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Research Article

Implantation with a novel micro-acoustic tag impairs aerobic metabolism of post-metamorphic sea lamprey

Evan P. Bellhouse[a], **Julia Xeni**[a], **Zhiqun Daniel Deng**[b,c], **Michael P. Wilkie**[a], **and Hugo Flávio**[a,d]

[a]Department of Biology and Laurier Institute for Water Science, Wilfrid Laurier University, Waterloo, ON N2l 3C5, Canada; [b]Energy and Environment Directorate, Pacific Northwest National Laboratory, Richland, WA 99354, USA; [c]Department of Naval Architecture and Marine Engineering, University of Michigan, Ann Arbor, MI 48109, USA; [d]Department of Biology, Dalhousie University, Halifax, NS B3H 4R2, Canada

Corresponding authors: **Evan P. Bellhouse** (email: bellevan58@gmail.com); **Hugo Flávio** (email: hflavio@dal.ca)

Abstract

One of the challenges in managing the invasion of sea lamprey in the Laurentian Great Lakes is understanding the early behaviour of parasitic juveniles. The eel and lamprey acoustic tag (ELAT; 12 mm × 2 mm, 0.08 g in air; akin to a 12 mm PIT tag) may finally open the possibility of tracking this poorly understood life-stage. Understanding if the ELAT alters the physiology and behaviour of the tagged animals is essential prior to wide application in the field. We implanted juvenile sea lamprey (4.95 ± 0.41 g) of wild and lab-reared origin with a mock ELAT and used intermittent-flow respirometry to quantify resting and maximum metabolic rates of control, sham surgery, and tagged groups. We found that ELAT implantation led to a 14% reduction in the maximum oxygen consumption capacity and a respective 15% reduction in the aerobic scope of juvenile sea lamprey over untagged controls, and also that juvenile sea lamprey of lab-origin had lower aerobic metabolic capacity than their wild counterparts. These physiological effects could translate to behaviour alterations after tagging and release, influencing management decisions if not accounted for.

Key words: telemetry, respirometry, sub-lethal effects, sea lamprey, metabolic rate

1. Introduction

Sea lamprey (*Petromyzon marinus*) are an ancient jawless vertebrate native to the Atlantic Ocean and the Baltic, Western Mediterranean, and Adriatic seas (Renaud 2011; Hume et al. 2021). Sea lamprey are generalist feeders and ingest blood by parasitizing a large variety of marine fishes (Renaud and Cochran 2019; Quintella et al. 2021). Following the invasion of the Laurentian Great Lakes, sea lamprey populations exploded, contributing to massive reductions and extirpations of native fish species such as lake trout (*Salvelinus namaycush*), whitefishes, and ciscoes (*Coregonus* spp.; Applegate 1951; Smith and Tibbles 1980; Siefkes 2017; Gaden et al. 2021). The need to control sea lamprey populations led to the creation of the Great Lakes Fishery Commission (GLFC) in 1955, which was given a mandate to implement a binational sea lamprey control program by the governments of Canada and the USA (Gaden et al. 2021). Sea lamprey populations were reduced by more than 90% from historic highs using an extensive network of barriers to prevent adults from reaching their spawning grounds, and through the application of 3-trifluoromethyl-4-nitrophenol (TFM) to kill larval sea lamprey in infested streams (Siefkes 2017; Sullivan et al. 2021).

Sea lamprey begin life as filter-feeding larvae that live burrowed in the soft sediment of streams (Sutton and Bowen 1994; Wilkie et al. 2022). After approximately 3–7 years, the larvae stop feeding and undergo metamorphosis, becoming free-swimming juveniles that then migrate downstream. While anadromous juvenile sea lamprey have been reported to begin parasitism while still migrating downstream (Beamish and Potter 1975; Farmer 1980), the Great Lakes juvenile sea lamprey are thought to start feeding only once they enter the lakes (Evans et al. 2021). This results in a long, natural period of fasting from the start of metamorphosis to the end of the downstream migration for the Great Lakes population. After 1–2 years of parasitism, the maturing sea lamprey cease feeding and migrate upstream where they spawn and die (Applegate 1951; Beamish 1980; Bergstedt and Swink 1995). Although the movements and behaviour of larval and adult life-stages are well documented and understood, comparatively little is known about the post-metamorphic juvenile stage, due in part to its migratory nature and primarily lacustrine habitat (i.e., a biological "black box"; Hume et al. 2021). Important information such as their preferred habitat following metamorphosis, timing and pattern of downstream migration (e.g., fall versus spring outmigration), early lake or marine behaviour, and the onset of parasitism is lacking (Evans et al. 2021). Gathering information on the juvenile life-stage is very difficult, as the animals' small size, slender body shape, and remarkable agility renders conventional tagging and tracking methods unsuit-

able (Applegate and Moffett 1955). This absence of information, in turn, translates into a lack of control measures targeting post-metamorphic sea lamprey in the Great Lakes (Evans et al. 2021; Miehls et al. 2021). Better understanding the post-metamorphic juvenile life-stage could open new management avenues not only to keep this invasive species under control in the Great Lakes, but also to support conservation initiatives in its native range across Europe and the Iberian Peninsula (Maitland 1980; Mateus et al. 2012; Hansen et al. 2016).

Acoustic telemetry allows researchers to capture the spatial ecology and behaviour of aquatic organisms beyond direct observation (Crossin et al. 2017; Matley et al. 2022). Most acoustic tags consist of a battery, microchip, and transducer, and are used on large animals, including fishes (Cooke et al. 2012; Li et al. 2024). While these tags provide high-quality data on fish movements, they cannot be implanted or attached to small fish without the risk of causing significant lethal or sublethal effects (Roussel et al. 2000). The recent development of micro acoustic tags, such as the Lotek JSATS PinTag (3.4 mm diameter, 15 mm length, 0.22 g in air), has allowed researchers to study smaller, juvenile fish (as small as ~10 cm fork length, Geist et al. 2018; Lennox et al. 2025; Notman-Grobler et al. 2025) without elevating the tag's weight burden (i.e., the weight of tag in relation to weight of animal). While these efforts to miniaturize the technology opened the possibility of tagging smaller, juvenile fish, they remained too large to safely tag animals with elongated body plans, such as juvenile sea lamprey.

Recently, a specialized eel and lamprey acoustic tag (ELAT; 12 mm length × 2 mm diameter, 80 mg in air, 42.3 mg in water, 30–60-day battery life; Mueller et al. 2019) was developed, representing a 72% reduction in volume and 63% reduction in weight compared to the JSATS PinTag described above. Mueller et al. (2019) reported 4.7% mortality in 120–160 mm juvenile Pacific lamprey (*Entosphenus tridentatus*) implanted with ELATs (tag to body weight burden of 1.3%–4.8%) compared to control animals during a 30-day post-implantation holding period. The same study also reported no mortality and no significant differences in swim performance for >130 mm juvenile American eels (*Anguilla rostrata*) implanted with ELATs, concluding that these tags are effective for use in both species. Haas et al. (2023) explored ELAT implantation in juvenile sea lamprey (tag-to-body weight burden of 1.87 ± 0.04%), showing a survival of 71% in tagged animals over a period of 60 days, with the tagged group survival only being significantly lower than the control group in the first four days (5 out of 59 tagged mortalities versus 0 out of 54 untagged control mortalities). However, the underlying causes for the observed mortality and the potential presence of sublethal effects of the tags were not addressed. The presence of sublethal tagging effects that alter the physiology and behaviour of the sea lamprey could bias any collected data, which would undermine interpretation and ultimately lead to incorrect conclusions and management decisions with respect to sea lamprey control and lamprey conservation. Hence, assessment of sublethal effects of the surgical procedures and tag burden on metabolism and behaviour of juvenile sea lamprey would provide valuable insight about the suitability, strengths, and weaknesses of ELAT implantation in this life-stage, improving our understanding of data collected in the wild. The study of sub-lethal impacts of tagging is highly relevant to accurately describe tracking data collected in the field, as changes in the physiology and behaviour of the tagged animals may occur even in the absence of lethal effects (i.e., absence of tagging-induced mortality should not be taken as a confirmation of normal behaviour).

In the present study, we used intermittent-flow respirometry to measure mass-specific oxygen consumption ($\dot{M}_{O_2}$) to determine if juvenile sea lamprey implanted with ELAT experienced any sub-lethal effects related to the procedure. $\dot{M}_{O_2}$ is a common physiological measurement that is highly sensitive to endogenous and exogenous factors such as life-stage, environmental conditions, and acute and chronic stressors (Sloman et al. 2000; Schulte 2015; Rosewarne et al. 2016; Zhang et al. 2018). Often referred to as indirect calorimetry, oxygen consumption indirectly reflects the energy expenditure of fishes (Cech 1990; Richards 2009), which could be a useful approach for monitoring the sub-lethal effects of tag implantation on juvenile sea lamprey physiology and behaviour. Variation in $\dot{M}_{O_2}$ has been correlated with altered behaviour, but this link is complex (Killen et al. 2013; Metcalfe et al. 2016*a*).

Limitations in O_2 delivery and use could impair aerobic swimming performance, as has been shown in numerous studies, thereby limiting predator evasion or foraging effectiveness (Killen et al. 2016; Metcalfe et al. 2016*b*; Bailey et al. 2022). Relationships have also been found between standard metabolic rate and aggression within fish dominance hierarchies, and reproductive success across a range of fish species (Sloman and Armstrong 2002; Metcalfe et al. 2016*a*). Such links underscore the potential value in using $\dot{M}_{O_2}$ to assess the potential sub-lethal impacts that tag implantation could have on behaviour and movements of juvenile sea lamprey and other fishes.

Measurements of $\dot{M}_{O_2}$ are made while the animals are at rest to determine standard metabolic rate (SMR), which is defined as the cost of living of an unstressed, nonbreeding, fasted ectotherm (Chabot et al. 2016). Measurements of $\dot{M}_{O_2}$ following exhaustive exercise can be used to estimate the maximum metabolic rate (MMR), usually defined as the oxygen consumed at the point of exhaustion (Clarke et al. 2013; Rosewarne et al. 2016). Because $\dot{M}_{O_2}$ is an indirect measure of aerobic energy expenditure by animals (Cech 1990; Richards 2009), measurements can provide an estimate of the energy available needed to perform all tasks beyond those needed to maintain homeostasis including feeding and digestion, growth, locomotion, and reproduction (Fry 1947; Claireaux and Lefrançois 2007; Clarke et al. 2013; Schulte 2015).

Another measure of metabolic capacity is the oxygen required to restore homeostasis after intensive exercise; commonly termed excess post-exercise oxygen consumption (EPOC; Scarabello et al. 1991; Zhang et al. 2018). EPOC is important for restoration of energy stores such as ATP, phosphocreatine, and glycogen, the correction of intracellular and extracellular pH and ion balance, and the clearance of metabolic wastes such as lactate and metabolic acid (Wood 1991; Kieffer 2000). Because the magnitude of EPOC reflects

Table 1. Body size and condition factor (CF) of the juvenile sea lamprey used in this study.

			At tagging				At testing			
Origin	Day	Group	*N*	Length (mm)	Weight (g)	CF	*N*	Length (mm)	Weight (g)	CF
Lab	10	Control	4	–	2.62 (0.39)	–	4	–	2.42 (0.31)	–
		Surgery	4	145 (6.13)	3.03 (0.73)	0.99 (0.15)	4	145 (6.13)	2.86 (0.79)	0.93 (0.17)
		Tagged	4	147 (5.74)	3.34 (0.56)	1.05 (0.08)	4	147 (5.74)	3.17 (0.57)	1.00 (0.10)
	20	Control	4	–	2.92 (0.30)	–	2	–	2.61 (0.60)	–
		Surgery	4	146 (2.22)	3.23 (0.21)	1.04 (0.05)	3	147 (1.53)	2.91 (0.10)	0.92 (0.05)
		Tagged	4	150 (10.05)	3.5 (0.66)	1.03 (0.07)	4	150 (10.05)	3.25 (0.99)	0.94 (0.10)
	30	Control	4	–	3 (0.13)	–	4	–	2.58 (0.22)	–
		Surgery	3	148 (4.58)	2.99 (0.30)	0.92 (0.07)	1	143	2.33	0.8
		Tagged	4	157 (11.09)	3.99 (0.67)	1.02 (0.06)	3	152 (4.36)	3.13 (0.05)	0.89 (0.06)
Wild	10	Control	6	–	4.98 (1.04)	–	6	–	4.45 (0.75)	–
		Surgery	6	161 (14.17)	4.8 (1.01)	1.15 (0.11)	6	161 (14.17)	4.73 (1.02)	1.15 (0.28)
		Tagged	6	163 (6.28)	5.22 (0.61)	1.21 (0.03)	6	163 (6.28)	4.61 (0.66)	1.07 (0.15)
	20	Control	6	–	4.42 (0.99)	–	6	–	4.12 (0.89)	–
		Surgery	6	159 (12.09)	4.96 (1.12)	1.22 (0.12)	5	156 (9.34)	4.08 (1.03)	1.07 (0.10)
		Tagged	6	167 (14.99)	5.63 (1.46)	1.19 (0.10)	6	167 (14.99)	5.16 (1.54)	1.08 (0.10)
	30	Control	6	–	4.34 (0.94)	–	6	–	3.80 (1.01)	–
		Surgery	7	159 (7.50)	4.94 (0.86)	1.23 (0.11)	7	159 (7.5)	4.30 (0.78)	1.07 (0.12)
		Tagged	6	164 (7.12)	5.27 (0.78)	1.18 (0.04)	5	163 (7.33)	4.43 (0.92)	1.01 (0.10)

Note: The values are divided by lab-reared and wild origin, with their respective treatment groups (Control, Sham surgery, Tagged) and sampling periods (10, 20, and 30 days). Animals were weighed at tagging and again prior to the respirometry trial. Data are presented as mean ± SD.

the restoration of homoeostasis following anaerobic exercise (Wood 1991; McDonald et al. 1998; Zhang et al. 2018), it provides important information about an animal's capacity to recover when faced with environmental stressors that require greater reliance on anerobic energy reserves. Understanding if tag burden compromises aerobic metabolism capacity and post-exercise recovery of juvenile sea lamprey could therefore be highly relevant because brief bursts of exercise are necessary to pursue host fishes and to evade predators (Evans et al. 2021).

2. Methods

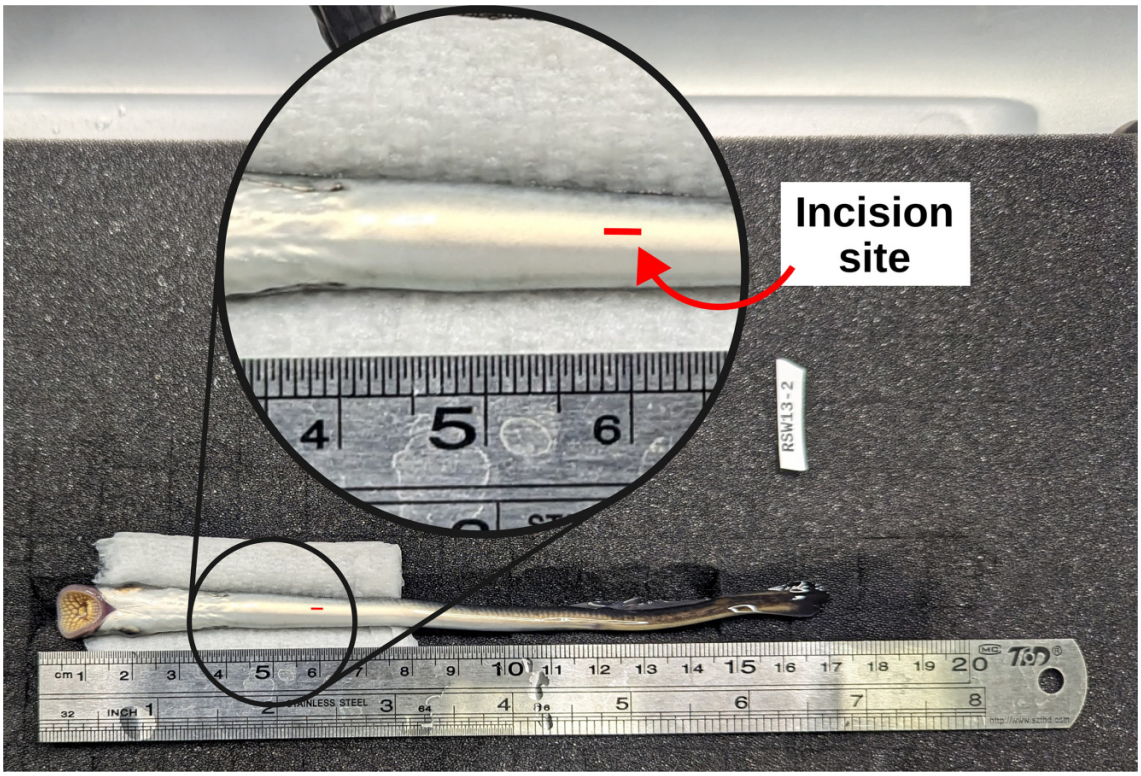
2.1. Animal procurement and holding

The majority of the juvenile sea lamprey used in this study (N = 55; 4.95 ± 0.41 g; 162.0 ± 3.2 mm; Table 1) were captured during their downstream migration by United States Fish and Wildlife Service (USFWS) or Fisheries and Oceans Canada (DFO) personnel in September–October 2022. Most of the juveniles were captured in the Marengo River (Lake Superior tributary, Ashland, Wisconsin, USA), with small contributions from the Cranberry River (Lake Superior tributary, Ontonagon, Michigan, USA), Garden River (Lake Huron tributary, Sault Ste. Marie, Ontario, Canada), and Ford River (Lake Michigan, Escanaba, Michigan, USA). The captured sea lamprey were held in the aquatic facilities at the US Geological Survey (USGS), Hammond Bay Biological Station (HBBS), Millersburg, Michigan, USA, for about four months in large aquaria continuously receiving Lake Huron water (~2 °C; pH ~ 8.0; alkalinity ~ 85 mg $CaCO_3$ L^{-1}; hardness ~ 150 mg·L^{-1} as $CaCO_3$), before shipment. Additional juvenile sea lamprey (N = 35; 3.18 ± 0.40 g; 149.0 ± 4.5 mm; Table 1) that had been captured as larval sea lamprey and spontaneously completed metamorphosis in captivity at the HBBS were also used in experiments (henceforth referred to as lab-reared juveniles). These lab-reared juvenile sea lamprey were intended to supplement the group sizes, under the assumption that they would be representative of the elusive wild-caught population. This assumption was then tested by including origin (lab vs. wild) as an explanatory variable in the statistical analysis, as further detailed below. The juvenile sea lamprey were transported to Wilfrid Laurier University (WLU; Waterloo, Ontario, Canada) in hard-sided coolers within plastic bags filled with ice-cold, O_2-saturated water in January 2023. Upon arrival at WLU, the sea lamprey were sorted according to origin into wild and lab-reared juveniles, but detailed information on the river of origin could not be kept due to space constraints. Juveniles were held in 40–80 L glass aquaria supplied with dechlorinated City of Waterloo tap water (pH ~8.0; alkalinity ~ 200 mg $CaCO_3$ L^{-1}; hardness ~ 450 mg·L^{-1} as $CaCO_3$) chilled to 10 °C with an inline chiller on recirculating flow. Juvenile sea lamprey residing in the Great Lakes naturally experience prolonged fasting from metamorphosis to the end the downstream migration, so the juveniles used in this study were not fed during holding or during experiments, which were initiated 41 days after arrival at WLU.

2.2. Surgical procedures

The 90 juvenile sea lamprey used for this study were divided into three groups: (1) controls, (2) sham surgery, and (3) tagged. Juveniles of wild and lab-reared origin were equally distributed among the groups. Control juveniles did not un-

Fig. 1. Top view of the V-shape closed-cell foam pad used for surgeries, including an anaesthetised sea lamprey ready for surgery. The approximate location and size of the incision are noted by the red dash on the lamprey's body.



dergo tagging or anaesthesia. Sham surgery juveniles underwent handling, surgical incision, but no tag was implanted. Tagged juveniles were implanted with a mock ELAT where the micro-battery was replaced with a PIT transmitter encased in epoxy (12.06 ± 0.1 mm length, 1.98 ± 0.03 mm diameter, 80.0 ± 2.4 mg in air, estimated 42.9 mg in water; i.e., identical to a real ELAT). The weight burden of the ELAT in the juvenile sea lampreys used in this study averaged 1.63 ± 0.15%, and the length burden averaged 7.45 ± 0.15%. The juveniles were anaesthetized in an 80 $\mu L \cdot L^{-1}$ solution of eugenol (Sigma–Aldrich, USA, C-8392-100ML, Lot 88H0082; preparation details available in Supplementary Material 1) until stage IV anaesthesia was induced (Summerfelt and Smith 1990), at which point their weight (nearest mg) and length (nearest mm) were measured. Time to full anaesthesia averaged 23 min (±33 s SEM). The juveniles were then transferred to a V-shape closed-cell foam pad. A 2–3 mm incision was made 1–2 cm below the last branchial pore (7th from front), slightly to the side of the mid-ventral line (schematic provided in Fig. 1). The tag was either (1) partly inserted and removed for the sham surgery group (to mimic stretch stress on the wound), or (2) fully inserted for the tagged group. The incision was then closed with a 2 × 2 braided suture stitch (Ethicon™ 5-0 Vicryl Braided Suture P-3 13 mm 3/8c reverse cutting needle). A braided suture was chosen over a monofilament suture because the braided suture is more pliable, allowing for better control of the small loop going through the thin body wall of the juvenile lamprey. The tagging procedure lasted on average 3 min 24 s (±10 s), during which the gills of the animal were kept wet by regularly spraying a 40 $\mu L \cdot L^{-1}$ maintenance solution of eugenol around the head region. All surgical tools were sterilized between procedures by soaking in a 1:3:1 Clidox-S® solution (Pharmacal Research Laboratories, Waterbury, Connecticut, USA), followed by a rinse with sterile water. The juvenile sea lamprey were placed into numbered mesh containers within 10 °C holding aquaria for monitoring. At 10, 20, and 30 days post surgery, 10 juveniles of each group were used for intermittent-flow respirometry experiments, as outlined below. All surgical and experimental procedures were approved by the WLU Animal Care Committee (Animal Use Protocol No. R23000) and adhered to the guidelines of the Canadian Council of Animal Care (CCAC).

2.3. Experimental setup

$\dot{M}_{O_2}$ was determined using intermittent-flow respirometry. The setup consisted of a recirculation system held at 10 °C using a temperature controller (TMP-REG, Loligo Systems), connected to a wet-table bath where eight respirometers were placed (schematics provided in Supplementary Material 2). Respirometers were custom-built using clear PVC piping (inner diameter = 20 mm, length = 200 mm) to accommodate the elongated shape of the animals, with a total volume of 75.4 mL. The respirometers were checked for leaks by filling them up, turning them on, and holding them above the water bath (with the flush pump still underwater) prior to the experiments. Each respirometer chamber was covered with a plastic sleeve during experiments to minimise animal disturbance. The experimental system was cleaned with 5% HCl and

70% ethanol at the end of each week to minimize calcium carbonate build-up and to combat biofilm accumulation, which could increase background oxygen consumption.

Each respirometer was equipped with an O_2 probe (OXFLOW-HS; PyroScience GmbH, Aachen, Germany). Temperature probes (TDIP15; PyroScience GmbH) were also installed on the 4th and 8th chambers to monitor temperature within the chambers. The probes were connected to a PyroScience Firesting O_2 (FSO2-C4; PyroScience GmbH) or a PyroScience Firesting Pro (FSPRO-4; PyroScience GmbH) oxygen meter. In-chamber oxygen concentration and temperature were recorded every second. Two flush pumps (model AD20P-0510 A, Shenzhen Giant Electric Tech Inc.) were used to flush the eight chambers (i.e., one pump flushed four chambers). These pumps were connected to a custom-built cycle controller (powered by an Arduino microcontroller board) set to perform 5 min of O_2 measurement followed by 3 min of flush. The first 20 s of the measurement phase were discarded from each cycle (wait phase). Background O_2 consumption was recorded both before and after the experiments to account for any microbial oxygen consumption that may have occurred throughout the duration of the experiment.

2.4. Experimental procedure

At each of the three designated time points (10, 20, and 30 days post-tagging), juvenile sea lamprey from each group (control, sham surgery, and tagged) were weighed in water to the nearest mg and then transported in a tube with water to their respective, individual respirometer. Four trials were run for each time point. Six to eight juveniles of both origins and all three treatment groups were mixed in each respirometry trial, and origin × group combinations were randomized through the chambers in different trials, to avoid time and chamber confounding factors. Measurements of $\dot{M}_{O_2}$ were initiated immediately following the transfer of each animal into the respirometer. The animal was left to rest within the chamber overnight (14–16 h) for the determination of SMR. The following morning, one by one, the animals were removed from the chambers and exercised for 5 min by manual chasing, which exhausted the animals (i.e., unresponsive to further stimulation). After chasing, the animals were immediately returned to the chamber, and $\dot{M}_{O_2}$ measurements were resumed to determine the MMR. The animals were then left to recover within the chambers for at least 4 h, during which EPOC was measured.

2.5. Calculations, statistics, and data analysis

2.5.1. $\dot{M}_{O_2}$ calculations

The $\dot{M}_{O_2}$ for each cycle was determined using the R package pyroresp (available at https://github.com/hugomflavio/pyroresp), using R v4.5.1 (R Core Team 2025). Recorded O_2 values (hPa) were converted to $\mu mol\ O_2 \cdot L^{-1} \cdot h^{-1}$ using the respirometry R package (Birk 2024). Pre-background respiration averaged 15% of SMR and post-background averaged 20% of SMR. Changes in background respiration were linearly modelled over time using the pre- and post-background readings. This linear model was then used to estimate the background $\dot{M}_{O_2}$ at the time of each cycle and to correct the recorded oxygen readings. The accuracy of the background estimates was verified by confirming that they correctly neutralized background oxygen consumption readings of an empty chamber. Linear models were then applied to the corrected O_2 readings to determine the slope and R^2 of the lines of best fit for each cycle. Cycles with an R^2 of 0.9 or above were considered valid for $\dot{M}_{O_2}$ determination. The respective slopes were converted into $\dot{M}_{O_2}$ ($\mu mol\ O_2 \cdot g^{-1} \cdot h^{-1}$) by accounting for the corrected volume of the respirometer and the mass of the animal, as follows:

$$\dot{M}_{O_2} = S \times V \times M^{-1} \quad (1)$$

where: S = rate at which oxygen decreased in the chamber ($\mu mol\ O_2 \cdot L^{-1} \cdot h^{-1}$), V = respirometer volume (mL; corrected for the mass of the animal, assuming a 1 g:1 mL animal density), M = mass of the animal (g). The $\dot{M}_{O_2}$ values calculated for each animal per cycle are available in Supplementary Material 3.

2.5.2. SMR, MMR, and aerobic scope calculations and statistics

SMR was calculated as the quantile 0.2 (Chabot et al. 2016) of the pre-chase measurements (average 114 measurements before chasing). MMR was determined as a two-step process. First, the post-chasing cycle with the highest $\dot{M}_{O_2}$ was determined. Then, that cycle was subdivided into rolling 30 s calculations of $\dot{M}_{O_2}$ progression. MMR was then determined as the highest 30 s $\dot{M}_{O_2}$ calculated in the previous step (96% of the resulting 30 s slopes were above an R^2 of 0.95; average $R^2 = 0.98$; lowest $R^2 = 0.91$). The SMR and MMR values calculated were used to calculate absolute aerobic scope (AAS) and factorial aerobic scope (FAS; Rosewarne et al. 2016), as follows:

$$AAS = MMR - SMR \quad (2)$$

$$FAS = MMR/SMR \quad (3)$$

Generalized Linear Models (GLM) with Gamma distribution and log link were applied to test for the effects of origin (factorial: lab, wild), treatment group (factorial: control, sham surgery, and tagged), and day (factorial: 10, 20, and 30) on SMR, MMR, AAS, and FAS. Because it was shown that origin had a significant effect on the response variables, additional models were calculated to assess the effects of the treatment group specifically on the SMR, MMR, AAS, and FAS of wild juveniles. Model fitting was confirmed by inspecting Q–Q and residual plots using the R package DHARMa (Hartig 2024). This revealed that the Gamma distribution was a bad fit for the factorial aerobic scope model, so a Gaussian distribution with identity link was used instead. ANOVA (type III) testing (car package; Fox and Weisberg 2019) was used to assess the significance of the tested variables. Where significant differences were found, Tukey post hoc tests were performed using the R package "emmeans" (Lenth 2025). To further confirm the absence of differences between wild control

Table 2. Effects of eel and lamprey acoustic tag (ELAT) implantation on the standard metabolic rate (SMR), maximum metabolic rate (MMR), absolute aerobic scope (AAS), factorial aerobic scope (FAS), weight loss, and excess post-exercise oxygen consumption (EPOC) of lab-reared and wild juvenile sea lamprey of control, sham surgery, and tagged groups.

Origin	Group	SMR (μmol $O_2 \cdot g^{-1} \cdot h^{-1}$)	MMR (μmol $O_2 \cdot g^{-1} \cdot h^{-1}$)	AAS (μmol $O_2 \cdot g^{-1} \cdot h^{-1}$)	FAS (fold over SMR)	Weight loss ($mg \cdot day^{-1}$)	EPOC (μmol $O_2 \cdot g^{-1}$)
Lab	Control	1.38 ± 0.06	8.6 ± 0.6	7.3 ± 0.5	6.3 ± 0.4	16 ± 2	3.83 ± 0.5
	Surgery	1.43 ± 0.06	11.6 ± 1.2	10.2 ± 1.1	8.1 ± 0.7	18 ± 2	4.01 ± 0.7
	Tagged	1.47 ± 0.07	11.1 ± 1.0	9.7 ± 0.9	7.5 ± 0.5	19 ± 2	4.01 ± 0.4
	All combined	1.43 ± 0.04^{B}	10.4 ± 0.6^{B}	9.0 ± 0.5^{B}	7.2 ± 0.3^{B}	17 ± 1^{B}	3.95 ± 0.3^{B}
Wild	Control	1.56 ± 0.05^{a}	14.0 ± 0.8^{a}	12.4 ± 0.7^{a}	9.0 ± 0.4	18 ± 2^{a}	5.64 ± 0.4^{a}
	Surgery	1.58 ± 0.05^{a}	13.2 ± 0.9^{ab}	11.6 ± 0.9^{ab}	8.3 ± 0.5	27 ± 3^{ab}	5.50 ± 0.7^{a}
	Tagged	1.53 ± 0.06^{a}	12.1 ± 0.8^{b}	10.6 ± 0.8^{b}	7.9 ± 0.4	25 ± 3^{b}	4.77 ± 0.5^{a}
	All combined	1.56 ± 0.03^{A}	13.1 ± 0.5^{A}	11.5 ± 0.5^{A}	8.4 ± 0.3^{A}	24 ± 2^{A}	5.31 ± 0.3^{A}

Note: Data presented as the mean ± standard error of the mean. Animals were subjected to no treatment (controls), incision but no ELAT implantation (sham surgery) or implanted with an ELAT (tagged) and followed for up to 30 days. Averages for all animals of either origin are also provided. Different lowercase superscript letters indicate statistically significant differences within columns for treatment groups of wild origin ($p < 0.05$). Different uppercase superscript letters indicate statistically significant differences within columns for origins, using combined (pooled) treatment groups ($p < 0.05$). Statistical tests between lab-reared groups were not performed due to the low number of lab-reared juveniles used in this study.

and wild tagged juveniles, the same models were also run using only those two groups. In the results, values are displayed as mean ± SEM unless otherwise stated.

2.5.3. Daily mass loss calculation and statistics

Mass difference was calculated by subtracting the weight measured at time of tagging (day 0) and weight measured at time of testing (corrected for tag mass where relevant), and dividing that difference by the number of days between measurements (10, 20, or 30 days). The mass change for four juveniles (all of different treatment combinations) was discarded as it was deemed unrealistic, likely resulting from an annotation error at the time of first weighing. A GLM with Gamma distribution and log link was applied to test for the effects of origin (factorial: lab, wild), treatment group (factorial: control, sham surgery, tagged), and day (factorial: 10, 20, and 30) on daily mass loss. Significance testing was performed as for the metabolic rate variables. To further confirm the differences between wild control and either wild sham surgery or wild tagged juveniles, models were also run using only two groups at a time (i.e., control vs. sham surgery and control vs. tagged).

2.5.4. EPOC calculations and statistics

To visualise the recovery trajectory, post-chase $\dot{M}_{O_2}$ values were converted to $\Delta\dot{M}_{O_2}$ by subtracting the respective SMR for each juvenile. These $\Delta\dot{M}_{O_2}$ values were then modelled using a generalized additive model (GAM) with Gamma family and log link. The recovery trajectory was allowed to vary between origins (factorial: lab, wild), treatment groups (factorial: control, sham surgery, tagged), day (factorial: 10, 20, and 30), and their three-way interaction. Model fitting was confirmed by inspecting Q–Q and residual plots, using the R package DHARMa and the R package gratia (Simpson 2024). This showed that the model was suboptimal at accounting for changes in variation over time (i.e., large variation in $\Delta\dot{M}_{O_2}$ during the first 30 min followed by low variation), but for the purpose of visualising the recovery trajectory we deemed the model to be satisfactory.

Finally, EPOC was calculated as the area between post-chase $\dot{M}_{O_2}$ readings and the animal's respective SMR (Zhang et al. 2018), until $\dot{M}_{O_2}$ reached 1.1 times SMR or 4 h had passed. A 4 h post-exercise monitoring period was selected based on previous observations showing that both larval and adult sea lamprey recover from exhaustive chasing within this period (Boutilier et al. 1993; Wilkie et al. 2001). A GLM with Gamma distribution and log link was applied to test for the effects of origin (factorial: lab, wild), treatment group (factorial: control, sham surgery, tagged), and day (factorial: 10, 20, and 30) on EPOC. Significance testing was performed as for the metabolic rate variables. To further confirm the absence of differences between wild control and wild tagged juveniles, the same model was also run using only those two groups.

3. Results

In addition to the figures and tables referred to below, details of all statistical analyses are summarized in Table 4.

3.1. SMR, MMR, AAS, and FAS

The SMR of all lab-reared juveniles was 8% lower than that of the wild juveniles across all treatment groups (i.e., control, sham-surgery, tagged; Table 2; Fig. 2A). As such, the effects of time and treatment group were further analysed for the wild juveniles only, which were more reflective of the true physiological state of animals likely to be tagged in the wild (see discussion for details).

The SMR of the wild juveniles was not affected by treatment group, averaging 1.56 ± 0.03 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$ for all sample periods combined (10 h, 20 h, 30 h; Table 2; Fig. 2A). This was also confirmed to be the case when comparing control and tagged wild juveniles directly (Table 2). Finally, the SMR of the wild juveniles (all treatment groups pooled) significantly decreased by 11% from day 10 to day 30 of the experiment (Tukey post hoc, $p = 0.025$; Table 3).

Fig. 2. Effects of ELAT implantation on $\dot{M}_{O_2}$ of lab-reared (orange boxes) and wild (blue boxes) juvenile sea lamprey. Animals were subjected to no treatment (controls), incision but no ELAT implantation (sham surgery) or implanted with an ELAT (tagged) and followed for 30 days. Intermittent-flow respirometry was used to measure (A) standard metabolic rate (SMR) and (B) maximum metabolic rate (MMR), followed by calculation of (C) absolute aerobic scope (AAS), and (D) factorial aerobic scope (FAS). Data are displayed as boxplots (median, 1st and 3rd quartiles, with whiskers expanding to 1.5 times the inter-quartile range) with the respective individual values overlaid. See Table 1 for details on the number of animals per group and sampling period. ELAT, eel and lamprey acoustic tag.

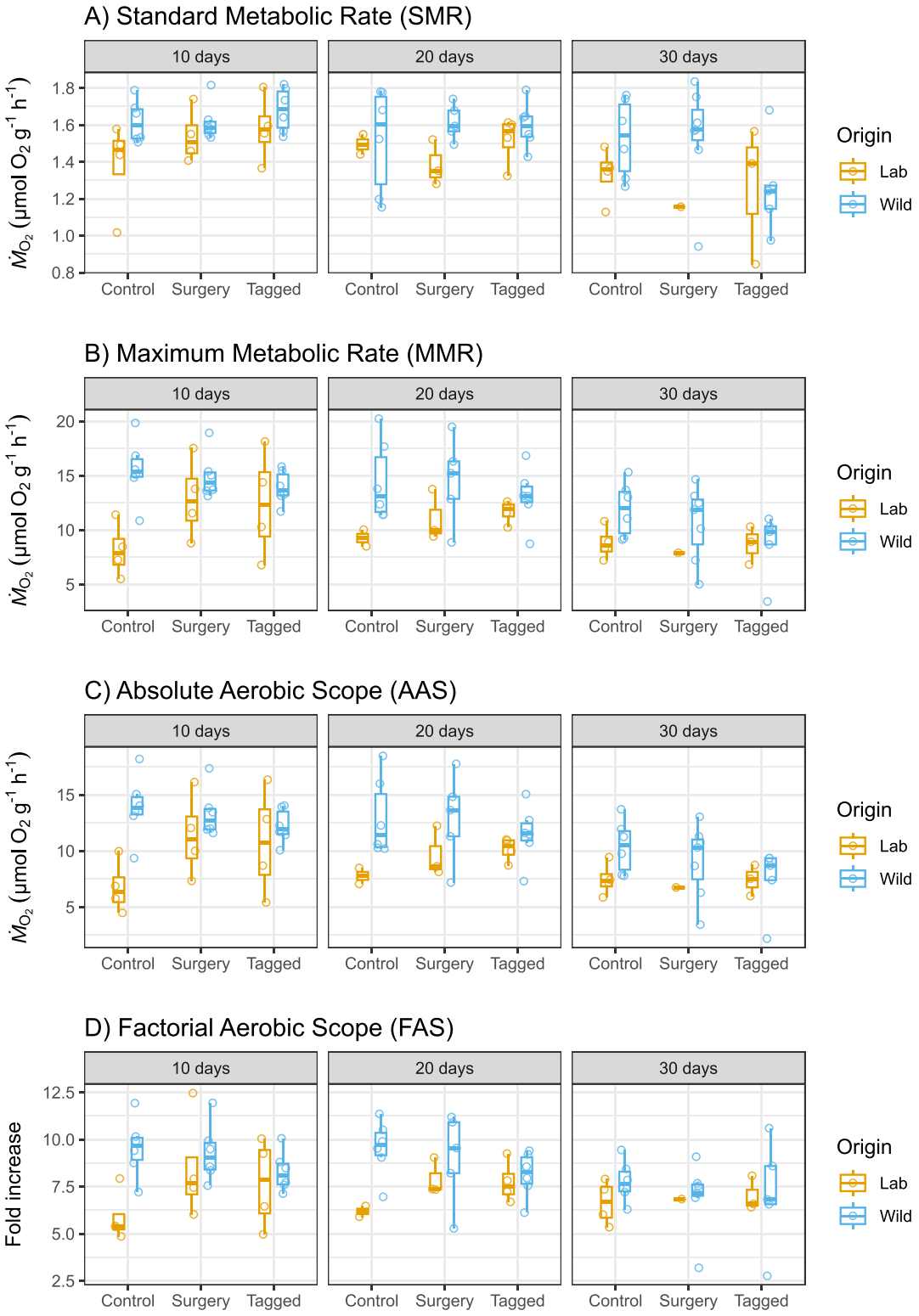


Table 3. Effects of eel and lamprey acoustic tag (ELAT) implantation on the standard metabolic rate (SMR), maximum metabolic rate (MMR), absolute aerobic scope (AAS), factorial aerobic scope (FAS), weight loss, and excess post-exercise oxygen consumption (EPOC) of lab-reared and wild juvenile sea lamprey measured 10, 20, and 30 days following procedure.

Origin	Day	SMR (μmol $O_2 \cdot g^{-1} \cdot h^{-1}$)	MMR (μmol $O_2 \cdot g^{-1} \cdot h^{-1}$)	AAS (μmol $O_2 \cdot g^{-1} \cdot h^{-1}$)	FAS (fold over SMR)	Weight loss ($mg \cdot day^{-1}$)	EPOC (μmol $O_2 \cdot g^{-1}$)
Lab	10	1.50 ± 0.06	11.2 ± 1.2	9.7 ± 1.2	7.3 ± 0.7	18 ± 2	3.88 ± 0.5
	20	1.47 ± 0.04	10.9 ± 0.6	9.5 ± 0.6	7.5 ± 0.4	18 ± 2	4.50 ± 0.5
	30	1.29 ± 0.08	8.7 ± 0.5	7.4 ± 0.4	6.8 ± 0.3	15 ± 2	3.43 ± 0.5
Wild	10	1.64 ± 0.03^{a}	14.8 ± 0.5^{a}	13.2 ± 0.5^{a}	9.1 ± 0.3^{a}	29 ± 3^{a}	5.36 ± 0.3^{ab}
	20	1.58 ± 0.04^{ab}	14.0 ± 0.8^{a}	12.4 ± 0.8^{a}	8.9 ± 0.4^{a}	22 ± 3^{a}	6.40 ± 0.7^{a}
	30	1.46 ± 0.06^{b}	10.5 ± 0.7^{b}	9.1 ± 0.7^{b}	7.26 ± 0.5^{b}	21 ± 2^{a}	4.23 ± 0.4^{b}

Note: Data presented as the mean ± standard error of the mean. Data is pooled by time point for animals that were subjected to no treatment (controls), incision but no ELAT implantation (sham surgery) or implanted with an ELAT (tagged). Different lowercase superscript letters indicate statistically significant differences within columns for treatment groups of wild origin ($p < 0.05$). Statistical tests between lab-reared groups were not performed due to the low number of lab-reared juveniles used in this study.

Table 4. Summary of the effects of origin (factorial: lab and wild), day (factorial: 10, 20, and 30), and treatment group (factorial: control, sham surgery, and tagged) on various response variables in juvenile sea lamprey.

	Origin			Day			Group			Group (control vs. tagged only)		
Variable	n	χ^2	***p*-value**	n	χ^2	***p*-value**	n	χ^2	*p*-value	n	χ^2	*p*-value
SMR	82	8.61	**0.003**	53	7.48	**0.024**	53	1.11	0.570	35	0.36	0.550
MMR	82	17.3	**<0.001**	53	23.5	**<0.001**	53	5.00	0.082	35	5.43	**0.021**
AAS	82	16.6	**<0.001**	53	23	**<0.001**	53	5.00	0.081	35	5.34	**0.021**
FAS	82	9.41	**0.004**	53	13.2	**0.001**	53	4.16	0.130	35	4.56	**0.030**
Weight loss	78	8.92	**0.003**	50	3.76	0.150	50	5.73	0.057	33	3.89	**0.048**
EPOC	82	9.41	**0.004**	53	11.8	**0.002**	53	3.06	0.210	35	4.56	0.065

Note: The effect of group is further detailed for the direct comparison between control and tagged wild juveniles. SMR, standard metabolic rate; MMR, maximum metabolic rate; AAS, absolute aerobic scope; FAS, factorial aerobic scope; EPOC, excess post-exercise oxygen consumption. *p*-values under 0.05 are highlighted in bold.

The MMR of all lab-reared juveniles combined was 21% lower than that of wild juveniles (Table 2; Fig. 2B). As such, the effects of time and treatment group were again analyzed for the wild juveniles only. The overall wild juvenile model was unable to detect a significant effect of experimental group on MMR when all groups (control, sham surgery, tagged) were examined (Table 4). However, direct comparison of wild control and tagged juveniles revealed that wild tagged juveniles had a mean MMR of 12.1 ± 0.8 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$, which was 14% lower than that measured in the control animals (which averaged 14.0 ± 0.8 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$) throughout the entire experiment (Table 2). Similarly to SMR, an effect of time on the MMR of all the wild juveniles combined was observed, significantly decreasing by 29% from day 10 to day 30 of the experiment (Table 3; Tukey post hoc, $p = 0.0001$), with the majority of the drop occurring from days 20 to 30 (25%; Table 3; Tukey post hoc, $p = 0.001$)

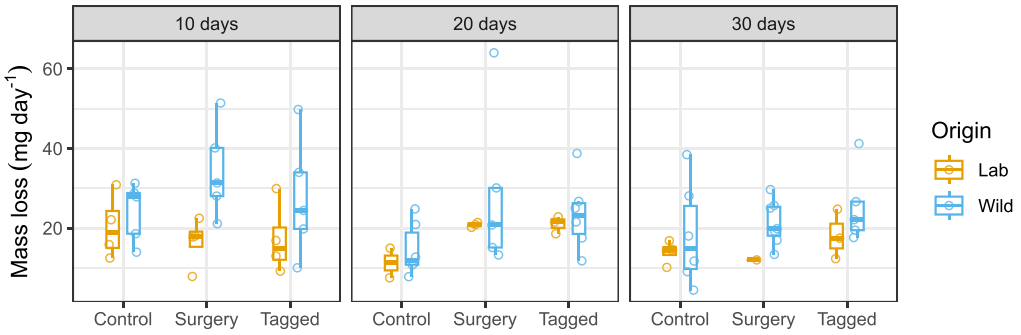
The lower SMR and MMR of the lab-reared juveniles translated to an overall 22% lower AAS in comparison to the wild juveniles (Table 2; Fig. 2C). Similar to MMR, the overall model for the wild juveniles could not detect a significant effect of experimental group on AAS (Table 4). However, the direct comparison of control and tagged wild juveniles revealed that the tagged juveniles experienced a 15% reduction in absolute aerobic scope from 12.4 ± 0.7 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$ in the controls to 10.6 ± 0.8 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$ in the tagged juveniles (Table 2; Fig. 2C). The AAS of the wild juveniles significantly decreased by 31% from day 10 to day 30 (Table 3; Tukey post hoc, $p = 0.0001$), with the majority of the drop (27%) occurring from days 20 to 30 (Table 3; Tukey post hoc, $p = 0.001$).

Not surprisingly, the FAS of the lab-reared juveniles (all groups combined) was also 14% lower than that of the wild juveniles (Table 2; Fig. 2D). While the overall model for the wild juveniles could not detect a significant effect of experimental group on FAS (Table 4), the direct comparison revealed that FAS of wild tagged juveniles averaged 7.9 ± 0.4 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$, which was 12% lower than that of wild controls (Table 2). As for the other measures, the FAS of the wild juveniles significantly decreased by 20% from day 10 to day 30 (Table 3; Tukey post hoc, $p = 0.005$), with the majority of the drop (18%) occurring from day 20 to 30 (Table 3; Tukey post hoc, $p = 0.013$).

3.2. Effects of time on body mass

The body mass of all juveniles decreased throughout the experiment in all treatment groups (Fig. 3). The overall loss rate was 29% lower for the lab-reared juveniles than for the wild juveniles (Table 2; Fig. 3). Sampling day had no significant effect on the mass loss rate of the wild juveniles (Table 4). While the overall wild model was unable to detect a significant effect of experimental group on daily mass loss (Table 4), the direct comparisons between groups revealed that the loss rates of wild controls were 33% lower than sham surgery juveniles (GLM, $N = 34$, $\chi^2 = 4.45$, *p*-value = 0.035), and 28% lower than tagged juveniles (Table 2; Fig. 3).

Fig. 3. Effects of ELAT implantation on the mass loss rate (mg·day^{-1}) of lab-reared (orange boxes) and wild (blue boxes) juvenile sea lamprey. Animals were subjected to no treatment (controls), incision but no ELAT implantation (sham surgery) or implanted with an ELAT (tagged) and followed for 30 days. Mass difference was calculated by subtracting the weight measured at time of tagging (day 0) and weight measured at time of testing (corrected for tag mass where relevant), and dividing that difference by the number of days between measurements (10, 20, or 30 days). Data are displayed as boxplots (median, 1st and 3rd quartiles, with whiskers expanding to 1.5 times the inter-quartile range) with the respective individual values overlaid. See Table 1 for details on the number of animals per group and sampling period. ELAT, eel and lamprey acoustic tag.



3.3. Excess post-exercise oxygen consumption

Post-exercise $\dot{M}_{O_2}$ declined sharply in the initial 30 min post-chase period, before the recovery trajectory switched to a slower, more gradual reduction as the $\Delta\dot{M}_{O_2}$ approaching SMR levels. The GAM revealed that recovery trajectory differed as a function of the three-way interaction between treatment origin, group, and day (GAM, $F = 7.61$, p-value < 0.001). In general, lab-reared juveniles had a lower recovery trajectory, and control juveniles (of both lab and wild origin) had higher curves than their sham surgery and tagged counterparts (Fig. 4). These patterns in recovery trajectory translated into differences in EPOC, with lab-reared juveniles having 26% lower EPOC than wild juveniles (Table 2; Fig. 5). The EPOC of the wild juveniles was not significantly affected by treatment group (Table 2). When compared directly, the EPOC of wild control and tagged juveniles were nearly significantly different from on another (Table 4; Tukey post hoc; $p = 0.07$). The EPOC of the wild juveniles significantly dropped by 34% from day 20 to day 30 (Table 3; Tukey post hoc, $p = 0.003$; Fig. 5).

3.4. Mortality

The vast majority of the juvenile sea lamprey survived the experimental period (91.1%). Most of the mortalities were lab-reared juveniles (6 out of 8), with no apparent trends relating to the size of the animals. One lab-reared control juvenile died due to an experimental holding mishap (which was then rectified), and another was unresponsive at the time of the experiment and was euthanized. Three lab-reared sham surgery juveniles were noted to have suffered an intestinal puncture during surgery, dying 14–17 days post-surgery. One lab-reared tagged juvenile mortality was deemed to be a direct lethal effect from carrying the tag (no intestinal puncture, no other visible damage; died 21 days post-surgery). Of the two wild juveniles that died, one sham surgery died after escaping the aquarium, and one tagged juvenile mortality was deemed a direct lethal effect from carrying the tag (no visible damage; died 30 days post-surgery, before experimentation).

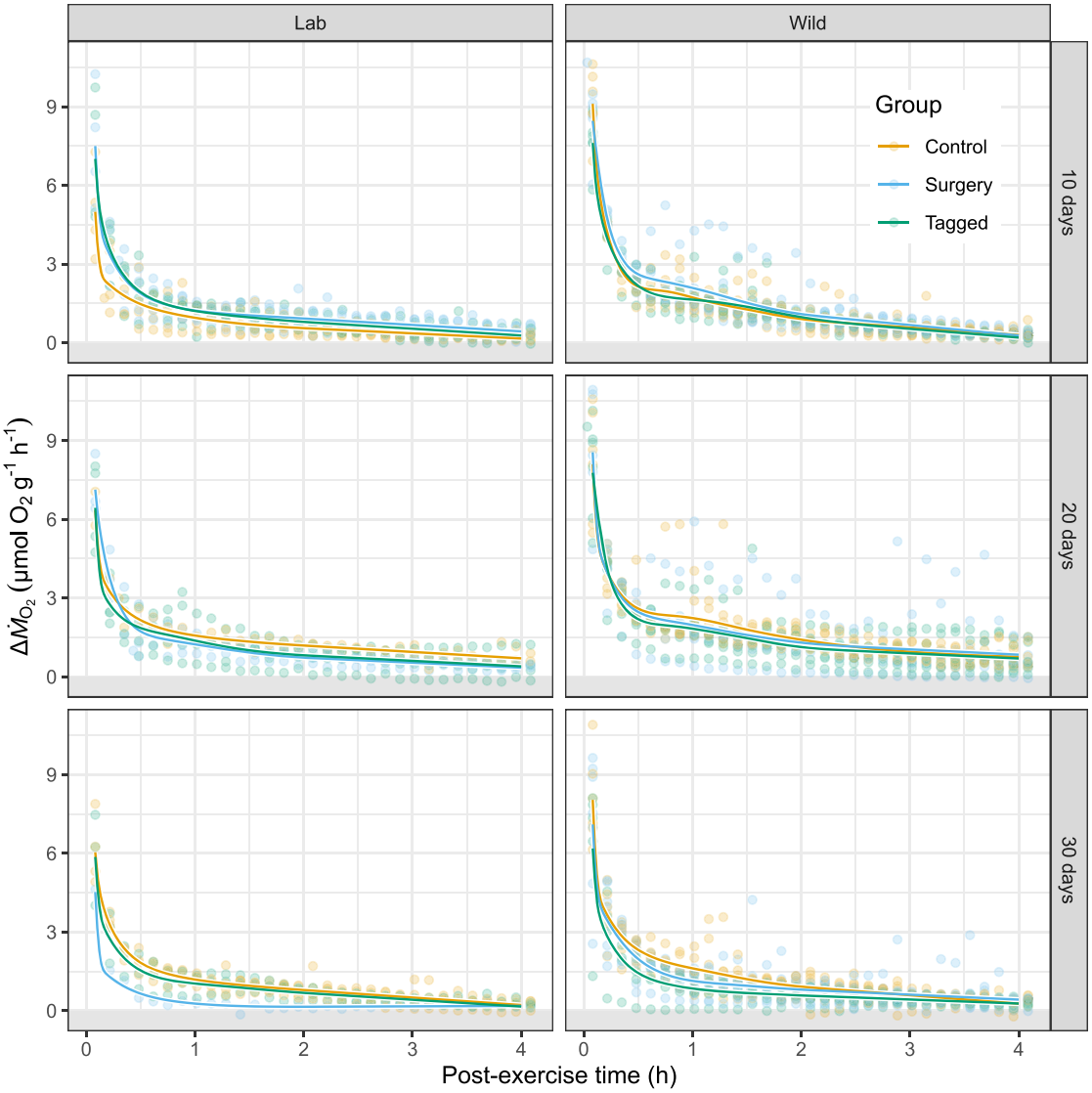
4. Discussion

Despite the widespread use of PIT, radio, and acoustic tags in telemetry studies, relatively few studies have addressed the effects of tag implantation on the physiological performance and growth of fishes (Brown et al. 2011; Cooke et al. 2011; Darcy et al. 2019). This is particularly true for fishes with elongated body forms, where commonly used thresholds (e.g., the 2% tag burden guideline) may fail to capture the true impact of the implanted tag. The present study revealed that implantation of eel/lamprey acoustic tags (ELAT; 12 mm length × 2 mm diameter, 80 mg in air, 42.3 mg in water) resulted in additional aerobic metabolic costs for wild juvenile sea lamprey compared to untagged (control) juveniles, as characterized by lower MMR, AAS, and FAS, even if the mass burden of the tag was only 1.63 ± 0.15% of the juvenile sea lampreys' body mass. However, no significant differences were observed between the EPOC of control and ELAT-implanted juvenile sea lamprey, suggesting that the tags had minimal impact on their capacity to recover from exhaustive exercise. These observations suggest that movement data obtained from migrating juvenile sea lamprey implanted with ELATs should be interpreted with caution to avoid accidentally misinforming future management and conservation efforts.

Lab-reared juvenile sea lamprey had lower aerobic performance than their wild counterparts

Lab-reared juvenile sea lamprey had a significantly lower standard metabolic rate (−8%), maximum metabolic rate (−21%), absolute aerobic scope (−22%), and factorial aerobic scope (−18%) than their wild counterparts. Interestingly, this generally lower aerobic capacity is in line with the 29% lower daily mass loss revealed for lab-reared juveniles (i.e., lab-reared juveniles had lower energy demands). The transition from wild conditions to laboratory conditions could have affected the feeding behaviour and physiology of the sea lamprey larvae that later metamorphosed into lab-reared

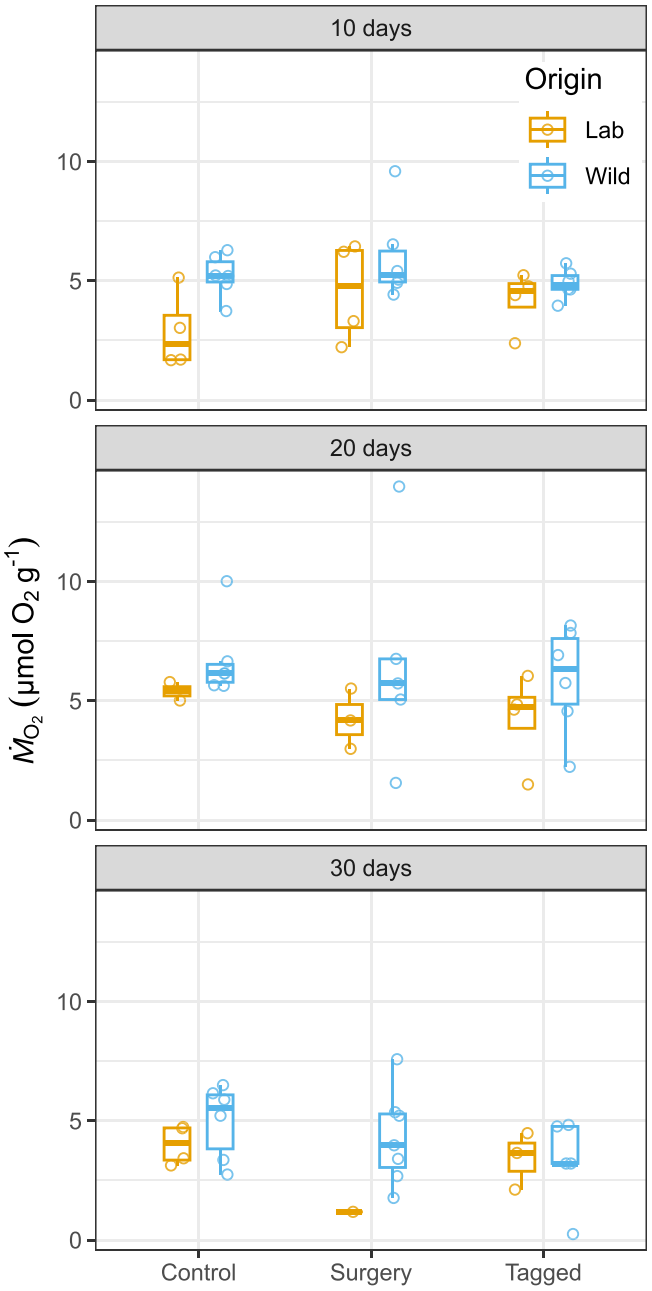
Fig. 4. Effects of ELAT implantation on post-exercise $\Delta\dot{M}_{O_2}$ recovery trajectory of juvenile sea lamprey. Animals were subjected to no treatment (controls; orange), incision but no ELAT implantation (sham surgery; blue) or implanted with an ELAT (tagged; green) and followed for 30 days. The recovery traces are displayed as GAM-modelled fitted curves overlaid on the cloud of recorded $\Delta\dot{M}_{O_2}$ values (31 data points per juvenile). See Table 1 for details on the number of animals per group and sampling period. ELAT, eel and lamprey acoustic tag.



juveniles, resulting in less energy allocation towards growth than in the wild. This interpretation is supported by Holmes et al. (1994), who reported that sea lamprey that underwent metamorphosis in the laboratory were smaller and had lower condition factor than individuals that metamorphosed in the field and were held under laboratory conditions for less time. These early energy limitations would impact the energy reserves of the lab-reared juveniles compared to the wild juveniles in the present study, as there is no further nutrient intake until parasitism begins (Evans et al. 2021). The smaller size (35% lower weight; 9% smaller length) and respective lower condition factor (8% lower; Table 1) of lab-reared juvenile sea lamprey could explain their lower SMR, MMR, and aerobic scope when compared to the wild animals (Fu et al. 2009; Luo et al. 2013).

Ultimately, physiological differences between lab-reared and wild juvenile sea lamprey could translate into diverging behavioural patterns. For example, differences in environmental conditions during rearing are known to affect the migration patterns of hatchery-raised and wild Atlantic salmon (*Salmo salar*; Jonsson et al. 1991). The differences we found between juvenile sea lamprey with two distinct prior histories (lab-reared vs. wild-caught) highlight the importance of animal origin in experimental design and the need for caution when interpreting data originating from nonwild individuals. Future studies need careful consideration when us-

Fig. 5. Effects of ELAT implantation on excess post-exercise oxygen consumption (EPOC) of lab-reared (orange box) or wild (blue box) juvenile sea lamprey. Animals were subjected to no treatment (controls), incision but no ELAT implantation (sham surgery) or implanted with an ELAT (tagged) and followed for 30 days. EPOC values are displayed as boxplots (median, 1st and 3rd quartiles, with whiskers expanding to 1.5 times the inter-quartile range) with the respective individual points overlaid. See Table 1 for details on the number of animals per group and sampling period. ELAT, eel and lamprey acoustic tag.



ing captive-reared individuals as proxies for wild juveniles to ensure that their conclusions are applicable to the conservation and management of wild populations.

ELAT implantation decreased the MMR and aerobic scope of wild juvenile sea lamprey

Carrying an ELAT significantly reduced the MMR and AAS of wild juvenile sea lamprey compared to wild controls. These findings highlight a decreased ability for tagged juvenile sea lamprey to elevate their aerobic metabolism beyond basic needs. Hanson and Barron (2017) noted increased mortality and growth suppression for fed larval Pacific lamprey (>83 mm) tagged with 8 mm × 1 mm PIT tags, suggesting the tag impaired food uptake, nutrient allocations to growth, and thus overall individual environmental fitness. Although suspension (filter) feeding by larval lampreys is very different from the mode of feeding in parasitic juvenile lampreys, their similar internal body plan suggests ELAT tags could potentially impair feeding in juvenile lampreys. It would therefore be very informative to explore how the implantation of ELATs, or other tag configurations, influences feeding behaviour, growth, and other sub-lethal physiological markers of naturally feeding juvenile lampreys. This would also indicate if prolonged starvation is a confounding factor that should be considered in future studies similar to this one.

Further evidence that body shape could be an important consideration when pondering tag burden limits was recently published by Notman-Grobler et al. (2025), who reported no significant effects on aerobic performance of juvenile brook trout (*Salvelinus fontinalis*) tagged with LOTEK JSATS PinTags that imposed similar tag weight burdens as in this study. The lack of impacts observed in juvenile brook trout compared to juvenile sea lamprey highlight the importance of testing tag effects on different species, particularly those with unconventional body shapes (subcarangiform vs. anguilliform; Lindsey 1978). Ultimately, the physiological effects noted here could translate to changes in behaviour after release into the wild, which could bias management decisions if uncounted for. Future studies addressing other sub-lethal impacts such as changes in growth, movement patterns, and behaviour of tagged juvenile sea lamprey would be highly informative.

The SMR of the wild juveniles was consistent with earlier reported SMR values for larval sea lamprey (ranging from 0.94 to 1.84 μmol $O_2 \cdot g^{-1} \cdot h^{-1}$; Wilkie et al. 2001; D'Souza et al. 2025), suggesting some continuity in resting metabolic demands from larval phase to parasitic juvenile phase. However, carrying the ELAT presented no effect on the SMR of wild juvenile sea lamprey. The lack of tag-induced effects on SMR is surprising given that both sham surgery and tagged wild juveniles displayed higher rates of mass loss than control wild juveniles. It was expected that the increased loss of mass would be accompanied by an increased SMR due to elevated energy expenditure. The presence of stressors such as xenobiotics, crowding, or social stress usually results in the mobilization of cortisol, which can lead to increased metabolic rate by promoting the catabolism of carbohydrates, proteins, and lipids, leading to increased $\dot{M}_{O_2}$ in many fish species (Mommsen et al. 1999; Morgan and Iwama 1996; Pfalzgraff et al. 2022). The primary stress hormone in lampreys is 11-deoxycortisol (Close et al. 2010; Shaughnessy et al. 2020; Shaughnessy and McCormick 2021), but its ef-

fects on $\dot{M}_{O_2}$ are not yet known. Shaughnessy and McCormick (2021) noted a 6-fold increase in 11-deoxycortisol within 6 h of an acute stress exposure, but information regarding 11-deoxycortisol during chronic stress, lasting days or weeks, is still lacking in lampreys (Shaugnessy et al. 2020). Information on the effects that prolonged 11-deoxycortisol elevation have on physiological process in sea lamprey and other lampreys could be very informative.

It is possible that the tag only causes distress while the animal is moving. This would likely impact MMR but not SMR, as observed. The mass burden of the tag in our study was 1.63 ± 0.15% of the juvenile sea lampreys' body mass. However, the length burden of these tags was 7.45 ± 0.15%, raising the possibility that the length of the ELAT may have hindered movement. Sea lamprey are anguilliform swimmers and, as such, they have long body oscillations that may be disrupted by long tags (Du Clos et al. 2019). The tag may cause discomfort during oscillations and/or hinder kinematics, leading to a loss of efficiency and thrust generation. With the loss of overall exercise efficiency and intensity, we expected to see a decrease in the amount of fuels used, corresponding to lower disturbances in acid-base and ion balance. The decreased efficiency and added discomfort, coupled with the lower physiological disturbances, may explain the lower MMR and aerobic scope observed for the wild tagged juvenile sea lamprey in this study. This raises interesting questions regarding potential effects of the tag burden while the sea lamprey is attached to a host, where the host's movement could then become a source of discomfort. The discomfort due to the tag presence could also make it more difficult for the sea lamprey to remain attached leading to decreased feeding time and growth rate. Additionally, this could also prevent the tagged juvenile from successfully attaching to highly mobile hosts/species and eventually attach to less mobile hosts/species. This could introduce a new layer of bias to tracking data collected in the field. Future investigation of host-parasite interactions with tagged sea lamprey would assist in elucidating if carrying an ELAT presents novel burdens for juvenile sea lamprey following successful attachment to a host.

SMR, MMR, and aerobic scope decrease with time in fasted juvenile sea lamprey

Wild juvenile sea lamprey of all treatment groups demonstrated a significant decrease in aerobic performance (SMR, MMR, AAS, and FAS) over the course of the experiments (30 days). This was likely attributable to a general decline in condition factor during the experimental period, as shown by the daily mass loss. Several studies have shown that SMR, MMR, and aerobic scope decrease with prolonged fasting in fishes (Fu et al. 2009; Luo et al. 2013; Fu et al. 2022). The total period of fasting experienced by the sea lamprey juveniles in this study, going back to the cessation of feeding following the initiation of metamorphosis (Beamish and Potter 1975; Youson and Potter 1979), would not be unusual in nature, during which sea lamprey often overwinter before beginning their downstream migration in the later winter or early spring (Beamish and Potter 1975; Swink and Johnson 2014). Conducting the experiments at 10 °C, rather than at much cooler temperatures that would be consistent with overwintering (i.e., just above zero), could have exacerbated the effects of starvation by increasing the metabolic demands of the sea lamprey, resulting in a negative energy balance and loss of body mass over the course of the study.

The present findings indicate that a lack of adequate food sources coupled with exposure to increased temperatures may negatively affect juvenile sea lamprey in the lab. Future studies involving prolonged fasting or restricted feeding should carefully consider lowering both holding and experimental temperatures, thus helping preserve energetic reserves and maintain physiological integrity over extended durations. Further, this problem translates into wild populations, because unlike anadromous populations of sea lamprey that have been observed to feed on riverine fishes during their out-migration, juvenile sea lamprey in the Great Lakes have not been reported to feed while migrating (Beamish and Potter 1975; Evans et al. 2021). Nonfeeding migratory juvenile sea lamprey could display altered behaviour and migration patterns under projected warmer conditions, which would be highly relevant for management, regardless of tag implantation.

ELAT implantation did not affect excess post-exercise oxygen consumption

The EPOC of wild juvenile sea lamprey during the first 4 h of recovery from exhaustive exercise was not significantly affected by ELAT implantation. Interestingly, the EPOC measured here for wild juvenile sea lamprey ($\bar{x}$ = 5.3 μmol $O_2 \cdot g^{-1}$) is 36% lower than that reported for larval sea lamprey ($\bar{x}$ = 8.3 μmol $O_2 \cdot g^{-1}$; Wilkie et al. 2001). This difference appears surprising, as larvae are burrow-dwelling animals and juvenile sea lamprey are free-swimming. However, this discrepancy in EPOC between life-stages could be explained by a difference in energetic condition. The magnitude of EPOC reflects the burning of anaerobic fuels to (1) rapidly generate ATP, (2) power metabolic enzymes, (3) eliminate metabolites, and (4) correct ion and acid-base balance (Luo et al. 2013; Wood 1991; Zhang et al. 2018). As sea lamprey stop feeding during metamorphosis and will not resume feeding until the onset of parasitism, the juvenile sea lamprey naturally undergo prolonged fasting. Following such a prolonged fasting period, juveniles tend to have lower lipid and protein content than larvae (Lowe et al. 1973; O'Boyle and Beamish 1977), which could have lowered the intensity of exercise in the juvenile compared to the larval sea lamprey in the two studies. This is in line with the findings of Luo et al. (2013), who observed a pronounced decrease in EPOC for starved Nile tilapia (*Oreochromis niloticus*) and suggested that prolonged starvation diminishes anaerobic capacity.

5. Conclusion

This study provides insight into the sub-lethal physiological effects of surgery and micro-acoustic tag implantation in juvenile sea lamprey by measuring aerobic performance at different time points post-tagging. We found that ELAT-

implanted, wild-caught juvenile sea lamprey experienced significant decreases in maximum metabolic rate and aerobic scope when compared to wild-caught controls. However, there was no evidence of a tag effect on their post-exercise oxygen consumption, suggesting that the tag does not impair their ability to recover from physiological disturbances such as exhaustive exercise. In addition, we found that lab-reared juveniles underperformed their wild-caught counterparts, showing lower maximum metabolic rates, aerobic scope, and EPOC across treatment groups and time. The sub-lethal effects revealed here could have consequences for the behaviour of these animals in the wild, which in turn could hinder the interpretation of data collected in the field. Ultimately, this would bias management decisions if unaccounted for, hindering conservation efforts. Future studies should focus on exploring behavioural changes imposed by ELAT implantation on wild-caught juvenile sea lamprey to ensure that data collected in the field is correctly interpreted and contributes towards informed management decisions.

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Copyright

Data availability

The respirometry data collected for this study and the respective R analysis scripts are available as a Zenodo repository: https://doi.org/10.5281/zenodo.17171546.

Author information

Author ORCIDs

Evan P. Bellhouse https://orcid.org/0009-0007-4136-9655
Julia Xeni https://orcid.org/0009-0007-2968-5671
Zhiqun Daniel Deng https://orcid.org/0000-0002-8300-8766
Michael P. Wilkie https://orcid.org/0000-0002-3844-8033
Hugo Flávio https://orcid.org/0000-0002-5174-1197

Author contributions

Conceptualization: ZDD, MPW, HF
Data curation: EPB, HF
Formal analysis: EPB, HF
Funding acquisition: ZDD, MPW, HF
Investigation: EPB, JX, HF
Methodology: EPB, JX, HF
Project administration: MPW, HF
Software: HF
Supervision: MPW, HF
Validation: MPW, HF
Visualization: EPB, HF
Writing – original draft: EPB
Writing – review & editing: EPB, JX, ZDD, MPW, HF

Competing interests

The authors declare there are no competing interests.

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2025-0333.

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