





tions of the thickness and conductance of fat and the feather air layer, Brinkman et al. (2003) estimate heat loss for eiders at 5°C to be 200 W m<sup>-2</sup> in water and 60 W m<sup>-2</sup> in air. The surface area of the 2 kg eider considered in their model is ~0.13 m<sup>2</sup> (Brinkman et al. 2003); so, assuming that approximately half of the bird is submerged while swimming on the surface, 0.065 m<sup>2</sup> would be subject to cooling by air and 0.065 m<sup>2</sup> to water. This yields a heat loss of 6.5 W kg<sup>-1</sup> to water and 1.95 W kg<sup>-1</sup> to air; at 5°C, when added to a BMR of 4 W kg<sup>-1</sup>, this gives an estimated cost for the whole bird of 7.9 W kg<sup>-1</sup> in air, and 12.5 W kg<sup>-1</sup> whilst resting on the water surface. Respirometry of common eiders in air (smaller sub-species weighing ~1.66 to 1.79 kg) has yielded values of 3.68 W kg<sup>-1</sup> at 5°C (Jenssen et al. 1989), 5.30 W kg<sup>-1</sup> at 5°C (Gabrielsen et al. 1991), and 4.29 W kg<sup>-1</sup> at an unspecified temperature (probably 14 to 19°C: Hawkins et al. 2000), suggesting that the biophysical model (Brinkman et al. 2003) overestimates costs in air at 5°C by 49 to 155%.

For resting on the water surface, respirometry yielded 5.03 W kg<sup>-1</sup> (Jenssen et al. 1989) for common eiders (1.66 kg) at 5°C, and 5.91 W kg<sup>-1</sup> for white-winged Scoters (1.09 kg) at 9°C (Richman & Lovvorn 2008), suggesting that the biophysical model overestimates costs of floating on water at 5°C by 136 to 249%. However, a higher value of 10.25 W kg<sup>-1</sup> was reported for common eiders at 14 to 19°C (Hawkins et al. 2000), indicating that the metabolic rate of floating eiders can be higher in some circumstances. For floating eiders in respirometry experiments, air temperature was probably very similar to water temperature (Kaseloo & Lovvorn 2006) and there was no appreciable air movement to enhance heat loss by convection. In contrast, floating eiders at our field site may experience above water air temperatures which are much lower than water temperatures, and high winds may cause substantial convective heat loss (Chappell et al. 1989). Equations provided by Jenssen et al. (1989) for air temperatures of -35°C suggested a cost of 5.91 W kg<sup>-1</sup> in air only; if a wind chill based on 25 km h<sup>-1</sup> winds is incorporated, a cost of 6.96 W kg<sup>-1</sup> in air only is suggested. We conservatively use a value of 6.0 W kg<sup>-1</sup> for costs of resting in air only (i.e. costs for resting on the ice edge). Lacking definitive measurements for floating on water, we used a value of 10 W kg<sup>-1</sup> for floating eiders at 14 to 19°C based on measurements by Hawkins et al. (2000), which is 82.5% higher than the value of 5.48 W kg<sup>-1</sup> for eiders floating on water at 0°C measured by Jenssen et al. (1989); this is likely to be conservative for conditions at our field site. Additional studies on thermoregulatory costs, particularly in colder air and water temperatures, are clearly required.

**Surface swimming.** An important component of the surface energy budget involves swimming, particu-

larly in maintaining position as tidal currents increase. Stephenson et al. (1989) report that drag increases strongly at swimming speeds over 0.5 m s<sup>-1</sup>. Hawkins et al. (2000) measured the oxygen consumption of common eiders swimming on the water at various speeds in a flume tank. They found that oxygen consumption increased exponentially above 1 m s<sup>-1</sup> and that no ducks were able to swim at speeds greater than 1.3 m s<sup>-1</sup> in their experiments. At 1.3 m s<sup>-1</sup>, the volume of oxygen consumed was 1.8 times that whilst resting on the surface of the water. They report no change in oxygen consumption up to 1.0 m s<sup>-1</sup>, however at 1.0, 1.1 and 1.2 m s<sup>-1</sup>, their data indicate an increase in oxygen consumption of 1.18, 1.36 and 1.6 times (respectively) that whilst resting on the water. As eiders could not swim against currents faster than 1.3 m s<sup>-1</sup>, we assume for the purposes of the present model that they would be carried by currents faster than this and would therefore maintain an oxygen consumption rate 1.8 times higher than at rest. This allows us to fully explore the influence of other energetic parameters instead of truncating the model at 1.3 m s<sup>-1</sup>. For currents <1.0 m s<sup>-1</sup>, Brinkman et al. (2003) similarly suggest only a slight increase of 0.3 W kg<sup>-1</sup> for speeds starting at 0.3 m s<sup>-1</sup>, which we applied for current speeds from 0.3 to 0.99 m s<sup>-1</sup>. Hawkins et al. (2000) did not provide a regression equation for oxygen consumption as a function of swimming speed. As it was desirable to keep our energetic equations continuous across their range, we performed a curve fitting exercise using the values of the multiplication factors listed above. The most accurate curve describing the relationship between the energetic multiplication factor for basal metabolic rate (MULTIPLE) and swim speed (SPEED) was a Gompertz curve, a sigmoidal function, which explained 99.6% of the variation. This equation was:

$$\text{MULTIPLE} = 1.016 + 0.7977 \cdot e^{-e^{[10.24(0.9631\text{SPEED}) + 1]}} \quad (1)$$

Given that eiders often maintain their position on the surface, we assumed that surface swimming speed was equal to current speed and used Eq. (1) to determine the energetic costs of swimming as a multiple of surface resting cost (BMR + surface heat loss) with respect to current speed.

**Descent.** Our previous research indicated that the total number of wing strokes and the duration of descent increased non-linearly with current speed. Stroke rate and swim speed (relative to the moving water) were maintained within a narrow range across current speeds (Heath et al. 2006). Therefore, while the total time and energy costs of descent change with current speed, the rate of energy expenditure during descent should be fairly constant. Heath et al. (2006)

noted that eiders always dove directly into oncoming currents, ending upstream of their surface departure point at an estimated dive angle of 0 to 20°. It is possible that increased drag in faster currents could lead to a decrease in dive angle (i.e. more vertical descent), although there is no data currently available to test this possibility. A slight change in dive angle induced by oncoming currents could compensate for increases in drag without entailing additional energetic costs. In either case, additional costs of drag not compensated for by small changes in dive angle are likely to be substantially smaller than the large increase in costs due to increased travel time and wing strokes on a given dive in fast currents (see Heath et al. 2006).

Changes in current speed could influence the rate of convective heat loss while underwater; however, given eiders swim at a relatively constant rate with respect to the water during descent (Heath et al. 2006), heat loss would not be expected to change substantially due to convective changes associated with current speed. Additionally, heat generated from exercise during diving likely compensates for heat losses (Kaseloo & Lovvorn 2006). Based on equations from a simulation model for spectacled eiders that accounts for changes in buoyancy with depth (Lovvorn et al. 2009), the total mechanical cost of a 9.46 s descent to 11.3 m is  $\sim 57.09 \text{ J kg}^{-1}$  ( $6.03 \text{ W kg}^{-1}$ ). New estimates of oxygen consumption for a wing-propelled sea duck descending to 2 m depth (Richman & Lovvorn 2008) suggest that the aerobic efficiency for that model should be  $\sim 0.37$  (J.R. Lovvorn, pers. comm.). For a dive to 11.3 m, those equations yield an estimated mechanical cost of  $6.03 \text{ W kg}^{-1}$ , for an aerobic cost of  $6.03 / 0.37 = 16.3 \text{ W kg}^{-1}$ . This value is about 4.03 times greater than the mechanical cost of 6.03  $\text{W kg}^{-1}$ .



Fig. 1. *Somateria mollissima sedentaria*. Estimated energy expenditure per dive cycle (rate of expenditure times duration of activity) for: (A) descending to depth, (B) foraging at depth, (C) ascending and (D) swimming on the surface, all as a function of current speed. Solid black line: baseline energetic estimates, light grey areas: 10% change in baseline parameters under sensitivity analysis, dark grey areas: 50% change in baseline parameters under sensitivity analysis. Note the difference in scale on the vertical axes

exclusively mussels in the gullet contained  $11.2 \pm 9.8$  g (95% CI = 3.8 g; S. Jamieson, unpubl. data), which suggests these values of gullet contents are reasonable. While the gullet can act as a storage organ (Guillemette 1994), unlike studies in other regions, eiders wintering at the Belcher Islands did not dive in regular foraging bouts before resting (see Heath 2007) and frequently paused for long periods on the surface before diving again ( $183 \text{ s} \pm 158 \text{ SD}$ ). This duration should be adequate to move most mussels from the gullet into the gizzard for processing; we therefore expect that many of the mussels present in the gullet of eiders at our study site could have been obtained within a single dive. We use 10 g as a baseline estimate of the mass of prey consumed per dive and consider a range of 5 to 15 g in our sensitivity analysis; the wide range should more than account for the possibility of

food in the gizzard being acquired from multiple dives. Of course, a wide variety of factors affect the abundance, quality and availability of prey in the field; natural variation is likely to be substantially greater than any minor changes we might make to this estimate. We demonstrate below that this intake rate is well within that observed for other eider species, suggesting it is quite reasonable.

To convert total intake of wet mussel mass into energy intake rate first requires assumptions about the size class of mussels taken on average. Eiders often select mussels within a narrow size range (Bustnes & Erikstad 1990, Bustnes 1998). A size distribution of mussels in the gullet contents were only available for a single individual that was diving at our specific field site (Ulutsatuq polynya); data for 26 individuals were available for common eiders wintering in Greenland



dicted by the energetic model. Tidal current speed was measured every 5 min for the duration of the study using Nortek Aquadopp current loggers (see Heath et al. 2006 for details).

## RESULTS

The change in energy expenditure for each component of the dive cycle (surface pausing, descent, foraging at the bottom and ascent) is presented in Fig. 1 as a function of current speed for the baseline values presented in Table 1, as well as the sensitivity analyses for a 10 and 50% change from baseline values (light and dark regions, respectively). The energetic costs of surface pausing increased sigmoidally as a function of current speed (due to the assumption that eiders swam at the same speed as currents in order to maintain position up to a maximum sustainable speed of  $1.3 \text{ m s}^{-1}$

gain in slack currents changed substantially with these large changes in prey intake. Compared to other parameters, intake rate had the greatest influence on model results in sensitivity analysis. The rate of energy intake during time spent foraging on the bottom therefore appears to be the most important parameter influencing energy budgets of eiders over the dive cycle.

Comparison of model output to observed  
diving behaviour



foraging. This has important implications for balancing energy budgets, particularly for eiders diving in sea ice habitats in mid-winter. We discuss below the relative influence of the various energetic parameters on the

be a major factor in determining the conditions under which diving is profitable.

While activities such as descent during diving are costly, they only occur for a brief proportion of the dive cycle. We found that resting and swimming on the surface, while cheaper than diving, still constituted a significant proportion of the energy costs per dive cycle. Travel time (descent and ascent) increases with tidal current speed, leading to a decrease in time available for foraging at depth within aerobic limits (Heath et al. 2007). Benthic prey is unlikely to be of sufficient energy content to make substantially more expensive anaerobic diving a profitable activity. The energetic model indicates that, under non-linearly decreasing bottom times as current speed increases, the cost of lost foraging time has a stronger negative influence on

a maximum of  $1.3 \text{ m s}^{-1}$  (e.g. surface position is influenced by currents). In addition to the constraint of net

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