

# Time budget and diving behaviour of chick-rearing Crozet shags

Y. Tremblay, T.R. Cook, and Y. Cherel

**Abstract:** Blue-eyed shags are known to be capable of the deepest dives in the cormorant family. Yet, the way these birds balance their energy and time budgets remains enigmatic. Using ventrally attached time–depth recorders on chick-rearing Crozet shags (*Phalacrocorax melanogenis* Blyth, 1860), we simultaneously described their time budget and diving behaviour. Crozet shags are diurnal, benthic foragers (mean foraging range 1.7 km) that spend 37% of the daytime at sea. While at sea, they spend 49% of their time on the water, 44% diving, and 7% flying, and consume mainly benthic nototheniid fish. Larger fish (>20 g) were caught at shallower depths during shorter trips. They made, on average, 4.4 trips/day, each including 2.5 diving periods of 14 dives. On average, Crozet shags dove to 28 m (max. 145 m) for 2 min 2 s (max. 6 min 11 s). Descent and ascent rates became less variable at a depth of 40 m, possibly owing to a change in bird relative buoyancy at that depth. Ten percent of dives exceeded the estimated behavioural aerobic dive limit (4 min) and diving depths showed a bimodal distribution at <5 and ~18 m for dives lasting ~1 min. This dive duration corresponded to dives with higher dive duration/postdive interval ratios. The Crozet shags managed their dive cycle to fully exploit their breathing capacities, thus optimizing foraging performance.

**Résumé :** Dans la famille des phalacrocoracidae, les cormorans à ventre blanc sont connus pour plonger le plus profondément. Pourtant, la manière dont ces oiseaux gèrent leur budget temps et leur budget énergétique reste énigmatique. En attachant ventralement des enregistreurs de plongée sur des cormorans de Crozet (*Phalacrocorax melanogenis* Blyth, 1860) élevant des poussins, nous avons déterminé simultanément leur budget temps et leur comportement de plongée. Les cormorans de Crozet sont diurnes et se nourrissent sur le benthos (jusqu'à 1.7 km des côtes en moyenne). Ils passent 37 % de la période diurne en mer, dont 49 % du temps posés sur l'eau, 44 % en plongée et 7 % en vol. Ils consomment principalement des poissons nototheniidés benthiques. Les plus gros poissons (>20 g) sont pêchés à de plus faibles profondeurs, pendant des voyages en mer plus courts. Les cormorans font en moyenne 4,4 trajets en mer par jour, chacun composé de 2,5 séquences de 14 plongées. En moyenne, les cormorans de Crozet plongent à 28 m (max. 145 m), durant 2 min 2 s (max. 6 min 11 s). Les taux de descente et de remontée deviennent moins variables à partir de 40 m, ce qui pourrait être dû à un changement de flottabilité relative des oiseaux à cette profondeur. Dix pour cent des plongées dépassent la limite comportementale de plongée aérobie (4 min). Les oiseaux plongent principalement à moins de 5 m et aux environs de 18 m, pendant des plongées d'une minute environ. Cette durée correspond à des plongées pour lesquelles le rapport durée de plongée/intervalle de récupération est le plus grand. Les cormorans de Crozet gèrent leur cycle de plongée de façon à pleinement exploiter leurs capacités respiratoires, optimisant ainsi leur performance d'approvisionnement.

## Introduction

As seabirds are major top predators in the oceans, their role and impact are crucial in understanding marine ecosystem structure and dynamics (Furness and Barrett 1985; Coyle et al. 1992; Woehler 1995; Mehlum et al. 1996; Woehler et al. 2003).

The foraging ecology of seabirds has been a long-standing mystery because seabirds generally feed out of human sight. The development of telemetry in the last 15 years has changed this situation. Progressive miniaturization and improvement of animal-borne devices have enabled researchers

to work on smaller and smaller species, and to monitor more and more parameters, including behavioural (Wanless et al. 1988; Jouventin and Weimerskirch 1990; Handrich et al. 1997; Benvenuti et al. 1998), physiological (Butler and Woakes 1984; Handrich et al. 1997), and environmental variables (Weimerskirch et al. 1995; Charrassin et al. 2002a, 2002b). Seabird activity at sea is crucial in determining animal energetics (Gremillet and Wilson 1999; Shaffer 2004) and prey abundance (Cairns 1987). Since the reaction of individuals to changes in their habitat can be recorded (Burger and Piatt 1990; Bryant et al. 1999), seabirds can now be used effectively as bioindicators of ecosystems.

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Among seabirds, cormorants (Phalacrocoracidae) are typical coastal, benthic, foot-propelled divers (Ashmole 1971; Cooper 1986). They are thought to be extremely efficient in finding and capturing food (Grémillet 1997). Because they have a wettable plumage, little blubber (e.g., compared with penguins), and exhibit high underwater costs of transport (Schmid et al. 1995), their field metabolic rate can be extremely high, especially in cold waters where heat loss is an important factor (Grémillet and Wilson 1999). Among cormorants, species from the "blue-eyed shag complex" (Bernstein and Maxson 1984), which is a complex comprising 13 species resembling each other morphologically and living scattered around the subantarctic ocean between the latitudes of 40°S and 70°S (Orta 1992), are capable of deep diving (Kato et al. 1992; Wanless and Harris 1993). The way these birds balance their energy budget is enigmatic and remains mostly unknown, in part, because obtaining accurate time budgets for birds that both fly and dive is difficult (Grémillet et al. 2003; Tremblay et al. 2003).

The Crozet shag (*Phalacrocorax melanogenis* Blyth, 1860) is the most inshore seabird species of one of the richest seabird communities in the world (Jouventin et al. 1984; Stahl et al. 1985), as it never forages offshore for more than a few kilometres. Yet, its foraging behaviour remains virtually unknown.

In this study, we used the ventral attachment technique (Tremblay et al. 2003) to record simultaneously the time budgets and diving behaviour of Crozet shags. The specific aims of the present study were (i) to test the ventral attachment method on a shag, (ii) to describe for the first time the foraging behaviour of the Crozet shag, and (iii) to explore the behavioural and physiological mechanisms involved in the adaptations of blue-eyed shags to diving.

## Methods

### Study site, birds, and general procedure

Fieldwork was conducted between 28 January and 9 February 1999 at Pointe Basse (46°21'S, 51°42'E), Possession Island, Crozet Archipelago (local time = UTC + 3 h 20 min, where UTC is the coordinated universal time). Twelve Crozet shags from a small colony (13 nests) were studied during the chick-rearing period. The birds were captured by hand at night, between 2220 and 0120. During this period both parents were present at the nest and the chicks had long since been fed. This sampling period gave the birds time to recover from the stress of capture before they went foraging at sea the next morning. Birds were weighed (precision  $\pm 25$  g) using a spring balance, measured for sexing, and a time-depth recorder (TDR) was attached ventrally for a 4- to 5-day period (total initial handling time  $\approx 5$  min). Chicks were counted, and weighed both when the TDRs were deployed on and when retrieved from the adults (age of chicks between 10 and 50 days, estimated from the curve of body mass versus age in chicks on Possession Island; Derenne et al. 1976).

TDRs were retrieved immediately when the birds came back from the sea. Birds were then reweighed and food samples taken. The stomach contents were sampled (one food sample per individual) from birds regurgitating spontane-

ously when handled. Four contents were not retrieved because the birds would not regurgitate. An additional three contents were sampled on chick-rearing individuals from the colony that were not the study birds. Contents were frozen for later analysis in the laboratory. Fish species were determined according to Gon and Heemstra (1999), using the whole fish when it was preserved or the otoliths in the absence of whole fish. Otoliths were measured (precision  $\pm 0.1$  mm), and were used to estimate standard length and wet mass of individual fish with the help of regression equations in the literature (Hecht and Cooper 1986; Hecht 1987; Ridoux 1994; North 1998).

All animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care. This study was approved by the Ethics Committee of the Institut Paul Emile Victor.

### TDR and the ventral attachment technique

Time budget and diving behaviour were studied using TDR MK7 (Wildlife Computers, Woodinville, Washington, USA). These devices were attached ventrally on 12 individuals with cyanoacrylate glue (Loctite 401) and secured with plastic ties (Tremblay et al. 2003). The TDRs were 8.6 cm  $\times$  2.0 cm  $\times$  1.1 cm and weighed 27 g, corresponding to  $\sim 1.1\%$  of the bird's mean body mass and  $\sim 1\%$  of the chest cross-sectional area of Crozet shags ( $\sim 200$  cm<sup>2</sup>). TDR tips were streamlined to reduce drag (Bannasch et al. 1994). The pressure and light sensors used reacted immediately to changes in the environment, while the temperature sensor had a slower reaction time. Thus, TDRs were programmed to record depth and light every 1 s and external temperature every 5 s. Depth and temperature resolutions were  $\pm 1$  m and  $\pm 0.1$  °C, respectively. Light (arbitrary scale) was linearly related to log(illuminance), which is measured in lux (Wanless et al. 1999). Memory was 2.03 MB.

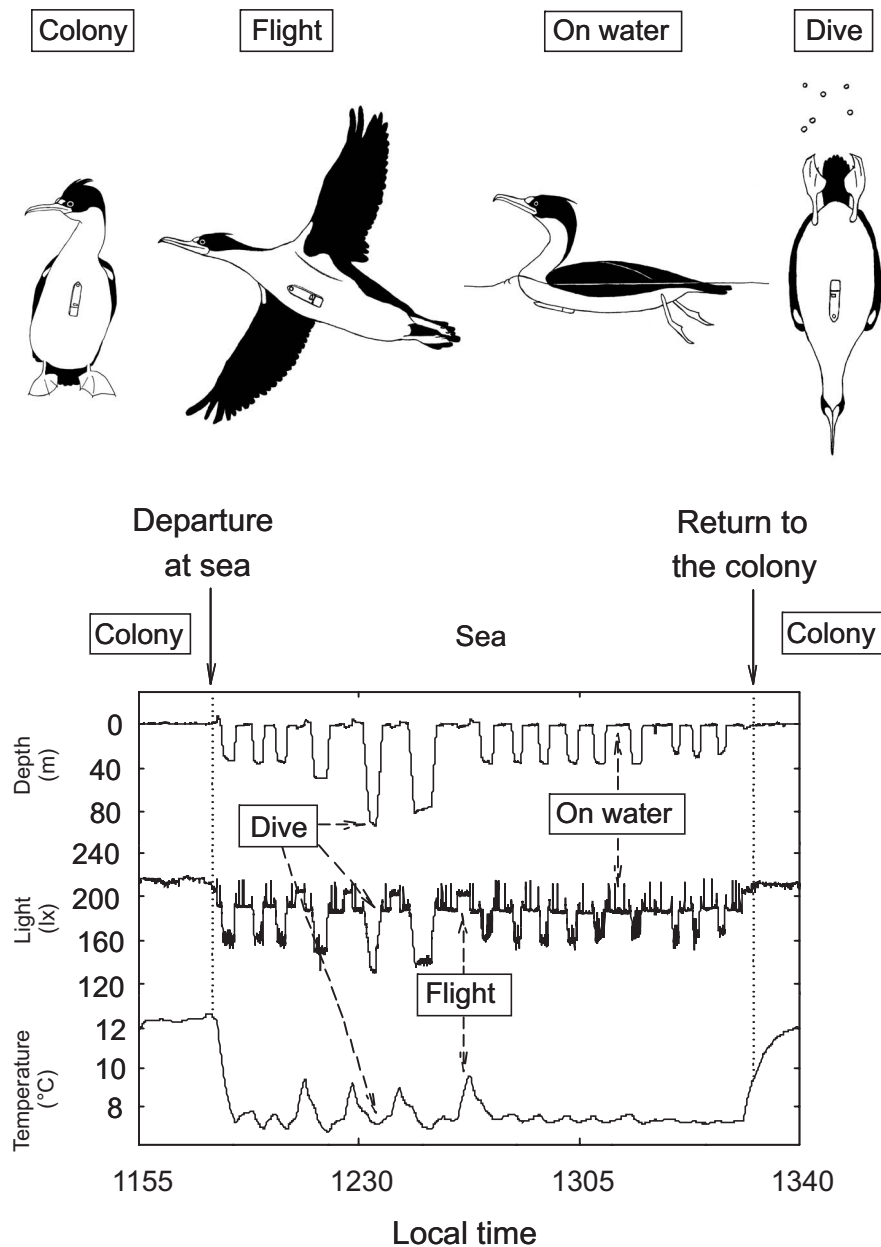
Time-budget analysis was performed using the advantages inherent in the ventral attachment technique (Tremblay et al. 2003) — foraging trips and flights were determined visually through simultaneous readings of depth, light, and temperature in relation to time (Fig. 1). Time at the colony was characterized by higher temperatures, while departures to sea were distinguished by a drop in temperature (owing to windchill). Upon landing on water, temperature dropped rapidly and the light profile shifted to low values. Flights at sea were characterized by rises in temperature and by high light values (Fig. 1). Finally, dives were recorded with the pressure sensor. The precision of the method for timing the beginning or the ending of a given behaviour was estimated to be within  $\pm 1$  s (dives) and  $\pm 5$  s (flights).

### Data analysis and statistics

Daily diurnal time budgets were calculated according to civil day time, which is the time bounded by the two moments when the sun is 6° under the horizon.

The mean radius of the foraging area was estimated using flight durations and a flight speed (m/s) calculated as  $V = 14.7 + 0.154W$  for a Crozet shag exposed to cross winds, where  $W$  is the wind speed (Spear and Ainley 1997). The average wind speed was 10 m/s from a west or northwesterly direction (Tchernia 1978; Aviso/Altimetry Project's 1999

**Fig. 1.** Illustration of the various bird activities recorded in this study, using selected recordings of light, temperature, and depth from a recorder placed ventrally on a chick-rearing Crozet shag, *Phalacrocorax melanogenis*.

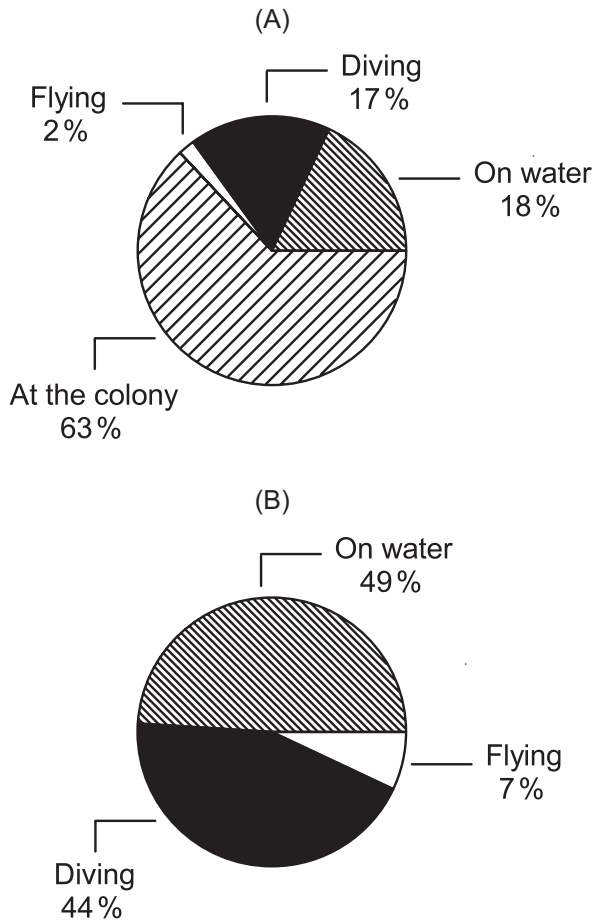


data from the Topex-Poséidon satellite at <http://www.aviso.oceanobs.com>). Crozet shag flight speed was thus estimated as 16.2 m/s. Birds were assumed to fly linearly from one point to another, and never to cut across land (Orta 1992). All recordings indicating that the Crozet shags were perched on land (Fig. 1) were considered to be at the colony.

The dives were analysed using our own software (Y. Tremblay and O. Logette, unpublished program). Since flying necessarily ended a dive bout because the bird potentially changed foraging zone and all dives bounded by two flight events belonged to the same dive bout (no long period of floating on the water without diving), a dive bout was defined as a series of dives bounded by two flights. Because of the resolution of the TDRs, a dive was considered only when it was  $\geq 2$  m. Bottom time was defined as the time spent in

the zone  $\geq 80\%$  of maximum depth (Kato et al. 1999). Rates of descent and ascent were calculated as the ratio between the depths where the bottom times began or ended and the time it took to commute from that depth to the surface, respectively. Postdive intervals (PDI, i.e., periods between successive dives) that were  $>13$  min 20 s (estimated graphically) were excluded from calculation of dive efficiency, because they were likely to represent non-recovery periods at the sea surface (e.g., bathing, preening). Behavioural aerobic dive limit (bADL, i.e., the breath-hold duration after which the organism uses anaerobic metabolism and starts producing lactate, and is estimated from behaviour) was estimated graphically following Kooyman and Kooyman (1995). To assess whether an animal dove serially to a similar depth, we calculated intradepth zone indices for all dives (Tremblay

**Fig. 2.** Daily time budget (A) and time budget at sea (B) of chick-rearing Crozet shags. The daily time budget is calculated for the period of daylight (civil day).

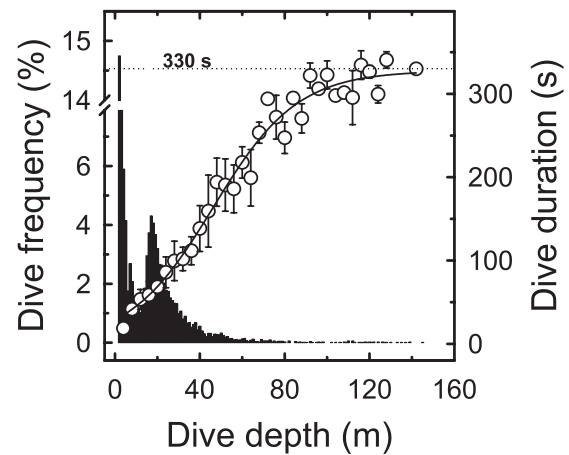


and Cherel 2000). If the maximum depth of a dive was  $\pm 10\%$  of the maximum depth of the preceding dive, it was considered an intradepth zone dive. A high percentage of intradepth zone dives suggests that dives are essentially benthic.

All birds did not contribute equally to the total number of dives, and dives are typically temporally pseudoreplicated (Hurlbert 1984), leading to autocorrelation in the data and thus to increasing probability of making type I errors. A simple way to deal with autocorrelation is to remove a certain number of data (i.e., "rarefaction") specified by a correlogram, which shows the degree of autocorrelation or the lag after which autocorrelation is not statistically different from zero. In our data set, the total number of dives was 8191, varying from 103 to 1377 dives/individual. The individual degree of autocorrelation varied between 3 and 33. By dividing the individual number of dives by the corresponding degree of autocorrelation, we obtained the number of statistically independent dives per individual. The smallest number obtained was 35. By randomly subsampling this number of dives for each individual, we further gave the same statistical weight to all individuals. Although the sample size was considerably reduced in the selected data sets, these were more appropriate for statistical analysis.

Dive parameters were only calculated for dives  $\geq 3$  m ( $N = 393$ ) because shallow dives did not have enough data points

**Fig. 3.** Dive frequency (bars) and dive duration (○; mean  $\pm$  SD) in relation to dive depth in chick-rearing Crozet shags.



to provide accurate measurements. We randomly sampled 10 flights for each bird (the smallest number of outbound/inbound flights per animal; total  $N = 120$ ). Data were analysed statistically using STATISTICA<sup>®</sup> version 6.1 (StatSoft Inc. 1984–2004) and SIGMAPLOT<sup>®</sup> version 8.0.2 (Systat Software Inc. 2002), with an  $\alpha$  level of  $P < 0.05$ . Values are means  $\pm$  SD.

## Results

A simultaneous reading of depth, light, and temperature profiles in relation to time enabled us to distinguish between the different bird activities in the same way that common guillemots, *Uria aalge* (Pontoppidan, 1763), were previously studied using this method (Tremblay et al. 2003). Four activities were identified: presence at the colony, flights, periods on the sea surface, and dives. No bird deserted its nest and no recorder was lost during the experiment. In all, 55 full cormorant-days were recorded, revealing a total of 243 trips at sea, 952 flights, 606 dive bouts, and 7770 dives.

### Time budget and foraging range

Trips at sea were exclusively diurnal (start of earliest trip 12 min after the beginning of civil day, finish of latest trip 8 min after the end of civil day). The number of trips per bird was  $4.4 \pm 0.9$ /day (range 2–9). Overall, 6.6% of the 243 trips did not include any dives, and 75% of such trips were the first one of the day, 18.8% the second, and 6.2% the last. Trips without a dive were short ( $9 \pm 7$  min) compared with trips (94.4%) that included dives ( $1 \text{ h } 25 \text{ min} \pm 25 \text{ min}$ , range 8 min to 6 h 23 min).

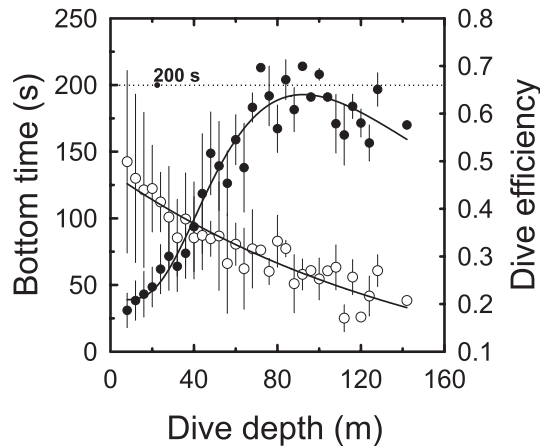
The intertrip interval (time spent at the colony between two trips) was  $1 \text{ h } 50 \text{ min} \pm 27 \text{ min}$  (range 2 min 31 s to 6 h 23 min). During the 15 h 50 min of day time, Crozet shags spent 63% and 37% of their time at the colony and at sea, respectively. While at sea, they spent 7% of their time flying ( $23 \pm 06 \text{ min}$ ), 49% resting on the sea surface ( $2 \text{ h } 56 \text{ min} \pm 37 \text{ min}$ ), and 44% diving ( $2 \text{ h } 39 \text{ min} \pm 46 \text{ min}$ ) (Fig. 2).

Pairs having more chicks to feed ( $1.8 \pm 0.7$  chicks, range 1–3 chicks) did not significantly change the number of foraging trips (Spearman's rank correlation,  $R_s = 0.80$ ,  $P = 0.191$ ), but there was a trend for increasing the total time

**Table 1.** Mean  $\pm$  SD values and range for the main diving parameters in the Crozet shag, *Phalacrocorax melanogenis* ( $N = 393$ ; see Materials and methods).

	Dive depth (m)	Dive duration (s)	Bottom time (s)	Dive efficiency*	Vertical descent rate ( $\text{m}\cdot\text{s}^{-1}$ )	Vertical ascent rate ( $\text{m}\cdot\text{s}^{-1}$ )	PDI (s)	Dive duration/PDI interval
Mean $\pm$ SD	28 $\pm$ 27	122 $\pm$ 22	84 $\pm$ 55	0.38 $\pm$ 0.13	1.41 $\pm$ 0.36	1.65 $\pm$ 0.46	138 $\pm$ 156	1.48 $\pm$ 0.94
Range	2–145	2–371	0–241	0–0.85	0.1–4	0.1–4	0–800	0.08–9

\*Dive efficiency is calculated as bottom time/(dive duration + PDI), where PDI is postdive interval.

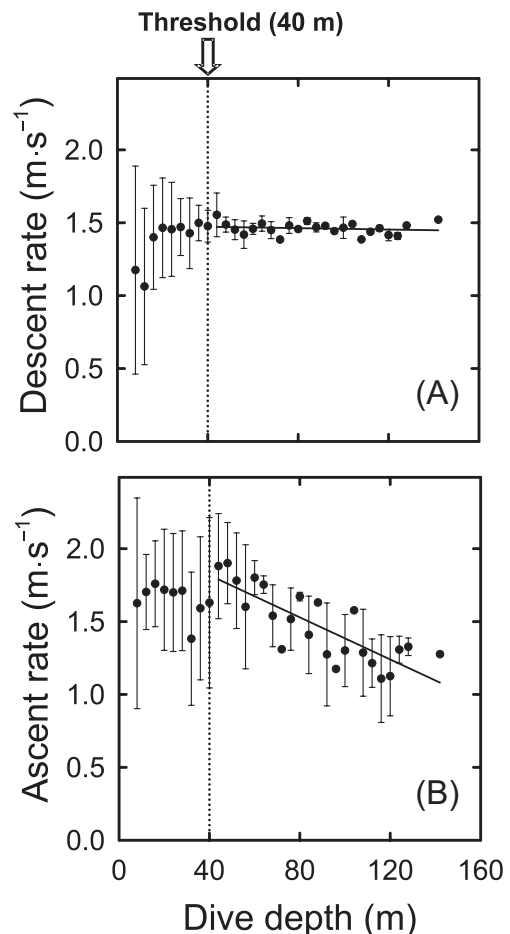
**Fig. 4.** Time spent at the bottom of dives (●) and dive efficiency (○; bottom time/(dive duration + PDI), where PDI is postdive interval) in relation to dive depth in chick-rearing Crozet shags. Values are means  $\pm$  SD.

spent at sea ( $R_S = 0.80$ ,  $P = 0.054$ ). There was also a trend for pairs feeding chicks with higher cumulative total mass ( $3313 \pm 1181$  g, range 675–6475 g) to increase the total time that they spent at sea ( $R_S = 0.77$ ,  $P = 0.072$ ) or to increase the total number of trips ( $R_S = 0.83$ ,  $P = 0.042$ ).

The 12 study birds completed a total of 260 inbound/outbound flight pairs (counting incomplete days of recording). The shortest flight (outbound) lasted 7 s, and the longest (inbound) lasted 11 min 27 s. Outbound flights were shorter than inbound flights in 65% of the cases. Outbound flights lasted 1 min 20 s  $\pm$  1 min 10 s, whereas inbound flights lasted 1 min 46  $\pm$  1 min 10 s (paired  $t$  test,  $t = 3.54$ ,  $P < 0.001$ ). Outbound flights of trips without dives lasted 32  $\pm$  19 s ( $N = 17$ ). The foraging radius was 1.7  $\pm$  1.1 km (estimated from return flights to the colony). Therefore, the foraging area was 4.7  $\pm$  2.0 km<sup>2</sup>, the equivalent of 3.5  $\pm$  2.3 km of straight coastline.

### Diving behaviour

All dives were carried out in water at 8 °C (sea surface) and at 6 °C (absolute maximum depth). The number of diving bouts per bird was 10.8  $\pm$  2.9/day (4–31) or 2.5  $\pm$  0.6 bouts/trip. The number of dives per bird was 141  $\pm$  82/day (range 1–157), with 31  $\pm$  15 dives/trip, or 14  $\pm$  10 dives/diving bout. The number of diving bouts increased with trip duration ( $R^2 = 0.24$ ,  $N = 606$ ,  $P < 0.0001$ ), as did the number of dives ( $R^2 = 0.44$ ,  $N = 7770$ ,  $P < 0.0001$ ). Eighty-nine percent of the trips included  $< 5$  dive bouts. Diving depths showed a bimodal distribution, with one peak at very shallow dives ( $< 5$  m) and a second peak at  $\sim 18$  m (Fig. 3). The

**Fig. 5.** Vertical descent (A) and ascent (B) rates in relation to dive depth in chick-rearing Crozet shags. The threshold at 40 m represents the depth at which the birds are hypothesized to be neutrally buoyant (see text and Fig. 8 for details). Values are means  $\pm$  SD.

maximum depth reached during any single dive was 145 m. Detailed diving parameters are shown in Table 1.

Dive duration increased with dive depth and levelled off at  $\sim 5$  min 30 s ( $R^2 = 0.98$ ,  $P < 0.0001$ ; Fig. 3). Bottom times, i.e., periods when the bird was at  $\geq 80\%$  of maximum dive depth, increased with dive depth ( $R^2 = 0.93$ ,  $P < 0.0001$ ; Fig. 4), levelled off at  $\sim 3$  min 20 s, and then decreased for dives  $\geq 90$  m in depth. Dive efficiency, calculated as bottom time/(dive duration + PDI), decreased with dive depth ( $R^2 = 0.87$ ,  $P < 0.0001$ ; Fig. 4).

The vertical rate of descent was highly variable for dives between 0 and 40 m, which then stabilized at  $\sim 1.5$  m/s for dives reaching greater depths ( $y = -0.0002x + 1.48$ ,  $R^2 = 0.025$ ,  $N = 111$ ,  $P = 0.466$ ; Fig. 5A). The vertical ascent rate

**Fig. 6.** Postdive interval (PDI) in relation to dive duration in chick-rearing Crozet shags (A;  $N = 8191$  dives). The abrupt slope change in the line joining the lowest values of PDIs theoretically defines the behavioural aerobic dive limit (bADL  $\approx 240$  s), and splits dives between aerobic (shorter dives) and anaerobic (longer dives) dives, respectively. The highest dive duration/PDI ratios occurred at  $\sim 60$  s (B). The PDIs of aerobic dives in relation to dive duration (C) showed a slope change at dives lasting 60 s, corresponding to the dive duration that was mostly used by the birds (D), in accordance with the optimal breathing theory (Walton et al. 1998). Dive frequencies correspond to the proportion of dives in the three duration classes defined by these two thresholds.

was also variable for dives between 0 and 40 m, which then decreased linearly for deeper dives ( $y = -0.0072x + 2.11$ ,  $R^2 = 0.66$ ,  $N = 111$ ,  $P < 0.0001$ ; Fig. 5B).

PDIs ( $< 13$  min 20 s) lasted  $2$  min  $16$  s  $\pm$   $2$  min  $29$  s. In terms of time budget, extended PDIs were insignificant because of their low occurrence (10 out of 8191) and their relatively small duration ( $16$  min  $40$  s  $\pm$   $3$  min  $20$  s).

Behavioural ADL was estimated at  $\sim 4$  min ( $N = 8191$ ; Fig. 6A), and  $\sim 10\%$  of dives lasting longer than that limit ( $N = 420$ ; Fig. 6D). The dive duration/PDI ratio increased rapidly for short dives, was maximum for dives lasting 1 min, and then decreased regularly to the longest lasting dives ( $R^2 = 0.60$ ,  $N = 420$ ,  $P < 0.0001$ ; Fig. 6C). A plot of the PDIs in relation to dive duration for dives lasting  $< 4$  min (aerobic dives) was linear with slope  $\approx 0$  for dives  $< 1$  min ( $y = 0.09x + 19.36$ ,  $R^2 = 0.12$ ,  $N = 153$ ,  $P = 0.490$ ; Fig. 6B), but positive and steeply inclined for dives lasting  $> 1$  min ( $y = 1.50x - 63.78$ ,  $R^2 = 0.74$ ,  $N = 226$ ,  $P < 0.0001$ ; Fig. 6B).

### Dive profiles and diet

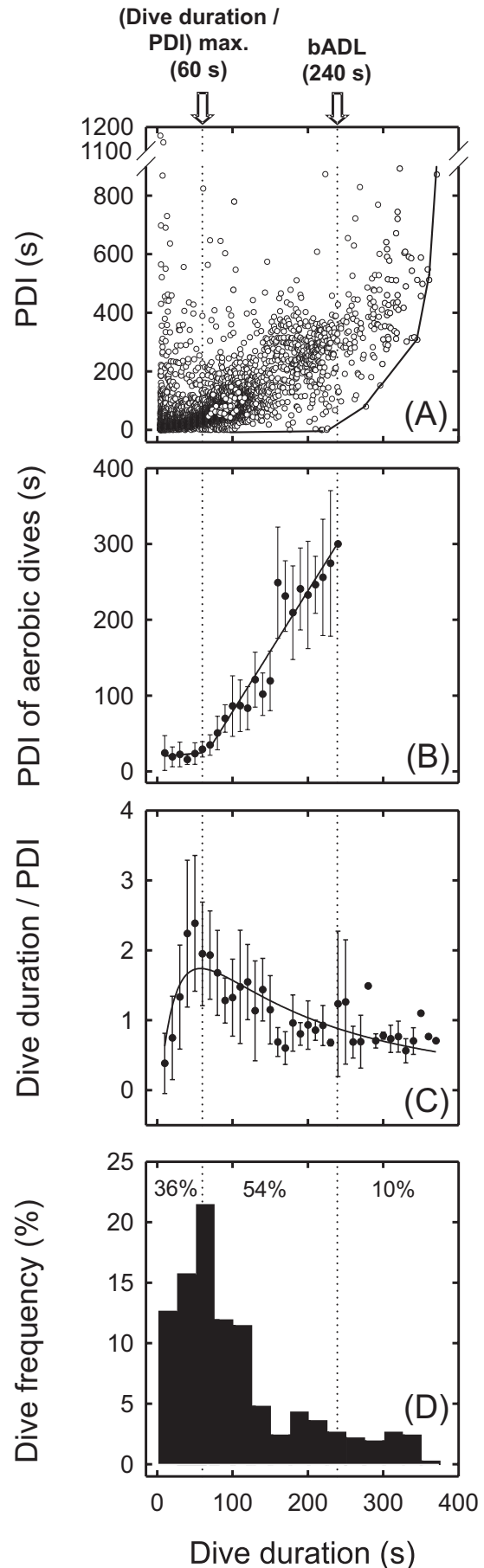
Eighty-three percent of dives were U-shaped (Fig. 1), while 12% and 5% were W- and V-shaped, respectively. There were  $57\% \pm 49\%$  intradepth zone dives.

Stomach contents produced fresh prey items (fresh fraction) and no accumulated fraction (except in one content with the beaks of two nereid annelids). Apart from one annelid (Polynoidae), two crustaceans (*Nauticaris marionis* Bate, 1888; Hippolytidae), and an undetermined species, 100% of the stomach contents were benthic nototheniid fish (Table 2). Stomach-content mass was  $164 \pm 73$  g (67–300 g,  $N = 11$ ). The number of fish items per content was  $21 \pm 20$ , and estimated wet mass of individual fish was  $10.8 \pm 19.3$  g ( $N = 156$ ). We were able to associate foraging trip parameters with seven of the stomach samples. Birds that preyed upon bigger fish tended to dive to shallower depths (mean fish wet mass =  $88.42e^{-0.097(\text{mean diving depth})}$ ,  $R^2 = 0.88$ ,  $N = 7$ ,  $P = 0.002$ ) and stayed at sea for shorter durations (mean fish wet mass =  $64.26e^{-0.012(\text{trip duration})}$ ,  $R^2 = 0.66$ ,  $N = 7$ ,  $P = 0.025$ ) (Fig. 7). Catch per unit time was  $0.15 \pm 0.11$  fish/min, corresponding to  $1.85 \pm 1.37$  g/min and  $0.6 \pm 0.8$  fish/dive.

## Discussion

### The method

The ventral attachment technique was a successful method for studying the time budget and the diving behaviour of the Crozet shag. It allowed the recording of four different be-



**Table 2.** Fish species, size, and numbers in stomach contents of 11 Crozet shags.

Fish species	Occurrence (no. of samples)		No. of individuals identified for each fish species		No. of individuals measured for each fish species		OL (mm)	SL* (mm)	Mass <sup>†</sup> (g)
	N	%	N	%	N	%			
<i>Paranotothenia magellanica</i>	8	72.7	154	73.3	115	73.3	63±24 (30–176)	8.5±15.7 (0.6–119.4)	
<i>Gobionotothen marionensis</i>	2	18.2	36	17.1	22	17.1	54±38 (8–121)	9.8±12.4 (<0.1–54.8)	
<i>Lepidotothen larseni</i>	1	8.3	18	8.6	18	8.6	104±29 (71–165) <sup>‡,§</sup>	18.9±16.8 (4.5–61.6) <sup>§</sup>	
<i>Notothenia corriceps</i>	1	8.3	1	0.5	1	0.5	186	151.2	
<i>Muraenolepis</i> sp.	1	8.3	1	0.5	1	0.5	—	—	

**Note:** Mean and range are given for measured otolith length (OL), and for estimated fish standard length (SL) and fish wet mass.

\*SL was estimated after calculating a regression between the measured SL of preserved fish individuals and OL (*P. magellanica*: SL = 64.8000OL - 8.6126, R<sup>2</sup> = 0.70, N = 14, P < 0.001;

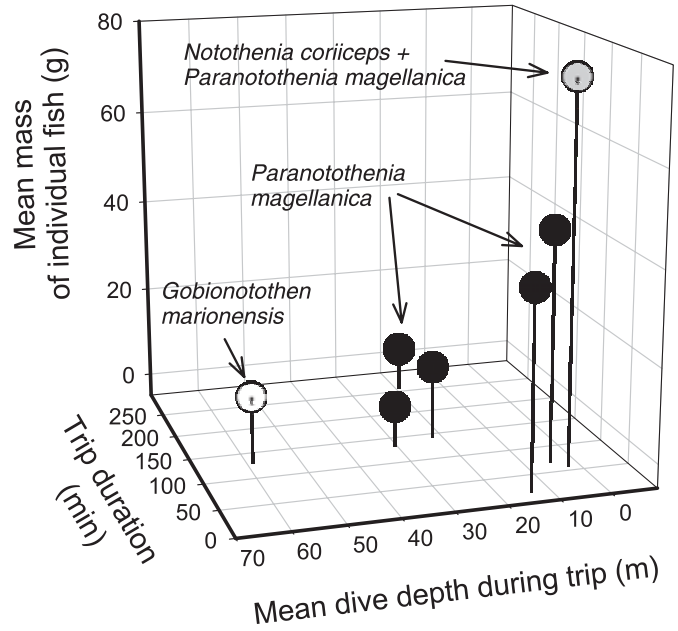
*G. marionensis*: SL = 35.6194OL - 25.8507, R<sup>2</sup> = 0.95, N = 8, P < 0.0001).

<sup>†</sup>Mass was estimated using the regressions calculated in Hecht and Cooper (1986) and North (1998).

<sup>‡</sup>Total length rather than SL.

<sup>§</sup>Total length and M were estimated according to Hecht (1987) and Ridoux (1994).

**Fig. 7.** Mean wet mass of individual fish in the stomach contents of chick-rearing Crozet shags in relation to trip duration and mean dive depth during the trip.



haviours: presence at the colony, flying, at the sea surface, and diving. Only one type of behaviour was observed at the sea surface (resting), contrary to the study by Tremblay et al. (2003) on the common guillemot where active periods were recorded, such as swimming, wing flapping, or preening. As for the common guillemot, the ventral attachment technique enabled the estimation of the foraging radius, using TDRs that were not initially conceived for this purpose. We also showed that 5.6% of all dives were followed by a PDI event, a flight event, and finally, an at surface pre-dive event. Such postdive flights indicate the end of a diving bout and are an energetically costly behaviour. Therefore, the intervals measured between the end of such dives and the beginning of a new dive were not equated to recovery times, as was potentially the case in other studies. This refinement cannot be obtained using a dorsal attachment, a method that may consequently lead to different PDI estimates in species that can change foraging areas between dives through flight.

Stress caused by the ventral attachment of the TDRs was not measured in this study. Tremblay et al. (2003) assessed the stress associated with the method in common guillemots by comparing variation in body mass and hormone levels in plasma between experimental and control birds. They detected no effects on the common guillemots, a species considerably smaller than the blue-eyed shag. A carried device constituting 3% of the animal's body mass has been suggested as the limit above which an animal is considered to be hampered (Kenward 1987), and that value was ~1.1% in our study. The success of the ventral attachment technique in blue-eyed shags encourages the general use of the method for investigating the foraging behaviour of diving and (or) nondiving flying seabirds.

**Time budget**

Birds spent 6 h/day at sea, 20 min of which were spent flying, 2 h 40 min diving, and 3 h at the surface. These val-

ues are similar to those found by Wanless et al. (1995) in chick-rearing shags from South Georgia. Their study was conducted using radiotelemetry, and is the only pre-existing work on the time budget of blue-eyed shags. These authors also observed 26 min/day spent on land, but not at the colony. The method used in our study did not distinguish between such behaviour, because all time spent on land was considered, by default, as taking place at the colony. Time at sea is also similar to the value found by Green and Williams (1997) in shags from Heard Island, although the stage of the chicks was not identified by these authors. The average number of foraging trips per day was of 2.5 in both South Georgia and Heard Island, whereas it was of 4.5 at Possession Island.

There was a trend for brood size, expressed as the number of chicks or as the cumulative mass of chicks, to positively influence the time spent at sea, but not the number of trips, as was the case in the study by Wanless et al. (1995) on chick-rearing South Georgian shags. This suggests that parents rearing more chicks could have worked harder, keeping the same number of daily trips, but extending these in time. Also, this could suggest that brood reduction may occur when suitable feeding conditions are not met. Since the relationships in the present study were weak, further studies are required that would better take into account chick brood size and age, follow parental investment over a longer period of time, and have a greater number of study birds.

Periods at sea were devoted almost exclusively to foraging activity. Indeed, birds rarely stayed at the sea surface for extended PDIs. In contrast, common guillemots studied with the ventral attachment technique showed periods of reduced activity at sea (Tremblay et al. 2003). This suggests that our study birds worked efficiently during this period and spent the minimum possible time in cold water.

A few short trips carried out mostly as the first trip of the day, which necessitated short commuting times and did not include dives, were assumed to be linked to bathing/preening activity. No trip or dive took place at night (outside civil day time), which confirms the high dependence of shags on daylight when foraging (Wanless et al. 1999). The use of the civil day to define the period when Crozet shags can forage seems appropriate, as the start of the earliest trip and the finish of the latest trip were just only slightly after the beginning and the end of civil day, respectively.

Mean flight time from colony to splash down was close to values reported in several other studies on the blue-eyed shag. In South Georgia, Wanless and Harris (1993) measured flights lasting, on average, 2 min 42 s, and Bevan et al. (1997) distinguished, on average, long flights lasting 3 min 41 s and short flights lasting <30 s. Flights to sea were significantly shorter than flights coming back to the colony. Thus, the birds moved progressively away from the colony while foraging. By moving away during a foraging trip, shags may have had to dive deeper and stay at sea longer, which could be associated with a change in targeted prey (Fig. 7). Conversely, targeting bigger fish (fresh mass over 20–30 g) might have permitted if successful a quicker return to the colony and to shallower dives, and thus, it may be a way of reducing energy costs at sea. We suggest that the availability of fish over 20 g is likely to be a crucial attribute in the foraging grounds used by Crozet shags.

### General diving behaviour and diet

The Crozet shag is a shallow diving bird with a deep-diving capacity that is only rarely used. Most dives (77%) were <40 m deep, with some dives reaching down to 145 m. To our knowledge, the deepest dive recorded previously was 125 m for the South Georgian shag (Wanless and Harris 1993).

The Crozet shag's foraging constitutes a strategy of inshore benthic feeding characterized by the vast majority of dives being U-squared shape, the percentage of intradepth zone dives being high, prey found in the diet being benthic, the trips at sea being numerous and short, and the rate of diving being high over depths within the calculated foraging range. This strategy was earlier described in blue-eyed shags (Croxall et al. 1991), and generally, is common to cormorants (Orta 1992). The prevalence of benthic nototheniid fish, as well as the few specimens of polychaetes and crustaceans also found in the stomach contents, corresponds to the diet earlier described by Ridoux (1994) for the Crozet shag. Our results also confirm that fish are the favoured prey of blue-eyed shags during the breeding season (Casaux and Barrera-Oro 1993; Coria et al. 1995; Casaux et al. 1997), and suggest that our study birds exhibited a typical behaviour for this time and place.

It is possible, because of thermoregulatory constraints and foraging effort, that the study birds digested some food at sea. Therefore, the fraction sampled at the colony could have been destined only for the chicks. In addition, prudence is needed when estimating the catch per unit time (calculated here as  $0.15 \pm 0.11$  fish/min), as digestion at sea may lead to the disappearance through the gastrointestinal tract of the smaller otoliths of digested fish. Also, the accumulated fraction, which contains the bigger otoliths of digested fish that enter the gastrointestinal tract with difficulty, does not appear in the contents sampled here. This fraction is usually evacuated as pellets (regurgitated casts). Casaux et al. (1997) estimated a daily regurgitation rate of 0.7 pellets in chick-rearing *Phalacrocorax bransfieldensis* Murphy, 1936 (South Shetland), representing 255 g of fish/day. It is therefore probable the catch per unit time was somewhat underestimated in this study.

Benthic diving is generally described as a costly strategy (especially at great depth), since the distances between the surface and the prey patches are at a maximum (Wilson and Wilson 1988). In addition, benthic foragers are restricted to areas where the benthos is accessible given the diver's physiological capabilities, thereby potentially promoting intraspecific competition. In response to such constraints, benthic divers tend to push their physiological limits (Tremblay and Cherel 2000, 2003; Costa et al. 2001; Costa and Gales 2003) and to manage their dive cycle to maximize bottom time.

### Dive-cycle management

#### *Transit rates and buoyancy*

In our study, rates of descent and ascent were highly variable for dives reaching <40 m. For dives >40 m, descent rates stabilized at 1.5 m/s, and ascent rates decreased linearly with dive depth (Fig. 5). To our knowledge, this is the first observation of such behaviour among diving animals. A constant descent rate of 1.5 m/s was also found in *Phalacro-*



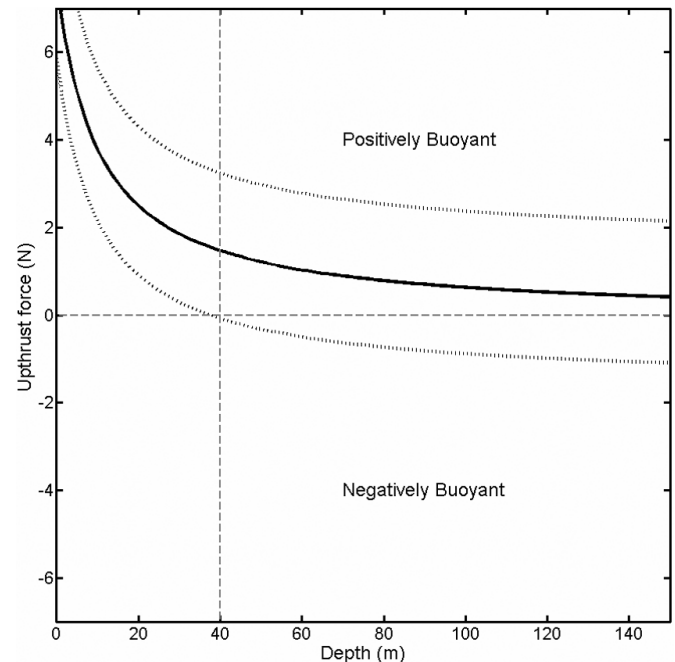
*orax atriceps* King, 1828, but the ascent rate was also 1.5 m/s and it remained constant with increasing depth up to 70 m (Wilson and Quintana 2004). Reducing ascent rates when diving deeper may be the outcome of an oxygen-saving strategy, because reducing swimming speed (thus ascent rate) permits reduced oxygen consumption (Kooymann and Davis 1987). Low ascent rates could also relate to a strategy for avoiding decompression sickness (Sato et al. 2002). This would be especially true when dives become very deep. In the future, using data loggers that measure underwater swimming speed, acceleration, and dive angles may improve our understanding of the ascent phase.

The ways in which our study birds managed the descent phase were also unclear. If the upthrust force remains positive for all dive depths, the bird must propel itself actively from the surface to the maximum depth. According to Wilson et al. (1992), a 1-kg cormorant is neutrally buoyant at 103 m of fresh water. Reusing the same model, we recalculated the upthrust force for a 2.3-kg cormorant in seawater (Fig. 8). According to this model, our study animals were never negatively buoyant within the depth range that they use. However, this model is based on air volume in the feathers and in body density calculated for two other species of cormorants exhibiting large differences in those parameters (see appendix in Wilson et al. 1992). Assuming a different volume of air in the feathers and body density, we calculated that our study birds would be negatively buoyant below 40 m if they had only 7% less air in the feathers and were only 7% denser, compared with the values given in Wilson et al. (1992) for cormorants (Fig. 8). If 40 m was the threshold depth at which the cormorant's apparent mass becomes negligible, descent could occur through passive sinking beyond that threshold. This strategy could be another way of reducing oxygen consumption during a dive.

Although blue-eyed shags are expected to have more air in the plumage as a response to cold water (Grémillet et al. 1998), there are no data available on this point. In addition, nothing is known about the ability of the blue-eyed shag to regulate its buoyancy by altering the volumes of air in its respiratory system or plumage, or about the effect of ingested prey on buoyancy. The relationship between upthrust force and depth (Fig. 8) implies that the depth threshold for change in buoyancy is extremely sensitive to body air volume and overall body density. It also shows that the upthrust force is about 5 times smaller at 40 m than at the surface, and mostly <1 N. Thus, even with a positive (but small) upthrust force, a combination of stroking and gliding could potentially be used for propulsion (Williams et al. 2000; Lovvorn et al. 2004). Passive sinking has been shown to reduce energy expenditure in diving Weddell seals (*Leptonychotes weddellii* (Lesson, 1826)) (Williams et al. 2000), and has been observed in other mammals and penguins (Crocker et al. 1997; Sato et al. 2002). This strategy may also apply to Crozet shags during deep dives, although closer examination of swim speed and propelling activity is needed to confirm this fact (Lovvorn et al. 2004).

The time allocated to the different dive phases (descent, bottom, ascent, and recovery period) is heavily dependant on the maximum dive depth attained, but also on parameters such as the predictability and density of prey (Cornick and Horning 2003). Based on optimal foraging considerations,

**Fig. 8.** Estimated upthrust force experienced by a 2.3-kg Crozet shag in salt water in relation to depth (solid line). The upper and lower broken lines represent the same force calculated for 7% more or less air in the plumage and 7% lower or higher body density, respectively. At the depth where the upthrust force becomes zero, birds switch from being positively to negatively buoyant. The proposed threshold at 40 m represents the depth at which the relationship between vertical transit rates and depth changed in this study (see text and Fig. 5 for details).



divers (particularly benthic divers) are expected to maximize the time they spend at the bottom of the dives (Charnov 1976; Pyke et al. 1977). Minimizing transit rates through changes in swimming speed or angles of descent and ascent (Wilson 1995; Ropert-Coudert et al. 2001; Charassin et al. 2002; Tremblay and Cherel 2003; Tremblay et al. 2003) — as discussed here — and relying on the management of the oxygen reserves are two common solutions to meet this demand.

#### Oxygen reserves

The longest dive lasted 6 min 11 s, a value similar to the maximum dive duration previously recorded for a blue-eyed shag (6 min 20 s for the South Georgian shag; Wanless et al. 1992). Therefore, unless new data change radically our knowledge on the blue-eyed shag complex, it appears that the physiological dive limit of this group is between 6–7 min.

Wanless and Harris (1993) found that dive duration reached a threshold at 3 min 45 s (for dives 50 m deep). They estimated the behavioural ADL at 2 min 54 s, with 50% of the dives lasting longer. In our study, a threshold was reached at ~5 min 30 s (for dives 140 m deep). We estimated a behavioural ADL of 4 min, with 10% of dives including an anaerobic phase. Given differences in methodologies, more work is needed to assess this apparent difference in diving capacities between species within the blue-eyed shag complex. So far, the diving performances of the Crozet shag seem to be maximal in the family.

Similar to *P. atriceps* in Argentina (Wilson and Quintana 2004), our study birds increased bottom time with increasing diving depth up to ~70 m. However, for the deepest “anaerobic” dives (>80–90 m), bottom time decreased with increasing dive depth. Dive efficiency, calculated as bottom time/(dive duration + PDI), decreased continuously with increasing dive depth. Burger (1991) hypothesized that the use of anaerobiosis was a strategy for extending bottom time, therefore increasing the probability of prey capture. In our study, deep-diving birds were unable to increase or even to maintain constant bottom time. Shorter bottom times and lower dive efficiencies at greater depth are only desirable for birds if deep dives provide particular advantages such as a greater probability of locating rich prey patches with a high catch per unit time.

The diving behaviour of *P. atriceps* in Argentina suggested that it submerged with substantial reserves of oxygen that went unused during a dive (Wilson and Quintana 2004). Because the Argentinian birds did not dive deeper than 70 m (half the range in our study birds), we believe that they were probably most frequently diving, as in our study, well below their maxima in terms of dive depth and duration.

The dive duration/PDI ratio of Crozet shags increased for short dives, was maximum for dives lasting 1 min, then decreased for dives >1 min (Fig. 6C) as described by Walton et al. (1998). The study of the PDIs in relation to dive duration for aerobic dives (<bADL = 4 min) revealed two linear relations: a horizontal one for dives lasting <1 min, and another, positive and steep, for dives lasting between 1 and 4 min (Fig. 6B). These two lines may represent two phases of oxygen consumption (from the respiratory tract and from haemoglobin/myoglobin stores, respectively). The relations fit with the model proposed by Walton et al. (1998) for oxygen usage in a diving bird. As long as the respiratory oxygen is not exhausted, recovery times do not vary — it takes the same time for a bird to renew its oxygen through the turnover of the respiratory gases after a 5-s dive as after a 1-min dive. Dives lasting 1 min would thus represent an optimal choice as far as the use of oxygen reserves is concerned. The frequency of dive duration showed a strong percentage of dives lasting ~1 min: 41% of all dives lasted between 30 s and 1 min 30 s (Fig. 6D). This suggests that this dive duration is targeted by the birds to optimize dive duration to PDI ratios.

### Thermoregulation and prey-patch requirements

Compared with *Phalacrocorax carbo* (L., 1758) in Greenland during the summer, our study birds spent more than 5 times longer and dove, on average, 8 times deeper in waters that were only 2 °C warmer (7 °C) than the waters off Greenland. They also caught about 15 times fewer fish (Grémillet et al. 2001). Bernstein and Maxson (1982) suggested that the blue-eyed shag’s plumage is as water repellent as any other cormorant. However, according to Grémillet et al. (1998), the blue-eyed shag’s plumage is more waterproof and they incorporate more air in their feathers when diving. Although *P. carbo* and *Phalacrocorax aristotelis* (L., 1761) maintain a high body temperature during diving (Grémillet et al. 1998), South Georgian shags decrease heart rate and abdominal temperature, thus minimizing thermoregulatory costs (Bevan et al. 1997). Because water

temperature and diving depth affect diving costs and energy requirements (Grémillet and Wilson 1999), it is likely that our study animals processed food at sea, and that our collected stomach contents did not represent the whole catch of the trip but only the portion brought to the chick.

Finally, given the record diving performance exhibited by Crozet shags and their relatively small estimated foraging area (4.7 km<sup>2</sup>), we believe that these birds are constrained to forage on very profitable prey patches. Such dependence has been suggested as an important condition for cormorants foraging in cold water (Grémillet et al. 2001). Biogeographically, the availability of rich prey patches is likely to be a key characteristic of ecosystems hosting any species from the blue-eyed shag complex.

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