UNDERWATER SWIMMING AT LOW ENERGETIC COST BY PYGOSCELID PENGUINS

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Summary

Energetic requirements of under-water swimming in pygoscelid penguins were studied in Antarctica, using respirometry together with a 21 m long swim canal and externally attached devices recording the swimming speed and dive duration of unrestrained animals. Field measurements were compared with measurements of the hydrodynamic properties of an Adélie penguin model in a circulating water tank. Minimum transport costs during underwater swimming in Adélie (*Pygoscelis adeliae*), chinstrap (*P. antarctica*) and gentoo (*P. papua*) penguins averaged 4.9, 3.7 and 7.6 J kg^{-1} m^{-1}, respectively, at their preferred swimming speeds of 2.2, 2.4 and 1.8 m s^{-1}, allowing the birds to dive aerobically for 110, 130 and 93 s, respectively. From the swim canal measurements, we calculated a drag coefficient (C_D) of 0.0368 for a typical Adélie penguin at 2.2 m s^{-1}. This value is significantly lower than the C_D of 0.04 of an ideal spindle and the C_D of 0.0496 measured on the model in the laboratory. The reasons for this difference are discussed.

Introduction

Penguins, seals, dolphins and other sub-surface swimmers appear to move effortlessly through the water, gliding for long distances. Determination of the energetic costs of swimming, however, has proved difficult. In water flumes (Woakes and Butler, 1983; Baudinette and Gill, 1985; Ponganis *et al.* 1990), animals mainly swim at the surface, are forced to maintain a stationary position, cannot move freely or chose their own swimming speeds and incur turbulence and increased drag from the surrounding cage. Energy consumption of animals in the wild has been measured indirectly through heart rate (Woakes and Butler, 1983; Williams *et al.* 1992) or by using doubly labelled water (Nagy *et al.* 1984; Culik and Wilson, 1992; Chappell *et al.* 1993*b*), a technique requiring a number of assumptions (Culik and Wilson, 1992; Wilson and Culik, 1993) and careful interpretation of results.

In Antarctica, we used a 21 m long, still-water canal in conjunction with respirometry to determine directly the energy requirements of freely swimming Adélie (*Pygoscelis adeliae*; Hombron and Jacquinot), chinstrap (*P. antarctica*; Forster) and gentoo (*P. papua*; Forster) penguins. Swimming speeds and dive durations of penguins in the wild were determined using externally attached (Wilson and Wilson, 1989) data-loggers measuring speed, depth and direction (Wilson *et al.* 1993), which had been specially shaped to minimize hydrodynamic drag (Bannasch *et al.* 1994; Culik *et al.* 1993). Results were compared with those from investigations on the hydrodynamic properties of a life-size, plastic-cast model (Bannasch and Fiebig, 1992) of a swimming Adélie penguin.

Materials and methods

All experiments on living penguins were carried out at Ardley Island (62°13′S, 58°55′W), South Shetland Islands, Antarctica, in January 1992. Adélie (*N*=12, body mass 4±0.4 kg; mean ± S.D.), chinstrap (*N*=7, body mass 3.8±0.3 kg) and gentoo (*N*=10, body mass 5.5±0.6 kg) penguins were caught on a nearby beach and inserted into one of two respiration chambers (one at each end of the canal) for experiments lasting up to 5 h. The canal (Fig. 1) consisted of a 21 m long plywood and steel frame construction (0.9 m wide and 0.7 m deep) sealed with a transparent polyethylene sheet and filled with sea water (4 °C). It was covered 10 cm beneath the water surface with transparent polyvinylchloride (PVC) sheets made conspicuous with netting, to prevent the birds from surfacing while allowing behavioural observations from above. For this purpose, an observer was positioned on a ladder, 10.5 m from both ends of the canal, his head approximately 3.5 m above the ground. The behaviour and position of the penguins in the canal were recorded orally onto a quartz-locked tape recorder (Sony Walkman) together with real time. These data were later transcribed onto a computer to determine activity type and duration, distance swum and speed for each interval between a penguin's departure from a respiration chamber and its subsequent departure from a chamber.

Penguins were allowed to breathe freely in two respiration chambers (volume 94 l) placed at either end of the canal, in which air was renewed at a rate of 3000 l h^{-1}. A subsample of the air from each chamber was dried (Drierite, Aldrich Chemicals) and passed into one of two paramagnetic oxygen analysers and one infrared carbon dioxyde analyser (Maihak, Hamburg). During the experiments, concentrations of O_2 and CO_2 in the respiration chambers remained between 20 and 21 % and between 0 and 1 %, respectively. Data from each analyser were sampled every 2 s by an IBM-compatible computer fitted with an analog–digital conversion card and using purpose-built software. The whole system was calibrated and checked daily. Mean measurement error (+5.7±1.7 %, *N*=11) was determined by recovery tests using known volumes of nitrogen pumped into the respiration chambers. Oxygen consumption was analysed with respect to swimming speed and averaged for 0.2 m s^{-1} speed classes ranging from 0.4 to 2.8 m s^{-1}

Fig. 1. Top: two gentoo penguins are observing a conspecific through the transparent section (6 m) of the 21 m long canal. Bottom: the canal was equipped with one respiration chamber at each end. Penguin activity during an experiment was observed from above using a ladder and a tape recorder.

(see Culik and Wilson, 1991*a,b*; Culik *et al.* 1990, 1991, 1993, for further details). Conversion into $W kg^{-1}$ was carried out assuming a conversion factor of $20.1 J ml^{-1}$ oxygen for a 'mixture of common food stuffs' (Schmidt-Nielsen, 1983).

In the investigation of penguin behaviour at sea, instruments carrying speed and depth sensors (Wilson *et al.* 1993) were attached (Wilson and Wilson, 1989) to breeding pygoscelid penguins at their nest site (N=17 Adélie, 11 chinstrap and 7 gentoo penguins). Speed sensors (paddle wheel) were calibrated on a life-size cast model of a swimming Adélie penguin (Bannasch and Fiebig, 1992), whose hydrodynamic properties were determined in the circulating water tank of the Versuchsanstalt für Wasserbau und Schiffbau, Müller-Breslau Strasse, D-10623 Berlin, Germany (Bannasch *et al.* 1994; Culik *et al.* 1993) as well as on living penguins in the swim canal in Antarctica. Typical accuracy of the speed sensors was 10 % at $1 m s^{-1}$, 5 % at $2 m s^{-1}$ and 3 % at $3 m s^{-1}$. Instrument recording interval was set to 10 s, yielding a total of 1695, 2255 and 1653 speed measurements and 1613, 1636 and 733 dives for analysis from Adélie, chinstrap and gentoo penguins, respectively. Depth sensors (accuracy ± 30 cm) were used to determine time spent under water.

Results

Penguins inserted into one of the chambers of the PVC-covered swim canal learned within minutes where they could surface to breathe. As opposed to earlier studies (Culik and Wilson 1991*a,b*; Culik *et al.* 1991), only two behavioural categories were used: 'resting' or 'swimming under water'. If the penguins showed erratic behaviour, such as jumping or struggling, the corresponding data were deleted from the analysis. As a result, the data presented here are for birds swimming freely from one end of the canal to the other, where they either surfaced to breathe or turned around to return to the chamber they had started from. The mean distance covered before surfacing in a chamber was 36±19 m (± S.D., N=754) at speeds ranging between 0.4 and $2.8 m s^{-1}$ (Table 1).

The measured power requirements while swimming (P_s, in $W kg^{-1}$) were best fitted (Fig. 2A, r^2=0.91) by a cubic function of the type $P_s=av+bv^2+cv^3+P_r$, where v is swimming speed ($m s^{-1}$) and P_r ($W kg^{-1}$) is the power required for resting at the water surface at v=$0 m s^{-1}$ (Culik *et al.* 1991). An allometric relationship between P_s, P_r and v would be suggested by simple hydrodynamic arguments, but it does not reflect the plateau phase observed at speeds between 0.8 and $2 m s^{-1}$ or the comparatively low power requirements for resting in cold water (at v=$0 m s^{-1}$). Discontinuous linear regression of the data is another alternative, but it is less elegant and has the disadvantage of not allowing transformation of the power curve into curves representing transport costs or aerobic dive distance (see below).

Transport costs (COT, the cost of transporting 1 kg of mass over 1 m, in $J kg^{-1} m^{-1}$) are obtained by dividing power ($W kg^{-1}=J s^{-1} kg^{-1}$) by speed ($m s^{-1}$). In this study, we obtained the best curve fit using the function COT=$(av+bv^2+cv^3+P_r)/v$ (Table 1). The data and corresponding curve obtained for Adélie penguins are shown in Fig. 2B. Power requirements while swimming, as well as transport costs were similarly analysed for chinstrap and gentoo penguins (Table 1).

Mean swimming speeds of wild Adélie, chinstrap and gentoo penguins measured by

Table 1. *Power input while swimming* (P$_s$, *in W kg^{-1}) and transport costs (COT, in J kg^{-1} m^{-1}) of pygoscelid penguins swimming under water in the swim canal*

	Adélie	Chinstrap	Gentoo
a	9.84	14.29	18.28
b	−6.75	−8.84	−14.72
c	1.7	1.66	3.89
P_r (W kg^{-1})	8.4	8.75	8.2
r^2	0.98	0.75	0.82
Animal *N*	12	7	10
Mass (kg)	4	3.8	5.5
S.D.	0.4	0.3	0.6
Speed in the canal			
Range (m s^{-1})	0.8–2.8	1–2.4	0.4–2.4
Mean (m s^{-1})	1.67	1.77	1.49
S.D.	0.4	0.3	0.4
N	387	228	139

Power input and cost of swimming are best described by $P_s = av + bv^2 + cv^3 + P_r$ and $COT = P_s/v$ where *v* is swimming speed (m s^{-1}) and P_r (W kg^{-1}) is power required for resting at the water surface (Culik *et al.* 1991).

r^2 gives the correlation coefficient for the COT curve fit; animal *N* indicates the number of birds used; mass is their mean mass; S.D. is the standard deviation of the mass, and *N* is the number of measurements made.

external speed and depth sensors, were 2.2±0.7, 2.4±0.7 and 1.8±0.6 m s^{-1} (±S.D.) respectively. Mean dive durations of birds in the wild were 85±28, 78±30 and 86±35 s (±S.D.) respectively (Fig. 3).

Hydrodynamic investigations on the Adélie penguin model in the circulating water tank in Berlin (see Bannasch *et al.* 1994, for details) yielded a drag coefficient (C_D) of 0.0496 at Reynolds numbers corresponding to a swimming speed of 2.2 m s^{-1} in sea water at 4 °C (the conditions encountered in the swim canal in Antarctica). The model was wingless, which meant that the drag coefficient of the body only was assessed.

Discussion

The energy requirements of swimming pygoscelid penguins have been determined previously, also using a swim canal in Antarctica and birds captured in the wild (Culik and Wilson, 1991*a,b*; Culik *et al.* 1991). However, in the earlier studies, only one oxygen analyser was used for both chambers, the renewal of air was at a rate of only 750 l h^{-1} chamber^{-1}, data sampling interval was 10 s, and data were averaged over 5 min intervals for analysis. Furthermore, in the past, the whole-system error had not been determined using known amounts of nitrogen. For these reasons, and because results from doubly labelled water studies showed significantly higher swimming energy requirements in penguins (e.g. Nagy *et al.* 1984; Davis *et al.* 1989; Kooyman *et al.* 1992; Chappell *et al.* 1993*b*), we have repeated these experiments using the improved and modified methods described above.
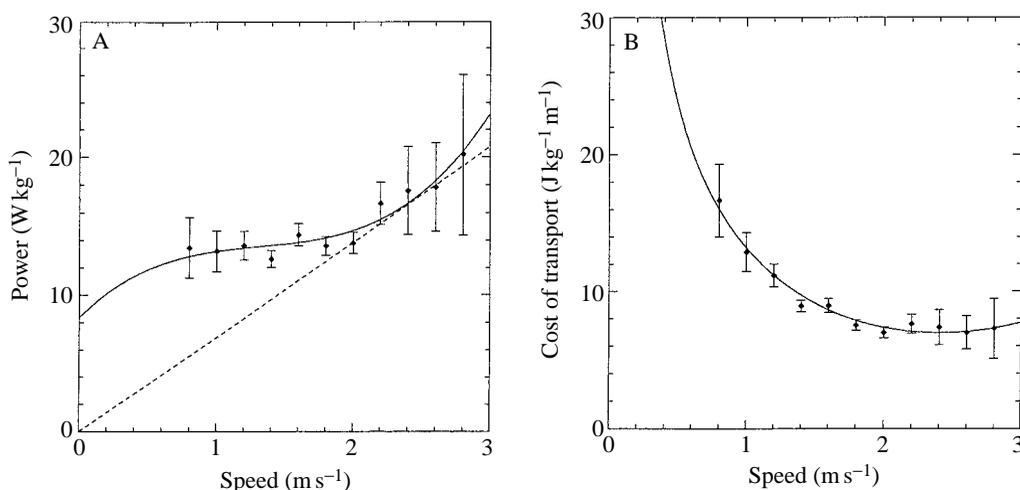
Fig. 2. (A) Power input (W kg^{-1}) in Adélie penguins (N=12) swimming freely in a 21 m long, seawater-filled canal in Antarctica (r^2=0.91). The dashed line meets the power curve where transport costs are lowest. (B) Transport costs (COT) in Adélie penguins calculated from power input (COT=power/speed; r^2=0.98). Bars show standard error of the means.

Comparison of the present study with earlier work (Culik and Wilson, 1991*a,b*; Culik *et al.* 1991) on power input in pygoscelid penguins swimming under water shows a difference in calculated COT values. Results for Adélie penguins are 6 % lower than previously reported (Culik and Wilson, 1991*a*), while those for chinstrap and gentoo penguins are 57 and 27 % higher, respectively (Culik *et al.* 1991). However, in the current study, neither chinstrap or gentoo penguins were as cooperative as Adélie penguins and often could not be induced to swim or engaged in escape behaviour while in the canal.

Because of the large number of measurements made, the relationship between swimming speed and corresponding energy requirements could be described and has been presented for the first time in the present paper by a single mathematical function (Table 1, Fig. 2). Because of the similarity of the results between the three pygoscelid penguin species, the Adélie penguin is used below to exemplify most of the points in the discussion.

Aerobic dive limits

Prior to a dive, penguins store oxygen in arterial and venous blood, muscle tissue and air sacs (Kooyman, 1989). The total amount of oxygen available to the birds while swimming under water can be calculated if variables such as the oxygen-binding capacity of blood and muscle and the oxygen saturation prior to the dive are known.

Oxygen stores in pygoscelid penguins were calculated from published data (Lenfant *et al.* 1969; Mill and Baldwin, 1983; Kooyman, 1989; Stephenson *et al.* 1989; Croll *et al.* 1992; Chappell *et al.* 1993*a*) and found to be 58.6, 57 and 63 ml kg^{-1} in Adélie, chinstrap and gentoo penguins, respectively (Table 2). It is now widely assumed that penguins and other birds dive after inspiration and use the oxygen in their respiratory system while
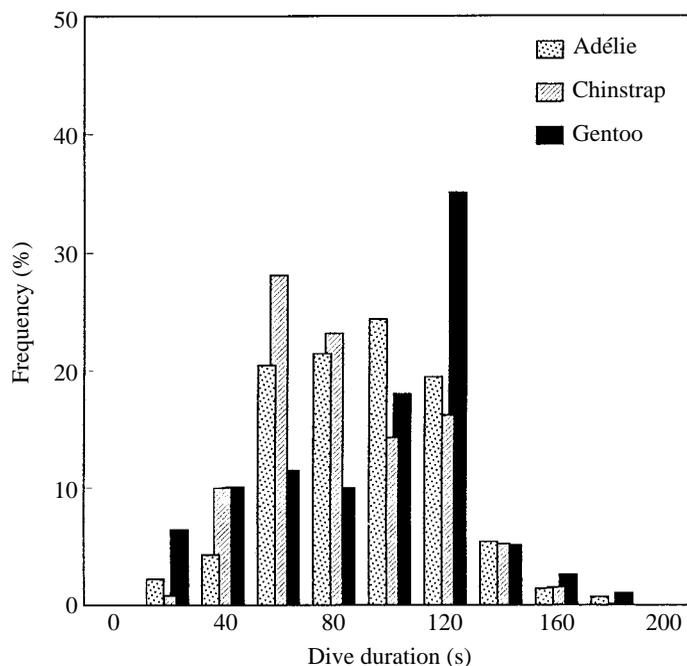
Fig. 3. Frequency of dive duration in wild Adélie (*N*=17 birds), chinstrap (*N*=13 birds) and gentoo penguins (*N*=7 birds). Means were 85, 78 and 86 s, respectively (see text for further details).

diving (Kooyman, 1989; Stephenson *et al.* 1989; Croll *et al.* 1992), although the mechanisms for this are still poorly understood. Nevertheless, it is surprising that pygoscelid penguins store more than 30 % of the oxygen required during the dive in their air sacs and use this, presumably by ventilating their lungs, without suffering from aeroembolism, i.e. 'the bends'. Presumably the oxygen in the respiratory tract is available to the exercising muscles during the dive. Although, as in most other air-breathing aquatic animals (Kooyman, 1989), penguins reduce their heart rate after submersion; heart rates only drop from pre-dive values of 250 beats min^{-1} to 107 beats min^{-1} during the dive (Culik, 1992).

Aerobic dive limits were calculated (Table 3) using mean speeds determined by data-loggers on pygoscelid penguins at sea, available oxygen stores (Table 2), and deriving the power requirements and transport costs for those speeds (Table 1). Using the transport costs determined in the swim canal, we calculated that the birds are able to dive aerobically for 76, 76 and 79 s, respectively, significantly longer than previously suggested (Chappell *et al.* 1993*a*).

However, penguins in the canal had to accelerate and decelerate at least once every 21 m (if they swam the whole the length of the canal), something which they would not normally do in nature. Trivelpiece *et al.* (1986), using radio transmitters on Adélie penguins, determined that the birds would swim for approximately 1 min below the water surface before stopping to breathe. At their normal cruising speed of 2.2 m s^{-1}, this

Table 2. *Calculation of the oxygen stores in Adélie penguins*

	Blood		Muscle	Air sacs	Source
	Arterial	Venous			
Proportion of body mass (%)	3.4	8.9	35		Chappell *et al*. (1993*a*)
Amount of respiratory pigment (g l^{-1})	175	193	36		Chappell *et al*. (1993*a*) Mill and Baldwin (1983)
Oxygen binding capacity (ml g^{-1})	1.37	1.37	1.34		Lenfant *et al*. (1969) Kooyman (1989)
Saturation prior to dive (%)	95	70	100	17.6	Stephenson *et al*. (1989) Croll *et al*. (1992)
Oxygen available during dive (%)	96	96	100	75	Stephenson *et al*. (1989) Croll *et al*. (1992)
Volume of air in respiratory tract (ml kg^{-1})				140	Chappell *et al*. (1993*a*)
Oxygen (ml kg^{-1})	7.43	15.81	16.88	18.48	

Prior to a dive, the total amount of oxygen available to Adélie penguins is 58.6 ml kg^{-1}. Of this, 12.2 % is stored in arterial blood, 26 % in venous blood, 29.5 % in the muscles and 32.3 % in the air sacs.

Table 3. *Aerobic dive limits calculated for swimming pygoscelid penguins from the energy requirements during swimming (Table 1), from available oxygen stores (Table 2) and from at-sea swimming speeds and dive durations (obtained using externally attached data-loggers) on wild penguins (see text)*

	Adélie	Chinstrap	Gentoo
Total oxygen stores (ml kg^{-1})	58.6	57	63
At-sea swimming speed (m s^{-1})	2.2	2.4	1.8
In the canal			
Power (W kg^{-1})	15.5	15.1	16.1
COT (J kg^{-1} m^{-1})	7.1	6.3	8.9
Aerobic dive time, ADT (s)	76	76	79
Dives exceeding ADT (%)	54	37	62
Minimum transport costs			
Power (W kg^{-1})	10.8	8.9	13.7
COT (J kg^{-1} m^{-1})	4.9	3.7	7.6
Aerobic dive time, ADT (s)	110	130	93
Dives exceeding ADT (%)	14	4	45

Transport costs (COT) obtained in the swim canal assume one acceleration and one deceleration for every 21 m swum, and minimum transport costs were calculated by assuming only one acceleration and subsequent sustained swimming until oxygen stores are depleted (see text).

Dives exceeding ADT (aerobic dive time) refers to the proportion of dives made by wild pygoscelid penguins lasting longer than the calculated ADT.

amounts to a distance of 132 m. In order to compensate for this, the physical energy required to accelerate and decelerate (P_a, in $W kg^{-1}$) was subtracted from the power requirements of swimming (Table 1). Distance (S) relates to speed as $S=v^2/2a$, where v is speed ($m s^{-1}$) and a is acceleration ($m s^{-2}$). Work (W) is given by $W=MaS$, where M is mass (kg), and simplifies to $W=v^2/2$ for acceleration and deceleration if a mass of 1 kg is assumed. Note that the value for a is of no consequence to the calculation of work. Finally, power (P) relates to work as $P=W v/S$. Thus, the correction term employed here was $P_a=-v^3/mfS$, where m is muscle efficiency (0.25, Schmidt-Nielsen, 1983), f is flipper efficiency (0.4, Oehme and Bannasch, 1989) and S is the length of the canal (21 m). The corrected power requirements are those for sustained swimming.

Aerobic dive time (ADT, s) for swimming penguins was calculated using $ADT=kOXY/(P_s-P_a+P_b)$, and corresponding dive distance (ADD, m) using $ADD=vADT$, where $k=20.1 J ml^{-1} O_2$, OXY is the O_2 store (ml) available prior to a dive, P_s is the energy required for swimming in the canal (W), P_a is the energy required for both acceleration and deceleration in the canal (W), P_b is the energy (W) required to accelerate and decelerate within given intervals (S, m) calculated as $P_b=v^3/mfS$, and v is the swimming speed ($m s^{-1}$). Aerobic dive limits calculated from the original data have $P_a=0$ and $P_b=0$ in the above equations. Assuming that penguins have to accelerate at least once during a dive, we obtained transport costs of 4.9, 3.7 and 7.6 $J kg^{-1} m^{-1}$ (Table 3) and predicted maximum aerobic dive times of 110, 130 and 93 s for Adélie, chinstrap and gentoo penguins, respectively.

When accelerating and decelerating every 21 m (original uncorrected data), aerobic dive distance in Adélie penguins (Fig. 4, thick line) shows a maximum of 175 m at 2.4 $m s^{-1}$. This is somewhat surprising, since the birds prefer to swim at 2.2 $m s^{-1}$ in the wild (Table 3). However, experiments with Adélie penguins carrying externally attached data-loggers in the swim canal (such as those employed here to measure swim speed in the wild) showed that swim speed was reduced by 7.7 % (Culik *et al.* 1993). Thus, without instrumentation, Adélie penguins in the wild could possibly have a higher mean speed of 2.4 $m s^{-1}$.

Because of the decrease of COT (cost of transport) with speed (Fig. 2B), ADD increases at higher speeds if the interval between each acceleration and deceleration is increased (Fig. 4, stippled lines). The maximum distance is reached if the Adélie penguin only accelerates *once* ($P_b/2$ in the above equations) and swims at a constant speed of 3 $m s^{-1}$; it can then travel 330 m and remain under water for 110 s before oxygen stores are depleted. A bird stopping every 0.5 m to catch prey will only be able to cover 42 m under water and spend 84 s below the surface at the best speed of 0.5 $m s^{-1}$. Maximum time under water is, of course, obtained if the penguin stops swimming completely, since energy requirements are lowest during rest. In water at 4 °C, Adélie penguins can remain submerged motionless for 140 s.

The probability of prey encounter is dependent on the distance travelled (Wilson, 1991), and therefore the overall rate of prey encounter depends on the swimming speed. However, since penguins are visual hunters (Wilson *et al.* 1989, 1993), the number of prey perceived and captured per unit time is likely to decrease if penguins swim too fast (Wilson, 1991). Thus, appropriate optimization for penguins swimming under water may

be time-, distance- or speed-dependent. The choice to optimize any of these variables is itself dependent on activity, e.g. travelling to foraging areas, searching or feeding. A detailed analysis of swimming speeds (R. P. Wilson, unpublished data) in Adélie penguins has shown that, during travel, the birds prefer to swim at $2.4\,\mathrm{m\,s^{-1}}$, whereas speeds around $1.5\,\mathrm{m\,s^{-1}}$ are preferred during searching and feeding dives. How often penguins 'stop and go' while at sea, however, has not been measured to date.

Using the data on penguin dive durations in the wild determined by the data-loggers, we calculated the percentage of dives exceeding the estimated aerobic dive limits (Table 3). In the wild, 54 % of all Adélie penguin dives exceed 76 s, which is the aerobic dive time for birds swimming in the canal (when accelerating and decelerating every 21 m). However, assuming minimal transport costs of $4.9\,\mathrm{J\,kg^{-1}\,m^{-1}}$ (one acceleration per 330 m), only 14 % of all dives in the wild exceed the maximum aerobic dive time of 110 s. Using the same procedure, only 4 % of all dives made by chinstrap penguins exceed the aerobic dive time (130 s) and 96 % of all dives are calculated to be aerobic, if the birds use sustained swimming for under water locomotion.

Contrary to the results of Chappell *et al.* (1993*b*), it would appear that Adélie penguins do not have 'swimming' costs of six times basal metabolic rate (BMR in thermoneutrality
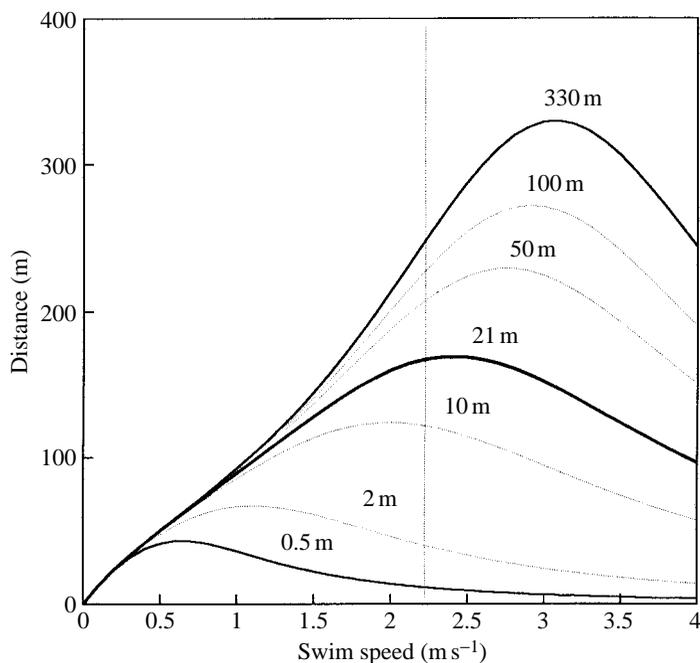

Fig. 4. Estimated aerobic dive distance against swimming speed for Adélie penguins calculated using the data from the swim canal experiments (thick line) and for various 'stop and go' intervals (stippled and solid lines). While accelerating and decelerating every 21 m, an Adélie penguin can cover 175 m at $2.4\,\mathrm{m\,s^{-1}}$ within its aerobic dive limits. If the animal only accelerates once to $3\,\mathrm{m\,s^{-1}}$ and maintains that speed, it can cover 330 m before its oxygen stores are depleted. A feeding Adélie penguin might have to stop every 0.5 m. In that case, it could cover 42 m under water before having to return to the surface.

on land is 3.6 W kg^{-1}; Culik and Wilson 1991a; Chappell et $al.$ 1993b) or 21.7 W kg^{-1}, which would allow aerobic dive times of only 54 s (Chappell et $al.$ 1993a, using time/depth recorders measured mean dive times of 73 s). It has been suggested (M. A. Chappell, personal communication) that the observed discrepancy between doubly labelled water studies and the swim canal experiments presented here may stem from the fact that in the wild, penguins spend a considerable time at sea porpoising. The energetic cost associated with this form of locomotion cannot be measured in the swim canal and could account for the comparatively high field metabolic rates calculated for penguins at sea (e.g. Nagy et $al.$ 1984; Davis et $al.$ 1989; Kooyman et $al.$ 1992; Chappell et $al.$ 1993b). However, by using radiotelemetry, Trivelpiece et $al.$ (1986) determined that the main mode of locomotion in gentoo and chinstrap penguins is underwater swimming, which accounts for 73 % of travelling time. Assuming metabolic rates of six times BMR for penguins at sea (i.e. swimming and porpoising; see Chappel et $al.$ 1993b) and underwater swimming metabolic rates of 2.9–4.3 times BMR (this paper), the energetic costs associated with porpoising would range from 10.6 to 14.4 times BMR. This seems unrealistically high (see Fig. 2A).

Using data-loggers to record penguin activity, we have observed (R. P. Wilson and B. M. Culik, unpublished data) that gentoo penguins injected in the pectoralis muscle with doubly labelled water (using the methods of Chappell et $al.$ 1993b) differ considerably in their behaviour from control birds. Generally, the penguins spent more time at the nest before returning to sea, swam at considerably slower speeds, showed different diving behaviour and had reduced foraging ranges compared with controls. This may be a hint that extrapolation of transport costs from doubly labelled water studies may be subject to a systematic error.

With respect to the energetic requirements of underwater swimming per se, there seems to be no requirement for the presence of anaerobic biochemical pathways in order to explain the long duration of dives. In fact, investigation of the muscle fibres of little penguin ($Eudyptula$ $minor$) pectoralis and supracoracoideus, the muscles employed in swimming, showed that they were basically aerobic with little capacity for producing ATP during muscle anoxia (Mill and Baldwin, 1983). These findings were mirrored for the Adélie penguin by Bannasch (1986). It seems that, rather than diving anaerobically, penguins simply consume very little energy (2.9–4.3 times BMR) while swimming under water, perhaps even less than calculated here. In this regard, it is important to note that the swim canal was 0.9 m wide, leaving only about 0.15 m on either side of the penguin flippers, thereby increasing the hydrodynamic drag on the swimming birds through wall effects.

Assuming the energy content of fresh krill to be, on average, 3.7 kJ g^{-1} (Culik and Wilson, 1992), a 4 kg Adélie penguin swimming in the canal requires 7.6 g of krill per kilometre travelled. With the energy liberated from 1 g of krill, the bird could swim 0.13 km. Assuming the stomach capacity of the 4 kg Adélie penguin in this example to be 1000 g, the bird would have a range of 130 km with the energy liberated from a full stomach. While swimming continuously at 3 m s^{-1} and pausing only every 330 m, krill requirements are reduced to two-thirds of this value, so that a full stomach would allow a penguin in the wild to cover nearly 200 km. This is considerably more than the distance a penguin could cover

by foot, since during walking, krill are consumed at a rate of $31\,\mathrm{g\,km^{-1}}$, which gives a maximum range of only 32 km (calculated from Pinshow *et al.* 1977).

Hydrodynamic drag

The low values reported for penguin swimming energetics using the swim canal were supported by independent measurements made on a plastic-cast true-to-life model of a swimming Adélie penguin. While maintaining a sustained swimming speed of $2.2\,\mathrm{m\,s^{-1}}$ (no acceleration or deceleration taking place), live Adélie penguins consume $10.5\,\mathrm{W\,kg^{-1}}$ or 42 W for a 4 kg bird. Assuming muscle and flipper efficiencies to be 0.25 (Schmidt-Nielsen, 1983) and 0.4 (Oehme and Bannasch, 1989), respectively, the mechanical power (P_m) generated by the swimming penguin is only 10 % of this value or 4.2 W (see Culik and Wilson, 1991*a*). Since the drag coefficient $C_D = 2F/dv^2 A$, where F is the drag force ($F = P_m/v^{-1}$), d is the density of the medium ($1028\,\mathrm{kg\,m^{-3}}$ for sea water at 4 °C), v is the swimming velocity and A is the frontal area of the bird ($0.02083\,\mathrm{m^2}$, Oehme and Bannasch 1989), a drag coefficient of 0.0368 was calculated for Adélie penguins at that speed. This value, as expected, is lower than the C_D of 0.0496, measured on the inflexible Adélie penguin model in Berlin at $2.2\,\mathrm{m\,s^{-1}}$ (calculated for sea water at 4 °C and 3.5 % salinity), and the drag coefficient of an ideal spindle ($C_D = 0.04$, Nachtigall and Bilo, 1980). However, the similarity of these results supports the validity of our findings on living penguins.

In order to calculate the drag coefficient of penguins from respirometry data obtained in the swim canal, it has been suggested that the basal metabolic rate ($3.7\,\mathrm{W\,kg^{-1}}$) should be subtracted from the power required for maintained swimming (Schmidt-Nielsen, 1977). The resulting net power input of $6.8\,\mathrm{W\,kg^{-1}}$ ($P_m = 2.7\,\mathrm{W}$) would yield a C_D of 0.0238, all other terms remaining constant. Could the C_D of a swimming penguin really be as low as 0.0238? The plastic-cast penguin model did not have the feathered surface structure and the compliant body of the living animal, characteristics that could reduce hydrodynamic drag by a large fraction. The values used in our calculations for muscle and flipper efficiencies (which will directly affect calculated values of C_D) are very difficult to measure *in situ* and were taken from the literature. They can only be approximate. The efficiency of a ship's propeller, for example, is 0.8, twice the value assumed here for a penguin's flipper. It is also possible that the assumed efficiency of 10 % for the combined muscles and flippers is too low, if, for example, elastic recoil allows for kinetic energy recovery (Schmidt-Nielsen, 1977) to be used by the propulsion system of penguins. Further investigations and modelling studies are obviously required.

Transport costs in sub-surface swimmers

Combining the values for minimal transport costs measured here for pygoscelid penguins with transport costs (measured in experiments considered 'realistic', see Culik and Wilson, 1991*a*) from other homeothermic sub-surface swimmers, such as seals (*Phoca vitulina*; Davis *et al.* 1985), sea lions (*Zalophus californianus*; Costello and Whittow, 1975; Feldkamp, 1987) and dolphins (*Tursiops truncatus*; Williams *et al.* 1992), where body mass (M) ranged between 3.8 and 145 kg, we obtained a general
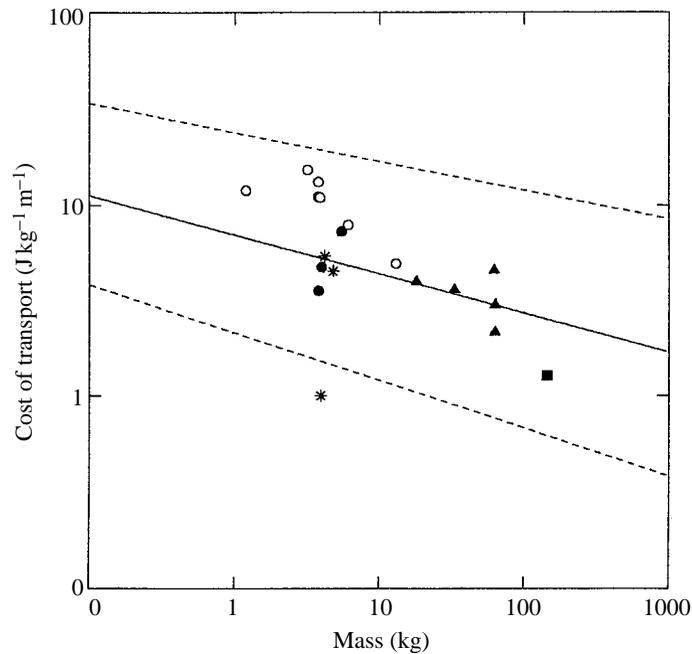
Fig. 5. Minimum transport costs (COT) in sub-surface swimming homeotherms were calculated from data presented in this study (filled circles) and published results on pinnipeds (Davis *et al.* 1985; Costello and Whittow, 1975; Feldkamp,1987; triangles) and bottlenose dolphins (Williams *et al.* 1992; square). The resulting regression is COT=7.01$M^{-0.205}$ (r^2=0.43, *N*=9). For comparison, previously published results on penguins, derived from experiments at slow speeds in water flumes or using doubly-labelled water (Nagy *et al.* 1984; Baudinette and Gill, 1985; Hui, 1988; Davis *et al.* 1989; Kooyman *et al.* 1992; Chappell *et al.* 1993*b*; open circles) and from earlier experiments using the swim canal (Culik *et al.* 1991; asterisks; data were corrected as in this study to determine minimal COT; the lower asterisk represents the value for chinstrap penguins) are also shown. The upper dashed line shows the COT in surface-swimming homeotherms (Williams, 1989), where COT=23.9$M^{-0.15}$, and the lower dashed line is the COT for fish extrapolated from values for swimming salmon (Brett, 1964), where COT=2.15$M^{-0.25}$.

relationship COT=7.01$M^{-0.205}$ (r^2=0.43, *N*=9; Fig. 5). Transport costs of chinstrap penguins are lower than predicted by this relationship, those of gentoo penguins are higher, and those of Adélie penguins are almost the same as predicted.

Unfortunately, data available on sub-surface swimmers are still sparse or not comparable because of the different methods employed. Swimming costs in dolphins (Fig. 5, square) for instance, were calculated from indirect measurements of energy consumption in open water using heart rate, with all the associated problems of diving bradycardia (heart rate had been calibrated in the laboratory using respirometry with the animals swimming against the drag of a load cell). Although the relationship shown in Fig. 5 is, therefore, only a first approximation, transport costs in sub-surface swimming homeotherms are approximately 3.3 times higher than those extrapolated for fish from

swimming salmon (Brett, 1964) and only one-third of those of surface-swimming homeotherms (Williams, 1989).

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