

Skating By: Low Energetic Costs of Swimming in a Batoid Fish

Valentina Di Santo¹, Christopher P. Kenaley^{2,1}

¹Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA,
vdisanto@fas.harvard.edu

²Department of Biology, Boston College, Chestnut Hill, MA, USA

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 much higher COT at approximately 5 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 $1.25 \text{ BL} \times \text{s}^{-1}$ (body length, defined as disc length: 5–6.5 cm), 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 and Blake, 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 et al., 2003). However, some species are quite mobile and swim above the substrate for prolonged periods during migrations (Frisk et al., 2010). Locomotor performance is critical to long-distance or prolonged movement; however, it is unclear whether swimming performance may limit dispersal of batoids due to tradeoffs associated with energetic costs.

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, 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-L tank at a constant temperature ($14.5 \pm 0.5^\circ\text{C}$), salinity (33 ppt), and a 12L:12D 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 post-absorptive state.

Swimming endurance and metabolic costs

We tested the energetic cost of swimming by quantifying oxygen consumption ($\dot{M}\text{O}_2$) in skates before swimming (routine, $\dot{M}\text{O}_{2\text{rout}}$), during prolonged steady swimming ($\dot{M}\text{O}_{2\text{swim}}$) at three constant speeds ($U=0.75, 1, \text{ and } 1.25 \text{ BL} \times \text{s}^{-1}$; body lengths as defined by disc length), and after fatiguing (recovery, $\dot{M}\text{O}_{2\text{rec}}$). Swimming endurance was calculated as 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. $\dot{M}\text{O}_2$ was measured by swimming individual skates in a custom-made 39.4-L Brett-type swim tunnel fitted with a 50W pump (Red Dragon[®] III, Royal Exclusiv, Germany) and a calibrated digital-flow controller (supplementary video S1). 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 $20 \times 12 \times 12 \text{ cm}$ (L \times W \times D). To ensure laminar, non-turbulent flow, a plastic honeycomb was inserted upstream in the working section. A 45° “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 (supplementary video S1). Dissolved oxygen was measured every 30 seconds 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 interindividual variation in performance. The sequence of experimental 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 (Lauder and Di Santo, 2015). 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 $\dot{M}O_{2rec}$ returned to $\dot{M}O_{2rout}$ levels).

Skate $\dot{M}O_{2swim}$ was calculated from the slope of oxygen decline over time in the respirometer according to the formula:

$$\dot{M}O_{2swim} = \text{slope} \times V \times M^{-b};$$

where V is volume of the swim tunnel in L, M is the mass of fish in kg. 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 $\dot{M}O_{2rout}$, individual quiescent skates were placed in an intermittent 0.465-L resting respirometer chamber while oxygen decline was measured at 30-second intervals over 1 h.

Cost of Transport

Cost of transport (COT; in $\text{kJ} \times \text{km}^{-1} \times \text{kg}^{-1}$) 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, $\dot{M}O_{2swim}$ was converted to $\text{kJ} \times \text{kg}^{-1}$ using an oxy-calorific equivalent of 3.25 cal per 1 mgO_2^{-1} (Solomon and Brafield, 1972) and calculated as:

$$\text{COT} = \dot{M}O_2 \times U;$$

where U is expressed as $\text{km} \times \text{h}^{-1}$. To obtain COT_{net} , $\dot{M}O_{2rout}$ was subtracted from $\dot{M}O_{2swim}$, giving the $\dot{M}O_{2net}$ at each speed.

Data Analyses

All metabolic rates, COT, and endurance time at different speeds were analyzed using 2-WAY repeated measures ANOVAs with individual skates and speed as factors, followed by Tukey-Kramer (TK) multiple comparison test for differences between group means. Recovery time following exhaustion was established by using a repeated measures ANOVA, followed by a Dunnett's test (DT) to compare $\dot{M}O_{2rec}$ to $\dot{M}O_{2rout}$. All values are presented as means \pm standard error. Statistical treatments were based on $\alpha=0.05$ and undertaken in R, version 3.2.

Results and discussion

$\dot{M}O_{2swim}$ decreased across the three speeds tested (ANOVA, $F_{2,8}=5.7$, $p=0.02$, Figure 1a). Mean $\dot{M}O_{2swim}$ and $\dot{M}O_{2net}$ were significantly different at 0.75 and 1.25 $\text{BL} \times \text{s}^{-1}$ (TK, $\alpha=0.05$; Figure 1a). Mean $\dot{M}O_{2swim}$ was minimum at 1.25 $\text{BL} \times \text{s}^{-1}$, establishing this as the optimal speed (U_{opt}) across the speeds tested. Moreover, swimming endurance did not differ

significantly across speeds (ANOVA, $F_{2,8}=1.94$, $p=0.2$; Figure 1b) suggesting a behavioral response rather than a physiological limit to swimming at these speeds (Peake and Farrell, 2006). Net COT was lowest at $1.25 \text{ BL} \times \text{s}^{-1}$, at $3.8 \pm 0.9 \text{ kJ} \times \text{km}^{-1} \times \text{kg}^{-1}$ (ANOVA, $F_{2,8}=12.42$, $p=0.003$; Figure 1c). Following exhaustion, skates exhibited an increase in oxygen consumption after swimming steadily at 0.75 and $1 \text{ BL} \times \text{s}^{-1}$ (DT, $\alpha=0.05$; Figure 2), suggesting swimming involved anaerobic metabolism at low speeds. After fatiguing at $1.25 \text{ BL} \times \text{s}^{-1}$ skates returned immediately to resting state indicating that aerobic metabolism sustained locomotion at this speed (Figure 2). The post-exercise $\dot{\text{M}}\text{O}_{2\text{rec}}$ was added to COT_{net} to obtain COT_{tot} , indicating that locomotion at $0.75 \text{ BL} \times \text{s}^{-1}$ is more inefficient than at 1 and $1.25 \text{ BL} \times \text{s}^{-1}$ (ANOVA, $F_{2,8}=15.63$, $p=0.002$; Figure 1d).

Little skates exhibit the lowest $\dot{\text{M}}\text{O}_{2\text{swim}}$ measured in any elasmobranch to date (for a review see Lauder and Di Santo, 2015). In fact, at $38.3 \text{ mgO}_2 \times \text{kg}^{-1} \times \text{h}^{-1}$, our results indicate that little skates achieve substantially lower $\dot{\text{M}}\text{O}_{2\text{net}}$ relative to the lowest value previously recorded for any elasmobranch (approximately $56 \text{ mgO}_2 \times \text{kg}^{-1} \times \text{h}^{-1}$ for *Squalus acanthias*, speed not controlled; Brett and Blackburn, 1978). Furthermore, little skate $\dot{\text{M}}\text{O}_{2\text{swim}}$ is comparable to the European eel, *Anguilla anguilla*, a species that has one of the lowest $\dot{\text{M}}\text{O}_{2\text{swim}}$ measured in fishes ($42 \text{ mgO}_2 \times \text{kg}^{-1} \times \text{h}^{-1}$; van Ginneken et al., 2005).

Although $\dot{\text{M}}\text{O}_{2\text{swim}}$ was significantly reduced with increasing speed, we were not able to quantify $\dot{\text{M}}\text{O}_{2\text{swim}}$ at speeds above U_{opt} , $1.25 \text{ BL} \times \text{s}^{-1}$, because at even slightly higher flow velocities ($1.35 \text{ BL} \times \text{s}^{-1}$), 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 and Blake, 1998). However, fishes at low suboptimal speeds experience increased induced drag, and thus require additional energy to maintain postural equilibrium (Webb and Blake, 1998). The combination of high-energy metabolic costs below and beyond U_{opt} contributes to the hypothetical “J-shaped” curve proposed by Webb (Webb and Blake, 1998); however, this has not yet been supported by empirical results from studies of fishes. In fact, published data address only the effect of high speeds on $\dot{\text{M}}\text{O}_2$, and thus overlook $\dot{\text{M}}\text{O}_{2\text{swim}}$ at low speeds. In our study, skates swimming at U_{opt} show no post-fatigue increase in $\dot{\text{M}}\text{O}_2$ and return to pre-swimming $\dot{\text{M}}\text{O}_2$ immediately after exercise. In contrast to this, $\dot{\text{M}}\text{O}_2$ increased significantly after exercise at the lowest speeds (0.75 , $1 \text{ BL} \times \text{s}^{-1}$), suggesting that skates incurred an oxygen debt at these speeds which 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 $\dot{M}O_{2net}$, COT_{net} in this species is much higher compared to other fishes (approximately 5 times higher than the European eel swimming at $0.5 BL \times s^{-1}$) 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 due to 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 to 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 et al., 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 $\dot{M}O_{2swim}$ and $\dot{M}O_{2rec}$ at low speeds suggest that swimming may be reserved for longer-distance movement rather than routine behaviors like 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 beyond $1.25 BL \times s^{-1}$, 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 $BL \times s^{-1}$ to evaluate swimming capability in fishes as a means 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, not

due to 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.

Acknowledgements. The authors thank George Lauder for logistical and conceptual support. James Sulikowski donated the skates used in this study. Research was conducted with approval of the IACUC protocol #20-03 at Harvard University.

Competing interests. We have no competing interests.

Authors' contribution. VDS and CPK designed and carried out experiments, analyzed data, and wrote the manuscript.

Funding. This work was supported by ONR MURI Grant #141410533 monitored by Dr. Bob Brizzolara to George Lauder.

References

- Bennett, A. F. and Huey, R. B.** (1990). Studying the evolution of physiological performance. *Oxford surveys in evolutionary biology* **7**, 251–284.
- Blevins, E. L. and Lauder, G. V.** (2012). Rajiform locomotion: three-dimensional kinematics of the pectoral fin surface during swimming in the freshwater stingray *Potamotrygon orbignyi*. *J. Exp. Biol.* **215**, 3231–3241.
- Brett, J. R. and Blackburn, J. M.** (1978). Metabolic rate and energy expenditure of the spiny dogfish, *Squalus acanthias*. *J. Fish. Res. Board Can.* **35**, 816–821.
- Di Santo, V.** (2015). Ocean acidification exacerbates the impacts of global warming on embryonic little skate, *Leucoraja erinacea* (Mitchill). *J. Exp. Mar. Biol. Ecol.* **463**, 72–78.
- Di Santo, V.** (2016). Intraspecific variation in physiological performance of a benthic elasmobranch challenged by ocean acidification and warming. *J. Exp. Biol.* **219**, doi: 10.1242/jeb.139204.
- Drucker, E. G.** (1996). The use of gait transition speed in comparative studies of fish locomotion. *Am. Zool.* **36**, 555–566.
- Frisk, M. G., Martell S. J. D., Miller, T. J. and Sosebee, K.** (2010). Exploring the population dynamics of winter skate (*Leucoraja ocellata*) in the Georges Bank region using a statistical catch-at-age model incorporating length, migration, and recruitment process errors. *Can. J. Fish. Aquat. Sci.* **67**, 774–792.
- Goodwin, N. B., Dulvy, N. K. and Reynolds, J. D.** (2005). Macroecology of live-bearing in fishes: latitudinal and depth range comparisons with egg-laying relatives. *Oikos* **110**, 209–218.
- Koester, D. M., Spirito, C. P. and Wood, R.** (2003). Punting: an unusual mode of locomotion in the little skate, *Leucoraja erinacea* (Chondrichthyes: Rajidae). *Copeia* **2003**, 553–561.
- Lauder, G. V. and Di Santo, V.** (2015). Swimming mechanics and energetics of elasmobranch fishes. In *Physiology of Elasmobranch Fishes: Structure and Interaction*

with *Environment*, Vol. 34A (R. E. Shadwick A. P. Farrell and C. J. Brauner, eds.), pp.219-253. New York: Academic Press.

Peake, S. J. and Farrell, A. P. (2006). Fatigue is a behavioural response in respirometer-confined smallmouth bass. *J. Fish Biol.* **68**, 1742–1755.

Perry, A. L., Low, P. J., Ellis, J. R. and Reynolds, J. D. (2005). Climate change and distribution shifts in marine fishes. *Science* **308**, 1912–1915.

Rosenberger, L. J. (2001). Pectoral fin locomotion in batoid fishes: undulation versus oscillation. *J. Exp. Biol.* **204**, 379–394.

Rosenberger, L. J. and Westneat, M. W. (1999). Functional morphology of undulatory pectoral fin locomotion in the stingray, *Taeniura lymma*. *J. Exp. Biol.* **202**, 3523–3539.

Sepulveda, C. A., Graham, J. B. and Bernal D. (2007). Aerobic metabolic rates of swimming juvenile mako sharks, *Isurus oxyrinchus*. *Mar. Biol.* **152**, 1087–1094.

Solomon, D. and Brafield, A. E. (1972). The energetics of feeding, metabolism and growth of perch (*Perca fluviatilis* L.). *J. Anim. Ecol.* **41**, 699–718.

Stebbing, A. R. D., Turk, S. M. T., Wheeler, A. and Clarke, K. R. (2002). Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960–2001). *J. Mar. Biol. Assoc. U. K.* **82**, 177–180.

van Ginneken, V., Antonissen, E., Müller, U. K., Booms, R., Eding, E., Verreth, J. and van den Thillart, G. (2005). Eel migration to the Sargasso: remarkably high swimming efficiency and low energy costs. *J. Exp. Biol.* **208**, 1329–1335.

Webb, P. W. and Blake, R. W. (1998). Swimming. *Physiol. Fishes*, 3–24.

Figures

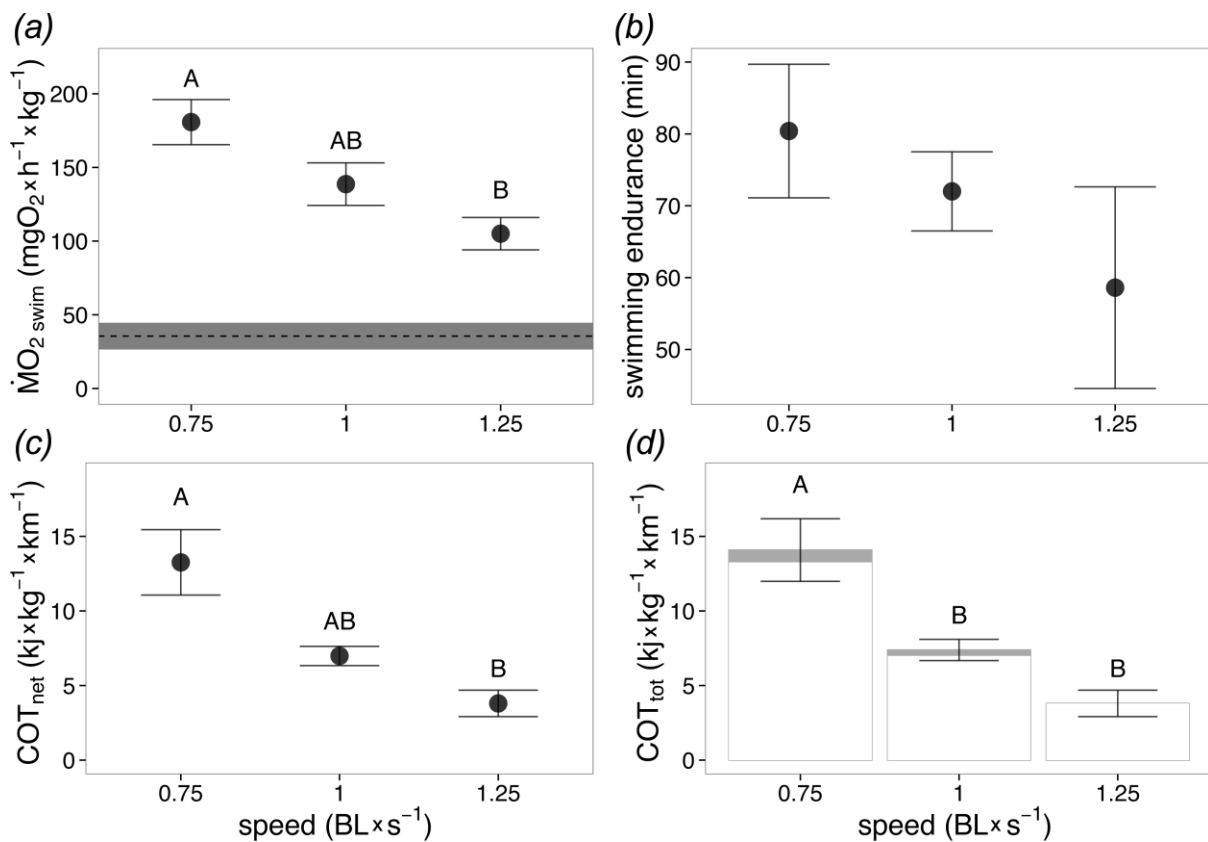


Figure 1. Swimming energetics of the little skate *Leucoraja erinacea* at different speeds.

(a) Routine (shaded) and swimming oxygen consumption rates ($\dot{M}O_{2\text{swim}}$), (b) swimming endurance, (c) net and (d) total cost of transport (COT_{net} and COT_{tot} , respectively; portion of post-fatigue COT in grey) as function of speed (mean \pm s.e.m.; n=5, repeated measures ANOVA, followed by a Tukey-Kramer MCT; different letters represent significance at $\alpha < 0.05$).

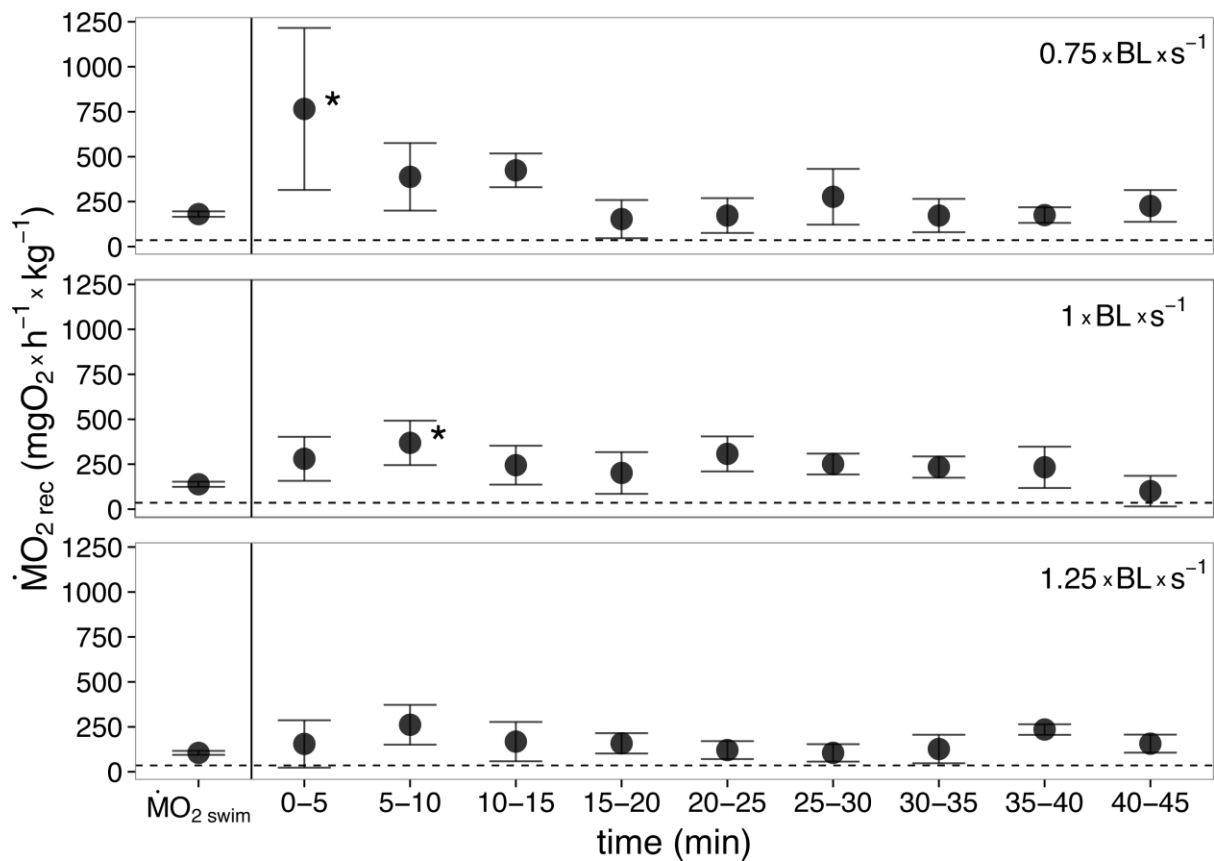


Figure 2. Oxygen consumption rates of the little skate *Leucoraja erinacea* recovering after exhaustive exercise. Oxygen consumption rates at 5-min intervals of skates recovering after exhaustive swimming exercise ($\dot{M}O_{2rec}$: mean \pm s.e.m.) at three speeds. Vertical line represents fatigue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



Movie 1. Little skate, *Leucoraja erinacea*, swimming in a Brett-type swim tunnel at 1.25 body lengths s^{-1} .