

forced and volitional exercise in fish

- an integration of swimming behaviour and physiology -

Christian Tudorache, Leiden University



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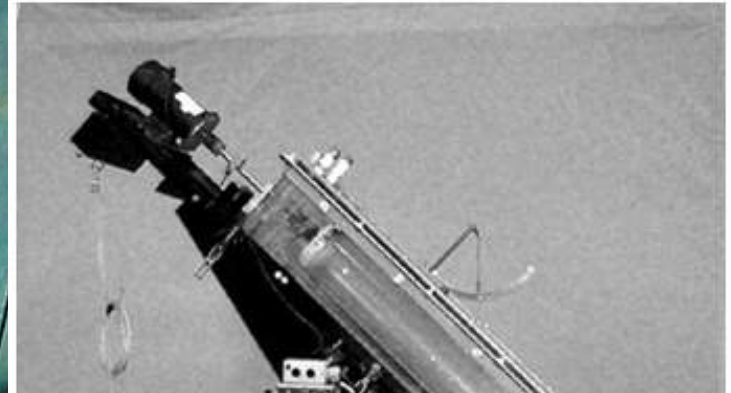
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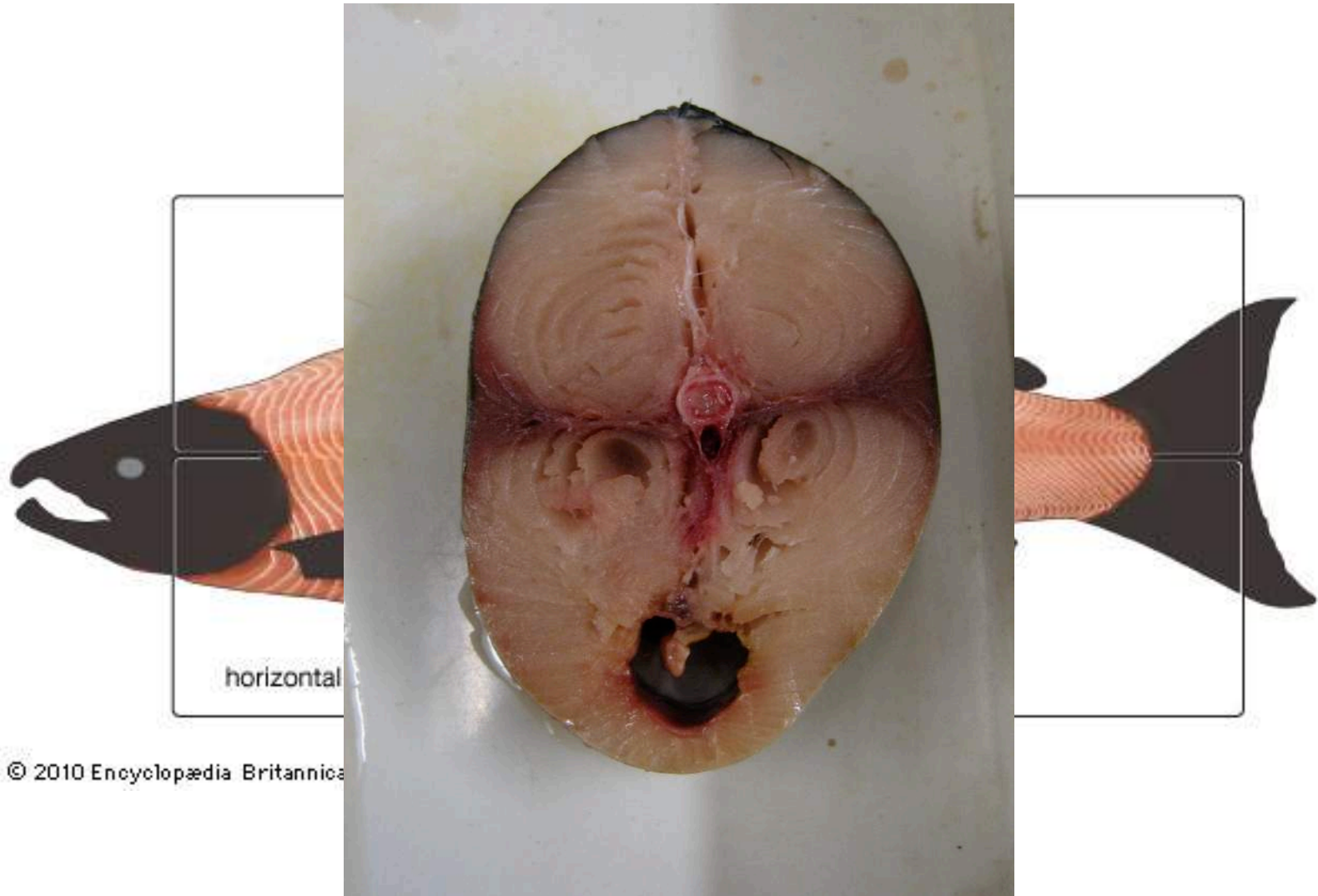
Wichita Mountains

Holyoke fish lift

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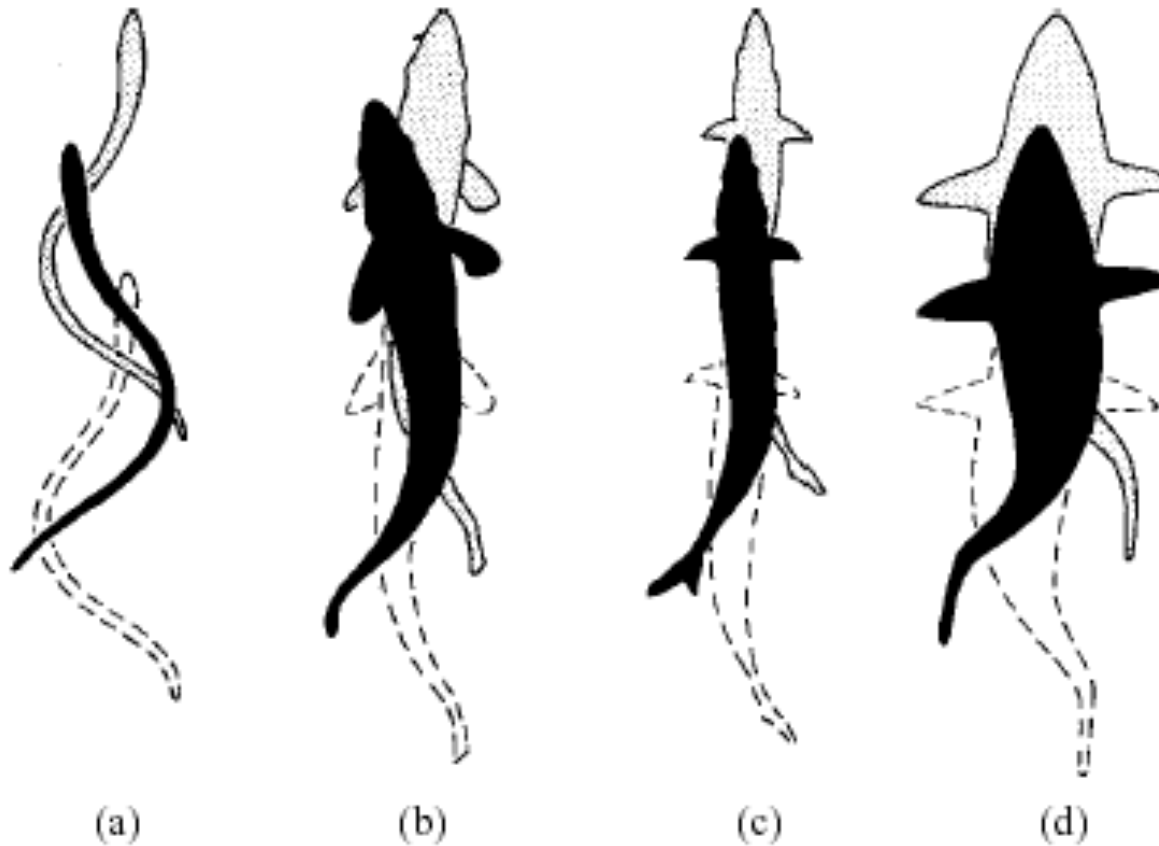
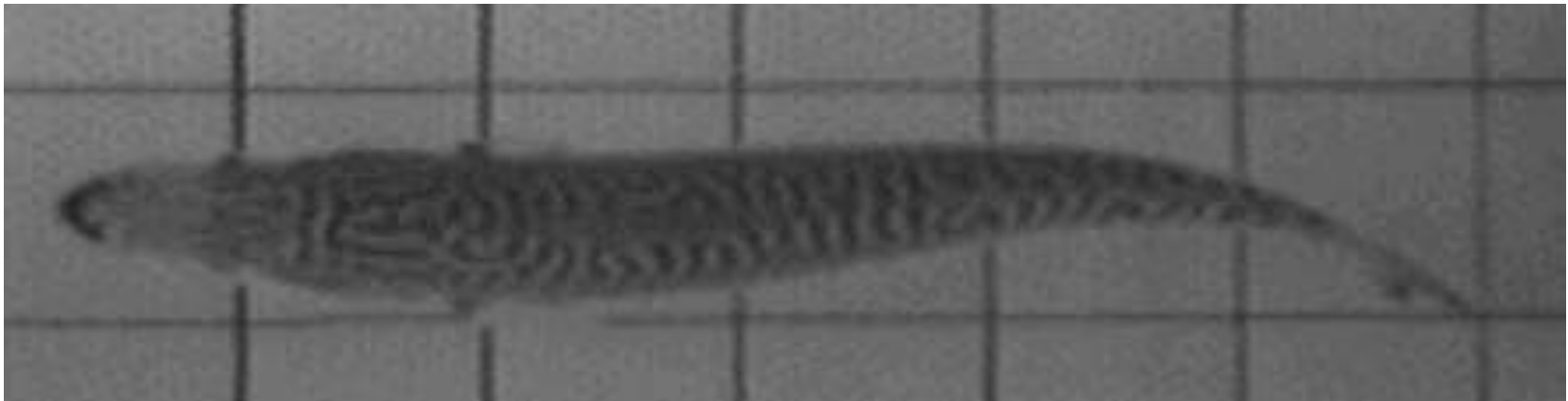
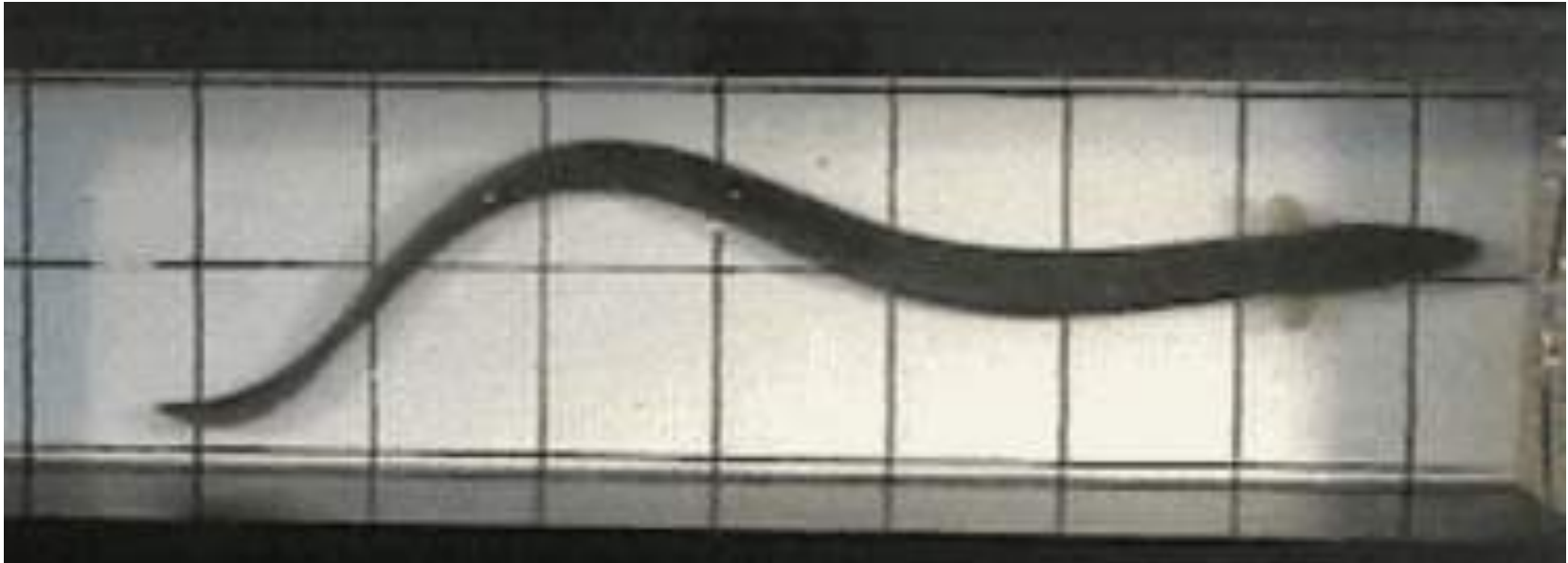


Fig. 7. Gradation of BCF swimming movements from (a) anguilliform, through (b) subcarangiform and (c) carangiform to (d) thunniform mode. (Taken from Lindsey [10].)



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swimming speeds

sustained

prolonged

burst

sustained swimming speeds

sustainable > 200 min

variable scope of speeds

aerobically powered

significance for
migration and aquaculture

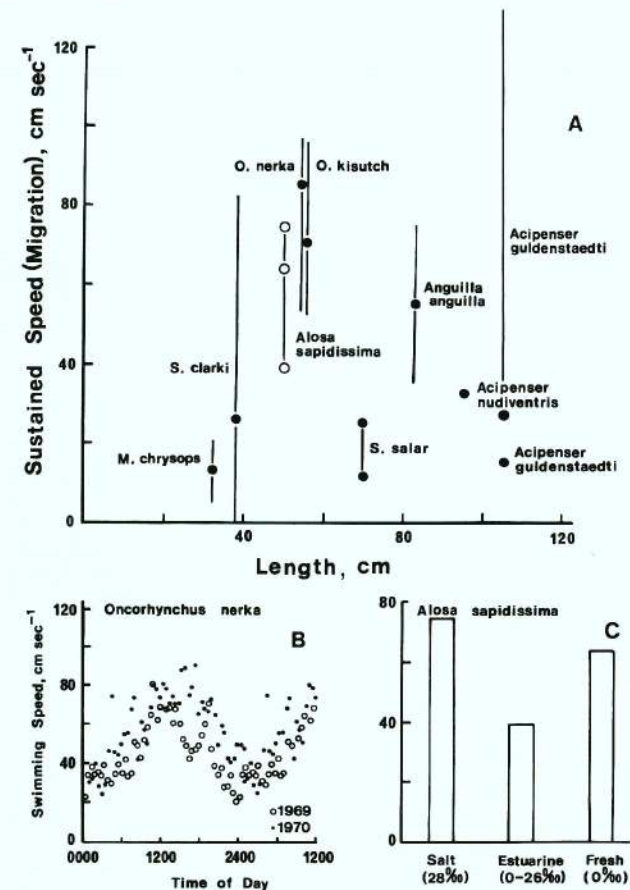


Fig. 1. Sustained cruising speeds of migrating fish. (A) Mean and range of sustained speed in relation to length (see text). (B) Diel fluctuations (redrawn from Madison *et al.*, 1972, *J. Fish. Res. Board Can.*). (C) Mean speed on entry into freshwater from the estuarine and marine environment (Dodson *et al.*, 1970, 1971, 1972).

2. SWIMMING CAPACITY

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sustained and burst speeds

ratio sustained / burst

burst: maximum speed

anaerobically powered

significance for
migration and aquaculture

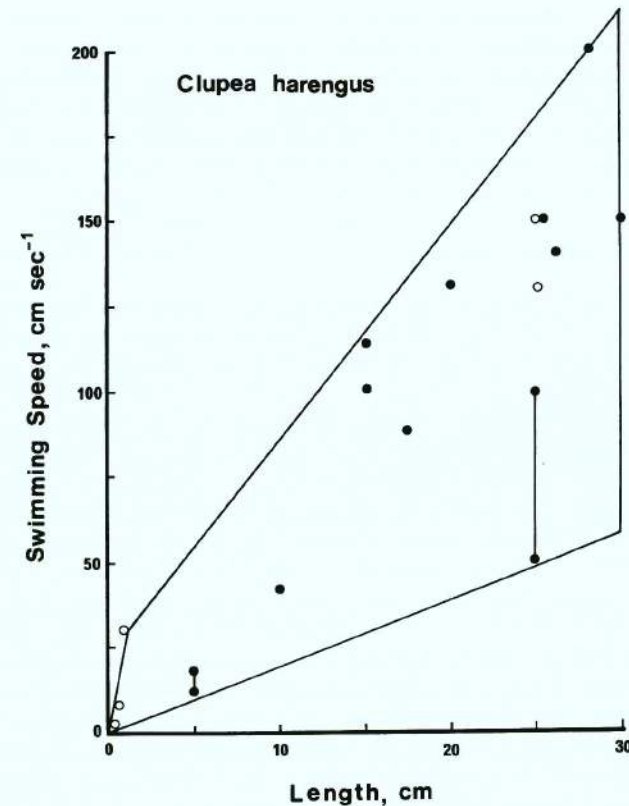


Fig. 2. Field and laboratory observations on the swimming capacity of herring, *Clupea harengus*, in relation to length. Sustained schooling and prolonged speeds are indicated by closed circles. Speeds reported as burst are recorded as open circles. [From Fridriksson and Aasen, 1952; Jones, 1957; Blaxter and Dickson, 1959; Bishai, 1960; Brawn, 1960; Schärfe, 1960; Boyar, 1961; Blaxter, 1962; Chestnoy (cited in Radakov, 1964); Blaxter and Parrish, 1966; High and Lusz, 1966.]

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Ecological implications

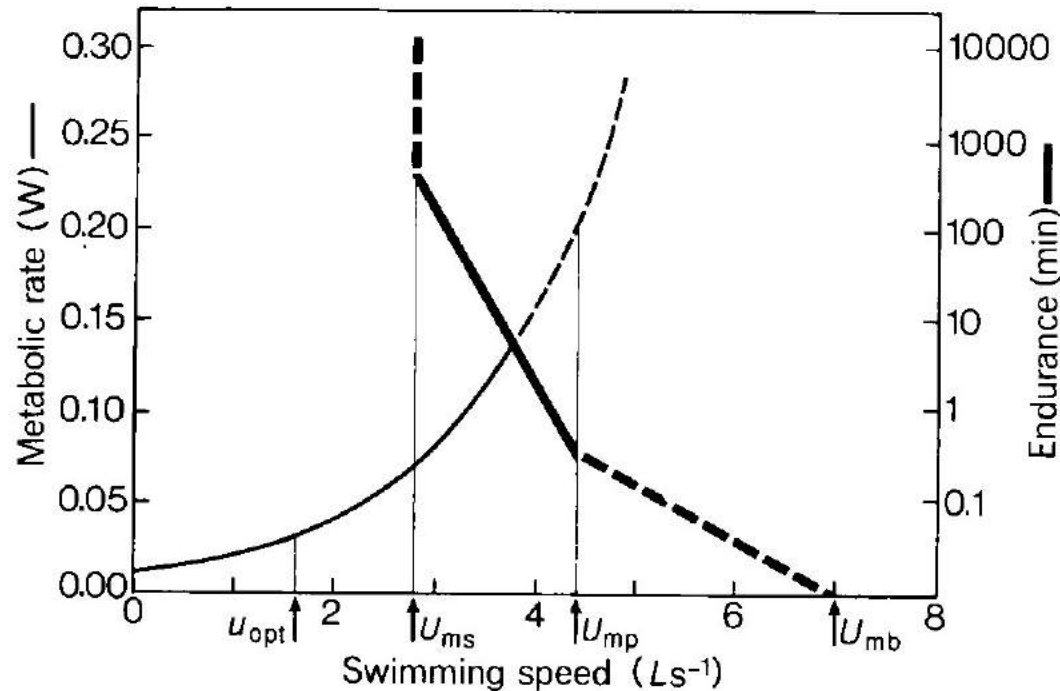
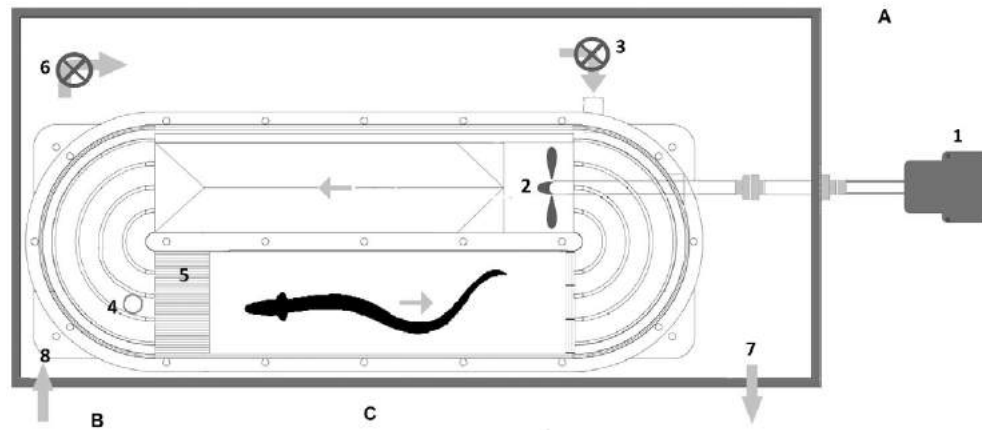
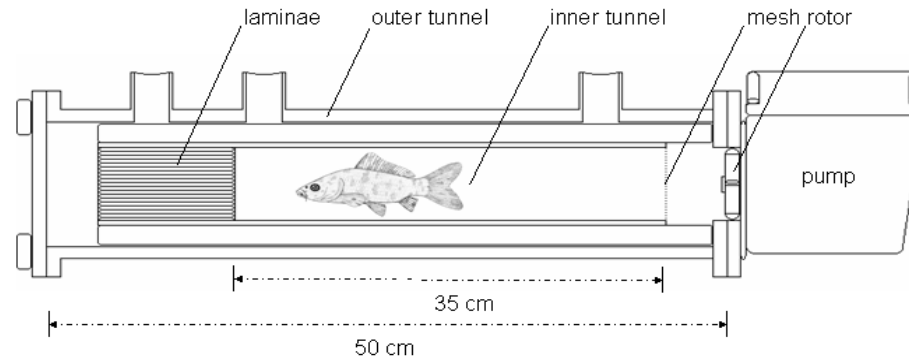
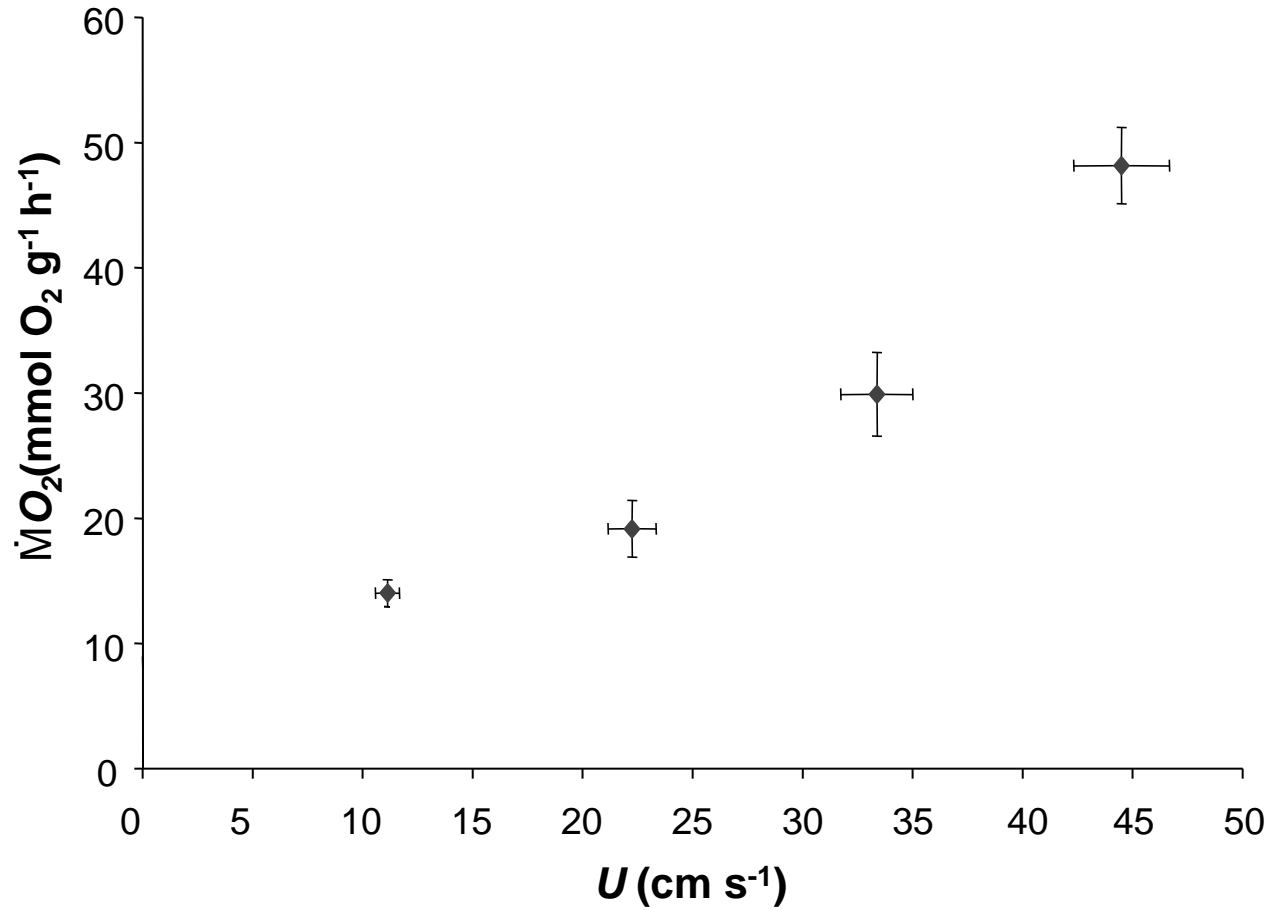


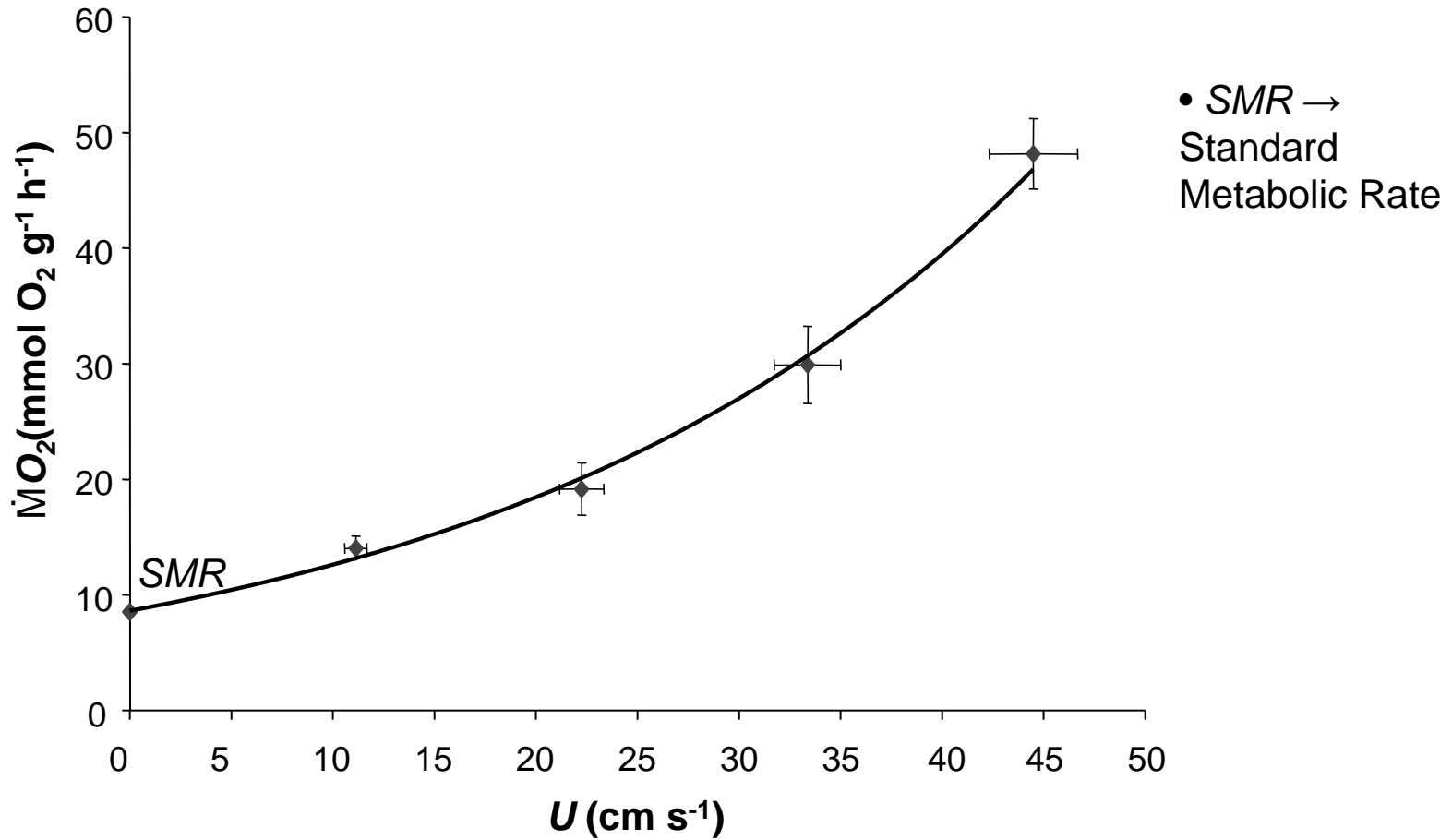
Fig. 10.3 The metabolic rate (linear scale) and the endurance (logarithmic scale) of a 0.18 m, 0.05 kg sockeye salmon as functions of swimming speed in Ls^{-1} . The water temperature was 15 °C. The optimum swimming speed (u_{opt}), the maximum sustained speed (U_{ms}), the maximum prolonged speed (U_{mp}) and an estimate of the maximum burst speed (U_{mb}) are indicated. Based on Brett (1964).

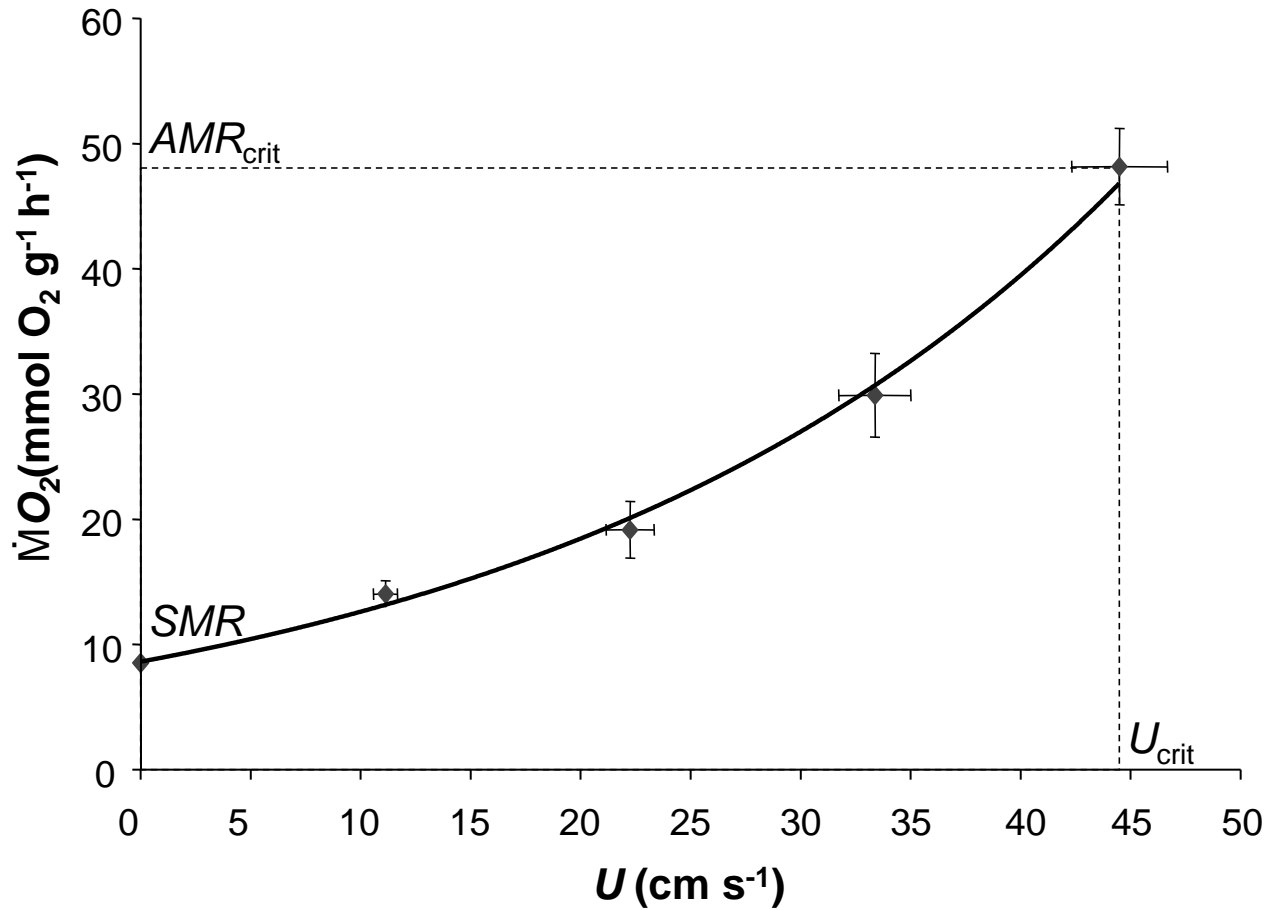


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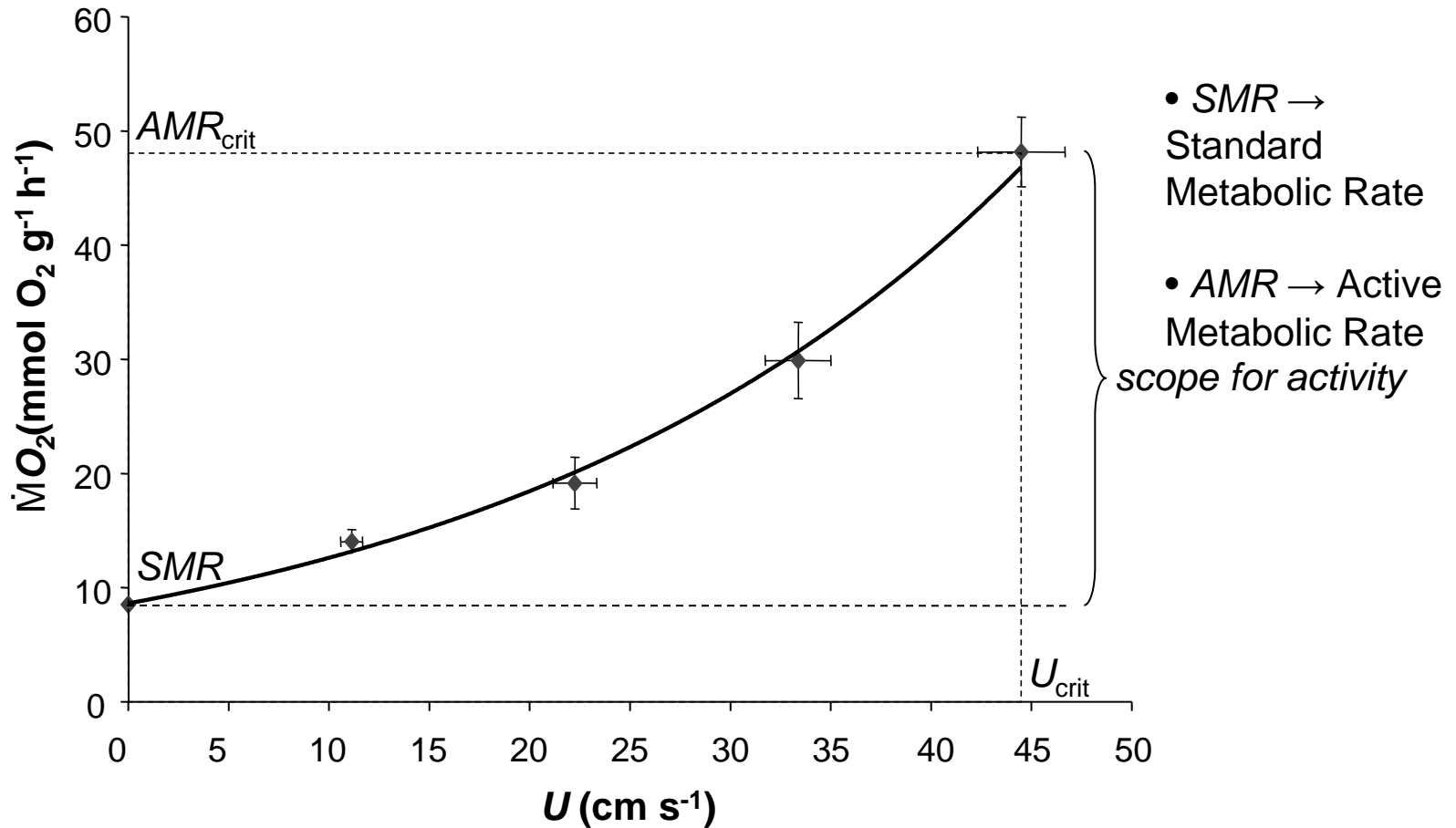


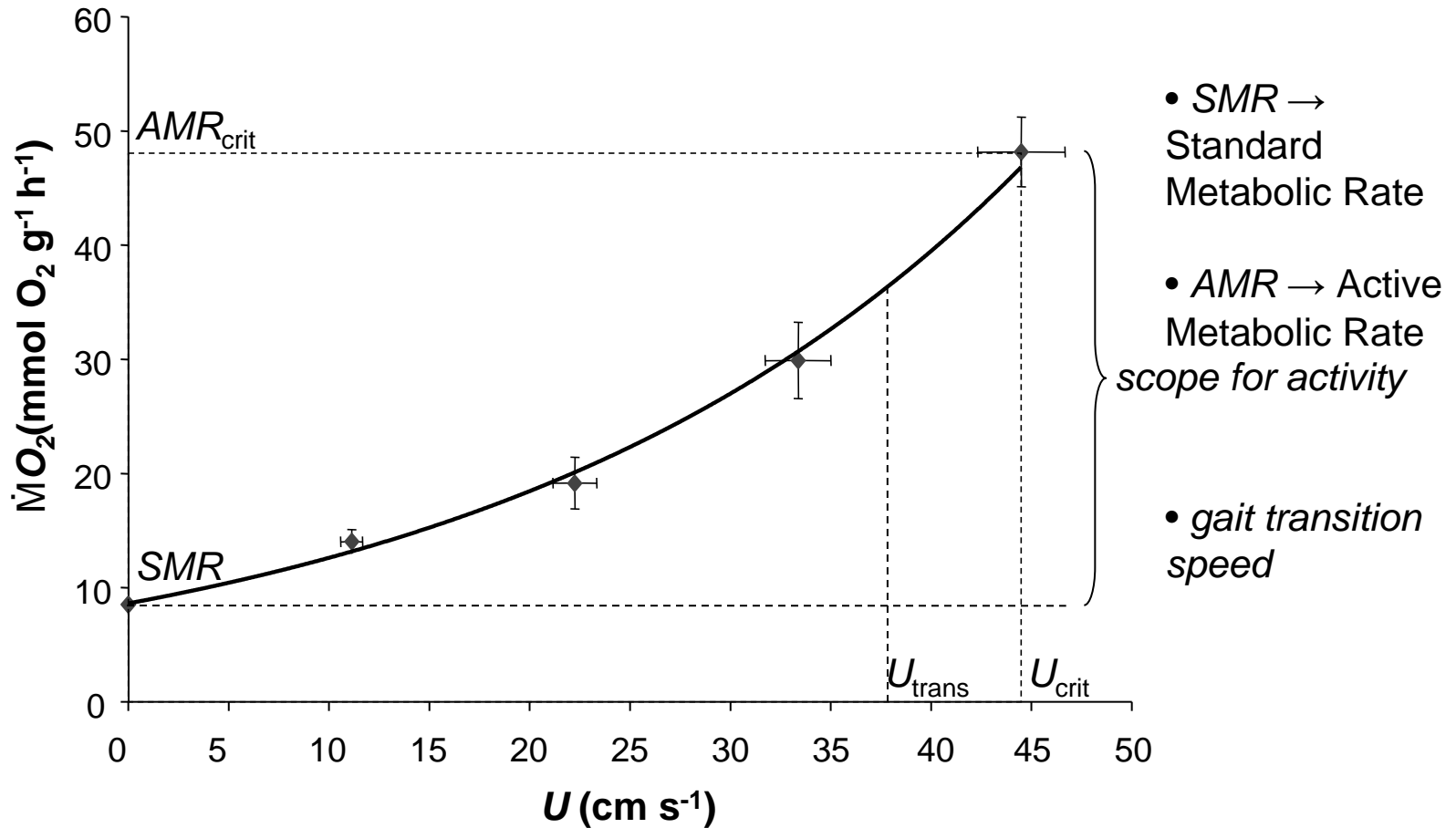
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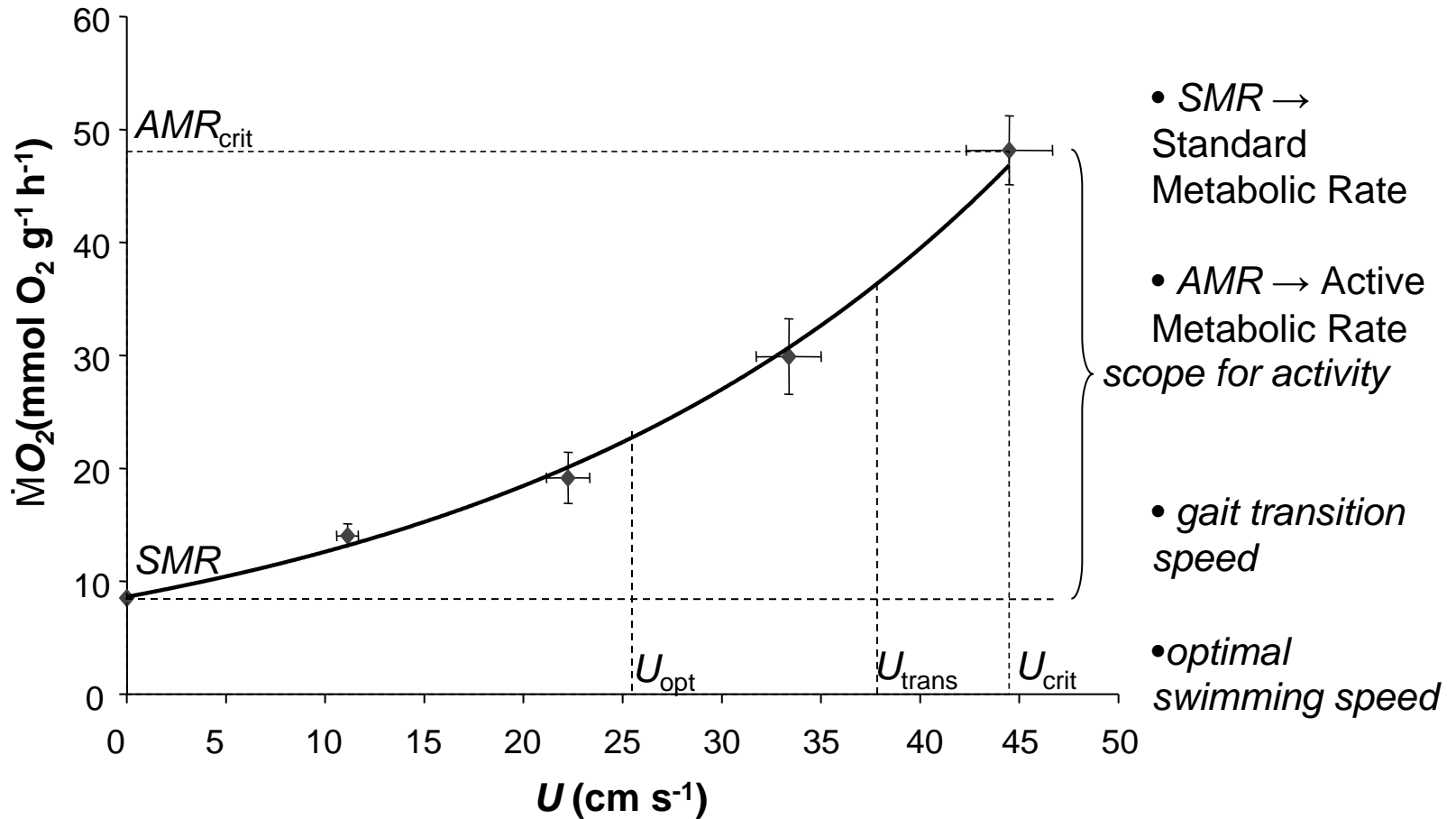


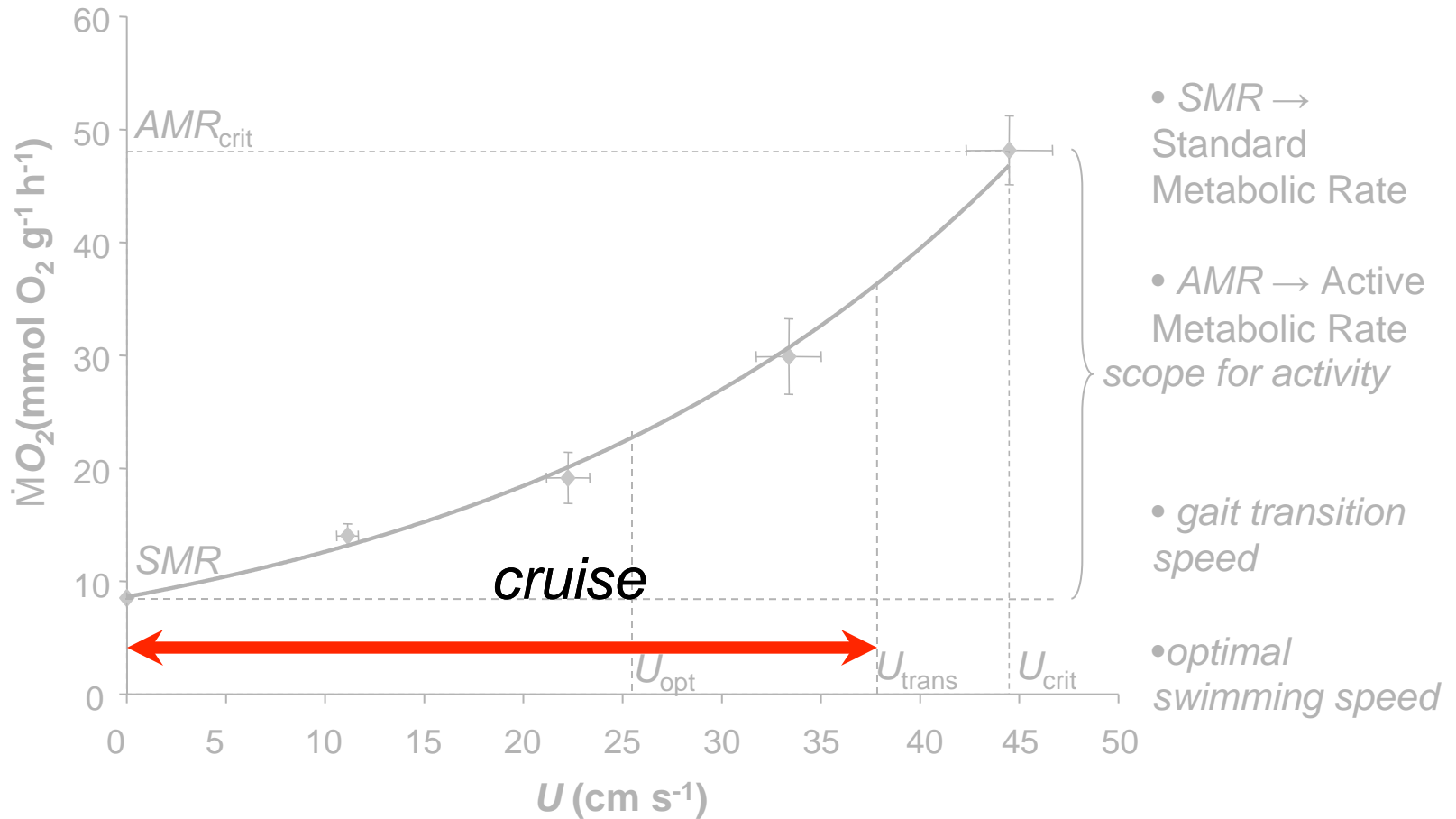


- SMR → Standard Metabolic Rate
- AMR → Active Metabolic Rate

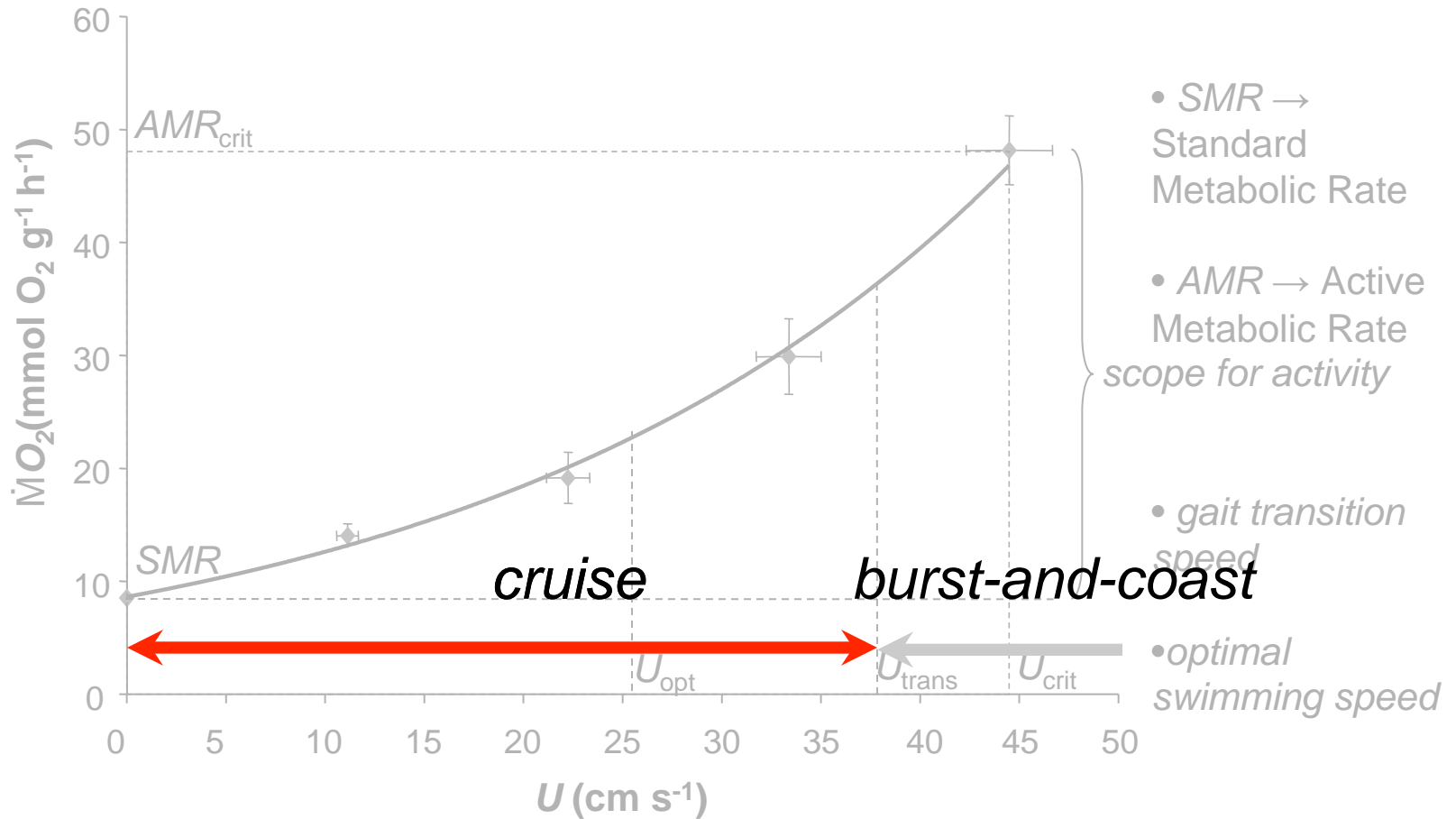








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2. SWIMMING CAPACITY

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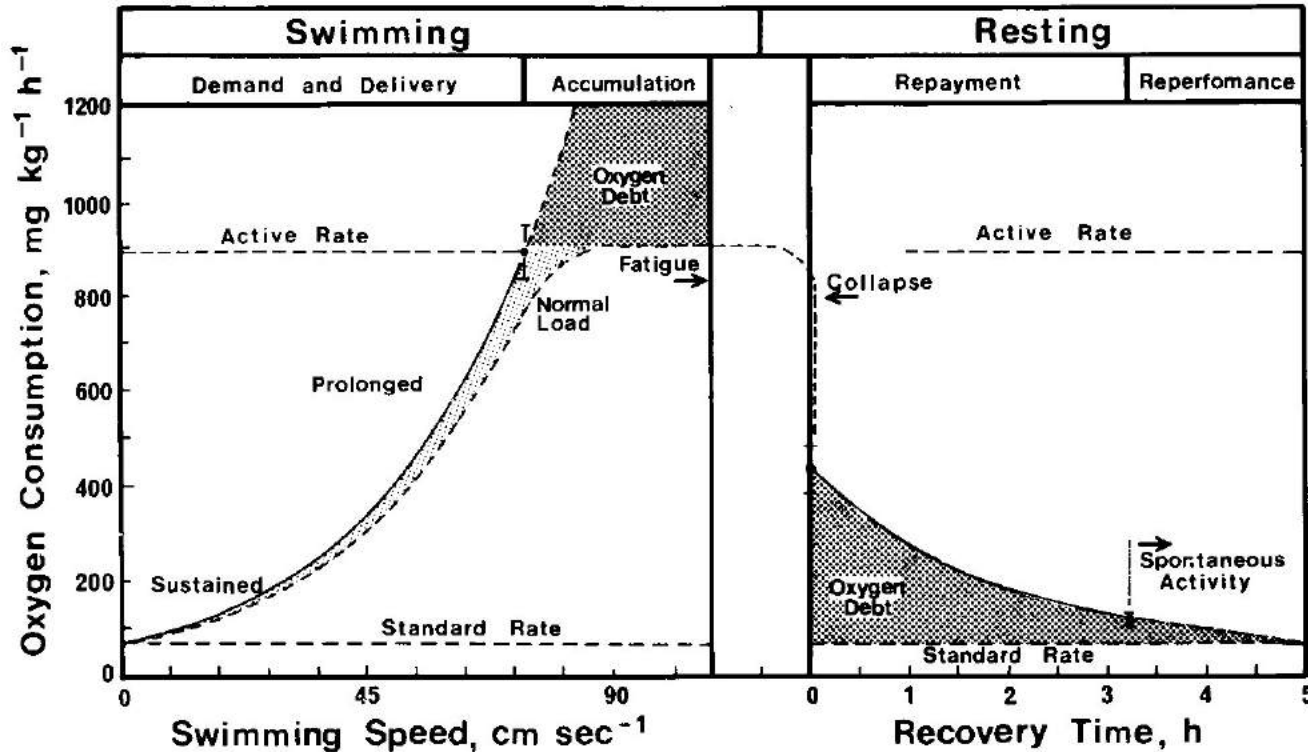
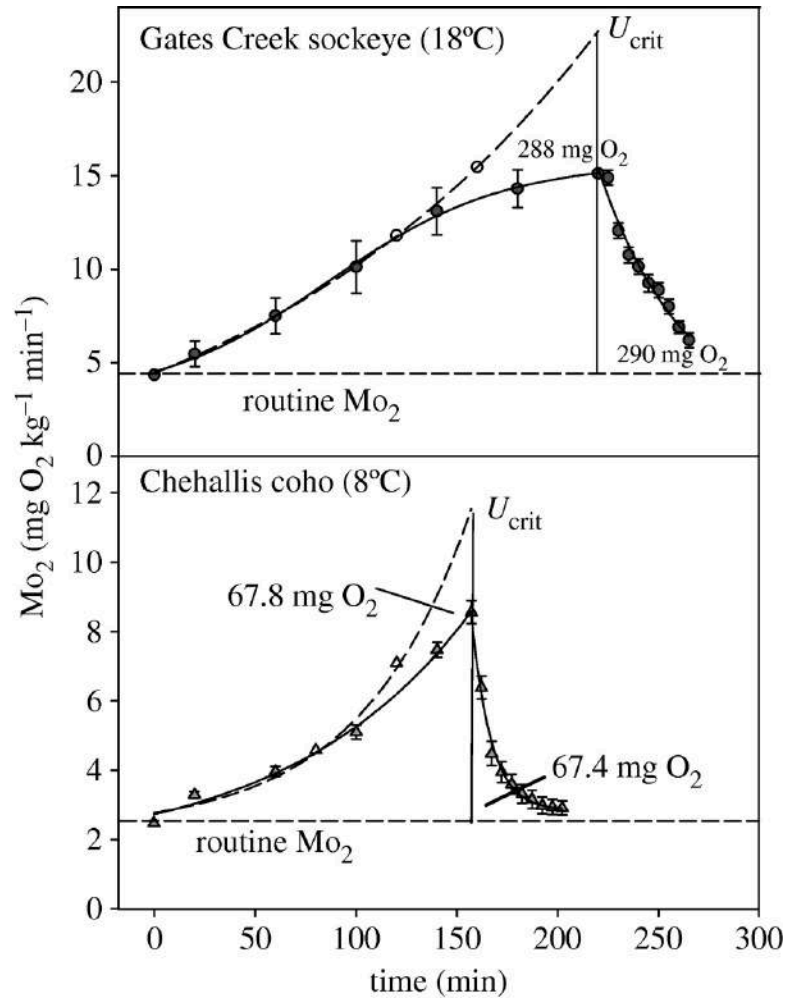


Fig. 17. Oxygen consumption and debt for sockeye salmon, *Oncorhynchus nerka* (18 cm), in relation to swimming speed and recovery at 15°C. (Redrawn from Brett, 1964, *J. Fish. Res. Board Can.*)



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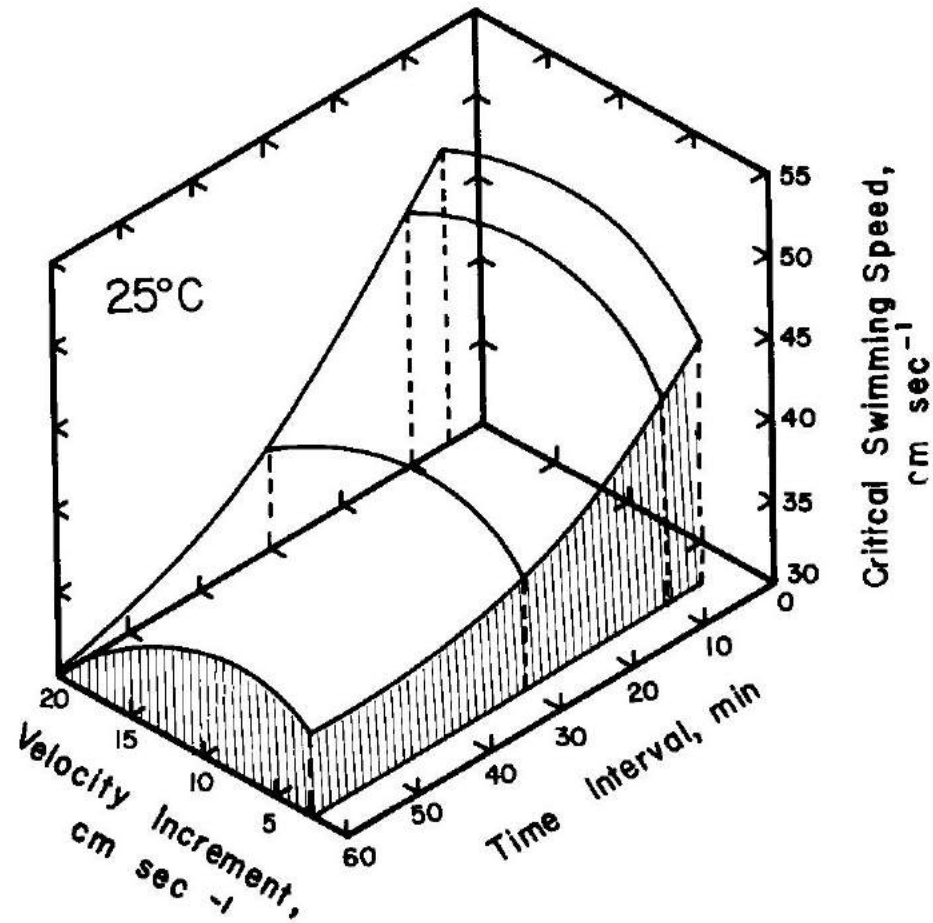
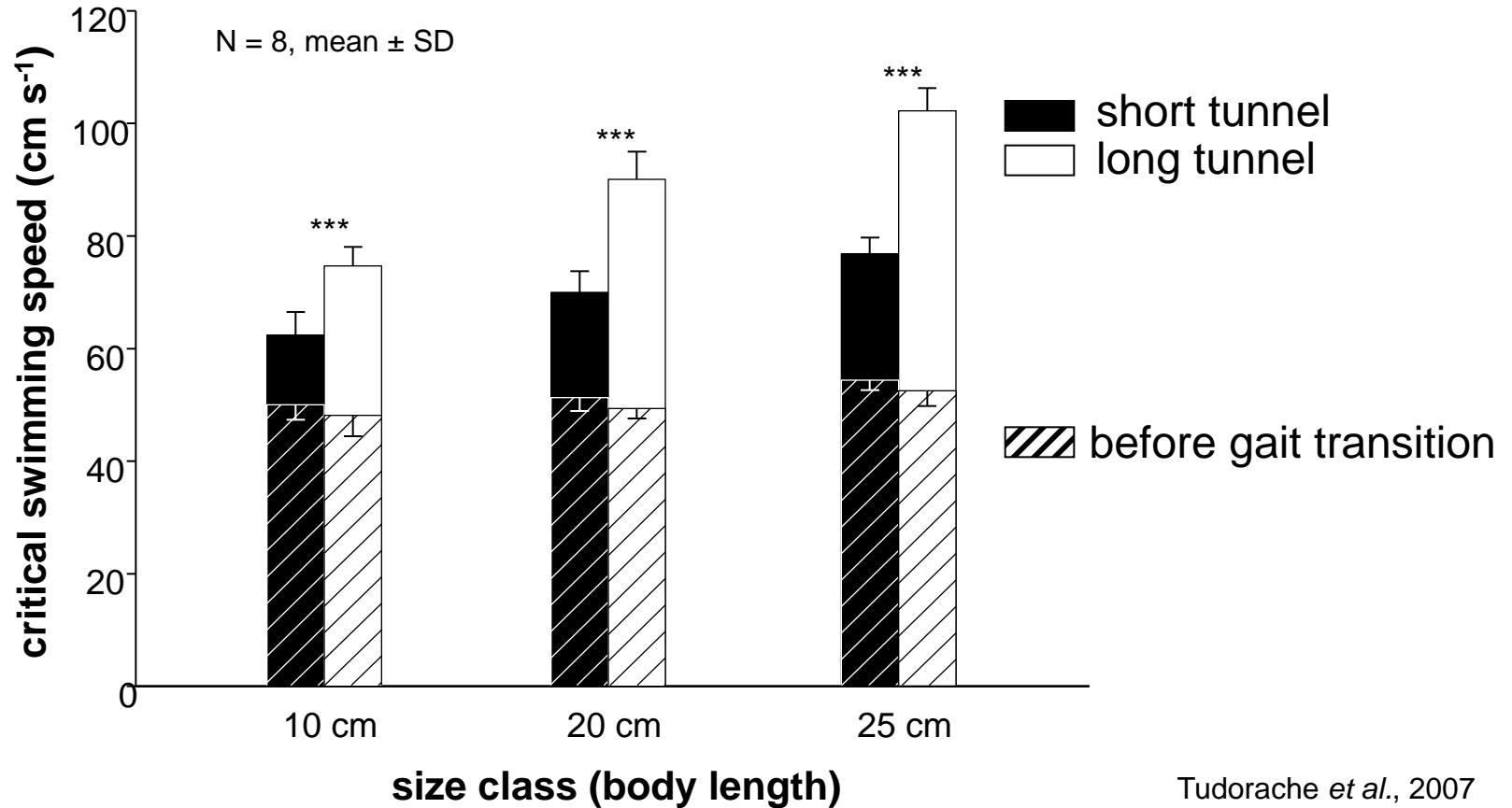
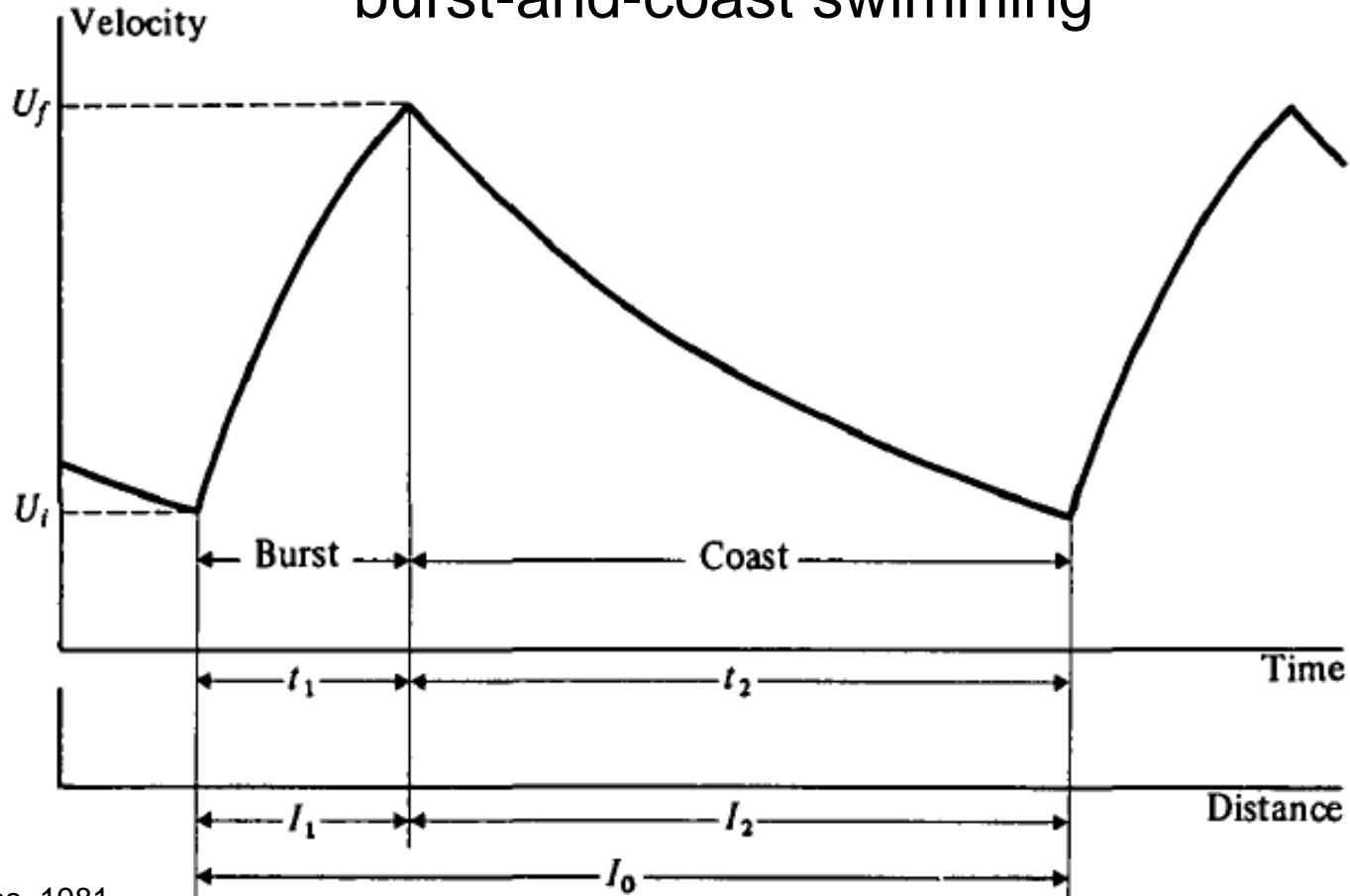


Fig. 5. Critical swimming speed of largemouth bass, *Micropterus salmoides* (10 cm), in relation to the interval between and magnitude of velocity increments. (Redrawn from Farlinger and Beamish, 1977.)

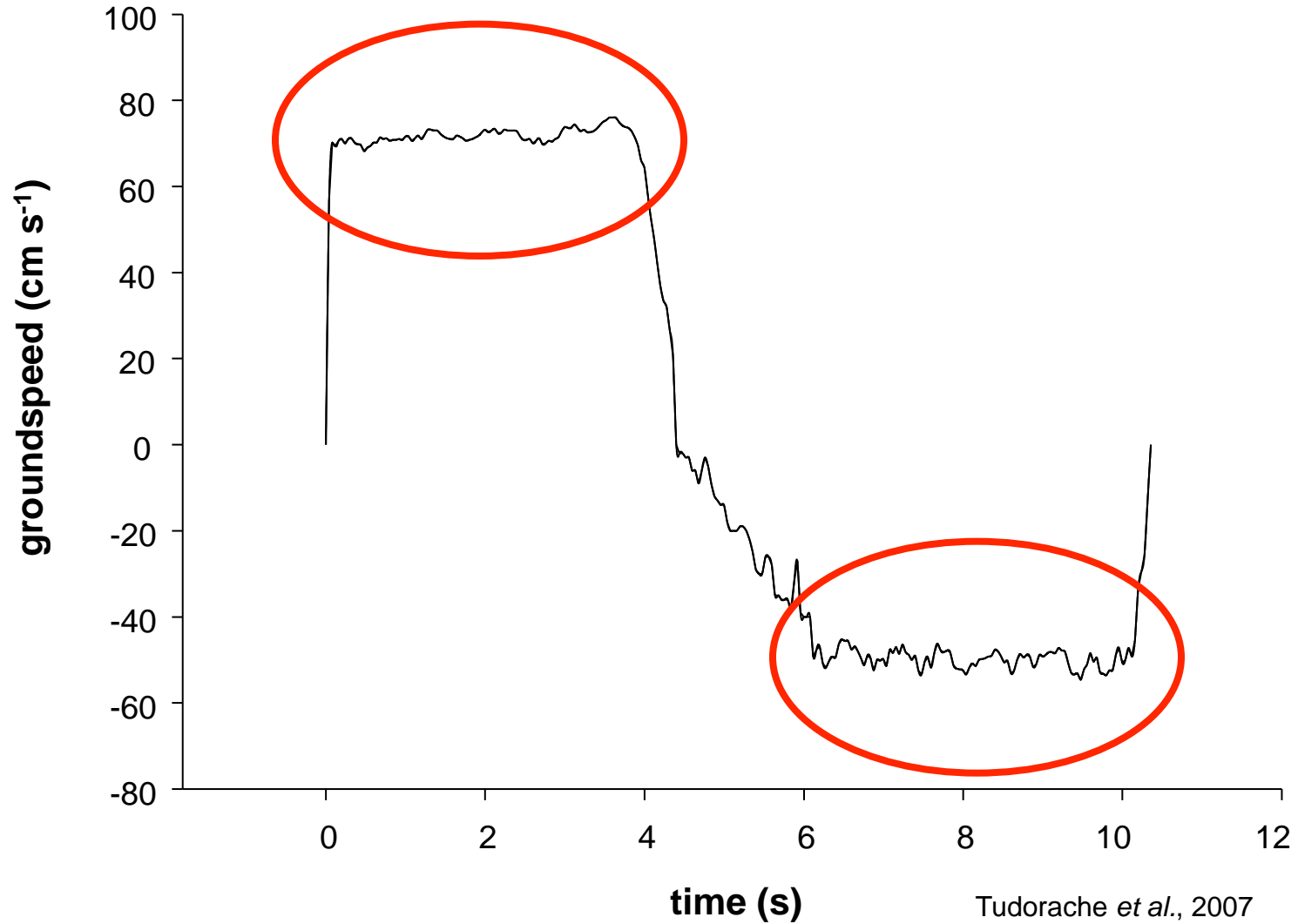




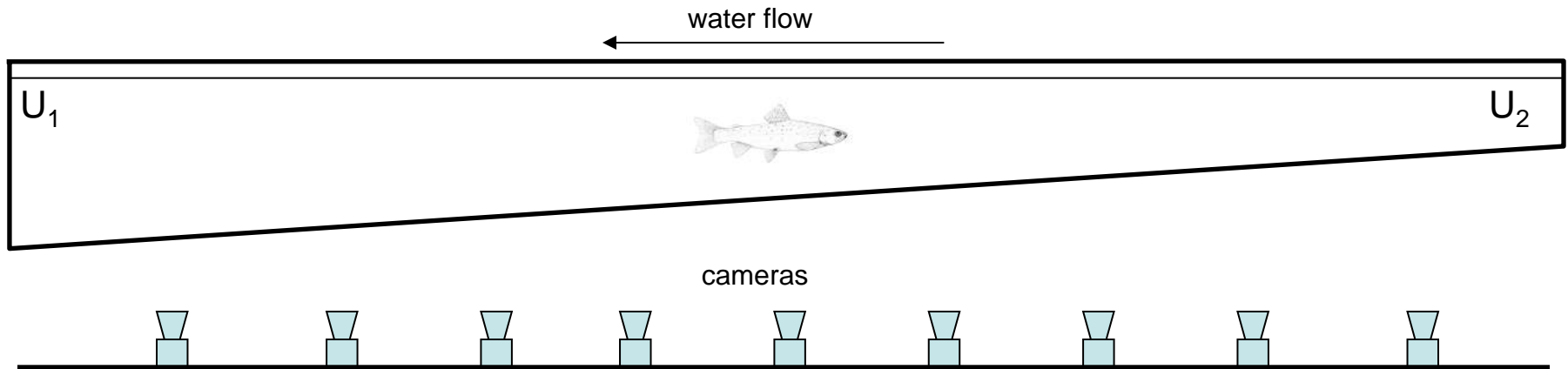
burst-and-coast swimming



Videler & Weihs, 1981



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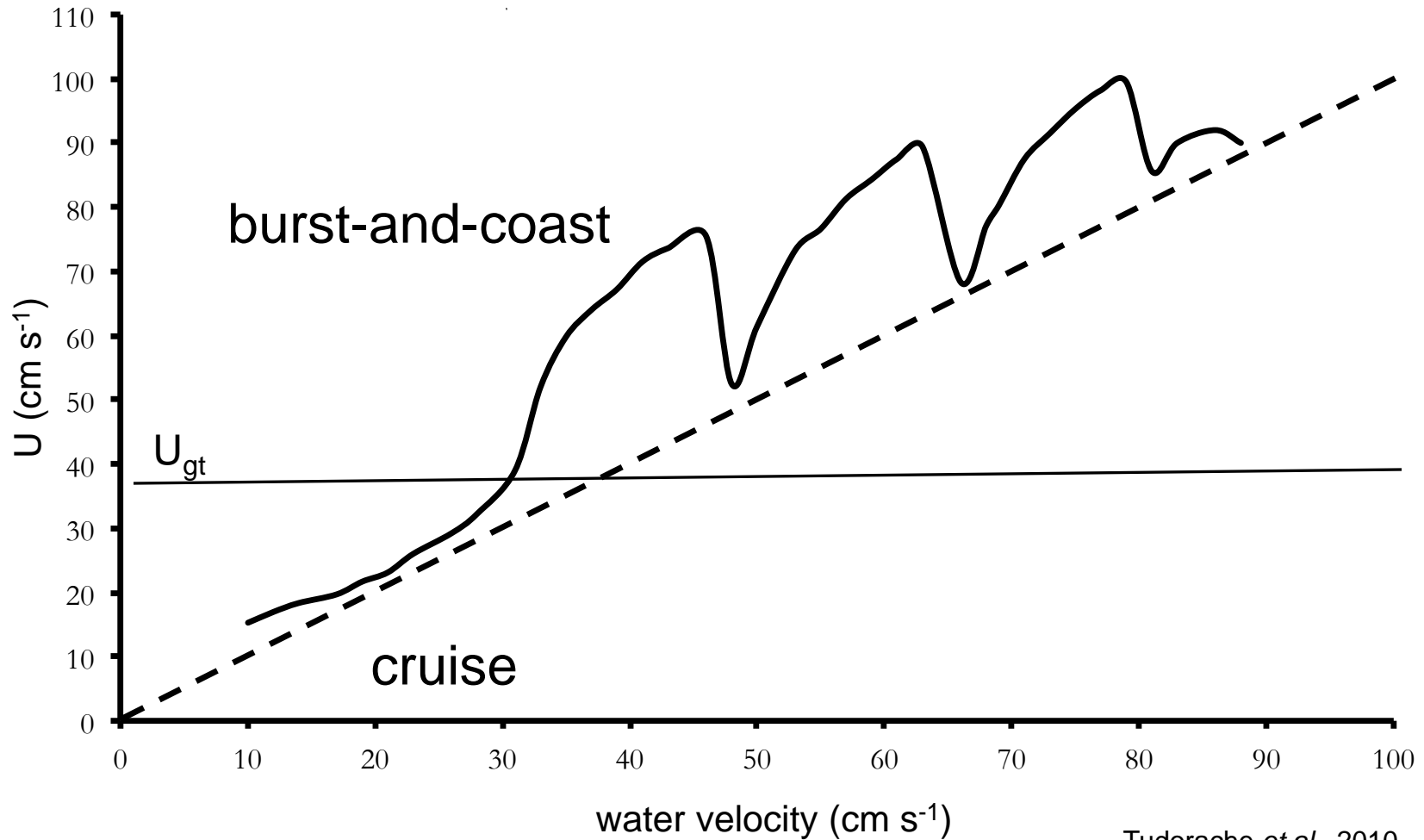


$$U = Q A^{-1}, U_1 < U_2, 5 - 120 \text{ cm s}^{-1}$$

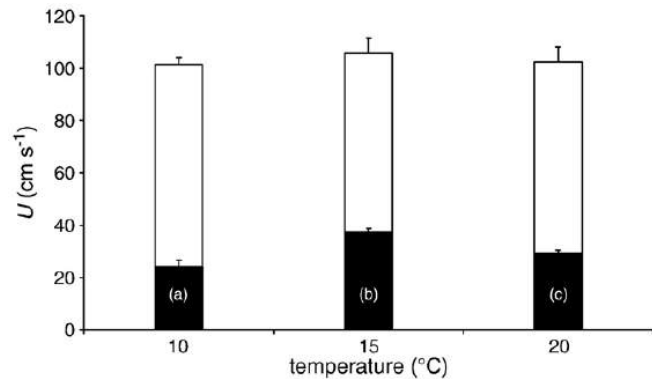
$$U_{gt}, U_{max}, A_{max}, \text{ kinematics } (a, f)$$

water temperature: 10, 15 (acclimation), 20°C

total ammonia (NH_3 and NH_4^+): 0, 14.38, 28.76, 43.14, 57.53 $\mu\text{mol l}^{-1}$

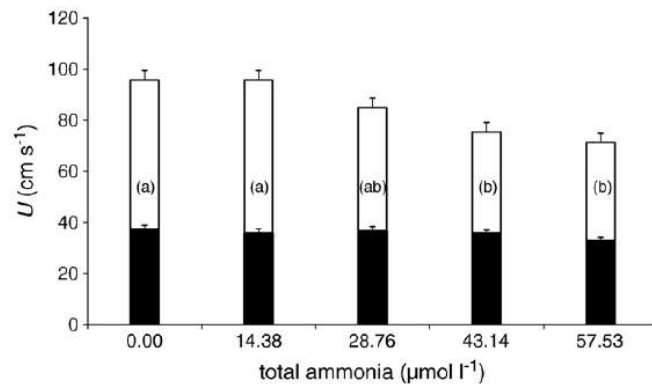


Tudorache *et al.*, 2010



temperature: aerobic apparatus

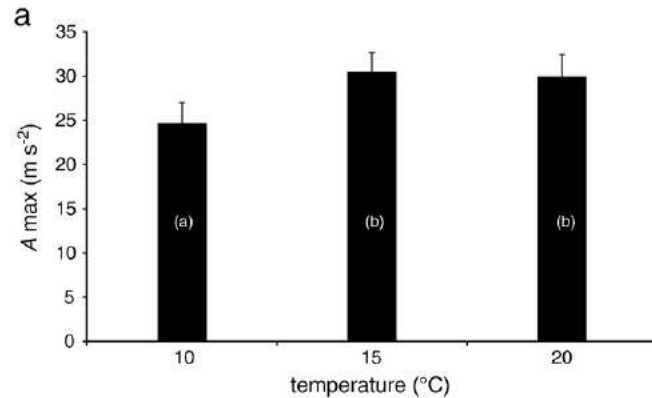
Fig. 2. Gait transition speed (U_{gt} , black) and maximum swimming speed (U_{max} , white) at 10, 15 and 20 °C. Letters indicate significant differences ($N = 10$, $p < 0.05$).



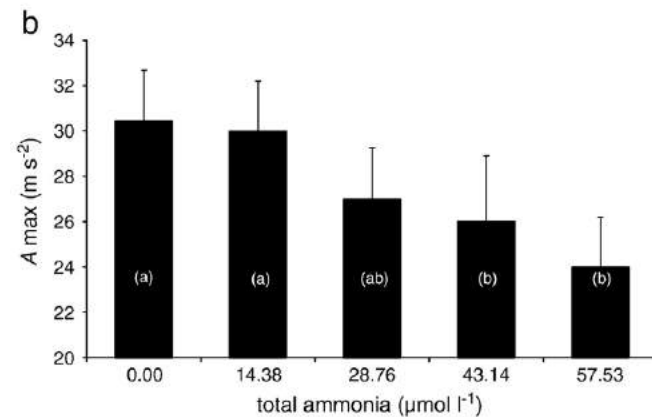
ammonia: anaerobic apparatus

Fig. 3. Gait transition speed (U_{gt} , black) and maximum swimming speed (U_{max} , white) at different total ammonia (NH_4^+ and NH_3) concentrations. Letters indicate significant differences ($N = 10$, $p < 0.05$).

Tudorache *et al.*, 2010



temperature: aerobic apparatus



ammonia: anaerobic apparatus

Fig. 6. Maximum acceleration (A_{max}) at different temperatures (a) and total ammonia (NH_4^+ and NH_3) concentrations (b). Letters indicate significant differences ($N=10$, $p<0.05$).

Tudorache *et al.*, 2010

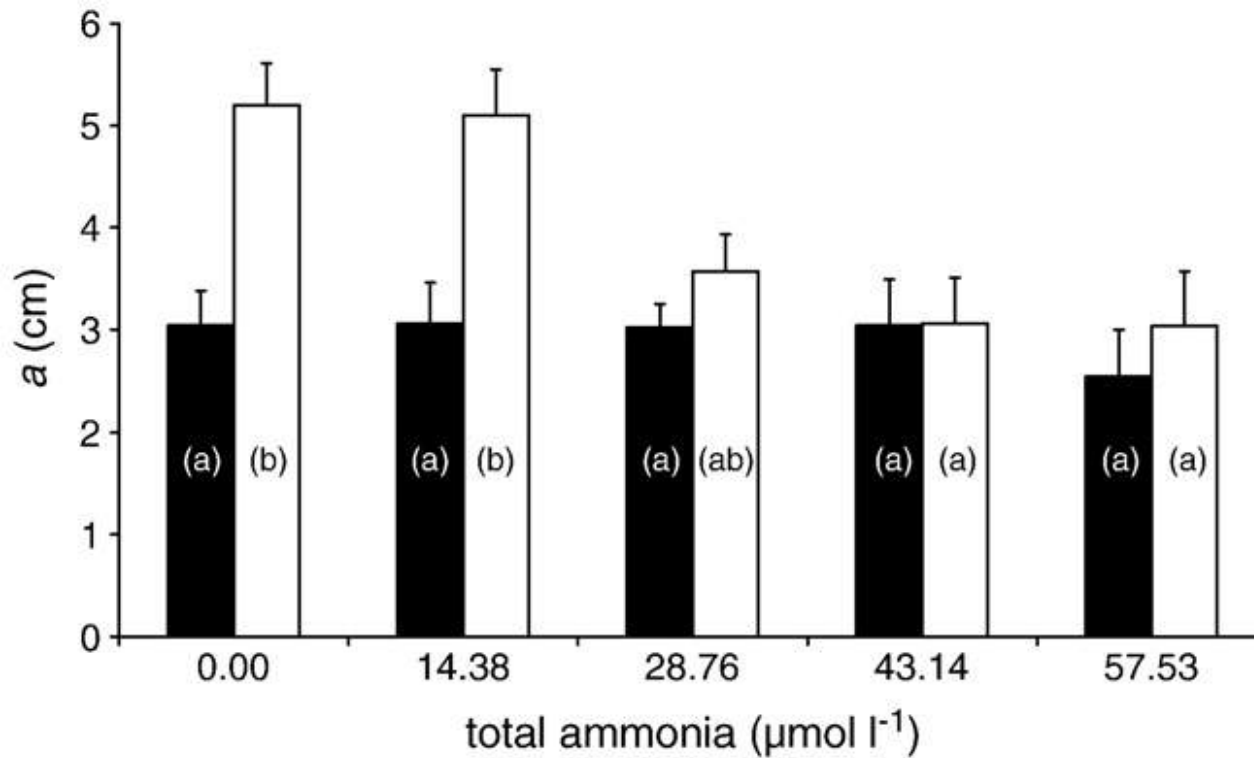


Fig. 5. Tail-beat amplitude (a) at different total ammonia (NH_4^+ and NH_3) concentrations before (black) and after (white) gait transition. Letters indicate significant differences ($N = 10$, $p < 0.05$).

Tudorache *et al.*, 2010

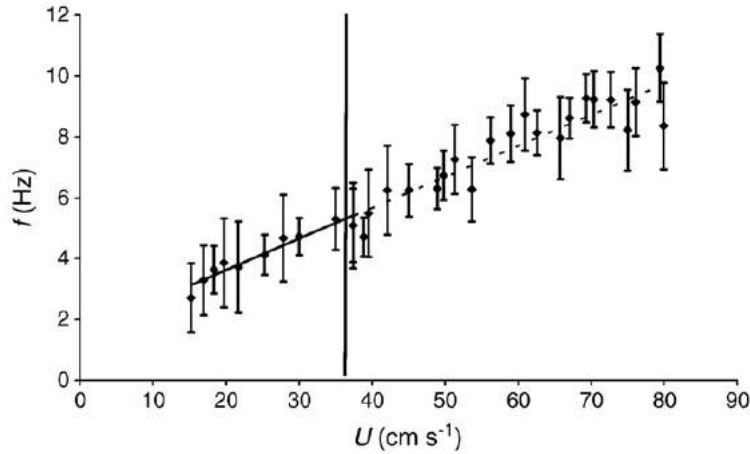


Table 1a

Regression values for tail-beat frequency (f , Hz) plotted against swimming speed (U , cm s^{-1}) with the formula $f = a + bU$ at different water temperatures.

Temperature (°C)	10	15 (control)	20
a (before U_{gt})	1.56 ± 0.13	1.57 ± 0.14	1.58 ± 0.15
a (after U_{gt})	1.58 ± 0.18	1.56 ± 0.11	1.58 ± 0.13
b (before U_{gt})	0.104 ± 0.042	0.104 ± 0.031	0.102 ± 0.020
b (after U_{gt})	0.105 ± 0.039	0.106 ± 0.024	0.107 ± 0.024

Fig. 4. Representative plot of tail-beat frequency (f) against swimming speed (U) for a control fish at 15 °C. The vertical line indicates gait transition speed and the resulting linear relationship can be described by the linear function $f = 1.5557 + 0.1033U$ ($r^2 = 0.92$) before and $f = 1.5793 + 0.102U$ ($r^2 = 0.85$) after gait transition ($N = 3$, $p < 0.05$).

Table 1b

Regression values for tail-beat frequency (f , Hz) plotted against swimming speed (U , cm s^{-1}) with the formula $f = a + bU$ under the influence of elevated ammonia concentrations in the water. *Indicates significant difference from control (one-way ANOVA, $p < 0.05$, $N = 10$).

Concentration ($\mu\text{mol L}^{-1}$)	0 (control)	14.38	28.77	43.15	57.53
a (before U_{gt})	1.57 ± 0.14	1.61 ± 0.15	1.58 ± 0.13	1.54 ± 0.17	1.53 ± 0.12
a (after U_{gt})	1.56 ± 0.11	1.57 ± 0.09	1.58 ± 0.12	$0.48 \pm 0.13^*$	$0.24 \pm 0.16^*$
b (before U_{gt})	0.104 ± 0.031	0.111 ± 0.025	0.112 ± 0.020	0.113 ± 0.012	0.118 ± 0.013
b (after U_{gt})	0.106 ± 0.024	0.106 ± 0.032	0.113 ± 0.024	$0.125 \pm 0.014^*$	$0.130 \pm 0.016^*$

Tudorache *et al.*, 2010

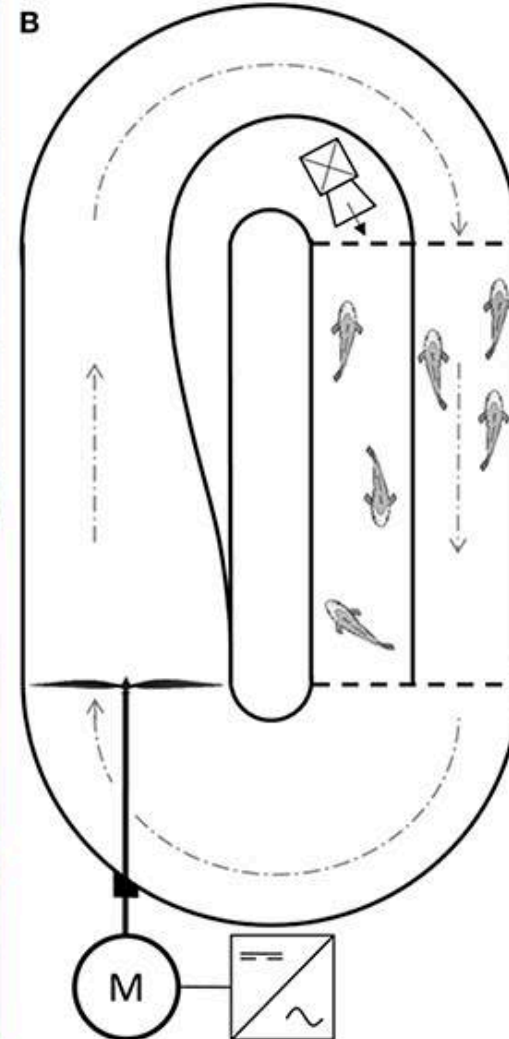


temperature: effect on aerobic apparatus

- $U_{gt} \downarrow$
- U_{max} , A_{max} , a , f not affected

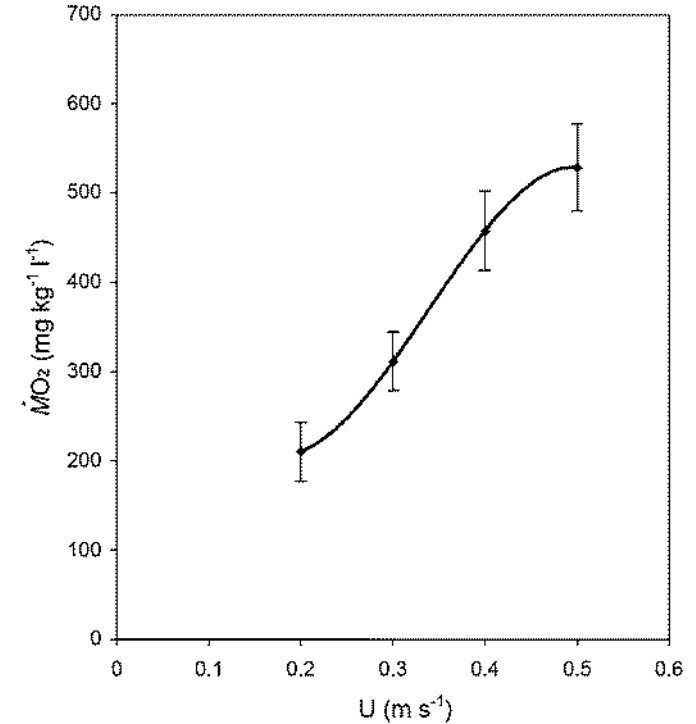
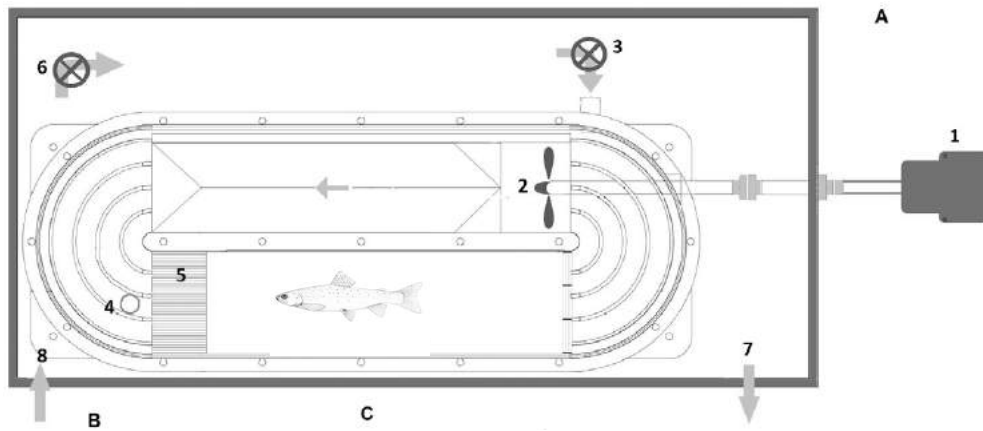
ammonia: effect on anaerobic apparatus

- U_{max} , A_{max} , $a \downarrow$
- f altered after U_{gt}
- \uparrow slope of burst-and-coast $\rightarrow \uparrow$ cost of transport



Palstra *et al.*, 2015

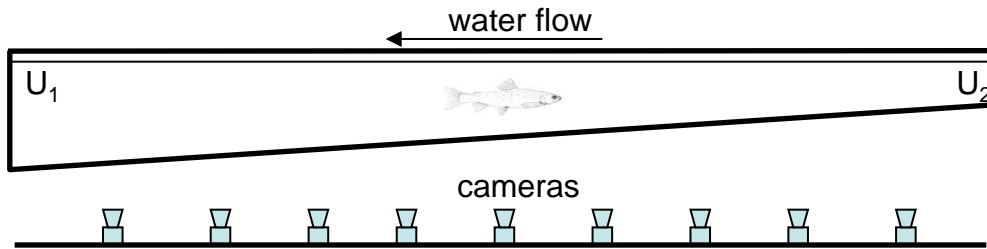
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$$U_{\text{opt}} = 22.77 \pm 4.54 \text{ cm s}^{-1}$$

Fig. 4 Relative oxygen consumption ($\dot{M}O_2$) plotted against swimming speed of brook charr swimming in a confined respirometer. The fitting curve is provided by the polynomial function $\dot{M}O_2 = -0.0105U^3 + 1.006U^2 - 18.665U + \text{SMR}$ ($r^2 = 0.99$, $N = 10$) with U being swimming speed (cm s⁻¹) and SMR, the standard metabolic rate, has a value of 258.77 mg O₂ kg⁻¹ l⁻¹

Tudorache *et al.*, 2011



$$U_{\text{opt}} = 22.77 \pm 4.54 \text{ cm s}^{-1}$$

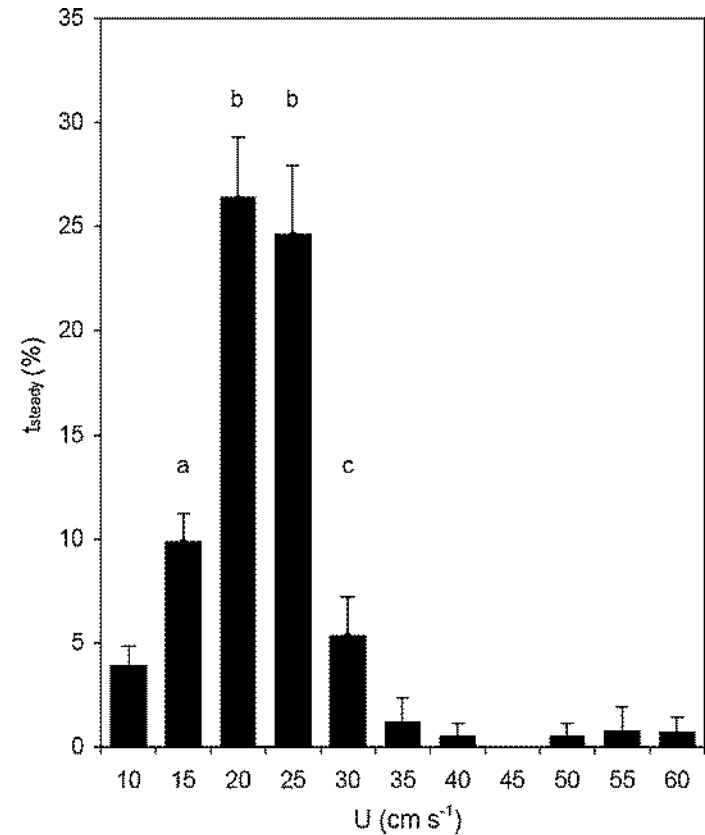
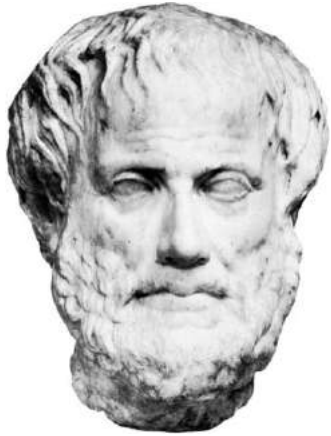
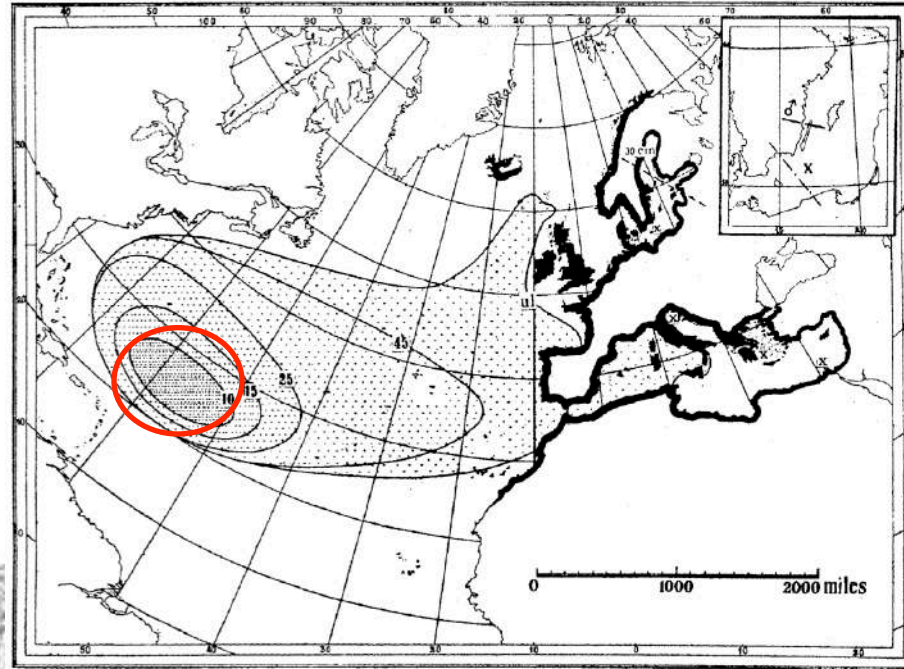


Fig. 3 The time (% total steady swimming time) spent swimming steadily plotted against clusters of swimming speeds of 5 cm s⁻¹ (see text for details). Letters indicate significant differences between values >5% of total steady time (one-way ANOVA, $P < 0.05$)

Tudorache *et al.*, 2011



Aristotle (384 BC - 322 BC)

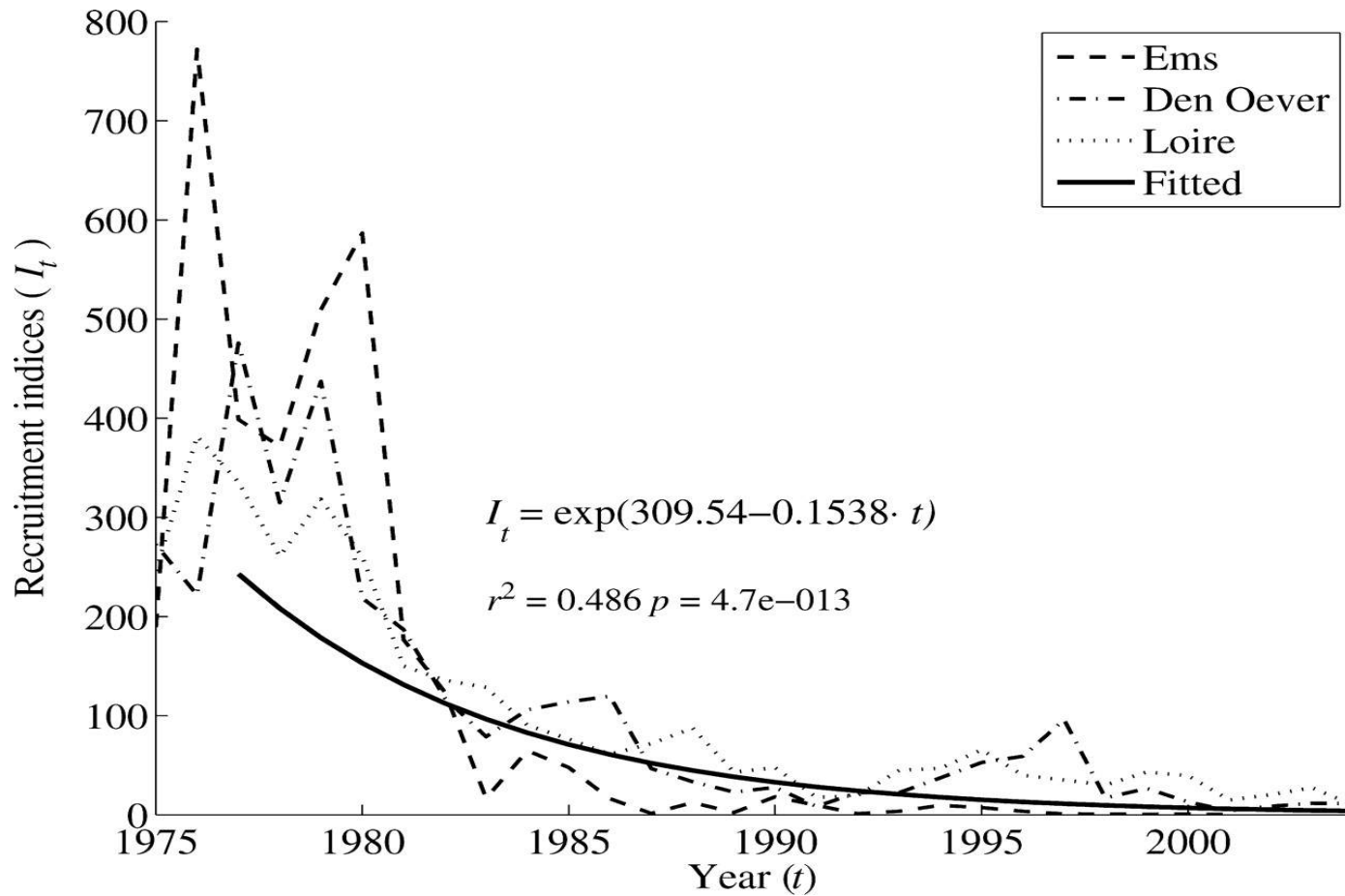


Schmidt, 1923



Johannes Schmidt (1877-1933)

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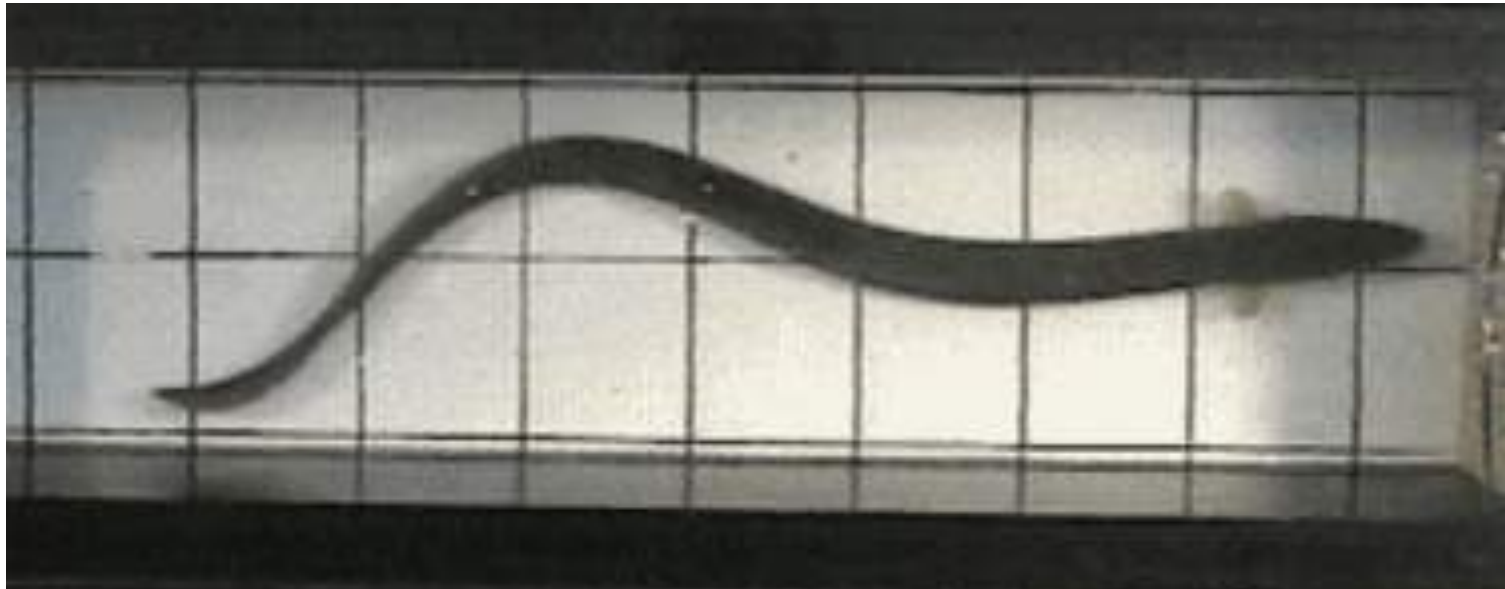


Arstrom & Dekker, 2007



Eel with a conventional satellite tag, Leiden University

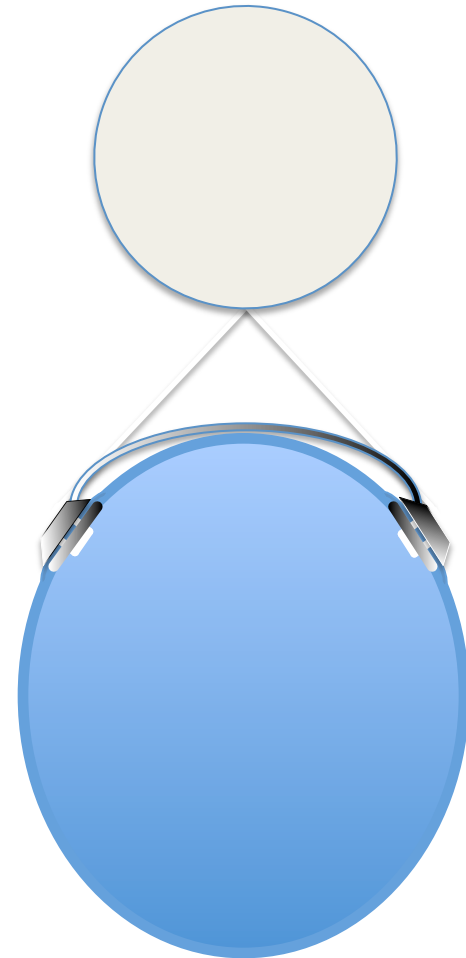
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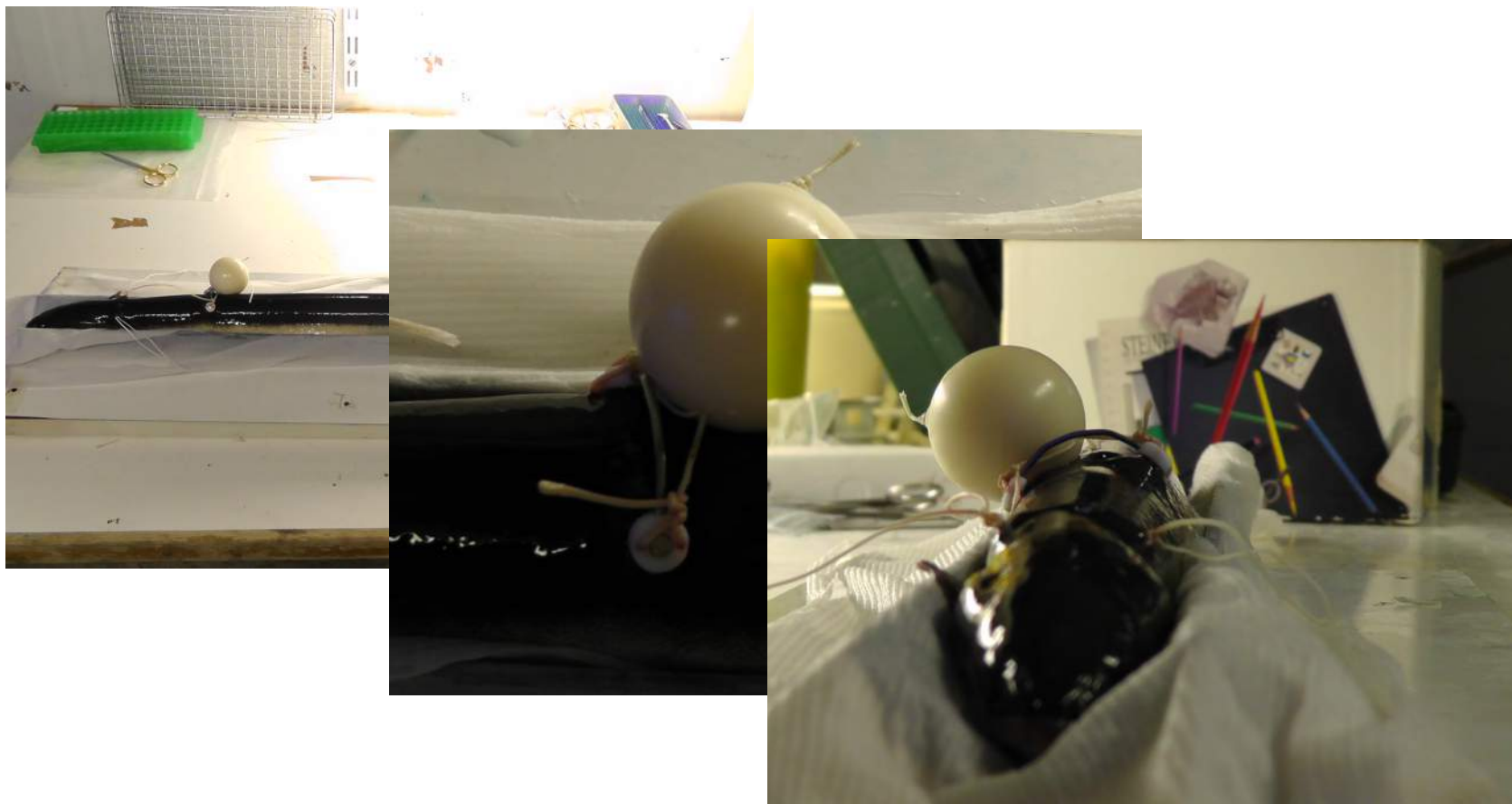
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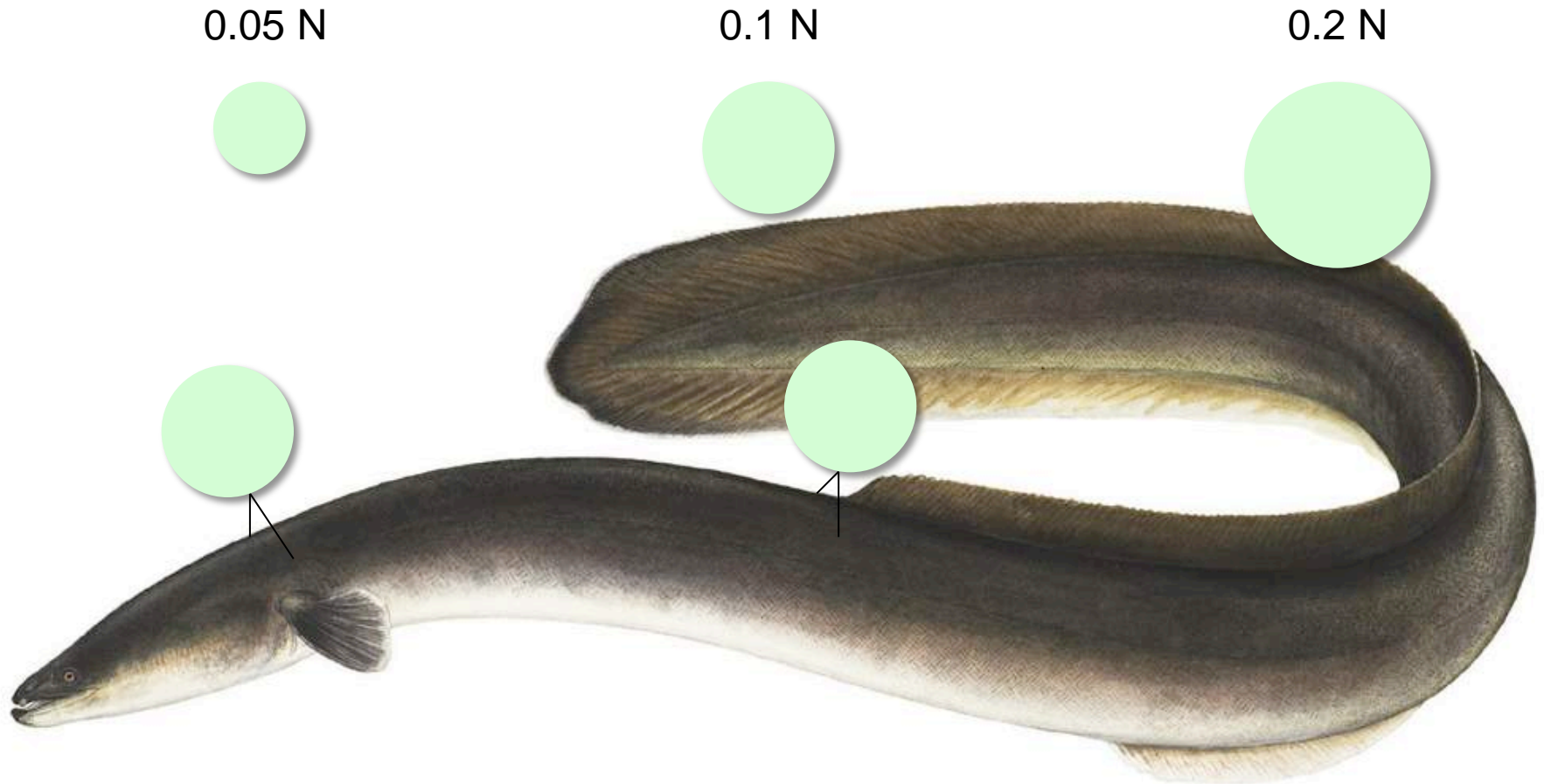
Jellyman and Tsukamoto, 2002



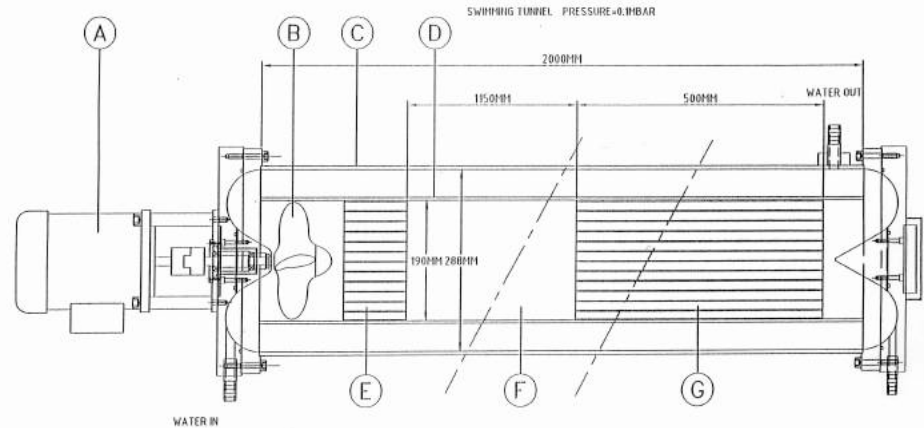
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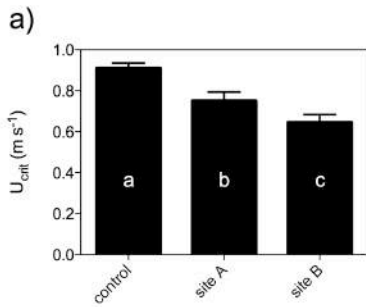


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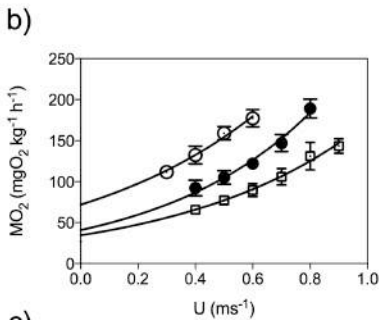
2m length A) motor; B) propeller; C) external tube; D) internal tube; E, honey comb; F) swimming section (1m); G) honey comb

v. d. Thillart *et al.*, 2003

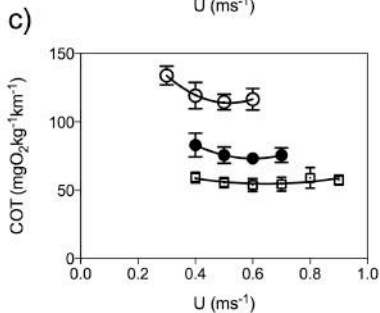


effect of place of attachment

critical swimming speed (U_{crit}): control > 20% A > 20% B



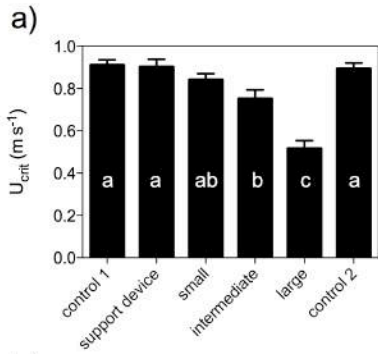
oxygen consumption (MO_2): control < 60-75% A < 70% B,
SMR control < 100% SMR B



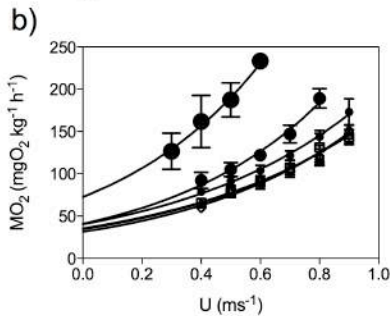
cost of transport (COT): control < 20% A < 40% B



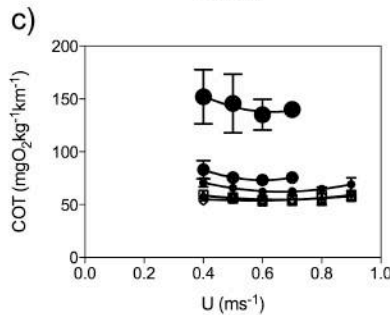
effect of added drag



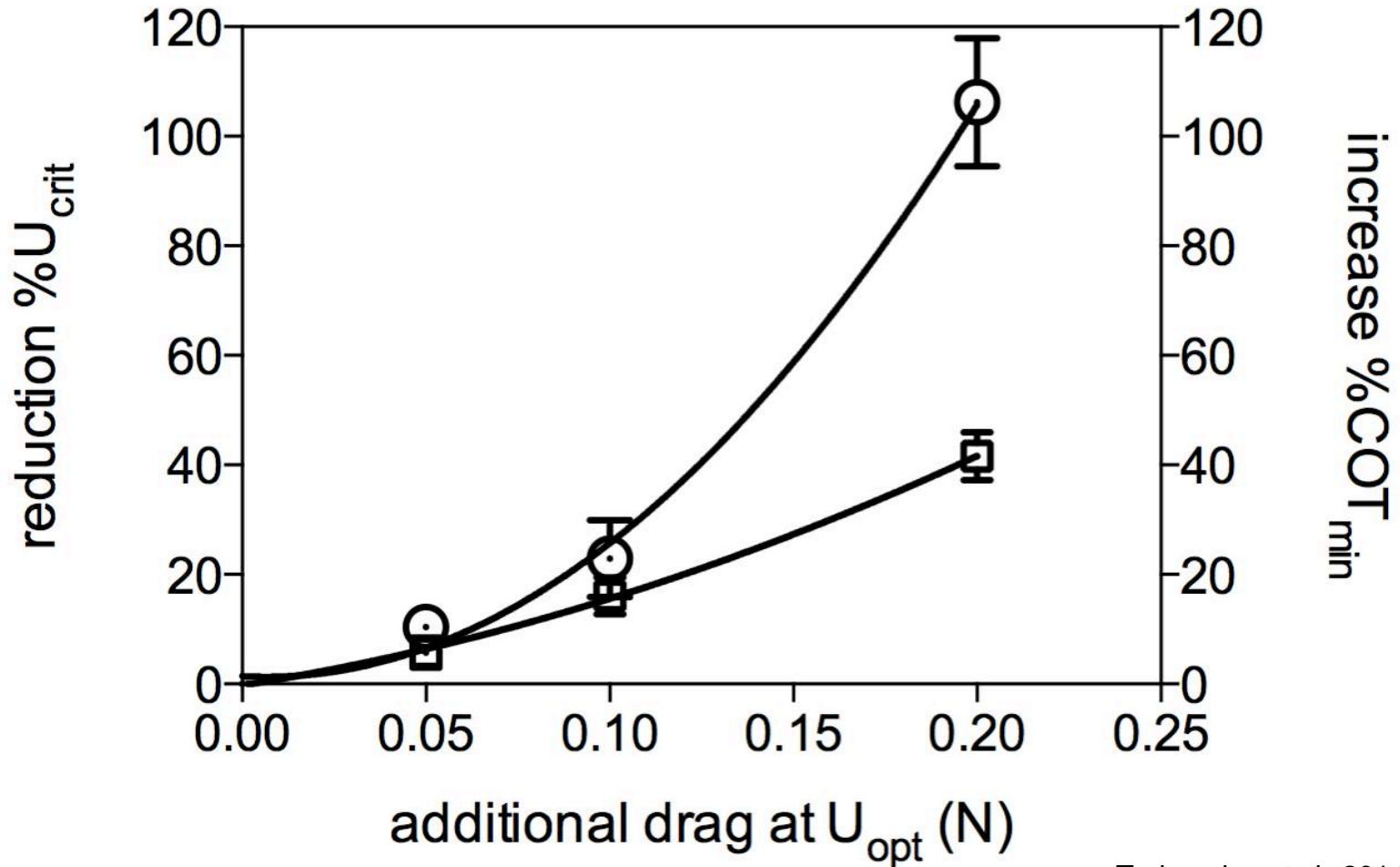
U_{crit} control = support device = 0.05N > 15% 0.1N > 60% 0.2N



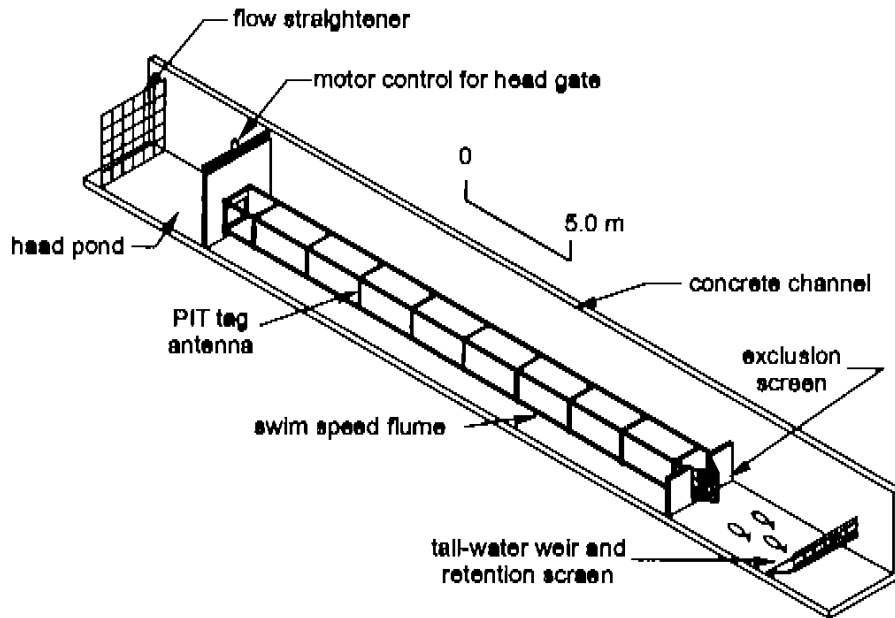
MO_2 control = support device = 0.05N < 20% 0.1N < 150% 0.2N; SMR control = support device = 0.05N = 0.1N < 100% 0.2N



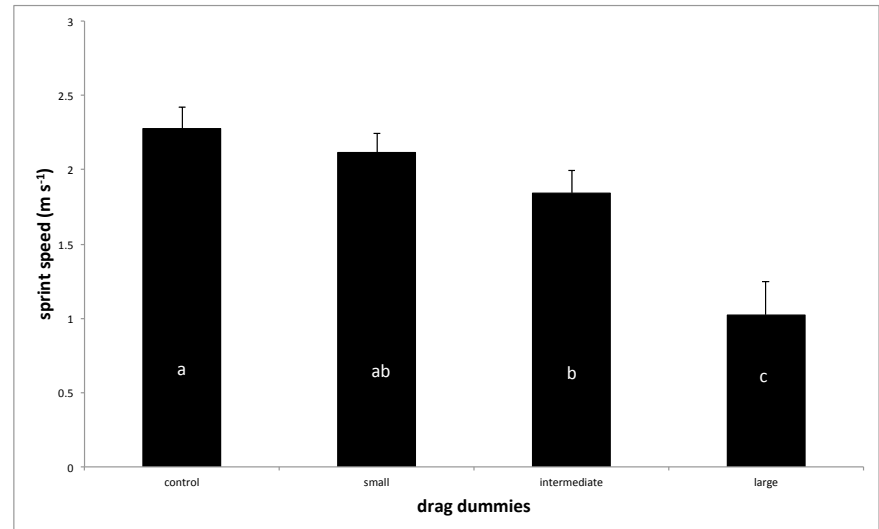
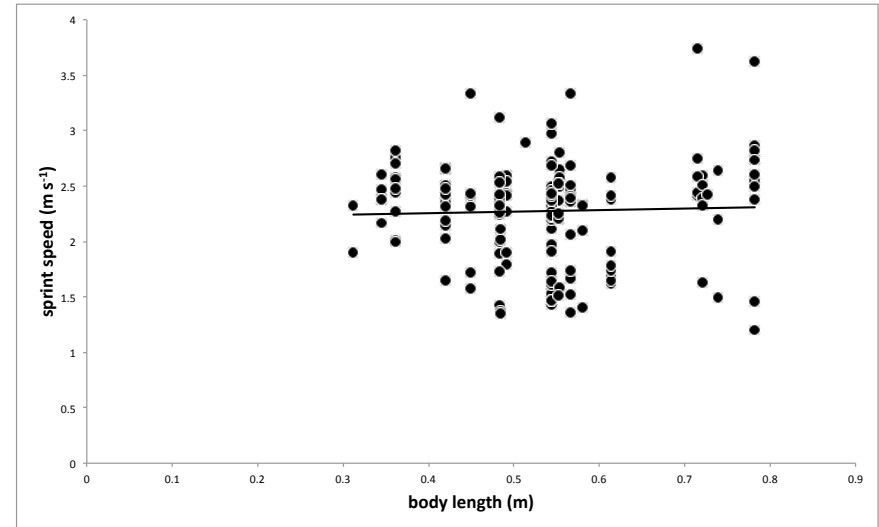
COT control = support device = 0.05N = 0.1N < 100% 0.2N



Tudorache *et al.*, 2014



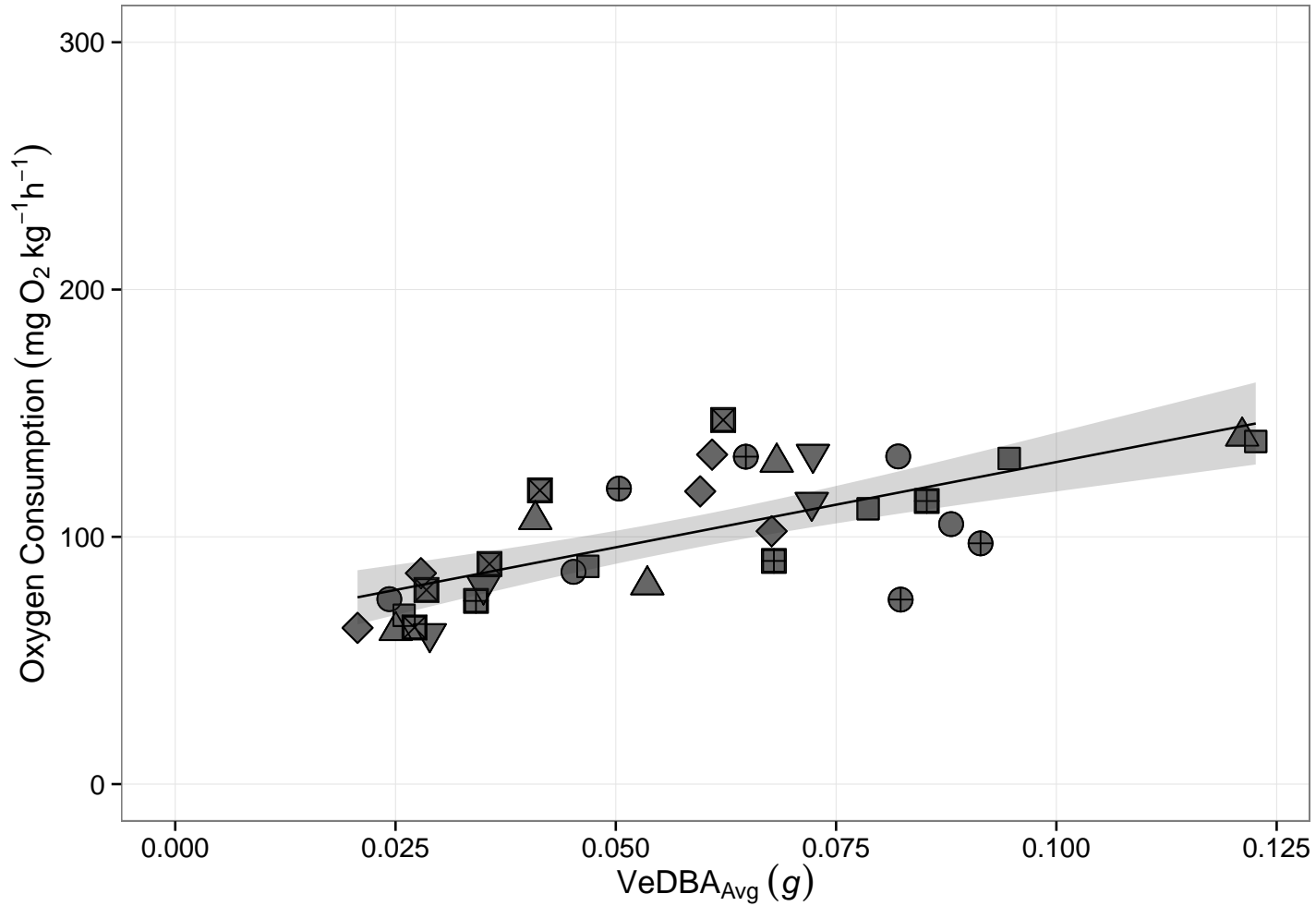
Tudorache *et al.*, in prep.



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Wright *et al.*, *in prep.*

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