

## ORIGINAL PAPER

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**Energy metabolism of underwater swimming in river-otters (*Lutra lutra* L.)**

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**Abstract** We used a still-water swim channel in conjunction with open-flow oxygen and carbon dioxide respirometry to examine the energy requirements of river-otters (*Lutra lutra* L.) swimming voluntarily underwater in Neumünster Zoo (Germany). While at rest on land (5 °C), river-otters had a respiratory quotient of 0.77 and a resting metabolic rate of 4.1 W kg<sup>-1</sup>. This increased to an estimated 6.4 W kg<sup>-1</sup> during rest in water (11–15 °C) and to 12.3 W kg<sup>-1</sup> when the animals were feeding in the channel. River-otters swimming under water preferred a mean speed of 0.89 m s<sup>-1</sup>, and their energy requirements attained 11.6 W kg<sup>-1</sup>. Cost of transport, however, was minimal at 1.3 m s<sup>-1</sup> and amounted to 0.95 J N<sup>-1</sup> m<sup>-1</sup>.

**Key words** Biomechanics · Swimming · Energetics · Mammals · Mustelids

**Abbreviations** ANOVA analysis of variance · PVC polyvinyl chloride · RMR resting metabolic rate · RQ respiratory quotient · TEB time-energy budget · COT cost of transport

**Introduction**

Semi-aquatic river-otters have a body mass of up to 12 kg and a body length of 120–150 cm (Festetics 1980). Although their bodies are hydrodynamically shaped and their feet are webbed for efficient propulsion in water, river-otters, unlike most other aquatic mammals, are capable of quadrupedal locomotion on land. This entails compromises with respect to functional anatomy and morphology, and is the reason why river-otters are

considered morphologically intermediate between terrestrial and aquatic mammals (Tarasoff 1974). Whereas aquatic mammals such as cetaceans and pinnipeds propel their body through oscillatory motion of their body or tail, river-otters do this only when swimming under water. On the surface, they employ pelvic paddling (Fish 1993), just as other semi-aquatic species do.

Earlier investigations on small semi-aquatic mammals (mink, *Mustela vison*; Williams 1983; muskrat, *Ondatra zibethicus*, Fish 1982) have yielded higher energy requirements for swimming than in aquatic mammals, apparently justifying conclusions on the efficiency of the different swimming modes (Fish 1993). Because a recent review on mammalian swimming energetics (Fish 1993) lacked data on the larger semi-aquatic species, we recently investigated beavers *Castor canadensis* (Allers and Culik 1997) to fill this gap. In the present study, we wanted to know how transport costs during submerged swimming compare between pelvic paddlers such as the beaver and the seemingly more adapted river-otter, and how river-otters perform in comparison to aquatic mammals and highly derived aquatic birds of similar size.

Determination of the energy costs of underwater swimming is difficult and several authors have attempted this with varying success. In the past, water flumes (Woakes and Butler 1983; Baudinette and Gill 1985; Williams 1989; Ponganis et al. 1990) seemed to be the only viable method, because they offered the possibility of keeping water flow (and thus “swimming” speed) constant. The price for this was, however, a stressful and noisy environment for the animals, the restriction of swimming at the surface or at best partially or intermittently submerged against a current, while maintaining a stationary position, and turbulence and increased drag from the surrounding cage. Worst of all, however, water flumes were only rarely able to simulate the swimming speeds the animals preferred in the wild, which resulted in overestimates of minimum transport costs (c.f. Culik and Wilson 1991).

As opposed to this, Allers and Culik (1997) presented a method whereby energy requirements of mammals

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such as beavers could be measured during submerged swimming under semi-natural conditions. They used a swim channel covered with transparent sheets and respiration chambers at each end to measure O<sub>2</sub> uptake after a dive. In the still-water channel, study-animals could be trained to swim freely, reaching the speeds at which they swim in the wild. Regular training and lack of handling reduced experimental stress, while at the same time providing an extensive data base.

After determining the energy expenditure of zoo-bred river-otters during rest on land, we adapted the method of Allers and Culik (1997) to measure the energetics of underwater swimming at speeds chosen by the animals and the minimum cost of transport at optimal speed and to examine how energy requirements during underwater swimming compare with those of other diving animals.

## Material and methods

All experiments were carried out under licence and in accordance with the principles and guidelines of the German laws on animal welfare (Bundesgesetzblatt, 1993, Teil I) at Neumünster Zoo and the Otter-Zentrum in Hankensbüttel, Germany, between July 1995 and January 1996. The river-otter display in Neumünster consists of a 3 m × 3 m × 2 m den which communicates with a swim channel (described below). The den holds 2 river-otters during experiments. We conducted 2 series of experiments, using a total of 4 zoo-bred animals (age 2–19 years; mean body mass 6.0 ± 1.1 kg), which were weighed prior to and after every experiment. Animals were fed twice daily between 1100 hours and 1500 hours and between 1900 hours and 2100 hours local time, receiving rations of approximately 1 kg fish (Cyprinids), and meat (beef).

### Resting metabolic rate

Energy requirements of the river-otters at rest were determined in an enclosure in the Otter-Zentrum in Hankensbüttel during the inactive phase (0600–1300 hours) by using a flow-through, wooden respiration chamber (48 L) with a sliding door (T<sub>a</sub> = 5 °C). The river-otters were conditioned to use the experimental setup for normal sleeping 1 week before experiments began. After an animal had entered the chamber (we could not determine when feeding had last occurred), the door was closed and air was circulated in the chamber via a 12 V fan (Trumavent TEB, Truma, Putzbrunn, Germany), which mixed the air volume within 2 s. Air from the chamber was cleared (negative pressure) at a rate of 50 Lmin<sup>-1</sup> by a pump (MC4, Vacuubrand, Wertheim, Germany) and fed directly to the laboratory via gas-impermeable tubing (9.5 mm diameter, Tygon, Norton, USA). In the laboratory, gas flow from the chamber was measured with a mass flow meter (MAS 3015, Kobold, Hofheim, Germany), and a subsample was dried (Drierite, Aldrich Chemicals) and passed into a paramagnetic O<sub>2</sub> analyser (OXYGOR) and subsequently an infrared CO<sub>2</sub> analyser (UNOR, both Maihak, Hamburg, Germany). During the experiments, O<sub>2</sub> and CO<sub>2</sub> concentrations in the respiration chamber remained between 20% and 21% and between 0% and 1%, respectively. Data from both gas analysers and the flow meter were sampled every 2 s by an IBM-compatible 386SX computer (Chicony, Hamburg, Germany) fitted with an analogue-digital conversion card and using customized software (resolution: 0.01% O<sub>2</sub> and CO<sub>2</sub>).

### Energy requirements during swimming

The swim channel was immersed into a pool and consisted of a 11-m-long U-shaped (in cross-section) zinc-plated metal sheet

construction 0.88–0.92 m wide and 0.77 m deep, pre-built in interlocking segments (1.25 m long). The channel was covered about 5 cm below the water surface with transparent polyvinyl chloride (PVC) sheets (5 mm thick, Richter, Kiel, Germany), bolted to the metal to prevent the river-otters from surfacing and breathing at locations other than in the respiration chambers. Water in the pool (mean temperature 12.8° ± 3.4 °C) had to be replaced twice a week owing to contamination with excreta and algae. During the experiments, the river-otters could breathe only in two open-flow respiration chambers made of transparent PVC, volume depending on water level, about 40L (chamber A) and 100L (chamber B) partially immersed at both ends of the channel and thus sealed from outside air. Both ends of the channel could be closed with sliding doors. One end (A) opened to the den area, while the other end (B) was closed.

Gas samples were treated in the laboratory as described above. The influence of O<sub>2</sub> and CO<sub>2</sub> exchange between air in the respiration chambers and the water in the channel during the experiment was assumed to be negligible (Williams 1989; A. Körtzinger, personal communication). The whole system was calibrated daily with outside air (20.95% O<sub>2</sub> and 0.03% CO<sub>2</sub>) and gas mixtures (Wösthoff pump, Bochum, Germany) of air and N<sub>2</sub> (19.90% O<sub>2</sub>) or air and CO<sub>2</sub> (1.03% CO<sub>2</sub>). Calibration checks with ambient air were made before and after each experiment. Recovery rates (99.5% ± 4.4%, *n* = 9) for the whole system (including mass flow meter, analysers, A/D converter, and computational techniques) were determined by pumping known volumes of nitrogen (99.995% pure, Messer Griesheim, Kiel, Germany) into the respiration chambers with a standard gas meter.

Prior to the experiments and over a period of 1–2 weeks, each pair of river-otters was conditioned daily to the experimental setup. Animals were allowed free access to the channel, and during the first days of the training phase, the water level in the pool was kept low so that the animals could breathe everywhere underneath the PVC sheets. Subsequently, the water level was raised gradually, and the animals had to dive through increasingly longer portions of the channel, breathing being finally restricted to one of the two respiration chambers. For experiments, individual river-otters were maintained in the channel for periods of approximately 1 h by closing the sliding door to the den-area. The animals never had to be handled.

Activity and position of the river-otters in the channel were recorded in real time using a Husky Hunter II field computer (Husky, Coventry, England) and specially designed software. Each key on the computer was associated with a particular behaviour or position of the animal (river-otters swimming past six markers), and when pressed, was recorded together with real time (to the nearest 0.1 s). A behaviour ended when a new behaviour was recorded. The data were analysed by means of specially designed software to obtain: (1) the duration of the various activities, (2) mean swim speed for a dive series (if an animal turned around between two markers, no speed was computed until the animal swam again in a straight line), (3) distance swum, and (4) dive duration for each individual pass.

### Oxygen consumption

Activity and respirometry data were individually matched for each interdive interval. Dives which were interrupted because the river-otters tried to lift the PVC sheets or showed other unquantifiable activity such as unrest were deleted from the analysis. The data set used in this study therefore only comprised observations from animals swimming in a straight line through the channel and surfacing, or turning around and surfacing in the original respiration chamber. When in the chambers, the otters were either resting or recovering quietly, followed by another swimming event. In total, we conducted 21 experiments with the four animals and obtained 478 individually analysed dives or dive series through the channel.

O<sub>2</sub> consumption in a respiration chamber was calculated for each 2 s interval using the formula of Woakes and Butler (1983) as modified by Culik et al. (1990), which accounts for analyser drift.

Measurements were corrected for respiratory quotient (RQ) according to Withers (1977) and summed for the duration of the surface interval for as long as values were above a threshold of  $1 \text{ mL s}^{-1}$  for three consecutive measurements (to account for system hysteresis). This ensured that any noise in the apparatus was not recorded while the river-otter was not in the chamber.

Culik et al. (1996) described three different methods for the calculation of  $\text{O}_2$  consumption rates from data obtained as above. Here, we assumed that river-otter  $\text{O}_2$  consumption in the chambers during surface time reflects  $\text{O}_2$  consumption while swimming (and breath holding) just prior to surfacing plus  $\text{O}_2$  consumption during the current recovery period (Castellini et al. 1992). The duration of the recovery period is defined as the time required for elevated  $\text{O}_2$  consumption rates after a dive or dive series to return to resting levels (in water). The total amount of  $\text{O}_2$  consumed during the recovery period after a dive series is therefore divided by the time of breath holding plus the time of recovery to obtain the rate of  $\text{O}_2$  consumption ( $\text{mL O}_2 \text{ s}^{-1}$ ) for the event (dive plus recovery). The corresponding power input reflects the energy expenditure of animals travelling or foraging in the water.

In order to analyse power input of diving river-otters with respect to swimming speed, power input was averaged for  $0.2 \text{ m s}^{-1}$  speed classes (e.g. power data obtained at mean swimming speeds between  $0.4$  and  $0.6 \text{ m s}^{-1}$  were summarized into the  $0.5 \text{ m s}^{-1}$  speed class, and so on). All statistical analyses were computed using SYSTAT. Means are presented  $\pm$  standard error.

## Results

### Resting metabolic rate (RMR)

During experiments, the animals (mean mass  $6.2 \pm 0.6 \text{ kg}$ ,  $n = 3$ ) were kept in the chamber for periods of 60 min. RMR was determined from minimum metabolism measured during 5 consecutive min. We registered a mean  $\text{O}_2$  consumption of  $0.205 \pm 0.07 \text{ mL kg}^{-1} \text{ s}^{-1}$  and an RQ of  $0.77 \pm 0.02$ , corresponding to an energy conversion factor of  $20 \text{ J mL}^{-1} \text{ O}_2$  (Eckert 1993). Energy consumption during rest therefore amounts to  $4.1 \pm 0.6 \text{ W kg}^{-1}$ .

### River-otter activity in the channel

During the experiments, when the channel was closed, the animals swam up and down, being submerged for an average of  $18 \pm 6 \text{ s}$  ( $n = 478$ ) prior to surfacing for mean periods of  $26 \pm 36 \text{ s}$  ( $n = 478$ ). Swim speed was constant during individual dives (but varied from one dive series to another) and averaged  $0.89 \pm 0.1 \text{ m s}^{-1}$  ( $n = 478$ ). River-otters did not always surface immediately after swimming from one end of the channel to the other; mean distance swum during dive series was  $11.5 \pm 1.7 \text{ m}$  ( $n = 478$ ).

### Energy requirements in the channel

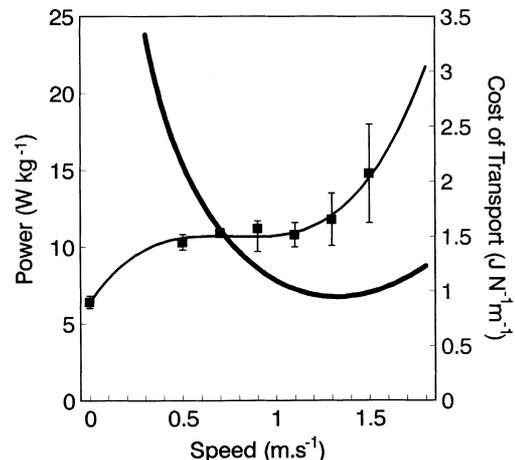
Because otters could never be induced to rest in the water for any length of time, this energy cost had to be determined by linear regression of oxygen consumption against duration of resting and diving (no constant). The resultant slope for resting in water yields  $0.321 \pm 0.016$

$\text{mL kg}^{-1} \text{ s}$  ( $n = 478$ ,  $r^2 = 0.854$ ,  $P < 0.0001$ ), which corresponds to  $6.4 \pm 0.4 \text{ W kg}^{-1}$ . Two of the four river-otters ( $5.8 \text{ kg}$  and  $7.8 \text{ kg}$ ) were trained to feed in the channel. Mean energy expenditure during feeding events was  $0.61 \pm 0.08 \text{ mL s}^{-1}$ , corresponding to  $12.3 \pm 1.5 \text{ W kg}^{-1}$  ( $n = 7$  measurements).

When swimming, the mean energy expenditure of all four animals ( $n = 478$  measurements) ranged from  $10.3 \pm 3.3 \text{ W kg}^{-1}$  ( $n = 38$ ) at  $0.5 \text{ m s}^{-1}$  to  $14.8 \pm 4.5 \text{ W kg}^{-1}$  ( $n = 2$ ) at  $1.5 \text{ m s}^{-1}$  (Table 1; Fig. 1), but differences between speed classes were not significant (ANOVA,  $P > 0.05$ ). Nevertheless, power input (in  $\text{W kg}^{-1}$ ) during sub-surface swimming was modelled for the six speed classes using a third degree polynomial function (Culik et al. 1994; Schmidt-Nielsen 1995) as  $P_1 = 10.19 v^3 - 23.31 v^2 + 17.47 v + P_{\text{rest}}$  ( $n = 6$ ,  $r_2 = 0.953$ ), where  $P_{\text{rest}}$  is the power input during rest at the water surface ( $6.4 \text{ W kg}^{-1}$ ), and  $v$  is swim speed ( $\text{m s}^{-1}$ ). The corresponding curve fit is shown in Fig. 1.

**Table 1** Power input and cost of transport of four river-otters in the swim channel averaged for different speed classes (see Fig. 1). Standard errors are given in parentheses

Speed ( $\text{m s}^{-1}$ )	Power ( $\text{W kg}^{-1}$ )	COT ( $\text{J N}^{-1} \text{ m}^{-1}$ )	Dives ( $n$ )
0.5	10.3 (0.5)	1.94 (0.11)	38
0.7	10.9 (0.2)	1.55 (0.03)	234
0.9	11.2 (0.5)	1.30 (0.06)	128
1.1	10.8 (0.8)	1.02 (0.08)	64
1.3	11.8 (1.7)	0.95 (0.14)	12
1.5	14.8 (3.2)	1.05 (0.23)	2



**Fig. 1** Power input ( $\text{W kg}^{-1} \pm \text{SE}$ , thin line) and dimensionless cost of transport ( $\text{J N}^{-1} \text{ m}^{-1}$ , thick line) of 4 river-otters in the channel with respect to different swim speeds ( $\text{m s}^{-1}$ )

Cost of transport ( $\text{JN}^{-1}\text{m}^{-1}$ , which is dimensionless) is power ( $\text{W kg}^{-1}$  or  $\text{J}\cdot\text{s}^{-1}\text{kg}^{-1}$ ) divided by speed ( $\text{m s}^{-1}$ ) and earth acceleration ( $9.81\text{ m s}^{-2}$ ), and is the amount of energy (in Joule) required to transport one Newton over a distance of 1 m (Videler and Nolet 1990). Cost of transport ( $n = 478$ ; Table 1, Fig. 1) ranged from  $1.94 \pm 0.68$  ( $n = 38$ ) at  $0.5\text{ m s}^{-1}$  to  $1.05 \pm 0.33$  ( $n = 2$ ) at  $1.5\text{ m s}^{-1}$  with a minimum of  $0.95 \pm 0.48$  ( $n = 12$ ) at  $1.3\text{ m s}^{-1}$ . Transport costs were significantly different (ANOVA,  $P < 0.001$ ) between the different speed classes ( $n = 6$ , Tukey test,  $P < 0.05$ ) and were fitted using  $P_i/v$ .

## Discussion

### RMR on land

RMR measured in three captive-born post-absorptive river-otters in the Otter-Zentrum in Hankensbüttel in a dark respiration chamber was 22.7% higher than the values reported by Kruuk et al. (1994) for river-otters under similar conditions and temperatures. Part of this difference can be accounted for by differences in body size. If metabolic rate is expressed as  $\text{W kg}^{-0.75}$  (Schmidt-Nielsen 1984), the difference is reduced to 16.4% ( $6.47\text{ W kg}^{-0.75}$  for  $6.2\text{ kg}$  river-otters). Because it was not possible to examine if the river-otters really were "totally quiet" in their sleeping-boxes during the experiments, slight, and acoustically imperceptible movements could have increased RMR.

RMR (in W) in terrestrial mammals is related to body mass ( $M$ , kg) as:  $\text{RMR} = 3.34 M^{0.75}$  (Schmidt-Nielsen 1984). Compared to this, the value for the RMR of river-otters reported here is 48.4% higher than expected, while that of Kruuk et al. (1994) was 38.3% higher. Irving (1973) proposed that semi-aquatic and aquatic mammals generally have a higher RMR than terrestrial mammals to compensate for heat loss in water, but this was not supported by the findings of, e.g., Allers and Culik (1997) for beavers. Iversen (1972), however, restricted his comparison to one of mustelids on the one hand and land mammals on the other hand and gave a figure of 20% for the differences in RMR. Based on this, Estes (1989) suggested that a high RMR is a general feature of mustelids.

### Rest in water

The metabolic rate calculated for river-otters resting in water is 36% higher than RMR on land. The main reason for this is presumably heat loss owing to the high thermal conductivity of water (25 times that in air; Schmidt-Nielsen 1995). According to Kruuk et al. (1994) the energy expenditure of active otters (9.2 kg) resting in water can also be derived from the following formula:  $E[\text{W/kg}] = 8.96 - 0.29 \times \text{TW}$  (TW is the Temperature in  $^{\circ}\text{C}$ ), which yields  $9.1\text{ W kg}^{-0.75}$  for the conditions

during our experiments (mean temperature  $12.9\text{ }^{\circ}\text{C}$ ). Our own results ( $10.0\text{ W kg}^{-0.75}$ ) compare well, the mass-corrected difference amounting to only 9.9%.

### Energy requirements while swimming in the channel

Culik et al. (1994) used a 3rd degree polynomial function to model the energy costs of wing-propelled *Pygoscelid* (body mass ca. 5 kg) and king penguins (*Aptenodytes patagonicus*, mass ca. 13 kg; Culik et al. 1996). The same approach was adapted by Bethge et al. (1997) on little blue penguins (*Eudyptula minor*, mass ca. 1 kg), Schmid et al. (1995) on foot-propulsed cormorants (*Phalacrocorax carbo sinensis*, mass ca. 2 kg); and Allers and Culik (1997) on beavers (mass ca. 18 kg). The 3rd degree polynomial offers the advantage of easy conversion from the units of power ( $\text{W kg}^{-1}$ ) to the dimensionless cost of transport when compared to other curve fits.

Power requirements in underwater-swimming otters increase at higher swim speeds (Fig. 1), but at speeds around  $1.3\text{ m s}^{-1}$ , cost of transport reaches a minimum. This is caused by the fact that at lower speeds, the proportion of energy used for maintenance and thermoregulation is higher than the energy requirements of propulsion. At the speed at which cost of transport is minimal, thermoregulation is in part a by-product of the metabolic heat generated by the muscles (Culik et al. 1996). At that speed, the propulsive muscles presumably work optimally, making full use of elastic energy storage and elastic rebound (Alexander 1988). Animals swimming at speeds above optimum (i.e. higher than  $1.3\text{ m s}^{-1}$  in river-otters), do this at the cost of increased power input (which increases with the third power of speed), caused by incrementing hydrodynamic drag. Transport costs rise only with the second power of speed, since they are given by power divided by speed (Culik et al. 1996; Allers and Culik 1997).

Interestingly, river-otters in the channel chose to swim at a mean speed of  $0.9\text{ m s}^{-1}$  which is 31% slower than their optimal speed of  $1.3\text{ m s}^{-1}$ . This can be explained by the limited size of the channel, which presumably caused the animals to slow down and accelerate more often than they would have done in the wild. Allers and Culik (1997) also found beavers to swim 28% slower than their optimal speed, and similar to the situation here, they had no independent speed measurements from free-living animals. During similar studies on birds, Culik et al. (1994, 1996), however, found Adélie, chinstrap, gentoo and king penguins to swim 25%, 27%, 20% and 25% slower, respectively, in a swim channel than at sea, and Bethge et al. (1997) even reported a difference of 45% for little penguins. These differences may be explained by the "stop and go" swimming activity in the channel, resulting in reduced mean speed during dives.

If we assume that the total oxygen stores of river-otters are comparable to those of the larger sea-otters ( $52\text{ mL O}_2\text{ kg}^{-1}$ , Lenfant et al. 1970) then river otters would

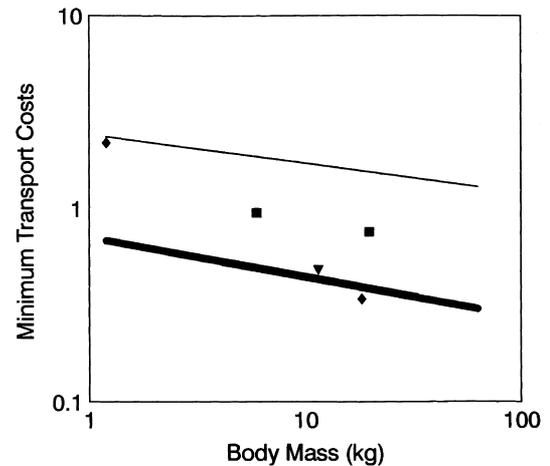
be able to dive for 90 s before their oxygen stores are depleted (at  $1.3 \text{ m s}^{-1}$  and  $0.59 \text{ mLO}_2 \text{ kg}^{-1} \text{ s}^{-1}$ ). This is only half the duration of 180 s calculated for sea otters (20 kg), which consume  $0.29 \text{ mLO}_2 \text{ kg}^{-1} \text{ s}^{-1}$  (Williams 1983). However, both species live in totally different environments and river-otters presumably do not need to conduct extensive dives while foraging.

#### Comparison with other subsurface swimmers

Most semi-aquatic mammals like beaver, mink and muskrat use the “paddling” swimming mode. This is a modification of terrestrial gait which is associated with slow swimming speeds and precise manoeuvrability. During the power phase of the paddling stroke cycle, the posterior motion of the webbed foot generates a drag force which is translated into forward thrust for the animal (Fish 1993). In order to reduce drag and minimize energy losses during the recovery or repositioning phase of the foot, its effective paddle area is reduced through configurational changes (Fish 1993). However, paddling animals only generate thrust during half of the stroke cycle and lose energy during repositioning of the limb and in accelerating the paddle mass (Fish 1993). As opposed to this, highly derived aquatic mammals and birds propulse themselves very efficiently by undulating their whole body or oscillating their appendages and employing hydrodynamic lift-based momentum exchange (Fish 1993). No repositioning is required and forward thrust is generated during both the up- and downstroke of body or limbs.

According to Fish (1982, 1993) and Thewissen et al. (1994) one of the key components in the evolutionary shift from quadrupedal terrestrial to fully aquatic mammals was a change from paddling or drag-based propulsion to undulatory propulsion. Semi-aquatic mammals are considered intermediate between terrestrial and aquatic mammals (Taylor 1914; Tarasoff 1974) and correspondingly, river- as well as sea-otters use both swimming modes, pelvic paddling and also body-undulation (Fish 1993). Consequently, we expected their underwater swimming metabolism to be on an intermediate level, higher than that of fully aquatic mammals but lower compared to paddling semi-aquatic mammals.

Dimensionless cost of transport can be used to assess the efficiency of different swimming modes and for that purpose it is not necessary to determine drag or thrust as a measure of power output in order to measure efficiency (Fish 1993). Culik et al. (1994) proposed that minimal cost of transport in sub-surface swimming homeotherms employing hydrodynamic lift-based momentum exchange for propulsion could be predicted based on their body mass ( $M$ , in kg) through cost of transport (COT) =  $0.71 M^{-0.205}$ . For a 6-kg river-otter, this would amount to 0.49, a value which is only about half of what we actually measured (0.95). However, homeotherms swimming at the surface have minimal transport costs given by  $\text{COT} = 2.43 M^{-0.15}$  (Williams, 1989), which



**Fig. 2** Minimal transport costs (in  $\text{J N}^{-1} \text{m}^{-1}$ , which is dimensionless) in river-otters (this study) and sea-otters (Williams 1989; squares) compared to surface paddlers (thin line, Williams 1989) and sub-surface swimming penguins and seals (thick line, Culik et al. 1994). Transport costs of muskrats (McArthur and Krause 1989), beavers (Allers and Culik 1997; diamonds), and king penguins (Culik et al. 1996; triangle) are included for comparison. For details, see text

would yield 1.86 for the river-otter or about double our result (Fig. 2).

The results of these comparisons compare well to minimal transport costs of sea-otters (*Enhydra lutris*, 20 kg) which were found to be 0.76 by Williams (1989). Again, her results are about twice as high as the 0.38 predicted by Culik et al. (1994) for sub-surface swimmers but only half of the estimate for surface paddlers (1.55). The measurements made on both otter species seem to support the hypothesis that these mustelids have reached an intermediate position between the truly aquatic mammals and the surface paddlers.

The “adaptation” hypothesis is further supported by the fact that minimal transport costs of semi-aquatic muskrats (*Ondatra zibethicus*, 1 kg), which propel themselves underwater by paddling (McArthur & Krause 1989), are as high as 2.2, or only 10% lower than predicted for surface paddlers by Williams (1989). Surprisingly, however, the beaver seems to be an exception to this hypothesis. Allers and Culik (1997) found that underwater, the minimal COT of the paddling beavers (*Castor canadensis*, 18.8 kg) are only 0.39, a value which is exactly in line with values for penguins and seals (Culik et al. 1994). The difference between the values for beavers and otters is difficult to believe at the first look. Intuitively, one would think that otters are much better adapted to an aquatic life.

A possible reason for this paradox is given by the results of Kurbatov and Mordvinov (1974). They conducted experiments aimed at measuring the hydrodynamic parameters characterising beavers (*Castor fiber*) and otters (*Ondatra zibethica*) and showed that the body shape of beavers provides a gradual tapering towards the tail, whereas the body of otters ends more abruptly, with a lancet-like, laterally compact tail. The result of

these shape differences is that in beavers, the boundary layer remains in contact with body and tail, which leads to a reduction in frontal drag resistance. As opposed to this, in the otters an interruption of the boundary flow in the region between body and tail results in strong turbulence generation and concomitantly, increased hydrodynamic drag. Flow visualisation around a swimming *Ondatra* showed the turbulences generated in the neck region and their strong magnification in the area of the hind limbs. From this, Kurbatov and Mordvinov (1974) concluded that the body shape of *Ondatra* was not very well adapted to life in the water when compared with beavers and seals (*Pagophilus groenlandicus*).

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