RESEARCH ARTICLE

Crossing the frontier: vertical transit rates of deep diving cormorants reveal depth zone of neutral buoyancy

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Abstract Knowing the depth zone of neutral buoyancy of divers is important because buoyancy can determine how animals manage their energy budget. In this study, we estimate the depth zone of neutral buoyancy of free-ranging cormorants for the first time, using time-depth recorders. We discovered that vertical ascent rates of 12 Crozet and 15 Kerguelen diving blue-eyed shags (respectively *Phalacrocorax melanogenis* and *P. verrucosus*) slowed down considerably at the 50–60 m depth zone. We suggest this was due to birds trying to reach the surface from that point upwards using reduced locomotor activity because the force of buoyancy becomes greater than the force of gravity at that depth. The results show a shift of this depth zone in relation to maximum targeted dive depth, suggesting cormorants may control buoyancy through respiratory air volume adjustment. Interestingly, 60 m is close to the maximum depth zone reached by these two species during dives lasting 4 min, their estimated behavioural aerobic dive limit. This suggests that the decision to swim deeper has a direct consequence on the energy budget, with time spent recovering at the surface (time thus lost to foraging) strongly increasing relative to the preceding time of submergence. Resources found in deeper waters must be of sufficient quantity or quality to justify crossing the frontier of physical neutral buoyancy.

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Introduction

Buoyancy is the upward force exerted on an object submerged in a fluid. Marine organisms have developed a large array of morphological adaptations to counter the effects of this force and those of an opposing force–gravity. Uncontrolled, these vertical forces can lead respectively, to undesired rising or sinking. Adaptations include gas-filled floats, low-density organic compounds, body fluids of unusual ionic composition and hydrofoils (Alexander 1990).

Because of their terrestrial lineage, diving air-breathing vertebrates are subject to important costs when they dive; they are limited by their capacity to store oxygen and underwater locomotion is a behaviour with high-energy expenditures. This is particularly true for diving endotherms, for which heat loss to the aquatic environment may greatly increase metabolism (Butler and Jones 1997). Hence, divers must submerge with respiratory air reserves on the one hand, and must sometimes load air in their plumage or accumulate blubber under their skin for purposes of insulation on the other. Overcoming the increase in the force of buoyancy these two factors generate can lead to important locomotor expenditures. This may occur during the descent or bottom phase of the dive if animals forage in waters shallower than their depth zone of neutral buoyancy (where the force of buoyancy and gravity cancel each other out), because they must constantly paddle to maintain depth.

Although there are morphological adaptations to reduce buoyancy, such as denser bones in penguins or partially wettable plumage in cormorants (Meister 2005; Grémillet et al. 2005), they do not entirely eliminate its impact. Buoyancy is a crucial parameter that animals must take into account, and working against it must be solved through behavioural adjustments. Pinnipeds are known to exhale

before they dive, thus partly solving problems related to pressure and deep diving, but also reducing the influence of upward force during descent (Kooyman et al. 1970). Depending on dive depth, animals can manage a trade-off between time spent underwater, maximum dive depth, energy used to overcome upward force, and gains related to passive ascent. This is demonstrated by the positive relationship between air volume intake before dives and maximum dive depths in penguins (Wilson and Zimmer 2004).

Consequently, to understand how divers incorporate buoyancy management into their decision-making processes (Wilson 2006), it is vital to estimate the depth zone in which the diver is neutrally buoyant and is a tail-, wing-, flipper- or foot-stroke away from floating up or sinking down. Such measurements are actually quite difficult to obtain. They can be done with simple experimental designs in the laboratory, followed by complex mathematical modelling (e.g. Wilson et al. 1992), or by measuring buoyancy of carcasses (e.g. Hustler 1992). In both cases, results are not actually measured on live animals, the difficult aspect probably being the correct estimate of lung and air sac volume (for birds).

Because changes in a diver's buoyancy under the effect of increasing pressure with dive depth can affect its vertical diving transit rate (e.g. Webb et al. 1998; Lovvorn et al. 2004; Elliot et al. 2007), this variable can be used to estimate the depth zone of neutral buoyancy. For example, it can be expected that animals crossing this frontier would develop increasing descent rates because the force of gravity becomes greater than buoyancy (Sato et al. 2002). On the other hand, animals returning to the surface can be expected to use the force of buoyancy in order to decrease their expenditures. By stopping or substantially reducing all locomotor activity once they cross the frontier, they will rise, slowly at first, but increasing buoyancy will accelerate their ascent the closer they get to the surface (Sato et al. 2002).

Field measurements using data loggers provide evidence concerning buoyancy management in sea mammals (e.g. Crocker et al. 1997; Skrovan et al. 1999; Williams et al. 2000), sea turtles (e.g. Hochscheid et al. 2003; Hays et al. 2004), and seabirds (e.g. Lovvorn et al. 1999; Sato et al. 2002). However, because bio-logging remains a recent field of research (Kooyman 2004), data are still lacking for many species of divers, including avian divers. In this study, we estimate the depth zone of neutral buoyancy in free-ranging cormorants for the first time. Foot propelled benthic divers, blue-eyed shags are sexually dimorphic and constitute a group of 13 sister species of cormorants living across the Southern Ocean (Orta 1992). We analysed vertical transit rates from 12 Crozet and 15 Kerguelen blue-eyed shags equipped with time-depth recorders. Our objectives were: (1) to estimate the depth zone of neutral buoyancy for these species, (2) to see if maximum depth reached during a dive has an effect on the depth of this particular zone (thus raising the possibility that cormorants may control their buoyancy through respiratory air volume adjustments), and (3) to compare the sexes in order to detect a possible influence of body size on buoyancy.

Materials and methods

Field work

Adult breeding Crozet and Kerguelen shags were equipped with time-depth recorders (TDRs). At Crozet, 12 Crozet shags (six females, six males) were equipped during 4–5 days with Mk7 models (Wildlife Computers, Redmond, WA, USA) at Pointe Basse (46°21′S, 51°42′E), Possession Island, Crozet Archipelago during the 1998–1999 breeding season (Tremblay et al. 2005). At Kerguelen, 15 Kerguelen shags (six females, nine males) were equipped during periods varying from one foraging trip to 2 days with Mk9 models (Wildlife Computers, Redmond, WA, USA) at Cap Cotter (49°03′S, 70°19′E), Mainland, Kerguelen Archipelago, during the 2002–2003 and 2003–2004 breeding seasons (Cook et al. unpublished). In both localities, TDRs sampled depth every second. Depth sensor resolution was ±1 m for Crozet shags and ±0.5 m for Kerguelen shags.

Dive data

The total number of dives recorded with the TDRs was 8,190 for Crozet shags and 541 for Kerguelen shags. Dive data represent a succession of depth values over time. A dive is characterized by a descent phase, a bottom phase, and an ascent phase (a post-dive interval, enabling recovery, separates one dive from the next). In this study, the bottom phase was defined as the time spent in the zone below 80% of maximum dive depth (Kato et al. 1999). Descent time is the time from the beginning of the dive at the surface to the beginning of the bottom phase. Ascent time is the time from the end of the bottom phase to the end of the dive at the surface.

Estimating the depth zone of neutral buoyancy (DZ) using individual dive profiles

Visual inspection of individual dive profiles from Crozet and Kerguelen shags reveals the presence of an important feature (Fig. 1), for all deep dives (>80 m). At one point during the ascent, dive profiles clearly show a change, with birds slowing down for several seconds before taking on speed again and ascending more and more rapidly the closer they get to the surface. This particularity may be
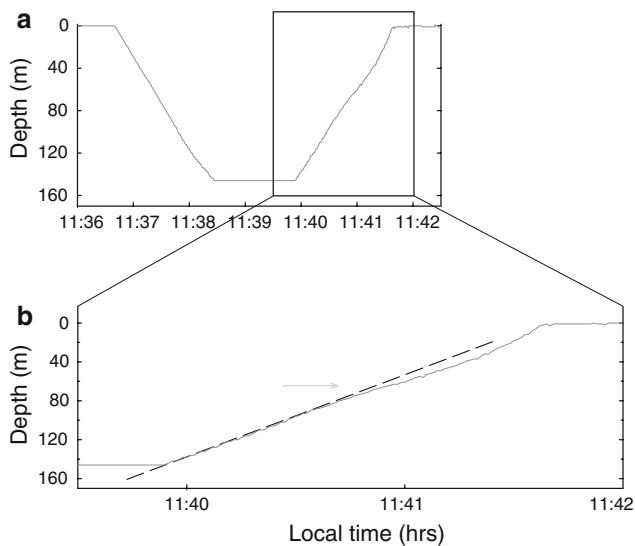
Fig. 1 Example of a dive profile from the Crozet shag. **a** A close-up of the ascent phase shows how the profile changes at a certain point, corresponding to the DZ (*horizontal arrow*). **b** The ascent follows a regular slope (*slashed black line*) from the bottom to the onset of the change and then slows down, before accelerating again closer to the surface

attributable to the influence of the DZ. However, at no point during the descent is there an inflection in the dive profile. For this reason, the method for estimating the position of the DZ has focused on the ascent phase.

We considered the DZ to occur when, for any dive, the current ascent rate of an individual slowed down. The current descent or ascent rates are the vertical speeds of a bird relative to its position in the water column (current depth). Hence, a current rate was estimated step by step for each dive, starting from the surface to the beginning of the bottom phase (current descent rate) and from the end of the bottom back to the surface (current ascent rate), respectively. For every 10 m depth class, the current rate was ten divided by the time spent inside the class. This was calculated using a program written with the software R 2.3.1 (Ihaka and Gentleman 1996). Dives of maximum depth <13 m deep were not taken into account (80% of $13 \approx 10$ m). Results for the deepest current depth classes from Crozet and Kerguelen shags (100–110 and 70–80 m, respectively) were not used because they contained too few data points (3 dives from only 1 bird for the Crozet shags, 18 dives from only 2 birds for the Kerguelen shags). The number of current transit rate values for all depth classes for Crozet shags totalled 6,776 for females and 5,529 for males, and for Kerguelen shags, 1,449 for females and 1,482 for males, for both the descent and ascent phases.

To determine whether the maximum depth reached during a dive has an effect on the position of the DZ, we separated dives into three categories of targeted depth (in parentheses: number of current rates for both the descent

and the ascent phases, and number of birds, respectively): dives reaching 50–80 m (Crozet shags: 1,025, 5; Kerguelen shags: 246, 7); 80–110 m (Crozet shags: 170, 3; Kerguelen shags: 871, 7); and 110–140 m (Crozet shags: 303, 3; Kerguelen shags: 0, 0). We then compared results from the three depth categories.

Finally, sex differences were studied in both species. For the Crozet shag, the 30–40 m female depth class was not used because it contained too few data points (17 dives from only one bird). The position of the DZ was not compared between sexes for the Crozet shags, because females did not dive deeper than 55 m (Cook et al. 2007). Both sexes of the Kerguelen shag carried out deep dives (max. female dive = 95 m, max. male dive = 108.5 m), making comparison possible.

Statistics

We studied differences between the sexes in current descent and ascent rates using an analysis of covariance. In all cases, we set the bird identity as a random factor. In order to compare the sexes independently from depth, current dive depth was set as a covariate. For the Crozet shag, sexes were only compared in the 0–40 m depth zone, as 55 m was the deepest female dive (80% of 55 = 43). For the Kerguelen shag, sexes were compared separately above and below the DZ. Dive parameters were log-transformed to adjust for skewed distributions. Data were analyzed statistically using R 2.3.1 (Ihaka and Gentleman 1996), with an α-level of significance of $P < 0.05$. The mean values are given ±SE.

Results

General depth zone of neutral buoyancy

Descent rates showed a fairly stable pattern during the total descent period, fluctuating around 1.5 m s^{-1} in both localities (Fig. 2). Descent rates were slightly higher for the Kerguelen shag than for the Crozet shag in shallow waters.

Ascent rates decreased in relation to increasing current depth, but started increasing again around 50 m for the Crozet shag and 60 m for the Kerguelen shag (Fig. 2). This threshold was considered as an estimate of the DZ.

DZ and maximum dive depth

Different targeted maximum dive depths had an effect on the position of the DZ for the Crozet shag only (Fig. 3). Dives to a maximum depth of 50–80 m resulted in the same position of the DZ as dives to 80–110 m; around 50 m

Fig. 2 Descent and ascent rates in relation to current depth in the Crozet shag (*n* = 12) (**a**) and the Kerguelen shag (*n* = 15) (**b**). Data points represent individual means averaged per depth class (−SD). *Shaded zones* correspond to the DZ
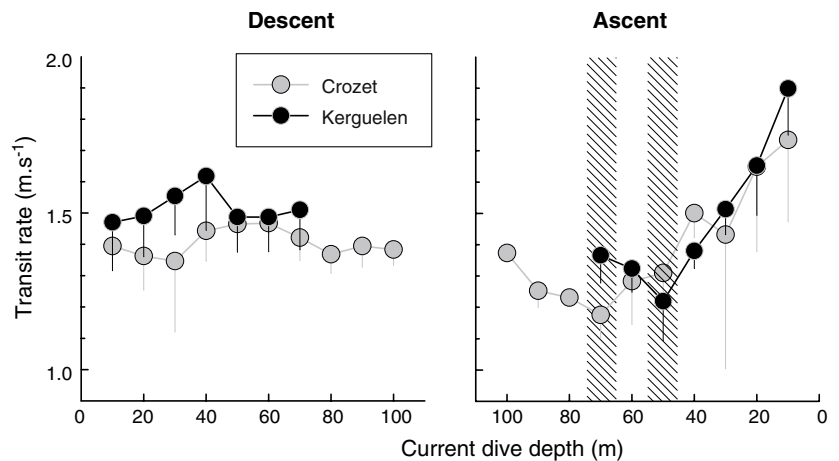

Fig. 3 Descent and ascent rates in relation to current depth in the Crozet shag (**a**) and the Kerguelen shag (**b**). Transit rates were separated into three categories according to the maximum depth reached during the dive (*parentheses*: number of Crozet and Kerguelen shags, respectively): 50–80 m (5, 7), 80–110 m (3, 7) and 110–140 m (3, 0). Data points represent individual means averaged per depth class (−SD). For the Crozet shag, DZ is close to 50 m in the first two depth classes, but switches to near 60 m in the last class (110–140 m)
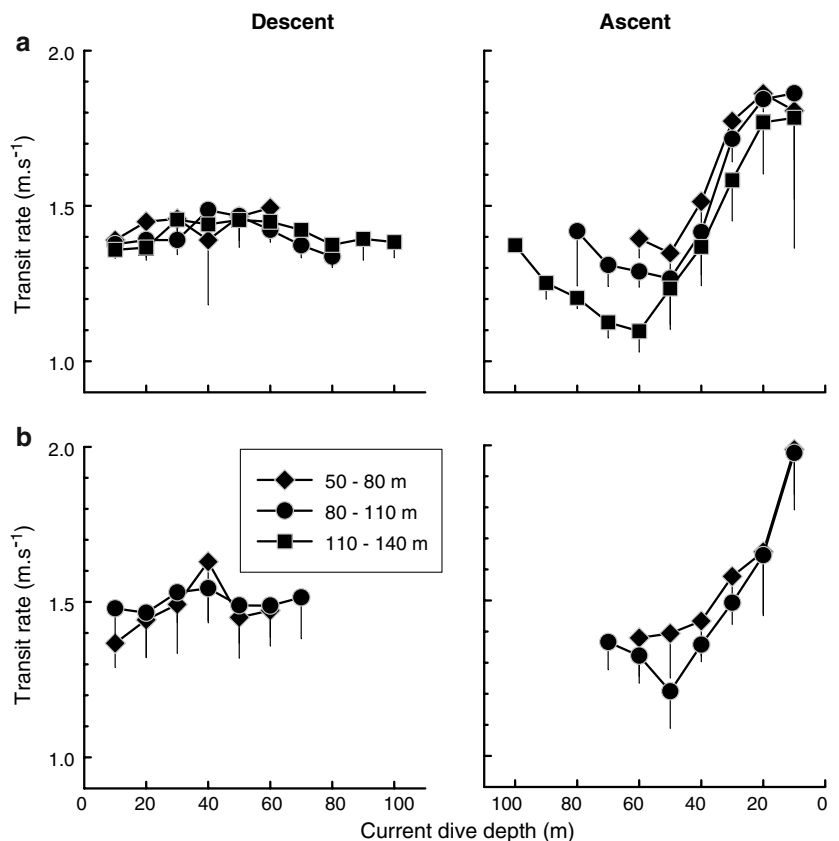
deep. But dives to a maximum depth of 110–140 m resulted in a shift of this value 10 m deeper, to around 60 m deep.

Sex differences

The two species of blue-eyed shag displayed sexual size dimorphism, with males larger than females (≈20% heavier in both localities, Table 1). We found no visible difference between male and female Kerguelen shags in the position of the DZ (Fig. 4). In both species however, there were significant sex differences in current descent and ascent rates,

males transiting faster than females by up to 0.1 m s^{-1} (Fig. 4; Table 2).

Discussion

The method

Tremblay et al. (2005) observed a major change in mean descent and ascent rates of Crozet shags around 40 m deep, with descent rates occurring at a constant value of

Table 1 Mean body mass, tarsus length, wing length and body condition index [ratio of body mass to (culmen + wing length), Chastel et al. 1995] for Crozet shags (six males, six females) and Kerguelen shags (nine males, six females)

Parameter	Crozet shag			Kerguelen shag		
	Females	Males	SSD (%)	Females	Males	SSD (%)
Body mass (g)	2,112 ± 109	2,542 ± 133	20.3	2,212 ± 135	2,635 ± 150	19.1
Tarsus length (mm)	65 ± 1	69 ± 1		62 ± 2	67 ± 2	
Wing length (mm)	278 ± 5	291 ± 9		276 ± 6	290 ± 4	
Body condition index	6.1 ± 0.2	7.0 ± 0.4		6.7 ± 0.4	7.4 ± 0.4	

Sexual size dimorphism (SSD) is expressed as the sex difference in body mass over female body mass ($\times 100$)

Fig. 4 Descent and ascent rates in relation to current depth, separated by sex, in the Crozet shag (6 males, 6 females) (**a**) and the Kerguelen shag (9 males, 6 females) (**b**). Data points represent individual means averaged per depth class (males +SD; females −SD)
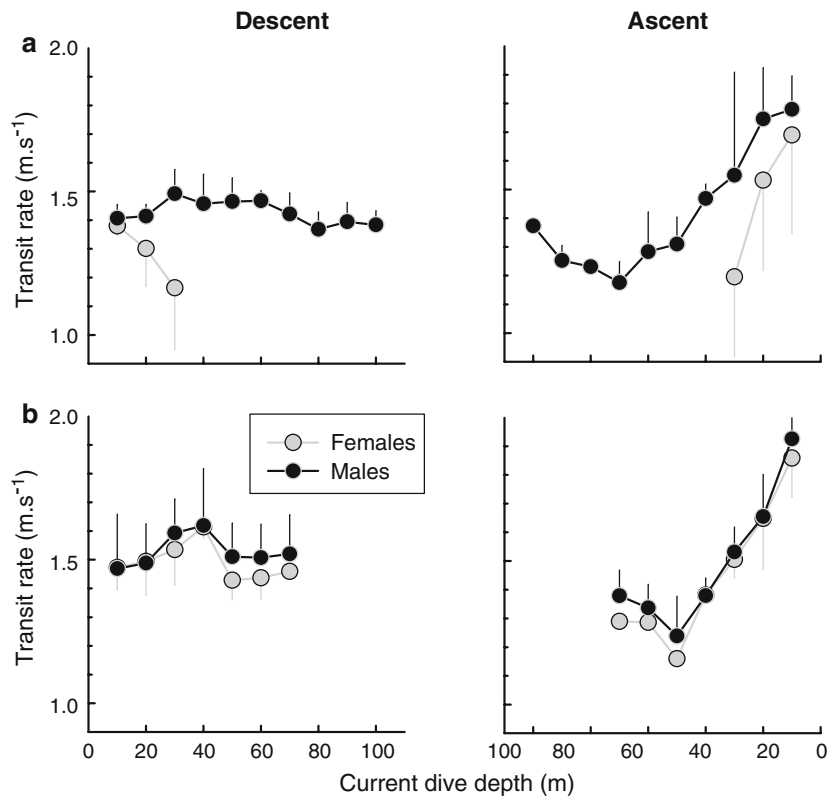

Table 2 Sex differences in transit rates in the Crozet shag (six males, six females) and the Kerguelen shag (nine males, six females) (ANCOVA)

Shag sp.	Parameter	Current depth zone (m)	Females	Males	F	P
Crozet	Descent rate (m s^{-1})	0–40	1.36 ± 0.01	1.43 ± 0.01	44.1	<0.0001
	Ascent rate (m s^{-1})	0–40	1.62 ± 0.01	1.80 ± 0.01	200.1	<0.0001
Kerguelen	Descent rate (m s^{-1})	0–50	1.48 ± 0.01	1.54 ± 0.01	25.4	<0.0001
		50–70	1.44 ± 0.02	1.54 ± 0.01	17.5	<0.0001
	Ascent rate (m s^{-1})	0–50	1.57 ± 0.01	1.63 ± 0.01	15.8	<0.0001
		50–70	1.22 ± 0.01	1.33 ± 0.01	25.1	<0.0001

Adjusted means are presented for each depth zone

1.5 m s^{-1} below this, while shallower dives were characterized by high rate variability (while descending or ascending). This was attributed to the effect of the DZ. Forty meters is shallower than the DZ estimated in the present study because mean transit rates do not depict the variation of vertical speed in the water column, as our method does,

but rather give only two average vertical speeds between the surface and 80% of maximum dive depth, for each dive. Thus, while mean transit rates remain a convenient parameter for exploring dive data because they are easily calculated using most available software for dive analysis, mean transit rates should not be used for studying the DZ.

In the present study, the use of TDRs combined with a method for calculating a dynamic estimate of vertical transit speed proved to be important. Because buoyancy affects a diver's locomotor behaviour, time-depth data often contains information about the animal's management of this force. We therefore encourage the use of time-depth data for such analyses. Nonetheless, the method has some points which need to be discussed.

First, it is based on several assumptions that cannot be demonstrated with the present data. We cannot be certain that our birds stopped paddling or reduced this activity during the second phase of the ascent in order to benefit from passive ascent. Also, as we did not have access to body angles or swimming speed, we assumed it was not an acute change in one or both of these parameters which caused the onset of the slow-down visible on the dive profiles. Loggers recording body angles, speed or acceleration in relation to depth provide data on propulsion behaviour (e.g. Minamikawa et al. 2000; Sato et al. 2002; Watanuki et al. 2003; Lovvorn et al. 2004; Miller et al. 2004). However, there are still too few studies using these loggers and this technology remains expensive, particularly for small species. In contrast, TDRs are now generally affordable and data sets collected with this generation of logger are available worldwide, for a large array of species. To date, studies with accelerometers on cormorants have been done on the great cormorant (*Phalacrocorax carbo*, Kato et al. 2006; Ropert-Coudert et al. 2005; Ropert-Coudert et al. 2006), the Patagonian blue-eyed shag (*P. atriceps*, Wilson et al. 2006), and the European shag (*P. aristotelis*, Watanuki et al. 2005). However, in all these studies, dives never exceeded 50 m deep. The importance of the present data is that both the Crozet and the Kerguelen shags dived to extreme depths, thus encompassing the DZ for these species.

Second, although mathematically neutral buoyancy corresponds to a precise depth of perfect equilibrium between the forces of buoyancy and gravity, from an animal's perspective it more likely corresponds to a zone of transition. Thus it is not particularly useful trying to pinpoint this value when using behavioural data. Furthermore, because of the modest resolution of the loggers (0.5–1 m), their low sampling frequency (1 s), and the method for calculating current transit rates (one value per 10 m depth class), precision is difficult in any case. This is why we use the term "depth zone" rather than "depth" of neutral buoyancy.

Finally, while ascending, the blue-eyed shags were slowest in the 50–60 m depth zone. But in fact, it is reasonable to assume they were neutrally buoyant just before entering the zone, as their behaviour probably reflects the fact their buoyancy has become strong enough to bring them to the surface with the least expenditure. This has important consequences, probably moving the DZ to a nearby, but deeper range, potentially 60–70 m.

Buoyancy in cormorants

The values found in this study for both species of blue-eyed shags are greater than the 5–6 m measured by Hustler (1992) using submerged carcasses of reed cormorants (*P. africanus*) and smaller than the estimate of 103 m obtained through modelling by Wilson et al. (1992) for the great cormorant (*P. carbo*) and the Cape cormorant (*P. capensis*). Although 5 m seems a very shallow estimate, DZ might vary from one species to another because of different air stores in the plumage, for example. Quintana et al. (2007) suggested that blue-eyed shags may have more plumage air than other species from the Cormorant family, as an adaptation to resisting the cold of sub-Antarctic waters, but this point remains to be demonstrated.

Buoyancy and dive cycle management

Captive great cormorants (*P. carbo*) normally prefer swimming at around 1.5 m s^{-1} (Schmid et al. 1995), while free-ranging ones swim optimally around 1.6 m s^{-1} (Ropert-Coudert et al. 2006). These values are consistent with the descent and ascent rates measured in the present study, suggesting blue-eyed shags transit with body angles close to 90° relative to the surface. Blue-eyed shags are on the water surface before they dive. They execute a pre-dive leap enabling them to penetrate the water in order to submerge their feet quickly so they can start paddling against buoyancy. Above the DZ, descent rates are variable, but on average relatively low ($\approx$1.5 m s^{-1}), since blue-eyed shags must work against the upward force of buoyancy. Descent rates in Kerguelen shags are higher during this first half of the descent phase than in Crozet shags (as are the ascent rates during the last part of the ascent), due to the influence on the data of very slow female Crozet shags (Fig. 4). Different foraging strategies, due to a different type of targeted prey (e.g. benthic vs. shoaling fish), could explain this difference (Cook et al. 2007); however, this is not clear. At the DZ and below, descent rates remain at 1.5 m s^{-1}. The absence of an obvious change of rhythm at this point (except for a small change in the descent rates of the Kerguelen shag) explains why the DZ was not evident on the dive profiles during the descent phase. Theory suggests shags should accelerate the deeper they go because buoyancy decreases with depth. However, because of Boyle's gas law, the greatest volume adjustments under the effect of increasing pressure occur in shallow waters (particularly in the first 10 m). Therefore, volume reductions of shag bodies might not be sufficient to provoke a clearly visible increase in descent rates. Also, below the DZ, because they benefit from a downward assisting force–gravity-shags may reduce paddling activity in order to save oxygen while maintaining swim speed. While ascending below the DZ, blue-eyed

shags have the lowest vertical transit rates of the dive ($\approx$1.2–1.3 m s^{-1}). This could be explained by the lack of buoyancy and the rise against gravity. Shags actually ascend more and more slowly the closer they get to the DZ. We suggest this is because shags feel the return of positive buoyancy and they save energy by reducing their locomotor activity. Vertical ascent rates above the DZ increase steadily from 50 to 60 m all the way back up to the surface. They range from $\approx$1.2 to 1.3 m s^{-1} at the depth of neutral buoyancy to $\approx$1.8–1.9 m s^{-1} near the surface (the highest transit rates of the dive). The increasing influence of buoyancy during ascent can explain how shags accelerate the closer they get to the surface. Future studies using data-loggers measuring locomotor activity (e.g. Watanuki et al. 2003; Wilson et al. 2006) will help clarify how paddling rhythm contributes to the transit patterns of deep diving cormorants.

The buoyancy of a diving air breathing vertebrate is subject to modification. For example, although the method used in this study is clearly not sensitive enough to detect this, prey items ingested throughout the foraging trip may decrease the force of buoyancy between the first and last dives. Similarly, varying fat reserves will cause changes in the buoyancy of divers (Biuw et al. 2003). Consequently, because body conditions of blue-eyed shags can deteriorate between the beginning and the end of the breeding season (personal observation), the costs associated with working against the upward force of buoyancy during the descent phase can be expected to decrease over this period (at Kerguelen, we collected only one carcass in sufficiently good condition to measure its mass and volume—2.202 kg for 2.437 L; the resulting estimated density of one Kerguelen shag carcass during summer is therefore equal to 0.90 kg L^{-1}).

Values for the body condition index were quite similar between the Crozet and Kerguelen shags (Table 1), suggesting this parameter would be insufficient to cause differences in DZ. Furthermore, since the index was slightly higher for the Kerguelen shag, we would expect this species to have the shallowest DZ, and not the opposite, as is the present case. Pre- or intra-dive modulation of respiratory air volume is thought to be a way for divers to regulate their buoyancy according to the maximum targeted depth: too much air and the costs of working against buoyancy during the descent are high, too little and oxygen reserves do not allow for deep dives (Wilson and Zimmer 2004). Penguins vary the depth at which they cease locomotor activity during ascent as a consequence of varying air reserves in relation to maximum dive depth (Sato et al. 2002), and we postulate that blue-eyed shags do the same. This may be why the DZ in Crozet shags switched from 50 to 60 m when targeted maximum dive depth changed from 80–110 m to 110–140 m. We suggest Crozet and Kerguelen

shags have a similar body density and that the reason we detected only one DZ for the Kerguelen shag, at around 50 m, is that its dives did not exceed 108.5 m. Had it dived deeper, then the DZ would probably have switched to a deeper area, as it did for the Crozet shag.

Sex differences

No difference in the depth of neutral buoyancy was observed between the sexes for the Kerguelen shag. Females can be expected to store proportionately more air in their plumage relative to their body mass compared to males, because body surface increases less rapidly than body volume when body mass is increased. This would consequently lead to a deeper DZ in females. If body density increases with body size in blue-eyed shags, our method was not accurate enough to detect this effect on the DZ.

However, significant sex differences were observed in the descent and ascent rates, males transiting faster than females by up to 0.1 m s^{-1} in both localities. Divers will swim at a speed which is optimal in terms of the energy spent relative to the time taken to transit. This is a function of body size, large animals swimming faster at their optimal rate than smaller ones because they are less susceptible to friction and turbulence (Schmidt-Nielsen 1983). Individual differences in swim speed have been detected in relation to body size in great cormorants (*P. carbo*) by Ribak et al. (2005), with larger ones swimming faster. These authors detected a difference of 0.4 m s^{-1} in the average swim speed between individuals with a 10 cm difference in body length. Sex differences in body sizes could be sufficient to explain slower female performance. These diverging performances have a direct consequence on dive cycle management, females being potentially unable to dive into very deep waters or to stay submerged for as long as males, since they lose more time (and therefore oxygen) transiting.

Conclusions

Estimating the DZ appears to be important, considering the implication of this physical frontier in terms of decision-making for divers. Cormorants, like penguins (Wilson and Zimmer 2004), show they may be capable of modulating the amount of air they store in relation to their dive depth, thus reducing buoyancy. The solution for making the best use of natural forces for descending or ascending, compared to the stages where the most effort is made working against these forces, becomes a complex behavioural trade-off.

Females are at a disadvantage, compared to males, if they wish to perform very deep dives. They transit more

slowly than males and, because of their smaller size, they also probably have a greater mass-specific metabolism (Eckert et al. 1999) and smaller oxygen reserves, which consequently limit their diving capacities in terms of dive duration (Schreer and Kovacs 1997; Halsey et al. 2006). Female Crozet shags never dived under 55 m (Cook et al. 2007) and female Macquarie blue-eyed shags did not dive below 62 m (Kato et al. 2000), depths which are close to the DZ defined in this study. The dive duration after which post-dive intervals begin to increase exponentially due to an elevation of anaerobic metabolism (behavioural aerobic dive limit) was defined at around 4 min for the female Crozet shag (Cook et al. 2007). This limit corresponds to the duration of dives that reach a maximum depth close to the 60 m zone. Future studies should tell us whether this is the result of a coincidence—deep dives (and therefore long dives) depleting oxygen reserves—or whether the energy spent per time unit when ascending under the neutral buoyancy barrier (with negative buoyancy and against gravity) is greater than for the other parts of the descent and ascent phases. If so, this can help explain the sudden increase in recovery periods. Whatever the relationship, reasons for crossing the line are probably a direct reflection of particular ecological factors. Diving below the DZ implies that prey found there, benthic fish in this case, are sufficiently large, abundant, or nutritive to compensate for the unfavourable physiological conditions (anaerobiosis) and time-budget constraints (longer post-dive recovery periods) associated with such a strategy.

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