

SHORT COMMUNICATION

Skating by: low energetic costs of swimming in a batoid fish

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ABSTRACT

We quantify the oxygen consumption rates and cost of transport (COT) of a benthic batoid fish, the little skate, *Leucoraja erinacea*, at three swimming speeds. We report that this species has the lowest mass-adjusted swimming metabolic rate measured for any elasmobranch; however, this species incurs a much higher COT at approximately five times the lowest values recorded for some teleosts. In addition, because skates lack a propulsive caudal fin and could not sustain steady swimming beyond a relatively low optimum speed of 1.25 body lengths s^{-1} , we propose that the locomotor efficiency of benthic rajiform fishes is limited to the descending portion of a single COT–speed relationship. This renders these species poorly suited for long-distance translocation and, therefore, especially vulnerable to regional-scale environmental disturbances.

KEY WORDS: COT, Elasmobranch, Locomotion, Metabolic rate, Performance

INTRODUCTION

Batoid fishes (skates and rays) are unique among elasmobranchs in having dorsoventrally flattened bodies with broadly expanded pectoral fins that form a disc. Most batoids use their pectoral fins to generate lift for swimming whereby thrust is generated by anterior-to-posterior propulsive waves directed through the pectoral fin. Because batoids are negatively buoyant and must use additional energy to accelerate water downward in order to offset their specific gravity and swim, the metabolic efficiency of this locomotor behavior may be limited. Moreover, metabolic costs typically increase at higher speeds as drag forces increase to the square of velocity (Webb, 1998). Although swimming kinematics have been analyzed in a number of batoids (Blevins and Lauder, 2012; Rosenberger, 2001; Rosenberger and Westneat, 1999), no study has yet quantified the energetic costs of swimming in a batoid, nor whether different speeds require aerobic or anaerobic metabolism (Lauder and Di Santo, 2015). This is despite a long-standing recognition that locomotor performance and the associated metabolic costs are traits linked to fitness because they determine the capacity to endure migrations, escape predators, explore the environment and forage over long distances (Bennett and Huey, 1990).

Many rajiform members of the batoid clade (skates) move along the substratum using modified pelvic fins to ‘punt’ (i.e. walk), and only occasionally swim in the water column to quickly escape potential predators (Koester and Spirito, 2003). However, some

species are quite mobile and swim above the substrate for prolonged periods during migrations (Frisk et al., 2010). Locomotor performance is crucial to long-distance or prolonged movement; however, because of trade-offs associated with energetic costs, it is unclear whether swimming performance may limit the dispersal of batoids.

In this study, we sought to characterize energetic costs associated with varying swimming speeds under the hypothesis that metabolic rate scales positively with speed. To do this, we quantified locomotor energetics of a small batoid, the little skate, *Leucoraja erinacea* (Mitchill 1825), by measuring: (1) whole-organism energetic costs during prolonged swimming; (2) swimming endurance; (3) cost of transport (COT); and (4) recovery after exhaustion, across three biologically relevant speeds.

MATERIALS AND METHODS

Animals

Juvenile little skates ($n=5$, mass: 0.0157 ± 0.0001 kg, disc length: 5.6 ± 0.02 cm) were maintained in a 1300-liter tank at a constant temperature ($14.5\pm 0.5^\circ\text{C}$), salinity (33 ppt) and a 12 h:12 h light:dark photoperiod. Skates were fed frozen mysis shrimp *ad libitum* daily. Before experimentation, fish were fasted for 24 h so that metabolic measurements were taken in a post-absorptive state. Research was conducted with approval of Harvard University IACUC protocol 20-03.

Swimming endurance and metabolic costs

We tested the energetic cost of swimming by quantifying oxygen consumption (\dot{M}_{O_2}) in skates before swimming (routine, $\dot{M}_{O_2, \text{rout}}$), during prolonged steady swimming ($\dot{M}_{O_2, \text{swim}}$) at three constant speeds [$U=0.75, 1$ and 1.25 BL s^{-1} , where body length (BL) is defined by disc length: 5–6.5 cm], and after fatiguing (recovery, $\dot{M}_{O_2, \text{rec}}$). Swimming endurance was calculated as the time at which the fish reached exhaustion, a behavior indicated by resting against the downstream baffle of the swim tunnel for at least 1 min. \dot{M}_{O_2} was measured by swimming individual skates in a custom-made 39.4-liter Brett-type swim tunnel fitted with a 50 W pump (Red Dragon[®] III, Royal Exclusiv, Germany) and a calibrated digital-flow controller (Movie 1). Water temperature ($14.5\pm 0.5^\circ\text{C}$) in the swim tunnel was maintained by an Aqualogic Chiller unit (San Diego, CA, USA) connected to the respirometer chamber. The working section of the swim tunnel was $20\times 12\times 12$ cm (length \times width \times depth). To ensure laminar, non-turbulent flow, a plastic honeycomb was inserted upstream in the working section. A 45 deg ‘ramp’ made of the same honeycomb was placed 15 cm from the downstream margin of the working section. This ramp produced laminar flow behind its pitched surface and elicited consistent swimming behavior even at the lowest speed (Movie 1). Dissolved oxygen was measured every 30 s using an optical oxygen meter (ProODO, YSI, Yellow Springs, OH, USA) calibrated with 100% air-saturated water. Each skate was tested at the three speeds in a repeated-measures experimental design to control for inter-individual variation in performance. The sequence of experimental

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speeds was randomized to minimize carry-over effects of training on performance. Skates were transferred to the swim tunnel and accustomed to the experimental set-up for 2 h prior to trials. Preliminary trials revealed that oxygen consumption in little skates returns to routine levels within 2 h after exhaustion (Di Santo, 2016). Following fatigue, the fish were allowed to rest in the tunnel for at least 1 h while oxygen consumption was recorded to determine recovery rates (when $\dot{M}_{O_2,rec}$ returned to $\dot{M}_{O_2,rout}$ levels).

Skate $\dot{M}_{O_2,swim}$ was calculated from the slope of oxygen decline over time in the respirometer according to the formula:

$$\dot{M}_{O_2,swim} = \text{slope} \times VM^{-b}, \quad (1)$$

where V is volume of the swim tunnel in liters and M is the mass of fish in kilograms. A scaling coefficient (b) of 0.67 was invoked to correct for the allometric relationship between metabolic rates and mass after Di Santo (2015). To quantify $\dot{M}_{O_2,rout}$, individual quiescent skates were placed in an intermittent 0.465-liter resting respirometer chamber while oxygen decline was measured at 30-s intervals over 1 h.

Cost of transport

COT (in $\text{kJ km}^{-1} \text{kg}^{-1}$) provides a measure of swimming efficiency and indicates the amount of energy an organism expends to displace its mass a fixed distance. At each speed, $\dot{M}_{O_2,swim}$ was converted to kJ kg^{-1} using an oxy-calorific equivalent of $3.25 \text{ cal } 1 \text{ mg}^{-1} \text{ O}_2$ (Solomon and Brafield, 1972) and calculated as:

$$\text{COT} = \dot{M}_{O_2} \times U, \quad (2)$$

where U is expressed in km h^{-1} . To obtain COT_{net} , $\dot{M}_{O_2,rout}$ was subtracted from $\dot{M}_{O_2,swim}$, giving the $\dot{M}_{O_2,net}$ at each speed.

Data analyses

All metabolic rates, COT and endurance time at different speeds were analyzed using two-way repeated-measures ANOVA with individual skates and speed as factors, followed by a Tukey–Kramer multiple comparisons test for differences between group means. Recovery time following exhaustion was established using a repeated-measures ANOVA, followed by a Dunnett's test to

compare $\dot{M}_{O_2,rec}$ with $\dot{M}_{O_2,rout}$. All values are presented as means \pm s.e.m. Statistical treatments were considered significantly different at $\alpha=0.05$ and undertaken in R, version 3.2.

RESULTS AND DISCUSSION

$\dot{M}_{O_2,swim}$ decreased across the three speeds tested (ANOVA, $F_{2,8}=5.7$, $P=0.02$, Fig. 1A). Mean $\dot{M}_{O_2,swim}$ and $\dot{M}_{O_2,net}$ were significantly different at 0.75 and 1.25 BL s^{-1} (Tukey–Kramer, $\alpha=0.05$; Fig. 1A). Mean $\dot{M}_{O_2,swim}$ was at a minimum at 1.25 BL s^{-1} , establishing this as the optimal speed (U_{opt}) across the speeds tested. Moreover, swimming endurance did not differ significantly across speeds (ANOVA, $F_{2,8}=1.94$, $P=0.2$; Fig. 1B), suggesting a behavioral response rather than a physiological limit to swimming at these speeds (Peake and Farrell, 2006). Net COT was lowest at 1.25 BL s^{-1} , at $3.8 \pm 0.9 \text{ kJ km}^{-1} \text{kg}^{-1}$ (ANOVA, $F_{2,8}=12.42$, $P=0.003$; Fig. 1C). Following exhaustion, skates exhibited an increase in oxygen consumption after swimming steadily at 0.75 and 1 BL s^{-1} (Dunnett's test, $\alpha=0.05$; Fig. 2), suggesting that swimming involved anaerobic metabolism at low speeds. After fatiguing at 1.25 BL s^{-1} , skates returned immediately to resting state, indicating that aerobic metabolism sustained locomotion at this speed (Fig. 2). The post-exercise $\dot{M}_{O_2,rec}$ was added to COT_{net} to obtain COT_{tot} , indicating that locomotion at 0.75 BL s^{-1} is more inefficient than at 1 and 1.25 BL s^{-1} (ANOVA, $F_{2,8}=15.63$, $P=0.002$; Fig. 1D).

Little skates exhibit the lowest $\dot{M}_{O_2,swim}$ measured in any elasmobranch to date (for a review, see Lauder and Di Santo, 2015). In fact, at $38.3 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$, our results indicate that little skates achieve substantially lower $\dot{M}_{O_2,net}$ relative to the lowest value previously recorded for any elasmobranch (approximately $56 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ for *Squalus acanthias*, speed not controlled; Brett and Blackburn, 1978). Furthermore, little skate $\dot{M}_{O_2,swim}$ is comparable to that of the European eel, *Anguilla anguilla*, a species that has one of the lowest $\dot{M}_{O_2,swim}$ measured in fishes ($42 \text{ mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$; van Ginneken et al., 2005).

Although $\dot{M}_{O_2,swim}$ was significantly reduced with increasing speed, we were not able to quantify $\dot{M}_{O_2,swim}$ at speeds above U_{opt} , 1.25 BL s^{-1} , because at even slightly higher flow velocities

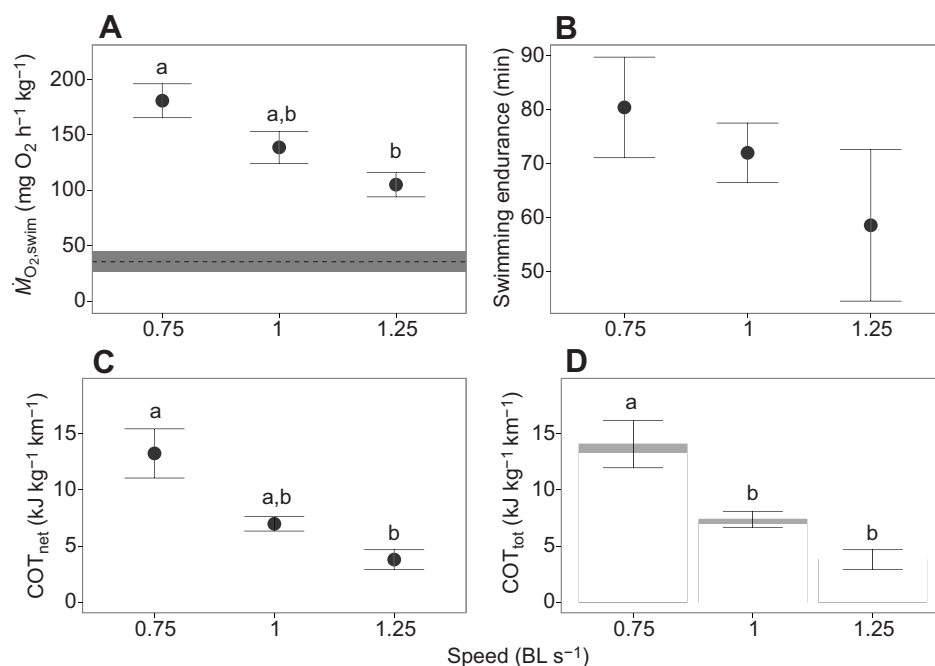


Fig. 1. Swimming energetics of the little skate, *Leucoraja erinacea*, at different speeds. (A) Routine (shaded) and swimming oxygen consumption rates ($\dot{M}_{O_2,swim}$), (B) swimming endurance, and (C) net and (D) total cost of transport (COT_{net} and COT_{tot} respectively; portion of post-fatigue COT in gray) as function of speed (mean \pm s.e.m.; $n=5$, repeated-measures ANOVA, followed by a Tukey–Kramer multiple comparisons test; different letters represent significance at $\alpha<0.05$).

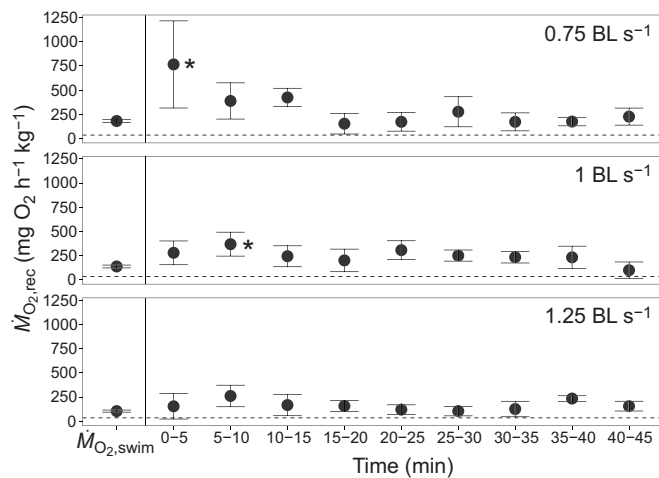


Fig. 2. Oxygen consumption rates of the little skate, *Leucoraja erinacea*, recovering after exhaustive exercise. Oxygen consumption rates at 5-min intervals of skates recovering after exhaustive swimming exercise ($\dot{M}_{O_2,rec}$: mean \pm s.e.m.) at three speeds. Vertical line represents fatigue point; horizontal dashed line indicates the mean routine metabolic rate ($\dot{M}_{O_2,rout}$). Asterisks indicate that $\dot{M}_{O_2,rec}$ is significantly higher than $\dot{M}_{O_2,rout}$ ($n=5$, repeated-measures ANOVA, followed by a Dunnett's test, $\alpha=0.05$).

(1.35 BL s^{-1}), skates were unable to swim steadily and fatigued within a few minutes of burst-and-coast swimming. Based on previous experiments, we expected an increase in oxygen consumption with speed beyond the U_{opt} (Webb, 1998). However, fishes at low suboptimal speeds experience increased induced drag, and thus require additional energy to maintain postural equilibrium (Webb, 1998). The combination of high-energy metabolic costs below and beyond U_{opt} contributes to the hypothetical 'J-shaped' curve proposed by Webb (1998); however, this has not yet been supported by empirical results from studies of fishes. In fact, published data only address the effect of high speeds on \dot{M}_{O_2} , and thus overlook $\dot{M}_{O_2,swim}$ at low speeds. In our study, skates swimming at U_{opt} show no post-fatigue increase in \dot{M}_{O_2} and return to pre-swimming \dot{M}_{O_2} immediately after exercise. In contrast to this, \dot{M}_{O_2} increased significantly after exercise at the lowest speeds (0.75, 1 BL s^{-1}), suggesting that skates incurred an oxygen debt at these speeds that increased metabolic rates during recovery. Consequently, skates at low speeds had an even higher COT_{tot} if the amount of energy consumed after exhaustion is considered. This suggests that, at low speeds, skates must also rely on anaerobic pathways to fuel this activity (Di Santo, 2016).

Despite the fact that little skates exhibit extraordinarily low $\dot{M}_{O_2,net}$, COT_{net} in this species is much higher compared with other fishes (approximately five times higher than the European eel swimming at 0.5 BL s^{-1}), and it is only surpassed by more active and larger species such as the mako shark, *Isurus oxyrinchus* (Sepulveda et al., 2007). Generally, COT is much greater in smaller fishes because of the increased energy required to cover a similar distance. It is not surprising then that smaller benthic species might exhibit limited geographic ranges, when compared with larger elasmobranchs. This perhaps also explains why skates often explore the environment by punting and only engage in swimming if startled by a potential predator (Koester and Spirito, 2003). It is possible that, similar to other animals, skates may switch gaits from punting to swimming to reduce metabolic costs over long distances; however, additional work is needed to evaluate this hypothesis. Combined, punting behavior observed in natural and laboratory settings and high $\dot{M}_{O_2,swim}$ and $\dot{M}_{O_2,rec}$ at low speeds suggest that

swimming may be reserved for longer-distance movement rather than for routine behaviors such as foraging. We also note that skates lack an expansive caudal fin and thus cannot transition from paired-fin to body-caudal-fin locomotion at higher speeds, a behavior common to teleosts, which swim at lower speeds using drag- or lift-based propulsion generated by the pectoral fins (Drucker, 1996). Because of this and our observations that skates would not swim steadily at speeds greater than 1.25 BL s^{-1} , these results suggest that skate locomotor efficiency is limited to the descending portion of a single COT –speed relationship.

However small, the energetic investment in swimming still represents a significant long-term cost. This cost is particularly relevant if a species must relocate to new, more favorable environments, especially in light of climate change, or migrate seasonally to breeding grounds. Although many fish species are known to have shifted their geographic range towards higher latitudes (Perry et al., 2005; Stebbing et al., 2002), a few studies have shown that skates do not seem to undertake large-scale migrations as a response to changes in the environment (Goodwin et al., 2005; Perry et al., 2005). As our results suggest, because little skates have some of the highest COT measured in fishes, they may be at a distinct disadvantage in regards to short-term translocation. Comparative physiologists have traditionally used BL s^{-1} to evaluate swimming capability in fishes as a means to account for the effect of size on locomotor performance. Such an approach reveals that comparing swimming efficiencies based on COT portrays a more accurate estimation of energetic costs of migration. In this framework, future studies may reveal that reduced locomotor ability, as a result of not high metabolic rates, but rather small body size, may limit large-scale translocation of smaller individuals and possibly render these more vulnerable to environmental changes.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

V.D.S. and C.P.K. designed and carried out experiments, analyzed data and wrote the manuscript.

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Supplementary information

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