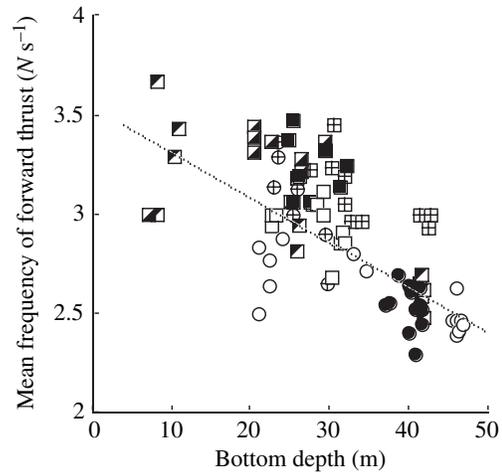The pattern of regulation used by a foot-propelled species such as the European shag, apparently differs markedly from that of wing-propelled divers such as penguins and auks. Magellanic penguins *Spheniscus magellanicus,* generate forward thrust on both the downstroke and the upstroke (Bannasch, 1995), and decrease the amplitude and the frequency of the wing stroke while they are descending (Wilson and Liebsch, 2003). Brünnich's guillemots have a higher frequency of forward thrust during descent to 20 m due to forward thrust being produced on the downstroke and the upstroke, but forward thrust occurs only on the downstroke at deeper depths (Watanuki et al., 2003).

Shags had a nearly constant swim speed throughout the descent (Fig. 4A). Brünnich's guillemots, however, increased the swim speed to counteract the strong buoyancy in shallow (<20 m) water and attained a nearly constant swim speed below 40–60 m (Watanuki et al., 2003). The rapid change of body angle at the start of dives in our shags almost certainly corresponded to the pre-dive leap (Wilson et al., 1992b), which is a conspicuous feature of European shag diving behavior. Birds did not stroke for 0.5 s after this (Fig. 3), indicating that they leap and enter the water using inertia. This could facilitate rapid acceleration of swim speed to overcome the strong buoyancy in shallow water.

Body angle and swim speed

Shags descended and ascended almost vertically and hence minimized transit time between the surface and foraging depth. However, below 5 m on the descent, body angle became significantly less vertical (–60 to –70°; Fig. 4). The reason for this change is obscure. One possibility is that birds make horizontal movements as they descend in response to shoals of fish near the bottom. This potential benefit in terms of increased prey capture presumably offsets the cost of increased transit time (for example a 3 s increase in descent time at a body angle of –70° and 1.6 m s^{-1} swim speed over a depth

range of 10–40 m). Hustler (1992) hypothesized that diving birds keep the body angle vertical in order to stay down, particularly in shallower water where buoyancy is greater because the birds have to direct force downward. In our study shags had a significantly shallower body angle when they foraged in deeper water, also supporting this hypothesis.

During ascent, body angle became less vertical (80–60°) above 5 m. An oblique ascent angle in penguins has been suggested to allow birds to search both the vertical and horizontal components of the water column (Wilson et al, 1996) or move horizontally by using increased buoyancy near the surface (Sato et al., 2004). However, shags are generally believed to feed almost exclusively during the bottom part of the dive rather than during the ascent. Sato et al. (2002) suggested that slowing down near the surface could be one way of potentially avoiding decompression sickness in King penguins *Aptenodytes patagonicus* diving deeper than 100 m. However, in shags ascending from depths of less than 40 m the decrease in body angle was small and ascent swim speed was still high near the surface (Fig. 4B), so this explanation is unlikely in this case.

Shags descended at an approximately constant swim speed (1.2–1.8 m s^{-1}). To minimize the energy lost to the water through friction, seabirds are suggested to keep within a range of speeds that minimize the drag coefficient (Lovvorn et al., 1999). During descent Brünnich's guillemots keep within a range of swim speeds (1.2–1.8 m s^{-1}) that are estimated to minimize the drag coefficient (1.2–1.5 m s^{-1}; Lovvoren et al., 1999; Watanuki et al., 2003). In contrast, in Brandt's cormorant *P. penicillatus* there is no clear evidence, based on the drag coefficient *vs* Reynolds number curve (fig. 8 in Lovvron et al., 2001), to support the idea that this species selects the maximum speed that avoids a rapid non-linear increase in drag. Thus the reason why shags keep within a narrow range of swim speeds while they descend is uncertain.

Effects of bottom depth

During the breeding season shags on the Isle of May feed predominantly on sandlance *Ammodytes marinus*, which they catch on or just above the seabed (Wanless et al., 1991a,b). In the present study we found that, on average, shags maintained a body angle of –35° during the bottom phase of the dive and rarely showed active horizontal swimming. This suggests that the birds may move relatively slowly over the seabed and concentrate their foraging effort in one place with the body pointing down towards the sand. Therefore, they are most likely to determine their foraging site and depth prior to each dive, and have the potential to regulate swim speed, body angle and stroke pattern depending on the depth finally attained as well as the depth changes during descent.

Because of air compression, buoyant resistance decreases dramatically with depth. Based on biomechanical modeling, it is suggested that seabirds can decrease mean mechanical power output when they make deeper dives (Hansen and Ricklefs, 2004). Assuming that shags do not change the pre-dive air volume according to the bottom depth, our data support this idea. Shags decreased the mean frequency of power stroke throughout the descent phase as they made dives with deeper bottom depth (Fig. 6). Maximum heave acceleration of the body by power stroke did not vary greatly with depth and actually decreased slightly with depth (Fig. 5). Thus mean mechanical power output per unit time should decrease as the birds make dives with deeper bottom depth.

In conclusion, we have shown that foot-propelled diving European shags descend almost vertically. They decrease the frequency of the power stroke with increasing depth, possibly in response to decreasing buoyancy. This regulation is achieved mainly by changes in glide duration. Birds appear to maintain the duration and maximum strength of the power stroke and thus optimize muscle contraction efficiency.

List of symbols

R	vertical depth change rate
V	swim speed
XG	total heave
XH	high frequency component of surge
YG	total surge acceleration
YH	high frequency component of heave
YL	gravity component along the surge axis
α	logger attachment angle
γ	logger axis angle
θ	body angle

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