MANUSCRIPT - cjfas-2025-0333

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

Evan P. Bellhouse[1†], Julia Xeni[1], Zhiqun Daniel Deng[2,3], Michael P. Wilkie[1], Hugo Flávio[1,4†]

[1] Department of Biology and Laurier Institute for Water Science, Wilfrid Laurier University, Waterloo, Ontario, N2l 3C5, Canada

[2] Energy and Environment Directorate, Pacific Northwest National Laboratory, Richland, Washington, 99354, USA

[3] Department of Naval Architecture and Marine Engineering, University of Michigan, Ann Arbor, MI 48109, USA

[4] Department of Biology, Dalhousie University, Halifax, Nova Scotia, B3H 4R2, Canada

[†] Corresponding authors: bell8980@mylaurier.ca, hflavio@dal.ca

ORCID:

Evan P Bellhouse: 0009-0007-4136-9655

Julia Xeni: 0009-0007-2968-5671

Zhiqun Daniel Deng: 0000-0002-8300-8766

Michael P Wilkie: 0000-0002-3844-8033

Hugo Flávio: 0000-0002-5174-1197

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; 12mm × 2mm, 0.08g in air; akin to a 12mm 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 migrating juvenile sea lamprey (4.95±0.41g) 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 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.

Keywords: 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 (Hume et al., 2021; Renaud, 2011). Sea lamprey are generalist feeders and ingest blood by parasitizing a large variety of marine fishes (Quintella et al., 2021; Renaud and Cochran, 2019). 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; Gaden et al., 2021a; Siefkes, 2017; Smith & Tibbles, 1980). 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., 2021b). 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 & 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 (Farmer, 1980; Beamish & Potter, 1975), 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 & 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 unsuitable (Applegate & 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 (Hansen et al., 2016; Maitland, 1980; Mateus et al., 2013).

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, 30-60d 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 >130mm 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 from 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 (Rosewarne et al., 2016; Schulte, 2015; Sloman et al., 2000; 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., 2016a).

Limitations in O_2 delivery and use could impair aerobic swimming performance, as has been show in numerous studies, thereby limiting predator evasion or foraging effectiveness (Bailey et al., 2022; Killen et al., 2016; Metcalfe et al., 2016b). Relationships have also been found between standard metabolic rate (SMR) and aggression within fish dominance hierarchies, and reproductive success across a range of fish species (Metcalfe et al., 2016a; Sloman et al. 2002). 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, non-breeding, 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; Clark 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 (Kieffer, 2000; Wood, 1991). Because the magnitude of EPOC reflects the restoration of homoeostasis following anaerobic exercise (McDonald et al., 1998; Wood, 1991; 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 in the fall of 2022 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 undergo 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 µl 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 minutes (± 33s 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 (7^{th} from front), slightly to the side of the mid-ventral line (schematic provided in Figure 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 13mm 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 3m24s (± 10s), during which the gills of the animal were kept wet by regularly spraying a 40 µl 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 each experiment. 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-0510A, 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 five minutes of O_2 measurement followed by three minutes of flush. The first 20 seconds 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 hours) for the determination of SMR. The following morning, one by one, the animals were removed from the chambers and exercised for five minutes 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 four hours, 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 μmol O_2 L^{-1} 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 $\dot{M}_{O_2}$ (μmol O_2 g^{-1} 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 (μmol O_2 L^{-1} 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-second calculations of $\dot{M}_{O_2}$ progression. MMR was then determined as the highest 30-second $\dot{M}_{O_2}$ calculated in the previous step (96% of the resulting 30-second 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, 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 & 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 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 minutes 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 four hours had passed. A four-hour 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 (Boutelier 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; Figure 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 g^{-1} h^{-1} for all sample periods combined (10 h, 20 h, 30 h; Table 2; Figure 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).

The MMR of all lab-reared juveniles combined was 21% lower than that of wild juveniles (Table 2; Figure 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 g^{-1} h^{-1}, which was 14% lower than that measured in the control animals which averaged 14.0 ± 0.8 μmol O_2 g^{-1} h^{-1} throughout the entire experiment (Table 2). As for SMR, an effect of time on the MMR of all the of 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; Figure 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 to 10.6 ± 0.8 μmol O_2 g^{-1} h^{-1} from 12.4 ± 0.7 μmol O_2 g^{-1} h^{-1} in the controls (Table 2; Figure 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; Figure 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 g^{-1} 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 (Figure 3). The overall loss rate was 29% lower for the lab-reared juveniles than for the wild juveniles (Table 2; Figure 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, χ^2 = 4.45, p-value = 0.035), and 28 % lower than tagged juveniles (Table 2; Figure 3).

3.3 | Excess post-exercise oxygen consumption

Post-exercise $\dot{M}_{O_2}$ declined sharply in the initial 30-minute 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 (Figure 4). These patterns in recovery trajectory translated into differences in EPOC, with lab-reared juveniles having 26% lower EPOC than wild juveniles (Table 2; Figure 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; Figure 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 unelongated 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 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 (Luo et al., 2013; Fu et al., 2009).

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 non-wild individuals. Future studies need careful consideration when using 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 & Barron (2017) noted increased mortality and growth suppression for fed larval Pacific lamprey (>83 mm) tagged with 8mm × 1mm 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 the other sub-lethal physiological markers, in addition to those explored in the present study to naturally feeding juvenile lampreys. This would also indicate if prolonged starvation is a confounding factor that should be considered in future similar studies 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 g^{-1} h^{-1}; D'Souza et al., 2025; Wilkie et al., 2001), 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 & Iwama, 1996; Pfalzgraff et al., 2022). The primary stress hormone in lampreys is 11-deoxycortisol (Close et al., 2010; Shaughnessy et al., 2020; Shaughnessy & McCormick, 2021), but its effects on $\dot{M}_{O_2}$ are not yet known. Shaughnessy & McCormick (2021) noted a 6-fold increase in 11-deoxycortisol within six hours 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; Fu et al., 2022; Luo et al., 2013). 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 (Youson and Potter 1979; Beamish and Potter 1975), 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). By 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). Non-feeding 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 four hours 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 g^{-1}) is 36% lower than that reported for larval sea lamprey ($\bar{x}$ = 8.3 μmol O_2 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 and Beamish 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.

Acknowledgements

Funding for this project was provided by the Great Lakes Fishery Commission (Grant 2023_FLA_541019). We thank the U.S. Geological Survey and the Hammond Bay Biological Station for supplying the juvenile sea lamprey used in this study, and M. Trzcinski and D. Mitrovic for help handling and tagging animals. The ELAT was developed by Pacific Northwest National Laboratory with funding from the U.S. Department of Energy Water Power Technologies Office and the U.S. Army Corps of Engineers. Finally, we would like to thank the reviewers for their constructive feedback and helpful suggestions.

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

Competing interests

The authors declare there are no competing interests.

References

Applegate, V. C. (1951). The Sea Lamprey in the Great Lakes. *The Scientific Monthly*, *72*(5), 275–281.

Applegate, V. C., & Moffett, J. W. (1955). The Sea Lamprey. *Scientific American*, *192*(4), 36–41. http://www.jstor.org/stable/24944609

Bailey, L. A., Childs, A. R., James, N. C., Winkler, A., & Potts, W. M. (2022). Links between behaviour and metabolic physiology in fishes in the Anthropocene [Review]. *Reviews in Fish Biology and Fisheries*, *32*(2), 555-579. https://doi.org/10.1007/s11160-022-09701-2

Beamish, F. W. H. (1980). Biology of the North American Anadromous Sea Lamprey,

Petromyzon marinus. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(11), 1924–1943. https://doi.org/10.1139/f80-233

Beamish, F. W. H., & Potter, I. C. (1975). The biology of the anadromous Sea lamprey (*Petromyzon marinus*) in New Brunswick. Journal of Zoology, 177(1), 57–72. https://doi.org/10.1111/j.1469-7998.1975.tb05970.x

Bergstedt, R. A., & Swink, W. D. (1995). Seasonal growth and duration of the parasitic life stage of the landlocked sea lamprey (*Petromyzon marinus*). *Canadian Journal of Fisheries and Aquatic Sciences*, *52*(6), 1257–1264. https://doi.org/10.1139/f95-122

Birk, M. A. (2024). respirometry: Tools for conducting and analyzing respirometry experiments [Manual]. https://CRAN.R-project.org/package=respirometry

Boutilier, R. G., Ferguson, R. A., Henry, R. P., & Tufts, B. L. (1993). Exhaustive Exercise in the Sea Lamprey (Petromyzon Marinus): Relationship Between Anaerobic Metabolism and Intracellular Acid–Base Balance. Journal of Experimental Biology, 178(1), 71–88. https://doi.org/10.1242/jeb.178.1.71

Brown, R. S., Eppard, M. B., Murchie, K. J., Nielsen, J. L., & Cooke, S. J. (2011). An introduction to the practical and ethical perspectives on the need to advance and standardize the intracoelomic surgical implantation of electronic tags in fish. *Reviews in Fish Biology and Fisheries*, 21(1), 1–9. https://doi.org/10.1007/s11160-010-9183-5

Cech, J. J., Jr. (1990). Respirometry. In C. B. Schreck & P. B. Moyle (Eds.), Methods for Fish Biology (pp. 335–362). Bethesda, MD: American Fisheries Society. ISBN: 0-913235-58-X.

Chabot, D., Steffensen, J. F., & Farrell, A. P. (2016). The determination of standard metabolic rate in fishes. *Journal of Fish Biology*, *88*(1), 81–121. https://doi.org/10.1111/jfb.12845

Claireaux, G., & Lefrançois, C. (2007). Linking environmental variability and fish performance:: integration through the concept of scope for activity. Philosophical Transactions of the Royal Society B-Biological Sciences, 362(1487), 2031-2041. https://doi.org/10.1098/rstb.2007.2099

Close, D. A., Yun, S.-S., McCormick, S. D., Wildbill, A. J., & Li, W. (2010). 11-Deoxycortisol is a corticosteroid hormone in the lamprey. *Proceedings of the National Academy of Sciences*, *107*(31), 13942–13947. https://doi.org/10.1073/pnas.0914026107

606 Cooke, S. J., Hinch, S. G., Lucas, M. C., & Lutcavage, M. (2012). *Biotelemetry and*
607 *biologging.* https://durham-repository.worktribe.com/output/1682787
608 Cooke, S. J., Woodley, C. M., Brad Eppard, M., Brown, R. S., & Nielsen, J. L. (2011).
609 Advancing the surgical implantation of electronic tags in fish: A gap analysis and
610 research agenda based on a review of trends in intracoelomic tagging effects studies.
611 *Reviews in Fish Biology and Fisheries*, *21*(1), 127–151.
612 https://doi.org/10.1007/s11160-010-9193-3
613 Crossin, G. T., Heupel, M. R., Holbrook, C. M., Hussey, N. E., Lowerre-Barbieri, S. K.,
614 Nguyen, V. M., Raby, G. D., & Cooke, S. J. (2017). Acoustic telemetry and fisheries
615 management. *Ecological Applications*, *27*(4), 1031–1049.
616 https://doi.org/10.1002/eap.1533
617 Darcy, A. P., Raby, G. D., Johnson, T. B., Pitcher, T. E., & Fisk, A. T. (2019). Effects of
618 intracoelomic transmitter implantation on metabolic rate, swimming performance,
619 growth and survival in juveniles of two salmonids. Journal of Fish Biology, 95(4),
620 1094–1106. https://doi.org/10.1111/jfb.14102
621 D'Souza, L., Flávio, H., & Wilkie, M. P. (2025). The lampricide 3-trifluoromethyl-4-nitrophenol
622 (TFM) stimulates oxygen consumption by larval sea lamprey in a dose-dependent
623 manner. *Journal of Great Lakes Research*, *51*(2), 102536.
624 https://doi.org/10.1016/j.jglr.2025.102536
625 Du Clos, K. T., Dabiri, J. O., Costello, J. H., Colin, S. P., Morgan, J. R., Fogerson, S. M., &
626 Gemmell, B. J. (2019). Thrust generation during steady swimming and acceleration
627 from rest in anguilliform swimmers. *Journal of Experimental Biology*, 222(22),
628 jeb212464. https://doi.org/10.1242/jeb.212464
629 Evans, T. M., Wagner, C. M., Miehls, S. M., Johnson, N. S., Haas, T. F., Dunlop, E., &
630 Manzon, R. G. (2021). Before the first meal: The elusive pre-feeding juvenile stage of
631 the sea lamprey. *Journal of Great Lakes Research*, *47*, S580–S589.
632 https://doi.org/10.1016/j.jglr.2021.02.005
633 Farmer, G. J. (1980). Biology and Physiology of Feeding in Adult Lampreys. *Canadian*
634 *Journal of Fisheries and Aquatic Sciences*, *37*(11), 1751–1761.

https://doi.org/10.1139/f80-220

Fox, J., & Weisberg, S. (2019). An R Companion to Applied Regression (Third). Sage. https://www.john-fox.ca/Companion/

Fry, F. E. J. (1947). Effects of the environment on animal activity. *Publications of the Ontario Fisheries Research Laboratory* **68,** 1–62.

Fu, S.-J., Dong, Y.-W., & Killen, S. S. (2022). Aerobic scope in fishes with different lifestyles and across habitats: Trade-offs among hypoxia tolerance, swimming performance and digestion. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *272*, 111277. https://doi.org/10.1016/j.cbpa.2022.111277

Fu, S.-J., Zeng, L.-Q., Li, X.-M., Pang, X., Cao, Z.-D., Peng, J.-L., & Wang, Y.-X. (2009). Effect of meal size on excess post-exercise oxygen consumption in fishes with different locomotive and digestive performance. *Journal of Comparative Physiology B*, *179*(4), 509–517. https://doi.org/10.1007/s00360-008-0337-x

Gaden, M., Brant, C., Stedman, R. C., Cooke, S. J., Young, N., Lauber, T. B., Nguyen, V. M., Connelly, N. A., & Knuth, B. (2021a). Shifting baselines and social license to operate: Challenges in communicating sea lamprey control. *Journal of Great Lakes Research*, *47*, S800–S808. https://doi.org/10.1016/j.jglr.2021.01.016

Gaden, M., O. Brant, C., & Lambe, R. (2021b). Why a Great Lakes Fishery Commission? The seven-decade pursuit of a Canada-U.S. fishery treaty. *Journal of Great Lakes Research*, *47*, S11–S23. https://doi.org/10.1016/j.jglr.2021.01.003

Haas, T. F., Castro-Santos, T., Miehls, S. M., Deng, Z. D., Bruning, T. M., & Wagner, C. M. (2023). Survival, healing, and swim performance of juvenile migratory sea lamprey (*Petromyzon marinus*) implanted with a new acoustic microtransmitter designed for small eel-like fishes. *Animal Biotelemetry*, *11*(1), 9. https://doi.org/10.1186/s40317-023-00318-1

Hansen, M. J., Madenjian, C. P., Slade, J. W., Steeves, T. B., Almeida, P. R., & Quintella, B. R. (2016). Population ecology of the sea lamprey (*Petromyzon marinus*) as an invasive species in the Laurentian Great Lakes and an imperiled species in Europe.

Reviews in Fish Biology and Fisheries, *26*(3), 509–535. https://doi.org/10.1007/s11160-016-9440-3

Hanson, K. C., & Barron, J. M. (2017). Evaluation of the Effects of Marking Pacific Lamprey Ammocoetes with Visual Implant Elastomer, Coded Wire Tags, and Passive Integrated Transponders. *Transactions of the American Fisheries Society*, *146*(4), 626–633. https://doi.org/10.1080/00028487.2017.1290681

Hartig, F. (2016). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models (0.4.7). https://doi.org/10.32614/CRAN.package.DHARMa

Holmes, J. A., Beamish, F. W. H., Seelye, J. G., Sower, S. A., & Youson, J. H. (1994). Long-term Influence of Water Temperature, Photoperiod, and Food Deprivation on Metamorphosis of Sea Lamprey, *Petromyzon marinus*. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*(9), 2045–2051. https://doi.org/10.1139/f94-207

Hume, J. B., Almeida, P. R., Buckley, C. M., Criger, L. A., Madenjian, C. P., Robinson, K. F., Wang, C. J., & Muir, A. M. (2021). Managing native and non-native sea lamprey (*Petromyzon marinus*) through anthropogenic change: A prospective assessment of key threats and uncertainties. *Journal of Great Lakes Research*, *47*, S704–S722. https://doi.org/10.1016/j.jglr.2020.08.015

Johnson, N. S., Miehls, S. M., Haro, A. J., & Wagner, C. M. (2019). Push and pull of downstream moving juvenile sea lamprey (*Petromyzon marinus*) exposed to chemosensory and light cues. *Conservation Physiology*, *7*(1), coz080. https://doi.org/10.1093/conphys/coz080

Jonsson, B., Jonsson, N., & Hansen, L. P. (1991). Differences in life history and migratory behaviour between wild and hatchery-reared Atlantic salmon in nature. *Aquaculture*, *98*(1–3), 69–78. https://doi.org/10.1016/0044-8486(91)90372-e

Kieffer, J. D. (2000). Limits to exhaustive exercise in fish. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *126*(2), 161–179. https://doi.org/10.1016/S1095-6433(00)00202-6

Killen, S. S., Glazier, D. S., Rezende, E. L., Clark, T. D., Atkinson, D., Willener, A. S. T., & Halsey, L. G. (2016). Ecological Influences and Morphological Correlates of Resting and Maximal Metabolic Rates across Teleost Fish Species [Article]. *American Naturalist*, *187*(5), 592-

606. https://doi.org/10.1086/685893

Killen, S. S., Marras, S., Metcalfe, N. B., McKenzie, D. J., & Domenici, P. (2013). Environmental stressors alter relationships between physiology and behaviour [Article]. Trends in Ecology & Evolution, 28(11), 651-658. https://doi.org/10.1016/j.tree.2013.05.005

Lenth R (2025). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.10.7. https://CRAN.R-project.org/package=emmeans

Lennox, R. J., Mastrodimitropoulos, P. M. B., Flávio, H., Cyr, K., Deng, Z. D., Cooke, S. J., & Piczak, M. L. (2025). How small can they go? Microelectronic tags for movement ecology of small aquatic organisms. *Fisheries*, *50*(5), 209–218. https://doi.org/10.1093/fshmag/vuaf002

Li, D., Du, Z., Wang, Q., Wang, J., & Du, L. (2024). Recent advances in acoustic technology for aquaculture: A review. *Reviews in Aquaculture*, *16*(1), 357–381. https://doi.org/10.1111/raq.12842

Lindsey, C. C. (1978). Form, Function, and Locomotory Habits in Fish. In W. S. Hoar & D. J. Randall (Eds.), *Fish Physiology* (Vol. 7, pp. 1–100). Academic Press. https://doi.org/10.1016/S1546-5098(08)60163-6

Liss, S. A., Brown, R. S., Deters, K. A., Walker, R. W., Deng, Z. D., Eppard, M. B., Townsend, R. L., & Seaburg, A. G. (2016). Mortality, Transmitter Retention, Growth, and Wound Healing in Juvenile Salmon Injected with Micro Acoustic Transmitters. *Transactions of the American Fisheries Society*, *145*(5), 1047–1058. https://doi.org/10.1080/00028487.2016.1176955

Lowe, D. R., Beamish, F. W. H., & Potter, I. C. (1973). Changes in the proximate body composition of the landlocked sea lamprey *Petromyzon marinus* (L.) during larval life and metamorphosis. *Journal of Fish Biology*, 5(6), 673–682. https://doi.org/10.1111/j.1095-8649.1973.tb04503.x

Luo, Y., Wang, W., Zhang, Y., Huang, Q., & Lim, D. (2013). Effects of starvation on the excess post-exercise oxygen consumption of juvenile Nile tilapia (*Oreochromis niloticus*). *Marine and Freshwater Behaviour and Physiology*, *45*(5), 333–342.

https://doi.org/10.1080/10236244.2012.750059

Maitland, P. S. (1980). Review of the Ecology of Lampreys in Northern Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(11), 1944–1952. https://doi.org/10.1139/f80-234

Masuda, R. (2011). Fish Locomotion: An Eco-Ethological Perspective - Edited by P. Domenici and B. G. Kapoor. *Journal of Fish Biology*, *79*(3), 819–820. https://doi.org/10.1111/j.1095-8649.2011.03077.x

Mateus, C. S., Alves, M. J., Quintella, B. R., & Almeida, P. R. (2013). Three new cryptic species of the lamprey genus Lampetra Bonnaterre, 1788 (Petromyzontiformes Petromyzontidae) from the Iberian Peninsula. *Contributions to Zoology*, *82*(1).

Matley, J. K., Klinard, N. V., Barbosa Martins, A. P., Aarestrup, K., Aspillaga, E., Cooke, S. J., Cowley, P. D., Heupel, M. R., Lowe, C. G., Lowerre-Barbieri, S. K., Mitamura, H., Moore, J.-S., Simpfendorfer, C. A., Stokesbury, M. J. W., Taylor, M. D., Thorstad, E. B., Vandergoot, C. S., & Fisk, A. T. (2022). Global trends in aquatic animal tracking with acoustic telemetry. *Trends in Ecology & Evolution*, *37*(1), 79–94. https://doi.org/10.1016/j.tree.2021.09.001

McDonald, D. G., Milligan, C. L., McFarlane, W. J., Croke, S., Currie, S., Hooke, B., Angus, R. B., Tufts, B. L., & Davidson, K. (1998). Condition and performance of juvenile Atlantic salmon (*Salmo salar*): Effects of rearing practices on hatchery fish and comparison with wild fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 55(5), 1208–1219. https://doi.org/10.1139/f98-003

Metcalfe, N. B., Van Leeuwen, T. E., & Killen, S. S. (2016). Does individual variation in metabolic phenotype predict fish behaviour and performance? *Journal of Fish Biology*, *88*(1), 298-321. https://doi.org/10.1111/jfb.12699

Metcalfe, J. D., Wright, S., Tudorache, C., & Wilson, R. P. (2016). Recent advances in telemetry for estimating the energy metabolism of wild fishes. *Journal of Fish Biology*, *88*(1), 284-297. https://doi.org/10.1111/jfb.12804

Miehls, S., Dawson, H. A., Maguffee, A. C., Johnson, N. S., Jones, M. L., & Dobiesz, N. (2021). Where you trap matters: Implications for integrated sea lamprey

management. *Journal of Great Lakes Research*, *47*, S320–S327. https://doi.org/10.1016/j.jglr.2020.06.023

Mommsen, T. P., Vijayan, M. M., & Moon, T. W. (1999). Cortisol in teleosts: Dynamics, mechanisms of action, and metabolic regulation. *Reviews in Fish Biology and Fisheries*, *9*(3), 211–268. https://doi.org/10.1023/A:1008924418720

Morgan, J. D., & Iwama, G. K. (1996). Cortisol-induced changes in oxygen consumption and ionic regulation in coastal cutthroat trout (*Oncorhynchus clarki clarki*) parr. *Fish Physiology and Biochemistry*, *15*(5), 385–394. https://doi.org/10.1007/BF01875581

Mueller, R., Liss, S., & Deng, Z. D. (2019). Implantation of a New Micro Acoustic Tag in Juvenile Pacific Lamprey and American Eel. *Journal of Visualized Experiments*, *145*, e59274. https://doi.org/10.3791/59274

Notman-Grobler, O. D. P., Mastrodimitropoulos, P. M. B., Bevilacqua, A., Lennox, R. J., & Flávio, H. (2025). Assessing metabolic rate and post-tagging recovery in juvenile fish. *Journal of Fish Biology*, jfb.70208. https://doi.org/10.1111/jfb.70208

O'Boyle, R. N., & Beamish, F. W. H. (1977). Growth and intermediary metabolism of larval and metamorphosing stages of the landlocked sea lamprey, *Petromyzon marinus* L. Environmental Biology of Fishes, 2(2), 103–120. https://doi.org/10.1007/BF00005366

Pfalzgraff, T., Lund, I., & Skov, P. V. (2022). Prolonged cortisol elevation alters whole body and tissue metabolism in rainbow trout (*Oncorhynchus mykiss*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *263*, 111098. https://doi.org/10.1016/j.cbpa.2021.111098

Quintella, B. R., Clemens, B. J., Sutton, T. M., Lança, M. J., Madenjian, C. P., Happel, A., & Harvey, C. J. (2021). At-sea feeding ecology of parasitic lampreys. *Journal of Great Lakes Research*, *47*, S72–S89. https://doi.org/10.1016/j.jglr.2021.07.008

R Core Team. (2025). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. https://www.R-project.org/

Renaud, C. B., & Cochran, P. A. (2019). Post-metamorphic feeding in lampreys. In Lampreys: Biology, Conservation and Control: Volume 2 (pp. 247-285). Dordrecht: Springer Netherlands.

Renaud, C. B. (2011). Lampreys of the world. An annotated and illustrated catalogue of lamprey species known to date. FAO Species Catalogue for Fishery Purposes. No. 5. Rome, FAO. 2011. 109 pp.

Richards, J. G. (2009). Metabolic and moecular responses of fish to hypoxia. . In J. G. Richards, A. P. Farrell, & C. J. Brauner (Eds.), Chapter 10 - Hypoxia (Vol. 27, pp. 443-485). Elsevier Academic Press Inc. https://doi.org/10.1016/s1546-5098(08)00010-1

Rosewarne, P. J., Wilson, J. M., & Svendsen, J. C. (2016). Measuring maximum and standard metabolic rates using intermittent-flow respirometry: A student laboratory investigation of aerobic metabolic scope and environmental hypoxia in aquatic breathers. *Journal of Fish Biology*, *88*(1), 265–283. https://doi.org/10.1111/jfb.12795

Roussel, J.-M., Haro, A., & Cunjak, R. A. (2000). Field test of a new method for tracking small fishes in shallow rivers using passive integrated transponder (PIT) technology. *Canadian Journal of Fisheries and Aquatic Sciences*, *57*(7), 1326–1329. https://doi.org/10.1139/f00-110

Scarabello, M., Heigenhauser, G. J. F., & Wood, C. M. (1991). The oxygen debt hypothesis in juvenile rainbow trout after exhaustive exercise. *Respiration Physiology*, *84*(2), 245–259. https://doi.org/10.1016/0034-5687(91)90121-X

Schulte, P. M. (2015). The effects of temperature on aerobic metabolism: Towards a mechanistic understanding of the responses of ectotherms to a changing environment. *Journal of Experimental Biology*, *218*(12), 1856–1866. https://doi.org/10.1242/jeb.118851

Shaughnessy, C. A., Barany, A., & McCormick, S. D. (2020). 11-Deoxycortisol controls hydromineral balance in the most basal osmoregulating vertebrate, sea lamprey (*Petromyzon marinus*). *Scientific Reports*, *10*(1), 12148. https://doi.org/10.1038/s41598-020-69061-4

Shaughnessy, C. A., & McCormick, S. D. (2021). 11-Deoxycortisol is a stress responsive and gluconeogenic hormone in a jawless vertebrate, the sea lamprey (*Petromyzon marinus*). *Journal of Experimental Biology*, *224*(11), jeb241943. https://doi.org/10.1242/jeb.241943

Siefkes, M. J. (2017). Use of physiological knowledge to control the invasive sea lamprey (*Petromyzon marinus*) in the Laurentian Great Lakes. *Conservation Physiology*, *5*(1). https://doi.org/10.1093/conphys/cox031

Simpson G (2024). gratia: Graceful ggplot-Based Graphics and Other Functions for GAMs Fitted using mgcv. R package version 0.10.0. https://gavinsimpson.github.io/gratia

Sloman, K. A., & Armstrong, J. D. (2002). Physiological effects of dominance hierarchies: laboratory artefacts or natural phenomena? [Review]. *Journal of Fish Biology*, *61*(1), 1-23. https://doi.org/10.1006/jfbi.2002.2038

Sloman, K. A., Motherwell, G., O'Connor, K. I., & Taylor, A. C. (2000). The effect of social stress on the Standard Metabolic Rate (SMR) of brown trout, Salmo trutta. *Fish Physiology and Biochemistry*, *23*(1), 49–53. https://doi.org/10.1023/A:1007855100185

Smith, B. R., & Tibbles, J. J. (1980). Sea Lamprey (*Petromyzon marinus*) in Lakes Huron, Michigan, and Superior: History of Invasion and Control, 1936–78. *Canadian Journal of Fisheries and Aquatic Sciences*, *37*(11), 1780–1801. https://doi.org/10.1139/f80-222

Sullivan, W. P., Lantry, B. F., Barber, J. M., Bishop, D. L., Bravener, G. A., Connerton, M. J., Hammers, B. E., Holden, J. P., Keffer, D. A., Lantry, J. R., Lapan, S. R., Morrison, B. J., Tallon, K. J., Todd, A. A., Van Kempen, T. N., & Zollweg-Horan, E. C. (2021). The path toward consistent achievement of sea lamprey abundance and lake trout marking targets in Lake Ontario, 2000–2019. *Journal of Great Lakes Research*, *47*, S523–S548. https://doi.org/10.1016/j.jglr.2021.06.002

Summerfelt RC, Smith LS (1990) Methods for fish biology. In: Schreck CB, Moyle PB (eds) Anaesthesia, surgery and related techniques. American Fisheries Society, Bethesda, pp 213–272

Sutton, T. M., & Bowen, S. H. (1994). Significance of Organic Detritus in the Diet of Larval Lampreys in the Great Lakes Basin. *Canadian Journal of Fisheries and Aquatic Sciences*, *51*(11), 2380–2387. https://doi.org/10.1139/f94-239

Swink, W. D., & Johnson, N. S. (2014). Growth and Survival of Sea Lampreys from Metamorphosis to Spawning in Lake Huron. *Transactions of the American Fisheries Society*, *143*(2), 380–386. https://doi.org/10.1080/00028487.2013.862182

Wilkie, M. P., Bradshaw, P. G., Joanis, V., Claude, J. F., & Swindell, S. L. (2001). Rapid Metabolic Recovery Following Vigorous Exercise in Burrow-Dwelling Larval Sea Lampreys *(Petromyzon marinus)*. *Physiological and Biochemical Zoology*, *74*(2), 261–272. https://doi.org/10.1086/319656

Wilkie, M. P., Johnson, N. S., & Docker, M. F. (2022). Chapter 10 - Invasive species control and management: The sea lamprey story. In N. A. Fangue, S. J. Cooke, A. P. Farrell, C. J. Brauner, & E. J. Eliason (Eds.), *Fish Physiology* (Vol. 39, pp. 489–579). Academic Press. https://doi.org/10.1016/bs.fp.2022.09.001

Wood, C. M. (1991). Acid-Base and ion Balance, Metabolism, and Their Interactions, After Exhaustive Exercise in Fish. Journal of Experimental Biology, 160(1), 285–308. https://doi.org/10.1242/jeb.160.1.285

Youson, J. H., & Potter, I. C. (1979). A description of the stages in the metamorphosis of the anadromous sea lamprey, *Petromyzon marinus* L. *Canadian Journal of Zoology*, *57*(9), 1808–1817. https://doi.org/10.1139/z79-235

Zhang, Y., Claireaux, G., Takle, H., Jørgensen, S. M., & Farrell, A. P. (2018). A three-phase excess post-exercise oxygen consumption in Atlantic salmon *Salmo salar* and its response to exercise training. *Journal of Fish Biology*, *92*(5), 1385–1403. https://doi.org/10.1111/jfb.13593

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

			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)

Table 2: Effects of 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. 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.

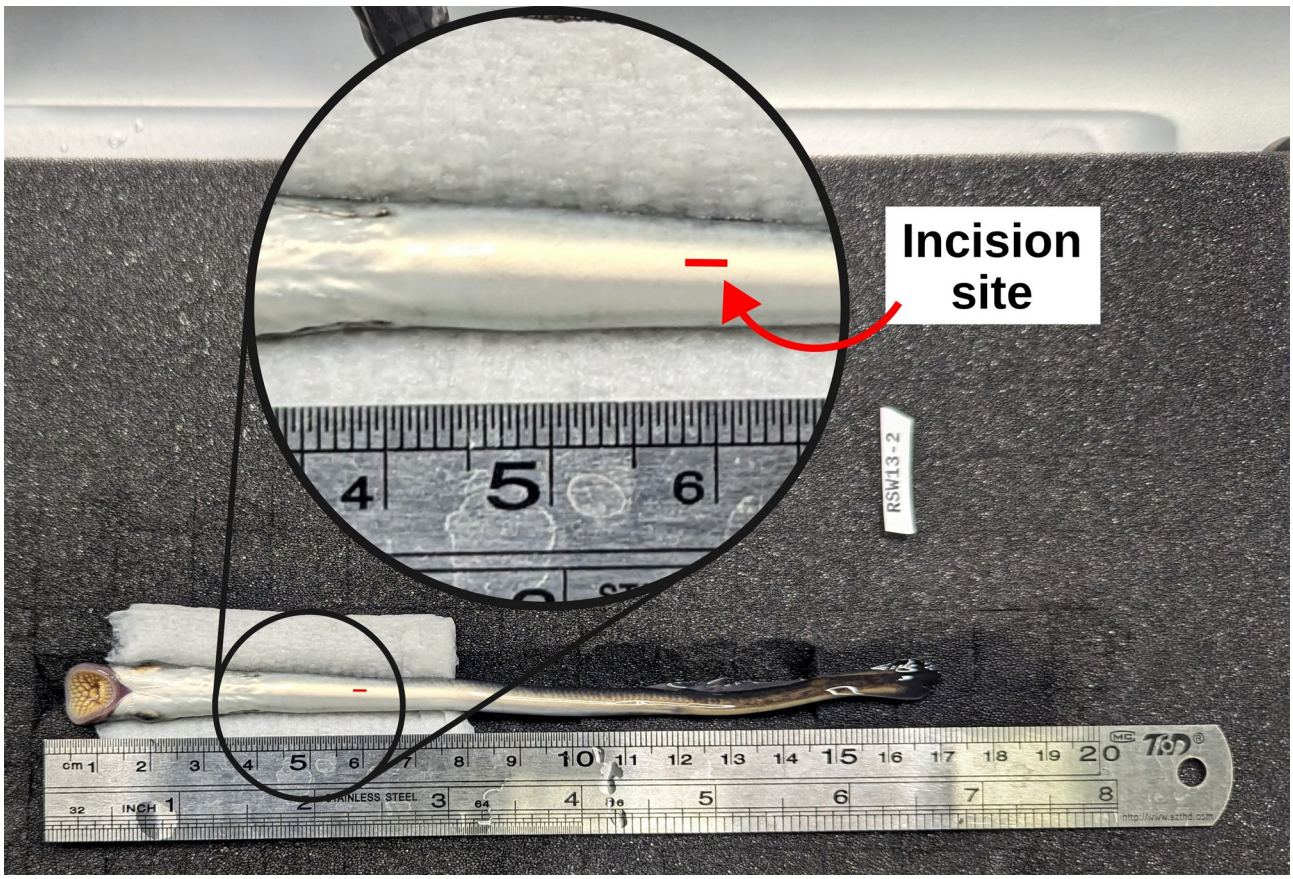
Origin	Group	SMR ($\mu mol\ O_2\ g^{-1}\ h^{-1}$)	MMR ($\mu mol\ O_2\ g^{-1}\ h^{-1}$)	AAS ($\mu mol\ O_2\ g^{-1}\ h^{-1}$)	FAS (fold over SMR)	Weight loss ($mg\ day^{-1}$)	EPOC ($\mu mol\ O_2\ g^{-1}$)
Lab	Control	1.38 ± 0.06	8.6 ± 0.6	7.3 ± 0.5	6.3 ± 0.4	16 ± 2	3.83 ± 0.5
	Surgery	1.43 ± 0.06	11.6 ± 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}

Table 3: Effects of 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 d, 20 d and 30 d following procedure. 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.

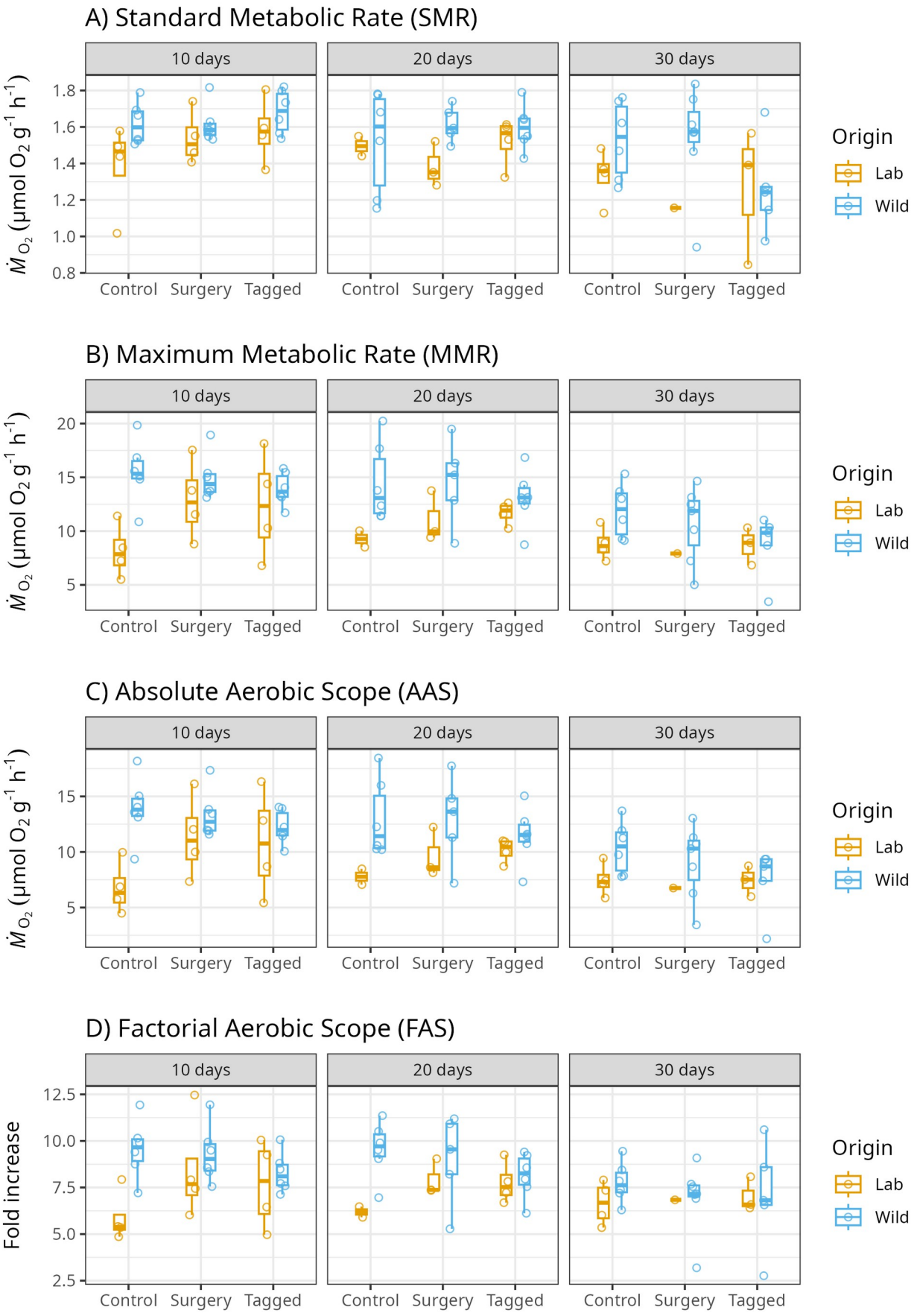
Origin	Day	SMR ($\mu mol\ O_2\ g^{-1}\ h^{-1}$)	MMR ($\mu mol\ O_2\ g^{-1}\ h^{-1}$)	AAS ($\mu mol\ O_2\ g^{-1}\ h^{-1}$)	FAS (fold over SMR)	Weight loss ($mg\ day^{-1}$)	EPOC ($\mu mol\ O_2\ g^{-1}$)
Lab	10	1.50 ± 0.06	11.2 ± 1.2	9.7 ± 1.2	7.3 ± 0.7	18 ± 2	3.88 ± 0.5
	20	1.47 ± 0.04	10.9 ± 0.6	9.5 ± 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}

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

	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



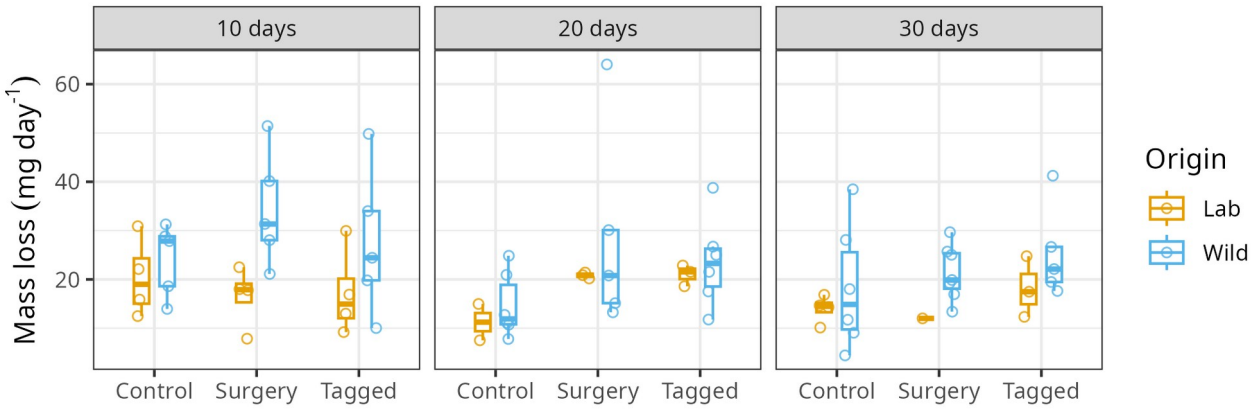
881 **Figure 1:** Top view of the V-shape closed-cell foam pad used for surgeries, including an
882 anaesthetised sea lamprey ready for surgery. The approximate location and size of the incision are
883 noted by the red dash on the lamprey's body.


A) Standard Metabolic Rate (SMR)
B) Maximum Metabolic Rate (MMR)
C) Absolute Aerobic Scope (AAS)
D) Factorial Aerobic Scope (FAS)
10 days
20 days
30 days
Control
Surgery
Tagged
$\dot{M}_{O_2}$ (µmol O_2 g^{-1} h^{-1})
Fold increase
Origin
Lab
Wild

884

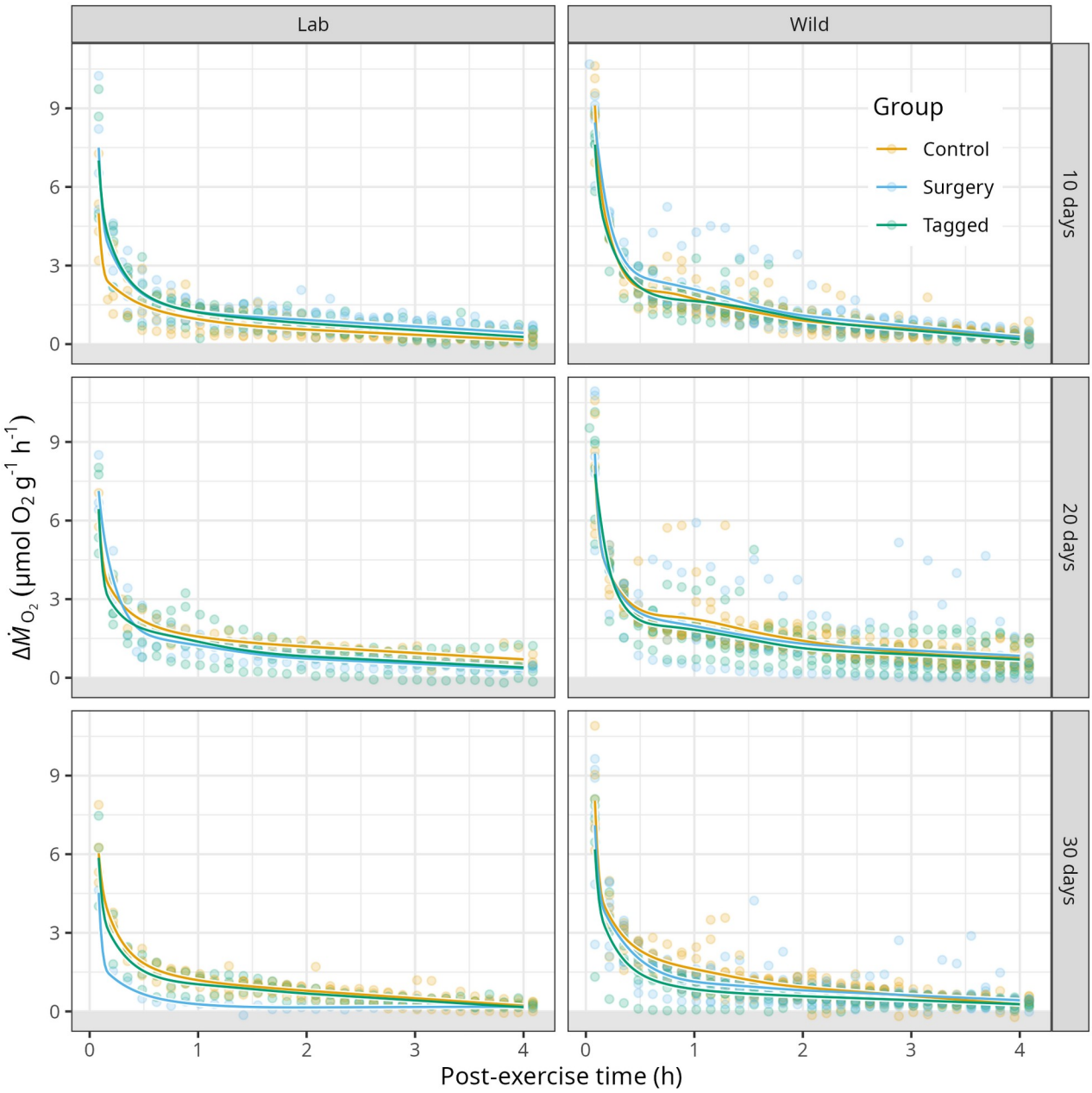
885

Figure 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.



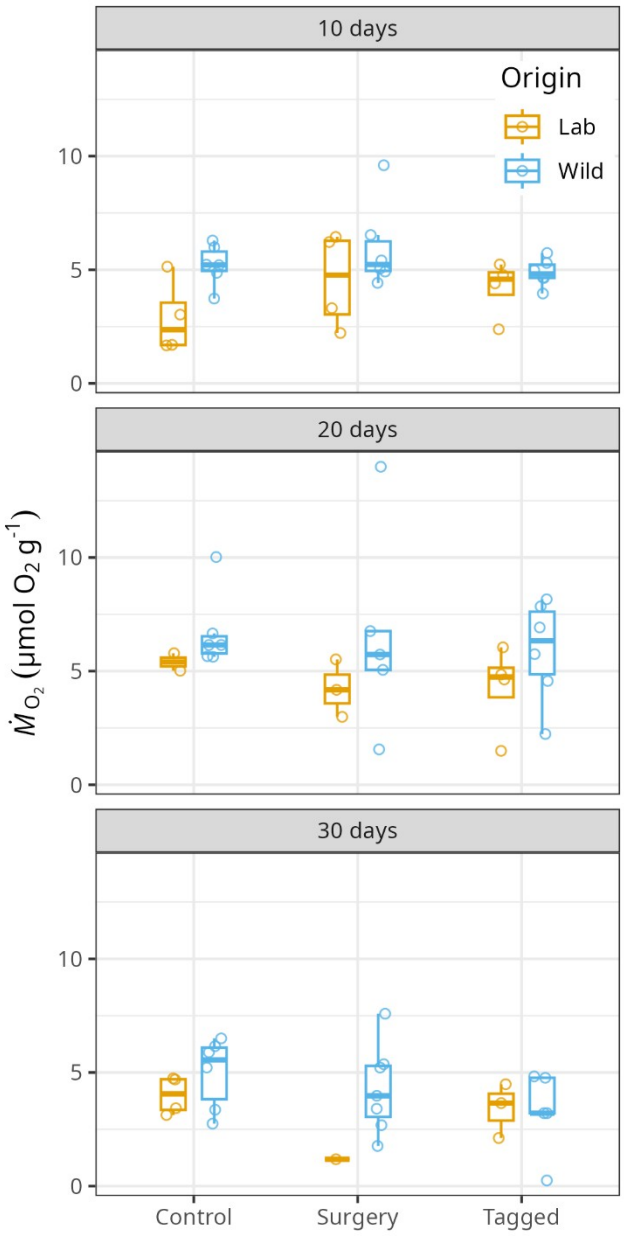
895

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



905

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



912

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