

Laurentian

Journal of the
Great Lakes Fishery Commission



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Scope

Launched in 2022, *Laurentian* replaces three historically separate, irregularly published Commission journals: *Technical Report*, *Special Publication*, and *Miscellaneous Publication*. *Laurentian* will continue to serve as an outlet for publication of interdisciplinary review and synthesis papers; narrowly focused material with special relevance to a single but important aspect of the Commission's mandate under the Convention; and scientific reports from committees that work under the umbrella of the Commission. In addition, relevant papers that do not fit the format of mainstream journals owing, for instance, to length, extensive datasets, or nature of the material and its presentation, will be considered. For further clarification, authors are encouraged to review recent papers published under the three former titles, all available on the Commission's website (www.glfc.org).

Editorial Process

All accepted submissions to *Laurentian* will be citation indexed by ProQuest®. In continuing with this scholarly process, all submissions will be reviewed by external experts, freelance editors, or staff reviewers as indicated by the nature of the material. Manuscripts should be submitted to the Commission's managing editor (randye@glfc.org) to begin the editorial process. The editor may also be consulted in advance of submission, if authors are unsure regarding whether a proposed paper is suitable for *Laurentian*. After a submission is determined to be suitable, the managing editor will forward it to one or more freelance editors, who will arrange for peer review as needed based on subject matter. Reviews by freelance editors and the managing editor may satisfy the requirement for review, or additional reviews may be sought. The managing editor will decide on acceptance and requirements for revision based on recommendations from freelance editors and the managing editor's own review. The production editor for *Laurentian* is Jill Wingfield (jwingfield@glfc.org) and the copy editor is Gail Mitchell (cranmercom@gmail.com).

Style

The Publication Manual of the American Psychological Association (APA), Seventh Edition has been adopted for *Laurentian* (<https://apastyle.apa.org/products/apa-style-manual>).

Laboratory Rearing, Growth, and Bioenergetics of Parasitic Juvenile Sea Lamprey *Petromyzon marinus*

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ABSTRACT

The behavior, physiology, growth, and bioenergetics of parasitic juvenile (non-metamorphosing) Sea Lamprey *Petromyzon marinus* (herein, juvenile) and its host fishes have been of interest since the Sea Lamprey invaded the Laurentian Great Lakes and contributed to the collapse of valued fisheries. However, questions concerning the ecology and control of Sea Lamprey remain unanswered because of difficulty in procuring juveniles from the wild and because there are few published methods for laboratory rearing that produce high survival of Sea Lamprey and their hosts. We describe methods developed to rear four Sea Lampreys from metamorphosis to the end of the juvenile feeding period in the laboratory using White Sucker *Catostomus commersonii* and Rainbow Trout *Oncorhynchus mykiss* as hosts. Wild-caught recently transformed juveniles fed on White Sucker *ad libitum* from their first feeding event starting in early May and continued feeding through July. From August through April of the following year, juveniles fed on Rainbow Trout for up to four days at a time and then were fasted for an average of 22 days (range 6–58 days) between feeding bouts. To evaluate if mass gain during short attachment bouts can be predicted, we applied a previously developed feeding model to data from 33 feeding bouts on Rainbow Trout. The feeding model was unbiased in predicting mass gained during short attachment bouts. Likewise, a bioenergetics model was unbiased in predicting mass loss during 29 fasting bouts. This report provides a protocol for humane rearing of juvenile Sea Lamprey and methods for predicting weight gain and loss for those conducting laboratory feeding experiments.

INTRODUCTION

The Sea Lamprey *Petromyzon marinus* (hereafter, lamprey(s)) invaded the upper Laurentian Great Lakes during the 1930s and 1940s and was a catalyzing factor in the collapse of valuable fish stocks and ecosystem function (Brant 2019; Smith and Tibbles 1980). As such, an international control program was developed and is overseen by the Great Lakes Fishery Commission (Gaden et al. 2021). Understanding lamprey biology is a critical component of this endeavor. For example, studies on lamprey life history in the Great Lakes determined that adults spawn in streams and die after spawning, a semelparous life history (Applegate 1950). Filter-feeding larvae remain in streams for several years before metamorphosing into parasitic juveniles that then migrate into the Great Lakes between September and April (Applegate 1950) and spend 12–18 months feeding on fishes before returning to streams in the spring as adults to spawn (Swink and Johnson 2014). After lamprey life history in the Great Lakes was understood, in-stream barriers and pesticides were used to block adults from accessing spawning grounds (barriers) and kill larvae prior to transformation and outmigration (pesticides) (Brant 2019). No direct methods have yet been developed to target juveniles in the Great Lakes (Hume et al. 2021).

While in the Great Lakes, juveniles attach to host fishes with their oral disc; use their rasping tongue to penetrate scales, skin, and musculature and then feed on host blood and tissues (Wilkie et al. 2022). In its native Atlantic Ocean environment, the lamprey is not considered a direct threat to fisheries, because host fishes are much more abundant and larger than in the Great Lakes, so they can better survive an attack (Beamish 1980; Wilkie et al. 2004). In the Great Lakes, lampreys have limited access to very large fishes and, therefore, become predacious on the relatively smaller fishes (as compared to marine fishes) like Lake

Trout *Salvelinus namaycush*, Lake Whitefish *Coregonus clupeaformis*, and Cisco *Coregonus artedii* (Harvey et al. 2008; Schneider et al. 1996).

Control has reduced the abundance of lamprey but has also made juveniles more difficult and costly to obtain for research. Reduced abundance impedes efforts to further study the biology of their maturation and new possibilities for control (Hume et al. 2021). Furthermore, the feeding behavior of juveniles presents some ethical concerns regarding the care of fish hosts in situations where juveniles are reared in a laboratory. Rearing protocols for juveniles that result in their long-term survival and low host mortality are not widely available (Swink 2003). For example, newly metamorphosed juveniles were collected from the wild during November 1950 ($n = 40$) and May 1951 ($n = 60$) and held until June 1952. Only six juveniles (15%) from the autumn group and 16 juveniles (27%) from the spring group survived to maturation. Combined, the 22 survivors each killed an average of 8.4 kg of fish. Furthermore, the mean final weight of the survivors (52 g) was well less than that of adults collected from Lake Huron (125 g) during 1952 (Parker and Lennon 1956). Additional laboratory studies occurring in the 1980s and 1990s documented that six of 292 juveniles survived to adulthood, and each survivor killed an average of eight hosts (range, 1–25) that weighed an average of 12.8 kg (range 1.2–34.4 kg; Swink 2003). More recent studies allowed juveniles to attach to Lake Trout for only four days (Firkus et al. 2022), because one goal was to prioritize host welfare and survival. This goal resulted in no mortality of Lake Trout, although sub-lethal effects occurred. The outcomes (growth and survival) for juveniles have yet to be reported from these studies, because juveniles were used as a tool to understand the physiological responses of hosts to lamprey feeding (Goetz et al. 2016; Smith et al. 2016; Firkus et al. 2021, 2022, 2023).

Given the challenges of directly observing juveniles feeding in the Great Lakes, the bioenergetics model developed by Kitchell and Breck (1980) has been incorporated into an individual-based population model to estimate the damage lampreys cause to native species like Lake Trout (Madenjian et al. 2003, 2008). This bioenergetics model was partially based on laboratory determinations of standard metabolic rate (Beamish 1964), which represents the predominant energy cost for a fasting juvenile (Kitchell and Breck 1980). A regression model relating juvenile feeding rate to number of days to death of the host was also incorporated into the individual-based population model (Farmer et al. 1975; Madenjian et al. 2003). In a related line of research, a juvenile feeding model was developed to estimate specific growth rate during an attachment to a host (Cochran and Kitchell 1986, 1989). This feeding model was largely based on data from laboratory work in which juveniles were attached to hosts in laboratory tanks (Farmer et al. 1975), and model development included the formulation of an empirical relationship between specific growth rate during attachment, size at the start of the attachment, and host–fish size at the start of an attachment (Cochran and Kitchell 1986, 1989). When this feeding model was tested against an independent set of laboratory observations from the 1980s and 1990s (Swink 2003), the predicted growth was like observed growth, but more error between observed and predicted growth was observed when the days attached were less than five (Cochran et al. 1999). Growth during these relatively short attachments may have been overpredicted, because an assumption of

the feeding model is that juveniles are feeding the entire time they are attached to a host (Cochran et al. 1999). This assumption fails to account for the time needed for juveniles to draw blood through the skin or pierce the host's skin (herein, initiation time). Indeed, non-penetrating Type-B marks (i.e., where the outline of the oral disk is evident but no gouge from the tongue is visible) are common in both laboratory and field settings (King 1980; Firkus et al. 2022). Initiation time and food consumption rates may also be influenced by where a juvenile attaches to a host, which adds to another potential source of error to the bioenergetics model if attachment site is not accounted for (Cochran et al. 1999).

The primary objective of our study was to evaluate previously developed feeding and bioenergetics models (Cochran and Kitchell 1989; Cochran et al. 1999; Kitchell and Breck 1980) for juvenile lampreys to assess their accuracy at predicting growth and weight loss. To accomplish this objective, we reared recently transformed juveniles captured in a Lake Huron tributary and tracked their growth and weight loss while they fed on Rainbow Trout *Oncorhynchus mykiss* (hereafter, trout) hosts over a 10-month period or fasted. Our secondary objective was to determine if variables such as attachment location, mark type, and host size explained error in model estimates. If the feeding and bioenergetics models are shown to be accurate, they can be used to estimate juvenile sizes before and after different feeding and fasting events, which is useful for estimating experimental host–fish size requirements.

METHODS

In the broadest terms, our experimental setup involved capturing recently transformed, wild Sea Lamprey *Petromyzon marinus* (hereafter, lamprey(s)). The setup involved temporarily holding the lampreys in our laboratory while allowing them to feed on White Sucker *Catostomus commersonii* (hereafter, sucker(s)) shipping them as juveniles to a laboratory at the University of Guelph where the actual research was to be conducted, and recording biometric data while they fed on trout to the end of the juvenile feeding period. This research was piggybacked on another project, which accounts for why lampreys were transferred between laboratories.

Procurement and Care of Recently Metamorphosed Lamprey

Via electrofishing, 33 recently transformed lampreys were collected (Jubar et al. 2021) from the Cranberry River, Michigan, a tributary to northern Lake Huron, on September 13, 2023. The lampreys were transported to the U.S. Geological Survey's Hammond Bay Biological Station (HBBS) in Millersburg, Michigan, on September 15, 2023, in coolers filled with aerated water from the Cranberry River. Upon arrival at the HBBS, the lampreys were in late stages of transformation (Stage 6+; Manzon et al. 2014) and averaged 4 g (2.3–8.5 g) in weight and 153 mm (129–192 mm) in total length. Between lamprey arrival and May 1, 2024, they were held at ambient photoperiod and ambient Lake Huron temperatures (1–16 °C), supplied at 3 L/min in tanks (0.4 m x 0.4 m x 0.3 m, 40 L) containing no substrate or hosts.

First Feeding and Care of Juvenile Sea Lamprey and Their Hosts

On May 1, 2024, all 33 lampreys, now at the juvenile stage, were moved to a 1,600-L circular tank (1.83 m in diameter; 0.61 m in depth) with Lake Huron water at ambient temperatures (7–18 °C) supplied at 3 L/min and with ambient photoperiod where light from a skylight in the ceiling entered the tank through a small window in the lid. The tank contained 58 suckers that averaged 420 mm (340–490 mm) in total length and 1,010 g (530–1,600 g). Suckers were captured from the Black Mallard River, Michigan, using traps (Johnson et al. 2021), and were fed sinking algae pellets (Tetra® PRO PlecoWafers™) *ad libitum* five days per week (roughly 0.1% of fish biomass). Lamprey juveniles were allowed to feed on the suckers *ad libitum* until July 29, 2024. None of the suckers but three of the juvenile lampreys died between May 1, 2024, and July 29, 2024. Size of juveniles was not tracked while feeding on suckers, because the goal was to keep the juveniles alive until they could be shipped. Animal care and use protocols for lamprey rearing at the HBBS were approved by Michigan State University (PROTO202100285).

Twelve juvenile lampreys were randomly selected and prepared for shipping to the University of Guelph on July 29, 2024. The shipping cooler (64 cm x 36 cm x 9 cm; Coleman® Chiller™ 45 L) was lined with two plastic bags; the interior bag contained 4.5 kg of cubed ice and 4.5 kg of lake water. The inner bag was filled completely with oxygen and sealed. The outer bag was also sealed. The cooler was taped shut and scheduled to ship overnight.

Unfortunately, delivery of the juveniles was delayed one day, so arrival was on July 31, 2024. Air temperatures exceeded 30 °C during the 48-hr shipping period and likely caused ice in the cooler to melt faster than in a typical shipment. Because the juveniles were allowed to feed on suckers right up to the shipping date, water in the cooler also contained feces. These problems resulted in eight of the 12 juveniles being dead upon arrival.

Feeding and Care of Juveniles to the End of the Life Stage

The four surviving juveniles were housed at the Hagen Aqualab at the University of Guelph in pairs in 40-L glass aquaria (50 x 26 x 30 cm) supplied with 10 °C ground water at 2 L/min under a 12 L:12 D photoperiod, with no access to hosts outside of scheduled feeding trials. Feeding trials started August 8, 2024, for two juveniles, and August 13, 2024, for the other two juveniles. Juveniles averaged 38.7 g at the beginning of their first feeding trial, representing approximately a 10-fold mass gain since their first feeding in May 2024. Care and use of animals at the University of Guelph were conducted in accordance with the Canadian Council on Animal Care and were approved by the University of Guelph's Animal Care Committee (AUP#5196). The feeding trials described below were based on recent feeding experiments where the goal was to determine sub-lethal effects of parasitism on trout (Smith et al. 2016; Firkus et al. 2022).

To serve as juvenile hosts, 34 trout were acquired from the Ontario Aquaculture Research Centre (Alma, Ontario, Canada) and held at the Hagen Aqualab in 2,000-L-capacity circular tanks (185 cm diameter x 75 cm height) supplied with a constant flow of 10 °C ground water. Trout were fed 0.5% of their initial body mass per day (Bluewater Fish Food; 4-mm pellet) and averaged 1,383 g (933–1,907 g) and 449-mm (392–515 mm) total length. Trout were implanted with passive integrated

transponders (PIT) tags (12-mm length, 2-mm width; Biomark®) under light anaesthesia upon arrival (80 mg/L MS-222 buffered 1:2 with 160 mg/L sodium bicarbonate) and acclimated for at least one month before inclusion in a trial. On the day prior to a feeding trial, an individual trout was lightly anaesthetized as above and its mass, length, and PIT-tag number were recorded. Trout were allowed to recover overnight in a 2,000-L-capacity circular tank (water depth reduced to ~25 cm) supplied with 10 °C groundwater at 15 L/min. The following day, a single juvenile lamprey was weighed and introduced into the trial tank with the preselected trout, and the time was recorded. Trout were not fed during the parasitism trial. Over the course of all feeding trials, the host:parasite wet-mass ratio prior to attachment averaged 27:1 (range = 17:1 to 39:1). To maximize host survival and to standardize attachment time, each juvenile was allowed to attach for no more than four days and was monitored three times per day at regular intervals during the light phase of the photoperiod (Firkus et al. 2022). If a lamprey failed to attach to a trout after two days, the trial was abandoned. If a lamprey self-detached prior to four days, the time was recorded and the trial was ended. Trials also ended prematurely if the trout was having difficulty maintaining equilibrium, however, there were no such instances throughout all feeding trials. A single host mortality occurred November 22, 2024, during the third night of an attachment. To prevent additional host mortality, feeding trials were occasionally limited thereafter to three days or less (based on expert judgement). Therefore, to account for variation in the total time of feeding trials, we hereafter use “feeding bout” to refer to the consecutive number of days a juvenile remained attached to its host.

At the end of a feeding trial, the trout was netted with the lamprey attached, and both were transferred to an anesthetic bath as above. The lamprey was manually removed, re-weighed, and returned to its home aquarium to fast until

its next feeding trial, which occurred 6–58 days later (hereafter, we use “fasting bout” to refer to the consecutive number of days between detachment from one host and attachment to a subsequent host). The anesthetized trout was re-weighed, the lamprey mark photographed, and the location of mark assigned according to Cochran (1986) as follows (Figure 1):

1. The anterior boundary was the farthest point of the mandible, and the posterior boundary was the edge of the operculum.

2. The anterior boundary was the farthest edge of the operculum, the posterior boundary was the insertion of the dorsal fin, and the ventral boundary was the lateral line.

3. The anterior boundary was the farthest edge of the operculum, the posterior boundary was the insertion of the dorsal fin, and the dorsal boundary was the lateral line.

4. The anterior boundary was the insertion of the dorsal fin, the posterior boundary was the insertion of the anal fin, and the ventral boundary was the lateral line.

5. The anterior boundary was the insertion of the dorsal fin, the posterior boundary was the insertion of the anal fin, and the dorsal boundary was the lateral line.

6. The anterior boundary was the insertion of the anal fin, and the posterior boundary was the farthest edge of the caudal fin.

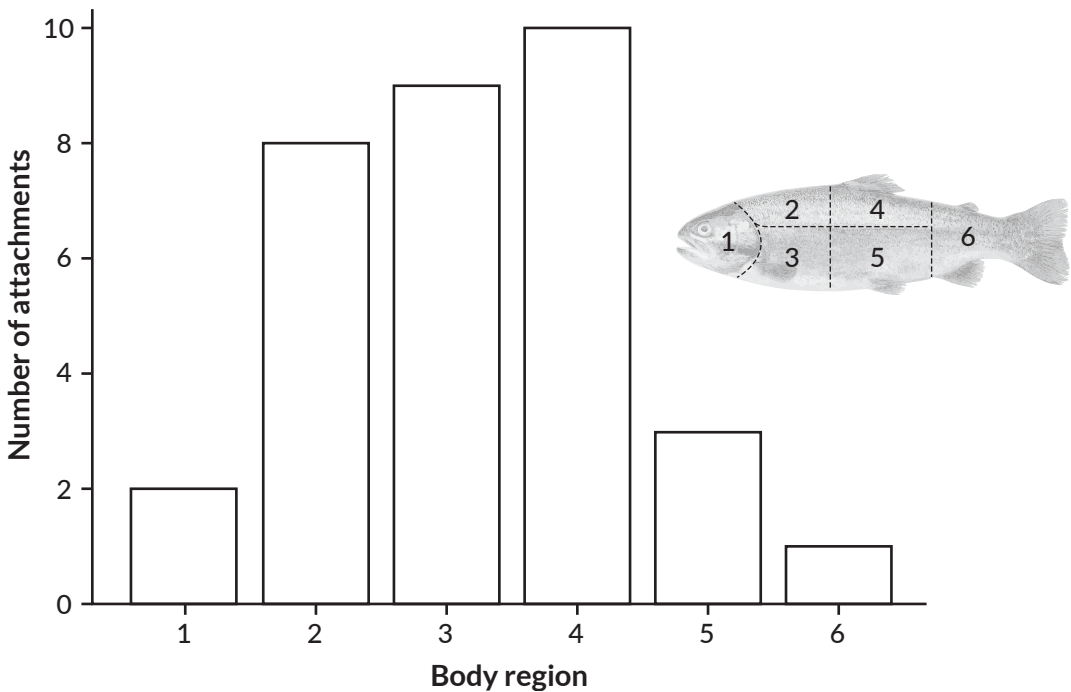


FIGURE 1. Sea Lamprey mark location on Rainbow Trout with body regions defined by Cochran (1986) and illustrated in the right portion of the figure.

Lamprey mark type was characterized as a Type-A mark (skin broken exposing underlying musculature) or Type-B mark (abraded skin but skin not broken; King 1980). Individual trout were either euthanized immediately or allowed to recover for up to one year following detachment as part of a separate study characterizing clotting response, and they were not used in any subsequent feeding trials. With the single exception noted above, all host trout survived until scheduled euthanasia. Juvenile lampreys were reused for feeding trials. When the lampreys were too large to safely feed on the remaining trout (trout:lamprey wet-mass ratio <17:1; juveniles 1, 2, and 4), or when their vigor for feeding diminished as judged by multiple feeding trials with no attachment or weight gained (juvenile 3), they were euthanized, weighed, and dissected to determine sex.

Application of Juvenile Feeding and Bioenergetics Models

Juvenile data were applied to a feeding model developed by Cochran and Kitchell (1989) and extended by Cochran et al. (1999) to evaluate deviations between predicted and observed growth rate. Specifically, observed instantaneous growth rate, G , was

$$G = \frac{\ln \left(\frac{W_f}{W_i} \right)}{t}$$

where W_f = final weight immediately after the feeding trial, W_i = initial weight at the start of feeding trial, and t = number of attachment days. According to Cochran and Kitchell (1989), predicted growth rate, $\hat{G}$, was

$$\hat{G} = 2.54 \left(\frac{W_i}{W_{host}} \right)$$

where W_{host} = weight of a host fish at the start of attachment.

Growth (G) and $\hat{G}$ were compared across all feeding bouts in relation to attachment time, initial juvenile mass (Cochran et al. 1999), and feeding location (Cochran et al. 1999). Error in predicted final mass (W_f and $\hat{W}_f$, respectively) of juveniles at the end of the feeding trial was also compared (Cochran et al. 1999), using the following equation to determine $\hat{W}_f$

$$\hat{W}_f = W_i e^{\hat{G}t}$$

where $\hat{G}$ = predicted instantaneous growth rate during the feeding trial, W_i = initial mass, and $\hat{W}_f$ = final mass.

The change in juvenile mass during a fasting bout was estimated using the Kitchell and Breck (1980) bioenergetics model, which has been coded in R into the Fish Bioenergetics 4 v1.1.6 package (released September 21, 2024; Deslauriers et al. 2017). The bioenergetics model simulated changes in juvenile mass over the course of the fasting period, given the water temperature regime experienced by the juvenile during that period. As mentioned above, water temperature was maintained at 10 °C during the fasting period. For each fasting bout, the initial mass of the juvenile in the corresponding bioenergetics-model simulation was set equal to the observed juvenile mass at the start of the fasting bout. The bioenergetics model generated an estimate of the juvenile mass at the end of the fasting bout. A time step of a single day was used in the bioenergetics-model simulations. Specific assumptions made in the package to predict the decrease in mass were:

- The juveniles did not feed during the fasting period.
- The standard or resting metabolic rate (Beamish 1973; Kitchell and Breck 1980) was the sole energetic cost during the fasting bout, which means that fasting lamprey had negligible swimming activity and there was no egestion, excretion,

or specific dynamic action, which is the energetic cost associated with processing of food.

- The energy density of the juvenile used in this study was the same as the energy density measured by Cochran et al. (2003) for juveniles from northern Lake Huron.
- The energy density of the juvenile remained constant during the fasting period.

Evaluating the Fits of the Feeding and Bioenergetics Models

Performances of the juvenile feeding and bioenergetics models were evaluated by determining if the model predictions were significantly biased. Specifically, the feeding-model predictions of juvenile mass at the end of an attachment period and the feeding-model predictions of specific growth rate during the attachment were tested for significant bias. Bioenergetics-model predictions of juvenile mass at the end of the fasting period were also tested for significant bias. For each set of predictions, an ordinary least-squares (OLS) regression was fit with observed values as the independent variable and predicted values as the dependent variable. For analyses of instantaneous growth during attachment, we evaluated both slope and intercept bias in the relationship between observed and predicted values. In addition to testing if the regression slope differed significantly from unity (1:1 expectation), we tested if the intercept differed significantly from zero. The slope test assessed if predicted instantaneous growth scaled proportionally with observed growth, while the intercept test evaluated if predictions were unbiased when observed growth approached zero. Predictions were considered without significant bias if the slope of the fitted regression line was not significantly different from unity and the intercept was not significantly different from zero. In addition, for specific growth rate during attachment, fit statistics (R^2 , root mean squared error [RMSE]

and mean absolute error [MAE]) were calculated and residual patterns inspected to further judge agreement between observations and model predictions, as per Cochran et al. (1999).

To identify factors contributing to discrepancies between observed and predicted values, the difference of observed minus predicted error was quantified and used to conduct multivariate OLS models using available covariates. We considered variables that could influence initiation time, rates of energy consumption, and metabolism. For feeding bouts, predictors included: pre-trial juvenile wet weight (initiation time, metabolism), Julian day at trial start (metabolism), trout: lamprey wet-mass ratio prior to the feeding bout (initiation time, energy consumption), duration of attachment (energy consumption), number of discrete marks on the trout (energy consumption), and categorical variables for sex (metabolism), mark type (initiation time, energy consumption), and body region (initiation time, energy consumption). For fasting bouts, predictors included: pre-fasting mass, Julian day at fasting start, fasting duration, number of marks, and the same categorical variables. If multiple lamprey marks of the same type were present, the region of the first mark was used. If a Type-A and Type-B mark were present, a Type-A mark and its region was used. ANOVA F -tests were used to evaluate predictor contributions, and residual diagnostics confirmed that OLS assumptions of normality and homoscedasticity were satisfied in all cases.

Because the same four juveniles were used repeatedly across trials, we also fit linear mixed-effects models with lamprey identity included as a random intercept. These models tested whether repeated measures altered inference relative to OLS and provided estimates of the intraclass correlation coefficient (ICC), representing the proportion of variance attributable to individual juvenile-level differences.

RESULTS

General Observations

No additional observations were recorded during attachments to suckers beyond those described in the Methods chapter. Forty feeding trials were carried out on trout with four individual juveniles. The majority of these trials included feeding bouts of up to four days with some exceptions: juvenile #1 did not attach to a trout on September 30, 2024, after two days of being with a host; juvenile #1 killed a host on November 22, 2024, after three days of attachment; juvenile #3 did not attach to a host on October 7 and November 25, 2024, and March 10 and March 24, 2025, after two days; juvenile #3 also attached to a host for one day (April 28, 2025) and lost weight during that time; juvenile #4 did not attach to a host on August 26, 2024, after two days. After excluding trials where juveniles did not attach or attached but did not gain weight, 33 feeding trials are reported herein where 26 trials resulted in Type-A marks and 7 attachments resulted in Type-B marks. Juveniles attached across all surface areas of hosts with the following frequency of marks in each region: Region 1 = 2; Region 2 = 8; Region 3 = 9, Region 4 = 10, Region 5 = 3, Region 6 = 1 (Figure 1).

Given the observed development of male and female gonads like that of adults and a reduced feeding vigor, we conclude that these lampreys were at the end of their juvenile life and were becoming adults as per Clemens (2019) when euthanized. Lamprey #1 was a female that weighed 100.5 g after its final feeding bout and was euthanized on January 31, 2025, after participating in six feeding trials (Figure 2 and herein). Lamprey #2 was a female that was 103.1 g when euthanized on May 9, 2025, after participating in 11 feeding trials. Lamprey #3 was a male that was 53.2 g after its final feeding bout and was euthanized on June 19, 2025, after participating in 14 feeding trials. Lamprey #4 was a female that was 121.5 g after its final feeding bout and was euthanized on March 14, 2025, after participating in nine feeding trials. Upon dissection of the females, the ovaries filled the entire abdominal cavity.

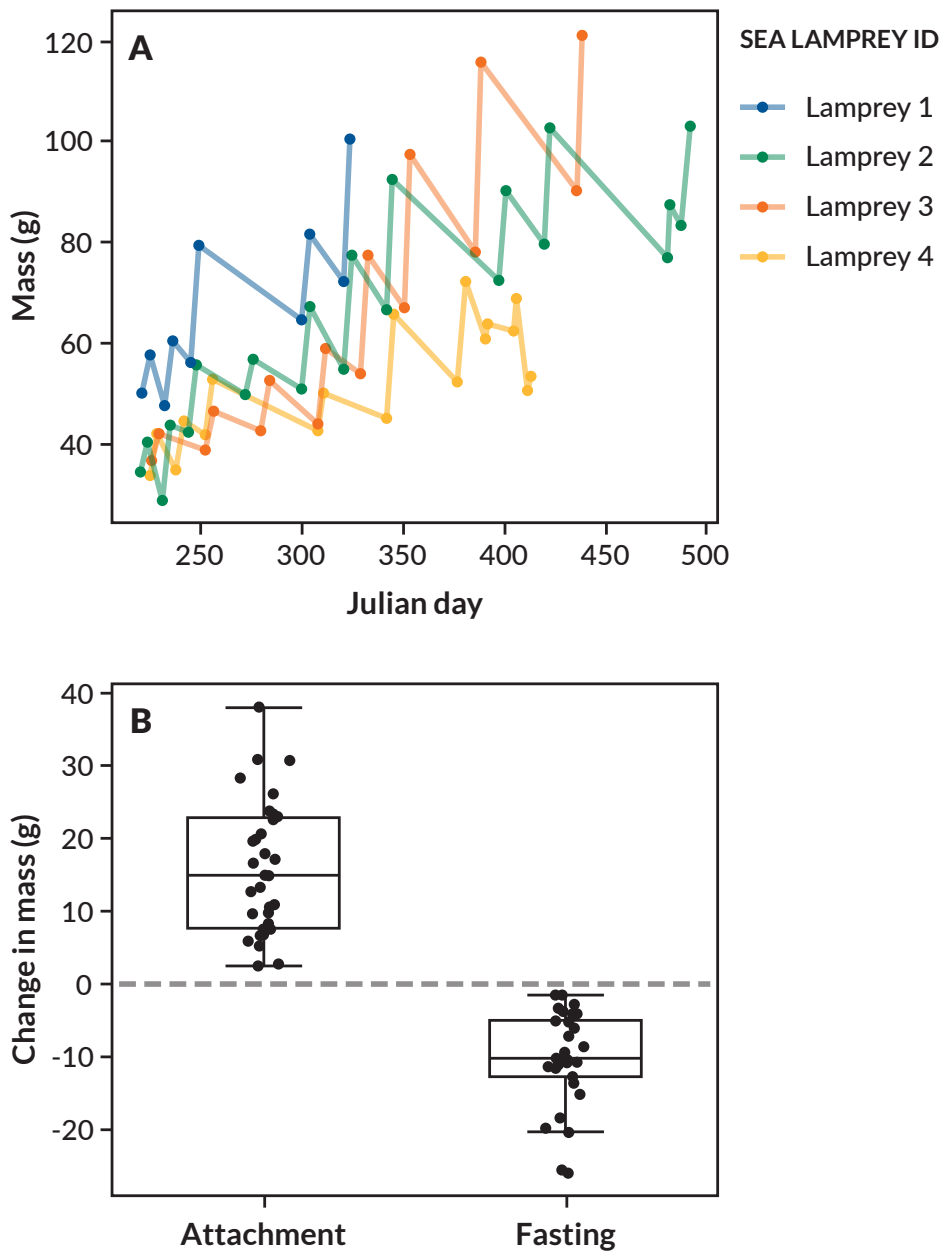


FIGURE 2. Observed Sea Lamprey mass (g) plotted through time (Julian day with continuous numbering after December 31, 2024) for individual juvenile lampreys over multiple consecutive feeding bouts on Rainbow Trout followed by periods of fasting (Panel A). Change in Sea Lamprey mass (g) during all attachment and fasting bouts with a box plot characterizing distribution (Panel B). The horizontal dashed line represents no change in mass. The boxes represent the interquartile range, the horizontal line inside the boxes is the median, the vertical lines outside the boxes (whiskers) are 1.5 times the interquartile range. The points outside the whiskers are outliers. [Panel B symbols all the same and some interjected noise.]

Weight Gain During Attachment

Predicted and observed wet mass after feeding were aligned (Figure 3; intercept = 6.97; slope = 1.00; 95% confidence interval [CI] 0.82–1.18). The slope was not significantly different from unity ($t = 0.02$, $P = 0.99$, $N = 33$), and the intercept was not significantly different from zero ($t = 0.81$, $P = 0.42$), indicating that predicted and observed

values were statistically indistinguishable. Residual variation around the fitted relationship was moderate (SD = 11.14 g). Error analysis of the residuals from the linear regression of predicted mass at the end of the attachment period as a function of observed mass at the end of the attachment period showed that 67% of the variance was explained by model predictors ($R^2 = 0.67$; adjusted $R^2 = 0.48$; $F_{12,20} = 3.43$, $P = 0.007$).

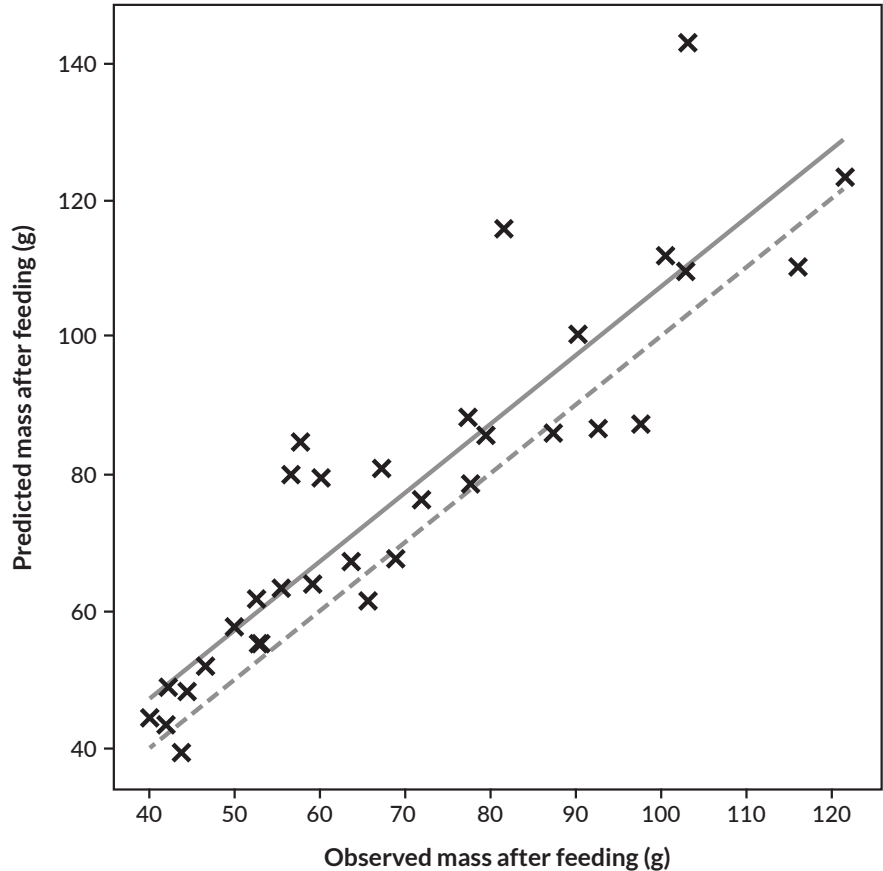


FIGURE 3. Predicted Sea Lamprey mass (g) after attachment to a Rainbow Trout according to the feeding model described in Cochran and Kitchell (1989) versus observed mass after attachment. Points (crosses) represent individual feeding bouts; the dashed line denotes the 1:1 expectation, and the solid line shows the fitted ordinary least-squares regression (intercept = 6.97; slope = 1.00).

The trout:lamprey wet-mass ratio was the strongest predictor of error ($F = 17.8, P < 0.001$; Figure 4), with higher ratios reducing error, while longer attachment durations increased error ($F = 5.32, P = 0.032$; Figure 4). Mark type was of marginal importance ($P = 0.075$) in explaining the error. Sex, body region, Julian

day, pre-trial weight, and the number of discrete marks were not significant ($P > 0.3-0.9$). Mixed-effects models confirmed these patterns: biomass ratio and attachment length remained highly significant, mark type was retained, and lamprey identity explained 10% of variance ($ICC = 0.10$).

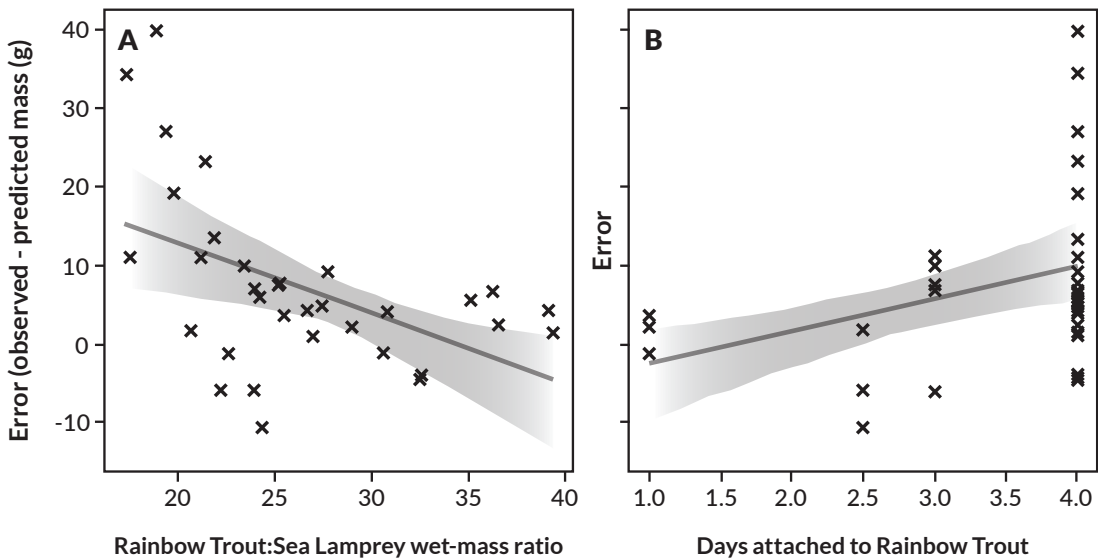


FIGURE 4. The difference between observed mass at the end of the attachment period and predicted mass at the end of the attachment period (Error) contrasted with Rainbow Trout:Sea Lamprey wet-mass ratio (Panel A) and days attached to the Rainbow Trout (Panel B). Points (crosses) represent individual feeding bouts, the solid line indicates the fitted ordinary least-squares regression, and the shaded region shows the 95% confidence interval.

Instantaneous Growth During Attachment

Agreement between observed and predicted instantaneous growth (or specific growth rate) was poor (Figure 5). The fitted regression had a slope of 0.138 and intercept of 0.091. The slope of the fitted regression line was significantly less than unity ($t = -6.90$, $df = 31$, $P < 0.001$), and the intercept of the line was significantly greater than zero ($t = 8.81$, $df = 31$, $P < 0.001$). Thus, the feeding-model estimates of specific growth rate

were significantly biased. Residual variation around the fitted relationship was relatively high ($SD = 0.0221$). In addition, estimates of R^2 (0.04), RMSE (0.043), and MAE (0.035) indicated weak model performance. Scatterplots and residuals indicated substantial variability and systematic underestimation of growth relative to the 1:1 line, suggesting that instantaneous growth was not well captured by the predictive framework.

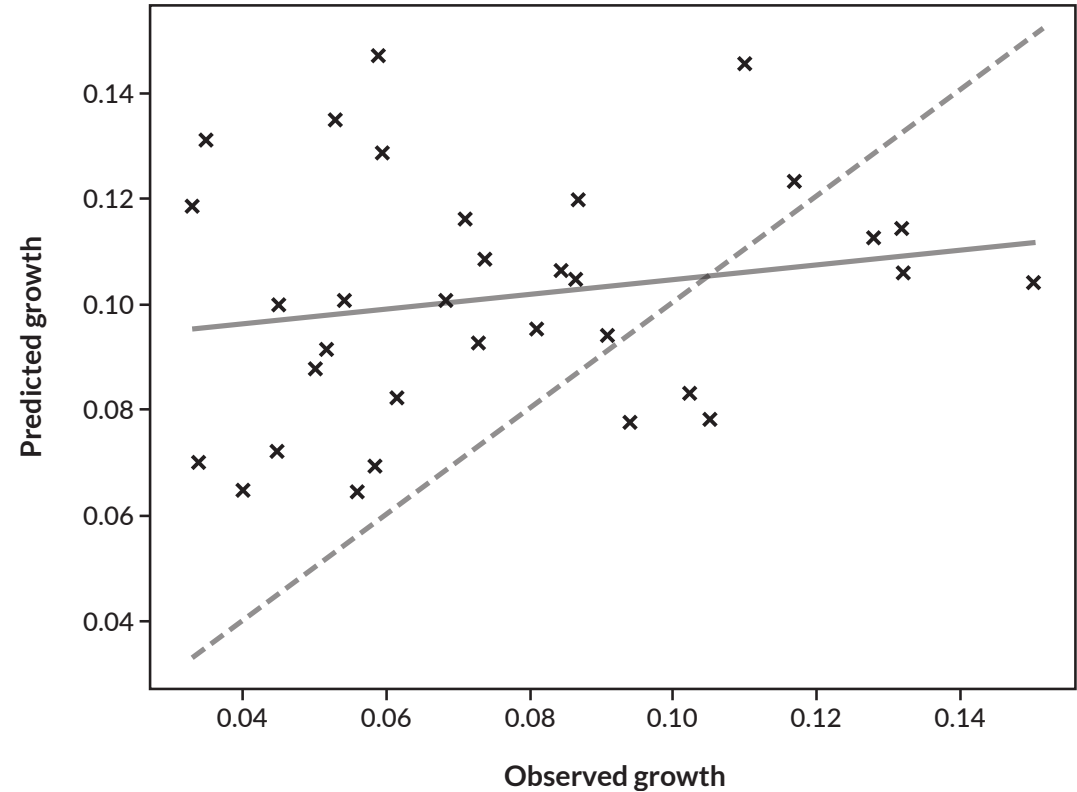


FIGURE 5. Linear relationship between predicted ($\hat{G}$) and observed (G) growth of Sea Lamprey attached to Rainbow Trout in this study according to a feeding model described by Cochran and Kitchell (1989). Points (crosses) represent individual feeding bouts; the dashed line denotes the 1:1 expectation, and the solid line shows the fitted ordinary least-squares regression (intercept = 0.091; slope = 0.138).

Loss in Juvenile Mass During Fasting

Predicted and observed post-fasting masses were closely aligned (intercept = 2.39, slope = 0.99, 95% CI 0.88–1.11), with the slope of the fitted regression line not significantly different from unity ($t = -0.16$, $df = 27$, $P = 0.87$, $N = 29$; Figure 6a), and the intercept of the fitted regression line not significantly different from zero ($t = 0.73$, $df = 27$, $P = 0.47$). Thus, the predictions of the change in Sea Lamprey mass during the fasting period were not significantly biased. Residual variation around the fitted relationship was low ($SD = 4.58$ g), indicating close agreement between predicted and observed post-fasting masses. Error analysis of the residuals from linear regression of predicted

post-fasting mass as a function of observed post-fasting mass indicated that 54% of variance of the residuals could be explained by the suite of covariates identified in the Methods chapter ($R^2 = 0.54$; adjusted $R^2 = 0.24$; $F_{11,17} = 1.79$, $P = 0.14$). Only fasting duration significantly influenced error ($F = 8.49$, $P = 0.010$; Figure 6b), with the observed mass loss being greater than the model-predicted mass loss when the fasting bout was short. All other predictors, including sex, body region, mark type, pre-fasting mass, trial start date, and number of discrete marks were non-significant (all $P > 0.2$). Mixed-effects models confirmed fasting duration as the dominant predictor with a secondary positive effect of initial mass and showed no evidence of lamprey-level clustering ($ICC = 0$).

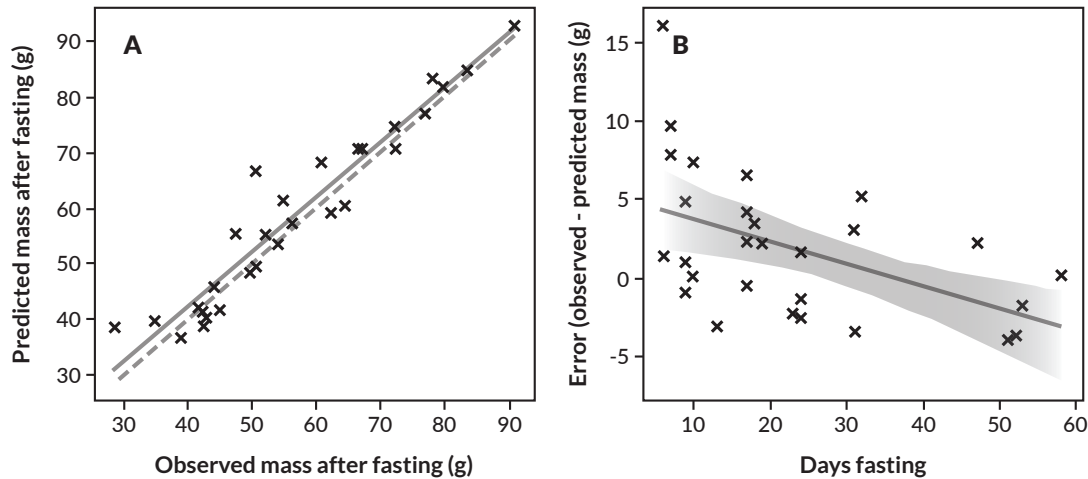


FIGURE 6. Performance and error structure of the fasting mass model for juvenile Sea Lamprey. (Panel A) Observed versus predicted mass after fasting. Points (crosses) represent individual fasting periods; the dashed line denotes the 1:1 expectation, and the solid line shows the fitted ordinary least-squares regression. (Panel B) Error in predicted mass after fasting (observed – predicted mass) as a function of fasting duration. Points (crosses) represent individual trials, the solid line indicates the fitted regression, and the shaded region shows the 95% confidence interval.

DISCUSSION

To our knowledge, this is the first detailed description of a method for rearing juvenile Sea Lamprey from metamorphosis through the juvenile feeding stage in a laboratory. This rearing process lasted 18 months, resulting in minimal host mortality (one Rainbow Trout) and lamprey mortality (~10%). All of the lampreys (100%) used in the experiment survived to adulthood after they were maintained in controlled environments with periodic access to hosts. Previous studies had reared juveniles in a laboratory from transformation to adulthood, but overall survival of lampreys was less than 27%, more than 8.4 kg of host fish were killed per lamprey, and some of the details of the rearing protocols were not provided (Parker and Lennon 1956; Swink 2003). Furthermore, the average lamprey mass at adulthood was smaller (average 52 g) in previous studies than reported here (average 81 g), which more closely aligns with mass of wild juveniles approaching maturation (Bergstedt and Swink 1995).

A key design advance in the present study is reporting growth and survival outcomes for juvenile lampreys when feeding is limited to short bouts. While high water quality and a constant temperature likely contributed to high lamprey survival, we further attribute the success of this rearing method to the adoption of short attachment times (less than four days), which others have used (Smith et al. 2016; Firkus et al. 2022). The high survival of juveniles using short attachment times and long fasting bouts aligns with what little is known about juveniles in the wild. Lampreys survive months-long fasting periods during metamorphosis (Manzon et al. 2014) and when migrating upstream to spawn (Johnson et al. 2014). Although the movement and feeding behavior of juveniles are poorly understood (Hume et al. 2021), the ability to endure unpredictable periods of fasting is consistent with the opportunistic nature of an ectoparasitic feeding strategy.

Significant bias in the feeding model of Cochran and Kitchell (1989) regarding prediction of lamprey mass at the end of attachment was not detected, indicating reasonably accurate model performance. Nonetheless, in about 75% of the attachment trials, the model overestimated mass at the end of attachment, suggesting a greater tendency to overestimate rather than underestimate mass. All attachment trials in our study were less than four days in duration. Similarly, Cochran et al. (1999) noted a greater tendency for the feeding model to overestimate rather than underestimate juvenile mass at the end of the attachment period when attachment was less than about 18 days, whereas this pattern was not apparent for longer attachments. This overestimation of mass by the feeding model for relatively short attachments was attributed to a delay in active feeding after attachment, which had a substantial influence on the cumulative amount of feeding during relatively short attachments (Cochran et al. 1999).

Based on our regression analysis, predictions of instantaneous growth rate by the feeding model were significantly biased. In their application of the feeding model to the extensive observations from the laboratory studies by Swink (2003), Cochran et al. (2003) decomposed the error in the feeding-model predictions of instantaneous growth rate into the following components: (1) error representing bias from the difference between mean observed and mean predicted instantaneous growth rate; (2) error resulting from the slope differing from unity; and (3) random error. They concluded, although the bulk (nearly 90%) of the error was random, model predictions were significantly biased, and most of the bias stemmed from the short-duration trials in which the model tended to overestimate rather than underestimate instantaneous growth rate.

A significant portion of the error in predicted mass gain during attachment was attributed to the difference in mass between the host and parasite prior to attachment. Specifically, host:parasite mass ratios below 20:1 led to a predicted mass increase that was greater than observed. This increase suggests that juvenile feeding is slower on smaller hosts and raises questions regarding whether feeding rate of juveniles is volitional. The difference in predicted results is not surprising since the model assumes that feeding rate during attachment is constant, regardless of host size. However, juveniles are more likely to fatally deplete blood supplies of smaller rather than larger hosts and do so more quickly (Farmer et al. 1975). Therefore, host:parasite mass ratios exceeding 20:1 may be optimal for rearing juveniles as it could encourage higher rates of feeding for longer periods of time. This is consistent with the conclusions of Farmer et al. (1975), which suggests a host:parasite ratio of at least 40:1 is necessary for host survival, with host survival time correlating with the rate of blood loss relative to blood volume. For example, Farmer et al. (1975) predict that Rainbow Trout and Lake Trout survive when $\leq 10\%$ of the host's blood volume is removed daily; that they survive ~ 14 days when 25% of blood volume is removed daily; and that, if blood removal rate approaches 100% per day, mortality occurs in less than two days. This may suggest that even if juveniles can alter their feeding rates, a large juvenile may be unable to lower the rate sufficiently to maintain host health, depending on the host's relative size. Therefore, in the context of rearing juveniles in captivity, access to large hosts may be important for scaling up sufficiently to maintain steady growth rates in a cohort of juveniles.

Error in predicted versus observed mass gain was also greater for four-day feeding bouts relative to those from one to three days; however, with fewer observations for feeding bouts of less than four days, this error may be a statistical artifact. In Cochran et al. (1999),

the greatest errors in predicted weight gain were observed during attachment bouts of less than five days, which they hypothesized was driven by variability in initiation time (the time between attachment and onset of feeding) and its proportionally greater influence on final mass when feeding bouts were less than four days. Initiation time is akin to handling time in the context of optimal foraging theory (e.g., King and Marshall 2022). To feed, a juvenile lamprey may need to rasp through the host's skin, remove scales, penetrate the musculature, and then generate anticoagulants to stimulate consistent blood flow (Renaud et al. 2009). The motivation to feed and these actions may take a varying amount of time between individual juveniles and their host species, thus decoupling the connection between attachment time and weight gain.

Interestingly, the location of an attachment on a host's body or even the type of mark induced (A or B) did not explain any of the error in difference between predicted and observed increase in mass during attachment as hypothesized by Farmer et al. (1975). Therefore, juveniles can access energy-dense food even when the skin is not broken, perhaps through the vacuum created by the oral disc. With the number of feeding trials investigated here being low, a lack of significance does not imply that mark type or location is not biologically important for juvenile growth but does imply that at least over short attachment bouts, juveniles are able to acquire high-quality food regardless of attachment location or type. Our observation supports the contention that both Type-A and Type-B marks may be useful for compilation of marking statistics since they both are generated by feeding juveniles. At present, only the number of Type-A marks per 100 fish is used by management agencies to direct control actions (Treska et al. 2021). Taken together, the ratio of the mass of the host relative to the mass of an attaching juvenile is perhaps more important for growth outcomes than attachment type or location.

Understanding weight loss during fasting bouts could be valuable for predicting what size juveniles will attain under different rearing conditions and the number and size of hosts to have available. We found that the lamprey bioenergetics model developed by Kitchell and Breck (1980) yielded unbiased estimates of juvenile mass at the end of the fasting period. However, we note that when fasting bouts were less than 10 days, the observed loss in mass tended to be greater than the predicted loss in mass. This tendency to slightly underpredict weight loss during shorter fasting bouts was likely due to egestion, excretion, and/or specific dynamic action occurring after a juvenile detached from the host trout. Because rates of egestion, excretion, and specific dynamic action were assumed to be zero for our bioenergetics-model simulation runs, the model apparently tended to slightly overestimate juvenile mass at the end of the fasting period for relatively short fasts. This type of error would be expected to substantially wane with increasing duration of a fast.

To the best of our knowledge, a portion of our study represented the first laboratory evaluation of the Kitchell and Breck (1980) bioenergetics model for lamprey, and our results indicated that the model provided a reasonably accurate accounting of the juvenile energy budget under fasting conditions. Significant bias in the model predictions of juvenile mass at the end of the fasting period was not detected. To more fully evaluate the model, water temperatures other than the 10 °C in our experiments should be tested. For the bulk of

the fasting trials, the influence of egestion, excretion, and specific dynamic-action effects was likely minimal such that the model yielded accurate estimates of juvenile mass at the end of fasting. In addition, observations of the juvenile behavior in laboratory tanks during fasting suggested that swimming activity was minimal, thereby supporting the contention that standard metabolic rate (SMR) was responsible for nearly all the energy expended during most of our fasting trials. Thus, the SMR component of the lamprey bioenergetics model appeared to be sufficiently accurate such that model predictions for fasting animals were not significantly biased. The SMR component was based on respiration-rate determinations of juveniles held in a laboratory respirometer (Beamish 1973; Kitchell and Breck 1980).

Uncertainties in parasite and host-fish biology can be addressed together in well-designed experiments and thereby minimize constraints on the availability of juveniles, host-fish welfare, laboratory space, and funding. Cochran et al. (1999) realized that a large data set funded by the Great Lakes Fishery Commission could be leveraged to better understand lamprey physiology and behavior. Likewise, we applied the rearing protocols of Smith et al. (2016) and Firkus et al. (2022) to the entire juvenile life stage and used the opportunity to test the predictive ability of bioenergetics models. In future work, newly generated data sets comprised of individual Sea Lamprey feeding data could be leveraged to further refine feeding protocols for specific rearing outcomes.

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Laboratory Rearing, Growth, and Bioenergetics of Parasitic Juvenile Sea Lamprey *Petromyzon marinus*

Nicholas S. Johnson, Sarah L. Alderman, Sean R. Avey, John B. Hume, and Charles P. Madenjian

