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What can commercial fishery data in the Great Lakes reveal about juvenile sea lamprey (*Petromyzon marinus*) ecology and management?

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ABSTRACT

The Laurentian Great Lakes of North America support a large and profitable freshwater fishery, but one continuously beset by parasitism from the invasive sea lamprey (*Petromyzon marinus*). Despite being the life stage that inflicts damage to the fishery, therefore necessitating a bi-national control program, our knowledge of juvenile sea lamprey ecology is poor and their response to control efforts are not assessed. Incidental capture of juvenile sea lamprey by commercial fishers is one means to collect data on this enigmatic life stage, and in Lake Huron such data have been collated since 1967. Here, we explore incidental captures of juvenile sea lamprey and their hosts from northern Lake Huron between 1987 and 2017 ($n = 33,246$ observations) to address four objectives. Firstly, we document collection efforts by fishers to provide historical context to the dataset. Secondly, we pose and test a series of questions related to fishery encounter, host selection, growth, distribution, and sex ratio to highlight how these types of data can be informative regarding juvenile sea lamprey ecology. Results presented here could be used to develop biological hypotheses to be addressed in future work. Thirdly, we directly assessed whether juvenile sea lamprey capture data could be useful in corroborating trends observed in adult sea lamprey abundance and wounding, as well as in identifying abundance and wounding hotspots. Lastly, we summarize research and outreach efforts that have benefited from the capture of juvenile sea lamprey in recent years.

Introduction

In the Laurentian Great Lakes of North America, parasitism of valuable fish stocks by juvenile sea lamprey (*Petromyzon marinus*) is a major concern for fishery managers. Consequently, sea lamprey are subject to a binational control program administered by the Great Lakes Fishery Commission (GLFC) and implemented by the Sea Lamprey Control Program (SLCP) and two control agents (U.S. Fish and Wildlife Service and Fisheries and Oceans Canada). The overarching control strategy is to reduce the number of juvenile sea lamprey encountering the fishery each year by employing barriers to block adult sea lamprey from accessing spawning habitat and applying pesticides to remove larval sea lamprey before they metamorphose into juveniles (Marsden and Siefkes, 2019). Despite being responsible for directly damaging the fishery, the juvenile life stage of sea lamprey is the one which we have least knowledge of. This stage is a biological "black box" that receives metamorphosed larvae and produces adults, but whose processes remain largely mysterious.

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Humans and juvenile sea lamprey tend to exhibit similar dietary preference for certain fishes and this overlap presents a significant opportunity to study this enigmatic life stage. For example, juvenile sea lamprey are seeking densely aggregated fishes with large volumes of blood and few scales; humans prefer to consume large-bodied fish with high aerobic capacity and muscle mass and which tend to form large shoals (Cochran, 1994). Thus, cooperation with a fishing fleet targeting potential juvenile sea lamprey hosts could provide a valuable source of data on juvenile foraging ecology, abundance, and impact on the Great Lakes fishery (e.g., Orlov and Baitaliuk, 2016). The SLCP has partnered with commercial fishers in the Great Lakes to gather incidentally caught juvenile sea lamprey and catch information since 1967. Johnson and Anderson (1980) summarized this collection effort from 1967 to 1978 in all five Great Lakes. Collection of juvenile sea lamprey in the Great Lakes has continued in recent decades and there is increasing interest in the ecology of juvenile lampreys in general, motivated by their potential to explain patterns of adult abundance and overall population health (Clemens et al., 2019; Hume et al., 2021a; Hume et al., 2021b; Lucas et al., 2020; Mateus et al., 2021; Quintella et al., 2021).

The purpose of this study is to explore a rich dataset from the Canadian waters of Lake Huron containing spatial, temporal, and biometric data for juvenile sea lamprey and their hosts from 1983 to 2017 in an update and extension of the work of Johnson and Anderson (1980). Our objectives are: 1) to document the collection effort and summarize those data collected since 1978; 2) to highlight the utility of such a dataset by asking a limited set of specific questions to reveal patterns in fishery encounter, host selectivity, growth, distribution, and sex ratio of juvenile sea lamprey that could be used to generate biological hypotheses and stimulate future research; 3) to describe how the data could be used to support sea lamprey control objectives; 4) to summarize the research and outreach output derived from this collection effort.

Juvenile sea lamprey collection program since 1978

In 1967, the SLCP began offering commercial fishers a reward of $1.00 (Canadian or U.S., according to country of origin) for each juvenile sea lamprey captured, in addition to information on the date, location, depth, gear, and species it was attached to (Johnson and Anderson, 1980). Currently, $7 is offered per capture. Juvenile sea lamprey collections have previously occurred in both Canada and the U.S., at times in all five Great Lakes. However, the collection effort and number of juvenile sea lamprey collected has varied by lake and year (Fig. 1). This variability is due to several factors, including changes in SLCP priorities, reduced numbers of commercial fishing licenses issued due to changes in fish communities, markets, and regulations, and fewer sea lamprey that can reduce incentive for collecting fewer juveniles.

In U.S. waters of the Great Lakes, juvenile sea lamprey collections occurred in Lakes Michigan, Huron, and Superior between 1969 and 1978 (Johnson and Anderson, 1980). Collections continued in Lakes Superior and Michigan until the early 1990's (GLFC, 1993; Fig. 1). In Lake Huron, collection efforts continued until 2003; however, catch records and biological data are not comprehensive for U.S. waters after 1978. In Canadian waters, collections of juvenile sea lamprey ceased in Lake Superior in 1985, Lake Ontario in 1986, and Lake Erie in 1991. However, collections in northern Lake Huron have continued for over 50 years (Fig. 1). Comprehensive capture data and biological information for juvenile sea lamprey are available from 1983 to 2017 in northern Lake Huron, providing the long-term dataset we explore in this study.

The commercial fishery in the Ontario waters of Lake Huron is managed by the Ontario Ministry of Natural Resources and Forestry (OMNRF), Upper Great Lakes Management Unit (UGLMU) in cooperation with commercial fishers and Indigenous communities throughout the basin. Licensed commercial fishers on Lake Huron are required to report fishing effort, catch, and harvest information. Fishing effort since 1984 has been variable for fishers cooperating in the sea lamprey collection program (Fig. 2a). The number of fishers has decreased: 14 fishers operated in 1985, nine in 1990, six in 2000, and four since 2008. The total annual length of gillnet used ranged from 12,248 km to 28,643 km but has not shown a consistent trend over the 35-year time period (Fig. 2b). The gear type and locations fished have remained generally similar in northern Lake Huron. The most used gear type was 4.5-, 4.75-, or 5-inch mesh gillnet (90% of the catch for all years), followed by trap nets, which are becoming more popular with some fishers. Dip nets and pound nets were sometimes used early in the time series.

The depth at which gear has been set since 1978 has varied, reflecting changes in the ecosystem and perhaps seasonal climate. On average, gear was set in deeper water during the late winter-early spring up to 2013, but no gear has been set at these times since, perhaps due to colder winters (December-February). In recent years, gear has been set in shallower water during spring (March-May) to find separation between lake whitefish (*Coregonus clupeaformis*) and rebounding populations of lake trout (*Salvelinus namaycush*), which tend to cohabit similar depths in the spring (David Carlson, commercial fisher, personal communication 2019). Depth of gear sets in the fall (September-November) has remained stable, perhaps due to lake whitefish spawning in similar habitats at this time of year, and in summer (June-August) gear set depths have been variable but showed no obvious trend.

Utility of commercial fishery data to reveal juvenile sea lamprey ecology

General methods

Data collection and preparation

When retrieving commercially valuable fish from Lake Huron with juvenile sea lamprey attached, fishers remove the sea lamprey and fasten plastic numbered tags to them with brass wire and store them in a 20 L pail with formaldehyde solution for preservation. Recorded data include tag number, capture date and location (fishery statistical district and grid number), gear used, mesh size (if gillnet), and host fish species. Capture data and preserved sea lamprey specimens are transferred to the Sea Lamprey Control Centre (SLCC), Sault Ste. Marie, Ontario at the end of each calendar year. For each preserved juvenile sea lamprey, SLCC staff record total length (TL, mm), weight (g), sex (male, female, unidentified), gut fullness (full, empty), and stage of sexual maturity (immature, maturing, and ripe). Host fishes were identified by fishers onboard and grouped to family or sub-family for analyses.

The juvenile sea lamprey collection effort database contained 45,593 unique observations (1 observation = a single row of data containing at least one record of a juvenile sea lamprey capture). Data used for analyses in this study were restricted to only those observations that included: juvenile sea lamprey sex (male or female), a condition factor $(K) < 6$ (calculated as $K = 100,000W/L^3$), host family or sub-family (Catostomidae, Coregoninae, Cyprinidae, Lotidae, Salmoninae), and fishery district (NC-1, NC-2, OH-1, corresponding to two portions of the North Channel and northern Main Basin of Lake Huron). Juvenile sea lamprey noted as having 'unidentified' sex were removed as it could not be determined if they would subsequently be classed 'male' or 'female'. Juvenile sea lamprey with a $K > 6$ were removed as this likely represents an error when recording length or weight; the cut off was determined by calculating mean and standard devia-

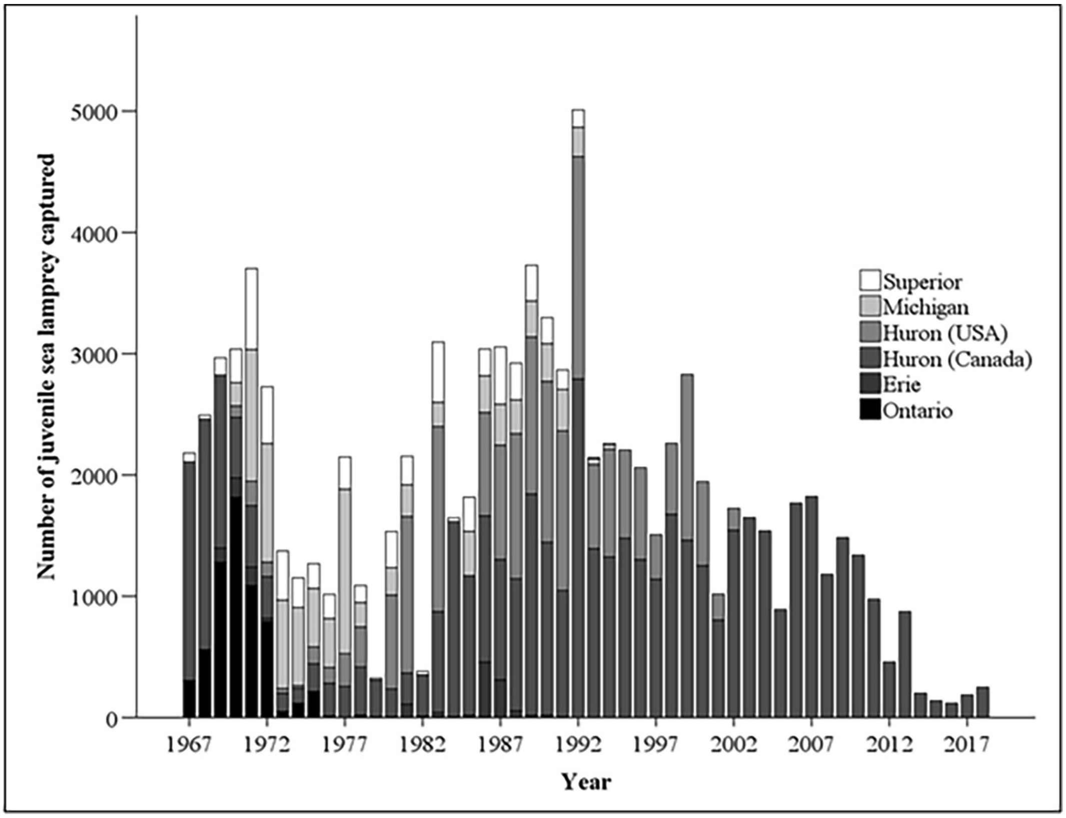

Fig. 1. Number of juvenile sea lamprey provided annually by cooperating commercial fishers in the Laurentian Great Lakes, 1967 to 2018. Captures for Lake Huron are separated by nation.

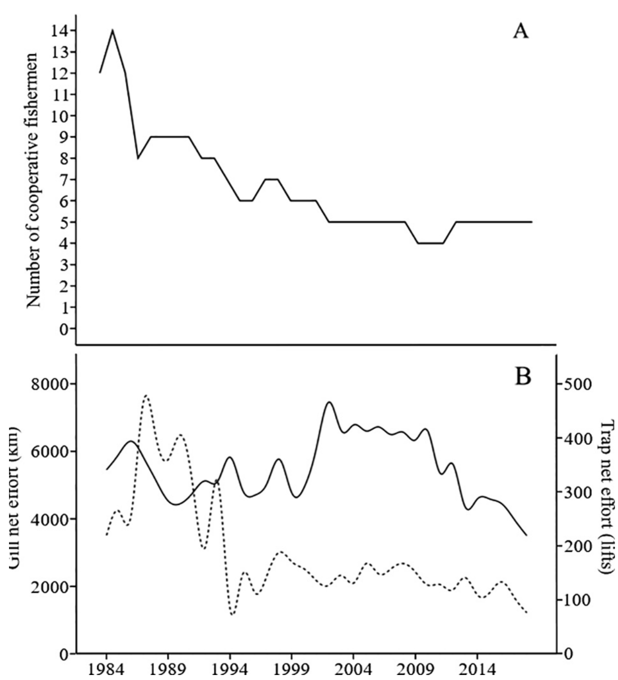

Fig. 2. Annual fishing effort in northern Lake Huron, 1984 to 2018. Panel A shows the number of licensed commercial fishers cooperating with the sea lamprey collection program; Panel B shows total effort for two gear types responsible for the majority of fish harvested in the region, gillnets (solid line) and trap nets (dashed line).

tion of *K* of juveniles in the dataset and excluding observations > *K* + 3*SD. Host identity and fishery districts were restricted to those with >500 observations. These steps reduced our total observations to 33,246 for use in analyses. Analyses were conducted in R (R Core Team, 2020) and IBM SPSS Statistics (v. 26).

Limitations and biases of the dataset

Despite providing a rich source of data, a commercial fishery does not provide a bias-free sample of a fish community. In this study, data were drawn from a fishery that now primarily targets lake whitefish. Gear selection, depth, and location were chosen nonrandomly, and the fish captured did not represent a random sample of potential hosts for juvenile sea lamprey. Consequently, certain potentially important hosts for juvenile sea lamprey were underrepresented in the dataset (e.g., large lake trout and burbot *Lota lota*). However, despite principally being considered a lake whitefish fishery since the year 2000 (~98% of the catch), this has not always been the case and fishers have quotas for several species (Adam Cottrill, OMNRF, personal communication, September 2020). Between 1985 and 2000, other fishes were regularly targeted, including suckers (*Catostomidae* spp.), yellow perch (*Perca flavescens*), bloater (*Coregonus hoyi*), walleye (*Sander vitreus*), and lake trout.

The fish community of Lake Huron has also changed over time and spatially. For example, lake trout abundance appears to be lower in certain parts of Lake Huron, which is another potential source of bias. However, we have included fishery data from both the North Channel (NC-1 and NC-2) and northern Main Basin (OH-1) of Lake Huron, which exhibit large differences in lake trout density to address this. Between 1979 and 2017 (oldest available to most recent datapoints used in this study) in the North Channel lake trout CPUE has averaged 7.27 (range = 2.35–13.29) compared to 16.87 (range = 1.06–92.1) in the northern Main Basin (Adam Cottrill, OMNR, personal communication, September 2020). Therefore, data presented in this study should be interpreted in the context of these limitations and biases.

Encounters with juvenile sea lamprey

- *Has the number of juvenile sea lamprey encountered by the fishery in northern Lake Huron changed over time?*

Declining or unpredictable captures of juvenile sea lamprey in many of the Great Lakes is one reason most collection efforts were discontinued by the 1990s. Despite consistently providing a source of juvenile sea lamprey to date, a similar decreasing trend in captures of juveniles in northern Lake Huron is suspected (Fig. 1). Based on a visual inspection of Fig. 1 we estimated that a decline may have started in the mid-2000s. To establish if there are fewer encounters with juvenile sea lamprey by the Lake Huron fishery and determine more precisely when this decline may have started, we performed a segmented (piecewise or broken-stick) linear regression on the number of juveniles captured over the time-series. The analysis was conducted using the *segmented* package in R (Muggeo, 2008).

The segmented regression estimated a breakpoint occurred at year 2006 (±1.86, $R^2 = 0.498$; Fig. 3). The slope prior to 2006 was positive (12.1) and after was negative (−149.4). This suggests that juvenile sea lamprey abundance has changed from gradually increasing (1983 to 2006) to sharply decreasing (2006–2017). A decline in juvenile sea lamprey captured by the fishery since the mid-2000s could reflect either a real change in their abundance, or a change in fishery operation that altered the likelihood of encounters. Changes to the depths of nets being set in winter or spring did not occur until the mid-2010s, which is several years after the decline initiated. Therefore, changes in fishery practices are an unsatisfactory explanation for the observed decline. However, it has been suggested that declines in abundance may be overestimated as fishers could be less likely to report juvenile captures if there are relatively few (Johnson and Anderson, 1980). The proximity of the St. Marys River to the fishery districts included in this study (NC-1, NC-2, OH-2) could strongly influence capture rates of juveniles. Beginning in the early 2000s, periodic largescale treatments of the St. Marys River with pesticide began, alongside annual pesticide applications, release of sterile males, and annual adult removal through trapping (Bravener and Twohey, 2016). A thorough examination of the hypothesis that changes in control efforts in the St. Marys River effect juvenile sea lamprey abundance is presented below (see *Management Applications*).

- *When does the fishery encounter juvenile sea lamprey?*

Larval sea lamprey complete metamorphosis by October-November, followed by downstream dispersal to the lakes to begin feeding as juveniles. Dispersal is correlated with increasing stream discharge and there are typically peaks in this outmigration coinciding with periods of extensive rainfall and snowmelt (Applegate and Brynildson, 1952; Hanson and Swink, 1989; Sotola et al. 2018). However, precisely when juvenile sea lamprey begin feeding in Lake Huron remains uncertain.

Visual inspection of a length-frequency plot of juvenile sea lamprey captured in different seasons (Fig. 4) indicates the presence of recently metamorphosed individuals (≤200 mm TL) within the fishery in spring (March-May) and winter (December-February), with fewer small juveniles captured during fall (September-November). Plotting the frequency of the smallest juveniles (range = 112–200, $n = 3066$) over Julian day (Fig. 5) indicates most sea lamprey juveniles are first encountered by the fishery between JD 110–200 (3rd week in April to 3rd week in July). There is a second pronounced peak between JD 320–360 (mid-November to late-December), followed by a steady rate of encounter with small juveniles through the winter and early-spring.

Fishers capturing recently metamorphosed juvenile sea lamprey more frequently in spring could be due to shallower gear sets during this period, compared to deeper sets in fall or winter. However, in our dataset winter gear sets averaged 24 m ($n = 439$) and spring 28 m ($n = 1378$) indicating this marginal difference in fishery effort is unlikely to explain the observed pattern. Based on an extensive, multi-year collection of out-migrating sea lamprey in a tributary of northern Lake Michigan, Applegate and Brynildson (1952) concluded most juveniles move into the lake during spring floods with additional pulses responding to increased precipitation in the fall and mid-winter thaws. Our data aligns with the observations of Applegate and Brynildson (1952) and suggests recently metamorphosed sea lamprey in Lake Huron rapidly locate potential hosts upon entering the lake and could initiate feeding either in spring or late-fall to early-winter.

Host selectivity

- *Does host selection change as juvenile sea lamprey grow larger?*

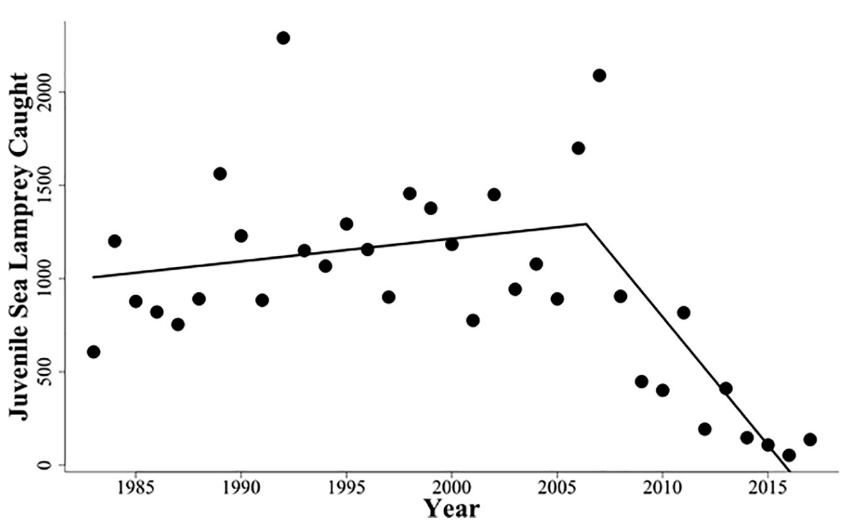

Fig. 3. Juvenile sea lamprey captured by year. Black line = predicted fit of segmented regression.

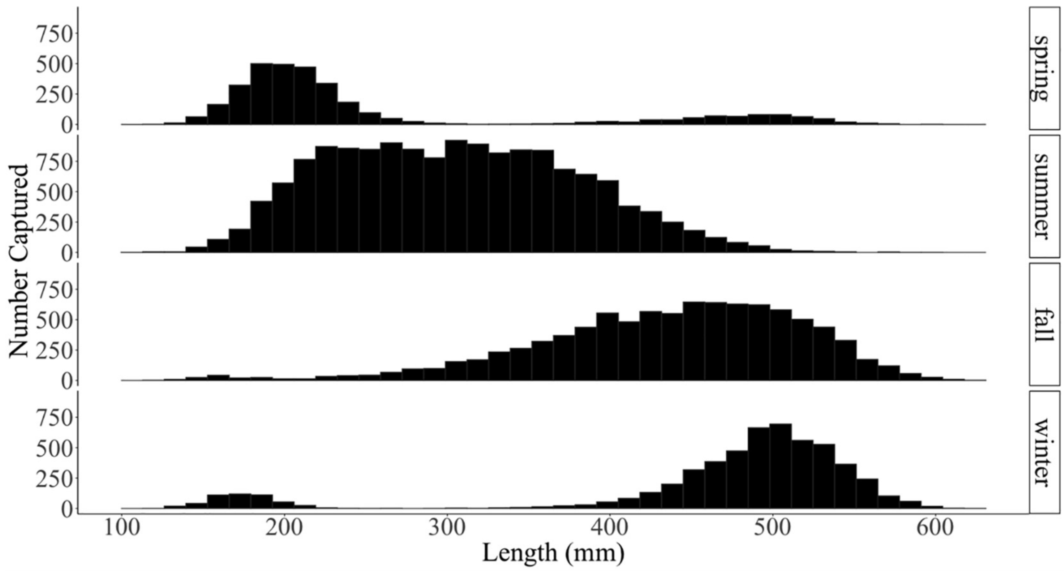

Fig. 4. Length distribution (total length, TL) of juvenile sea lamprey by season.

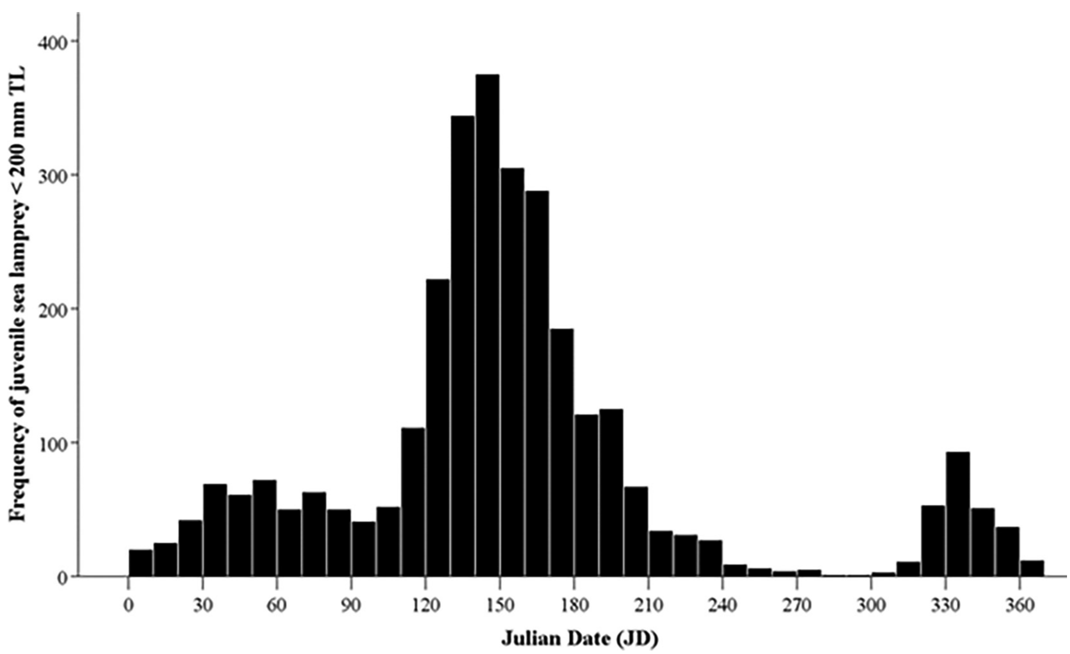

Fig. 5. Length distribution (total length, TL) of newly transformed sea lamprey captured by the Lake Huron fishery throughout as a function of Julian day.

Juvenile sea lamprey are capable of feeding parasitically as soon as metamorphosis is complete (Manzon et al., 2015; see above *Encounters with juvenile sea lamprey*), and at least in marine environments 10 – 30% of small juveniles remain in nearshore habitats to feed for several months before locating larger hosts offshore (Silva et al., 2013). If a similar feeding strategy was expressed by sea lamprey in the Great Lakes, we should expect to see a shift in host selection as juveniles increase in size, from fishes inhabiting littoral or shallow nearshore habitats to deep water or pelagic species. Plotting the proportion of hosts selected by juvenile sea lamprey across 10 mm TL size bins (range = 112–630; Fig. 6) reveals patterns that could support the findings of Silva et al. (2013). Only one observation was available for the 110–120 bin, and two observations for the 630–640 bin so values for those juvenile sea lamprey are not discussed below.

In the North Channel (NC-1 and NC-2, n_{obs} = 20,965) the majority of juvenile sea lamprey were found attached to coregonines across all sizes bins (76–88%), followed by salmonines (2–16%), and catostomids (2–12%). Juvenile sea lamprey were more commonly attached to burbot and cyprinids in the North Channel once they reached ~360 mm TL, but generally encompassed only small proportions of attachments to hosts (0–5% and 0–5%, respectively). In the northern Main Basin (OH-1, n_{obs} = 12,256), juvenile sea lamprey exhibited a different pattern of host selection. Attachments to coregonines were still the most frequently observed within sea lamprey size bins (36–88%), particularly among juveniles larger than ~380 mm TL. However, cyprinids and salmonines were selected by greater proportions of juvenile sea lamprey in the northern Main Basin compared to the North Channel (0–44% and 6–28%, respectively). Higher proportions of juveniles were also

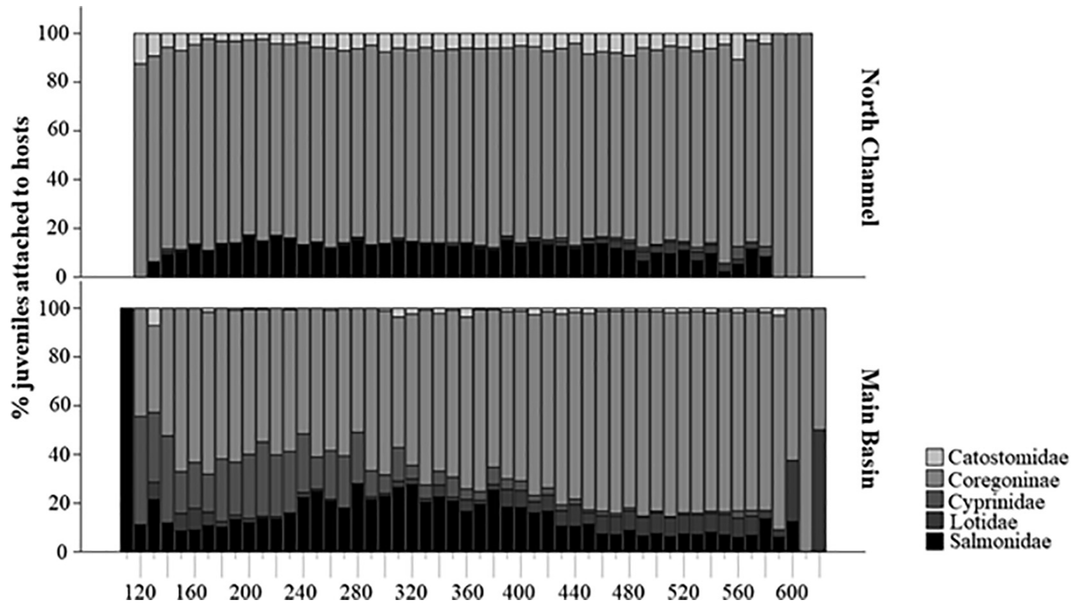

Fig. 6. Percent of juvenile sea lamprey attached to hosts in northern Lake Huron, with sea lamprey placed in 10 mm size bins (112 – 630 TL mm).

attached to burbot in the northern Main Channel (0–9%), particularly in sizes greater than ~340 mm TL. Almost the opposite trend was observed for proportions of juveniles attached to cyprinids, with attachments appearing to decline as juvenile sea lamprey reached ~380 mm TL.

Juvenile sea lamprey have been observed, or inferred to have fed on, most fish species in the Great Lakes (Christie and Kolenosky, 1980; Johnson and Anderson, 1980; Smith and Tibbles, 1980). Combined with recent diet assimilation studies, juvenile sea lamprey are likely pursuing a generalist feeding strategy at the population level, with some evidence for host preference within lakes (Harvey et al., 2008; Happel et al., 2017), or in response to changes in host abundance (Adams and Jones, 2021). Our data suggest that, in the northern Main Basin of Lake Huron, at least a proportion of recently metamorphosed sea lamprey feed on cyprinids for the first few months of their juvenile life stage, possibly in shallow nearshore environments. It also may be the case that as they reach a certain size some juveniles move to deeper water to feed on burbot. Whether and how host selection in the wild impacts growth of sea lamprey remains uncertain, but coregonines are apparently preferred in both the North Channel and northern Main Basin of Lake Huron. Host preference could, in general, be tracking abundance in these areas (Adams and Jones, 2021), with more abundant coregonines in the North Channel attracting a greater proportion of juveniles. Alternatively, these proportions reflect the likelihood of capturing hosts by the fishery and are therefore not reflective of true selectivity. In addition, there is no evidence from these data that juvenile sea lamprey systematically switch to feeding on lake trout as they grow larger, as the majority of juveniles equivalent in size to adults undertaking spawning migrations were observed feeding on coregonines in both lake regions. However, it should be reiterated that the observations of hosts in this study are likely to under sample large lake trout.

- *Is there a cost to juvenile sea lamprey selecting certain hosts?*

Juvenile sea lamprey in the Great Lakes are likely to be highly efficient feeders due to their ability to reach a maximum size of ~650 mm TL in a relatively short period of time (12–20 months; Renaud and Cochran, 2019). Two factors influence feeding efficiency, the time lag and energy expended between feeding bouts, and both are a function of host density, aggregation tendencies, and scale or skin thickness (Cochran, 1994). Therefore, foraging juvenile sea lamprey should seek a high density of hosts with a tendency to aggregate, and which bear few or no scales. However, many fish species are frequently parasitized by sea lamprey in the Great Lakes (e.g., Harvey et al., 2008; Happel et al., 2017). It is possible that inter-individual variation in host selection is at least partly responsible for the observed variation in adult sea lamprey size, but this has not been explored previously.

As noted previously most juvenile sea lamprey enter the Great Lakes in two pulses, spring and winter (see *Encounters with juvenile sea lamprey*). To examine a single cohort therefore requires excluding those individuals likely to spawn in spring (>400 mm TL) and newly metamorphosed individuals entering the lake in late-fall through winter (<200 mm TL). We removed individuals captured in the spring that were >400 mm TL and individuals captured in the winter that were <200 mm TL from the data. Removing these observations from our dataset (n = 1066) reduced the total number of observations for additional analyses to 32,180. We compared total body length of sea lamprey observed feeding on different hosts using a linear mixed effects model with host species as a fixed effect and fishery statistical district and year as random effects. We used Tukey's HSD to test for differences within seasons. To reduce unwanted comparisons between seasons, models were fit separately for each season.

No statistically significant differences in TL of juvenile sea lamprey feeding on different hosts were observed in spring, but juveniles feeding on cyprinids during summer were significantly smaller ($P < 0.0001$) than sea lamprey observed on catostomids (−44 mm), coregonines (−34 mm), burbot (−67 mm), and salmonines (−39 mm) (Fig. 7). Whereas juveniles found attached to burbot (+33 mm, $P = 0.032$) and catostomids (+9 mm, $P = 0.013$) were significantly larger than those feeding on coregonines. During fall months, juvenile sea lamprey attached to burbot were still the largest group, significantly larger ($P < 0.0001$) than those observed on catostomids (+28 mm), coregonines (+21 mm), and salmonines (+41 mm). Salmonine-feeding juveniles were significantly smaller than juveniles attached to catostomids (−14 mm, $P = 0.007$), coregonines (−21 mm, $P < 0.0001$), or cyprinids (−31 mm, $P = 0.0002$). Juvenile sea lamprey attached to cypri-

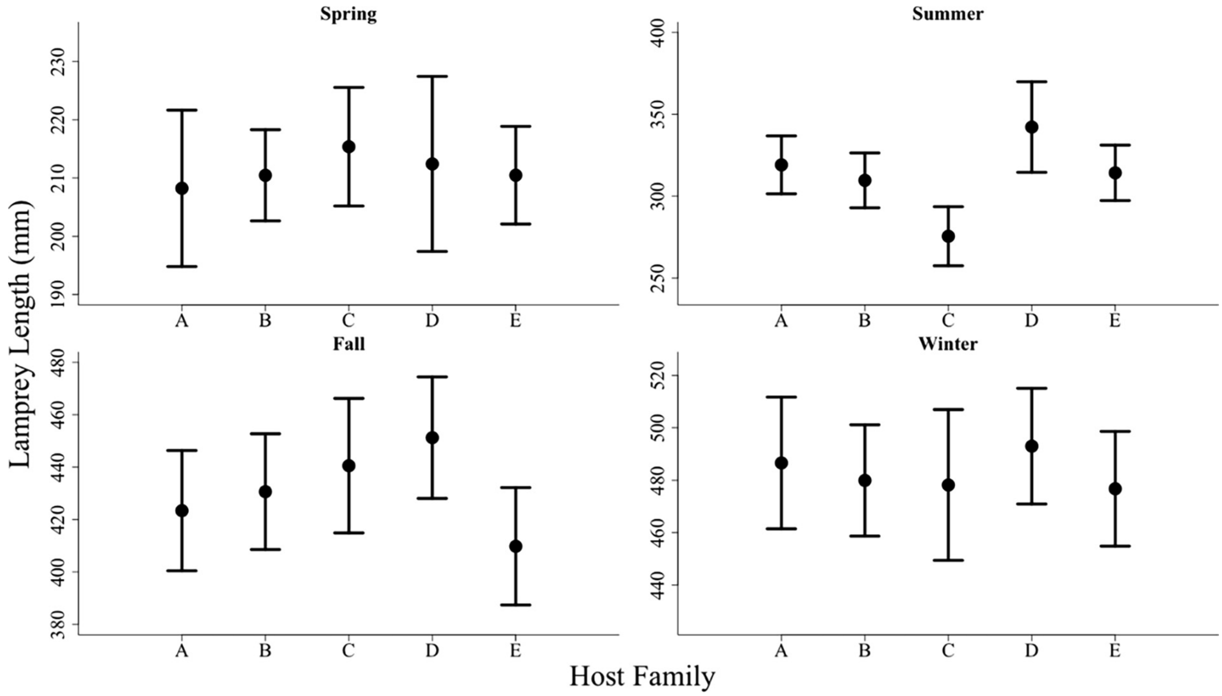

Fig. 7. Body size of juvenile sea lamprey observed on different hosts across seasons (A = Catostomidae, B = Coregoninae, C = Cyprindae, D = Lotidae, E = Salmoninae). Whiskers = 95 CI of means.

nids in the fall were 165 mm larger than those attached to the same fishes in summer. In winter months size differences among juveniles attached to different hosts have mostly disappeared, except sea lamprey observed on burbot remain significantly larger than those on coregonines (+13 mm, $P = 0.0007$) and salmonines (+16 mm, $P = 0.002$).

Based on these data, juvenile sea lamprey begin feeding on different host species at approximately the same size. However, individuals selecting cyprinids in the spring following metamorphosis grow slowly compared to other hosts. During fall, juveniles feeding on cyprinids are far larger than those in the spring-summer, indicating they either experienced a large growth rate increase that enables them to catch up with juveniles feeding on other hosts, or this represents a whole new group of juveniles newly attracted to cyprinids. These patterns could indicate that smaller juvenile sea lamprey feed ineffectively on cyprinids, potentially due to the presence of heavy scales that increase prey handling times (Cochran, 1994). As juveniles increase in size, they perhaps feed on cyprinids more effectively due to better penetration of the scales and skin, and they would also have access to large numbers of densely aggregated hosts reducing lag between feeding bouts (Cochran, 1994). These data also suggest even the smallest juvenile sea lamprey can feed effectively on burbot, likely due to the presence of very small scales reducing prey handling time. However, as the sea lamprey-host body size ratio declines as we progress toward winter, the rate of blood consumption may also decline (Madenjian et al., 2003), rendering even large hosts like burbot less profitable.

Growth

- *Does lake temperature influence juvenile sea lamprey body size and condition?*

Juvenile sea lamprey growth increases linearly through summer in Lake Huron, with a sharper upward inflection in fall (Bergstedt and Swink, 1995). The increase in fall growth rate is suspected to be related to water temperature and an increase in appetite of juvenile sea lamprey brought on by gonadal development. Understanding changes in juvenile sea lamprey size (body length) and condition in response to environmental change, including differences between sexes and seasons, could be important to improve individual-based models of feeding and better estimate the effect of sea lamprey on the fishery.

Mean daily surface temperature data of Lake Huron was obtained from NOAA buoy 45,003 (45.351 N, 82.840 W), and covered the time period April 1984 to December 2017. To examine the relationship between juvenile sea lamprey size (TL, mm) and mean seasonal temperature (°C) of Lake Huron, a linear regression was fit to juvenile length with mean seasonal temperature, sex, season of capture, and year as fixed effects. Additionally, interaction effects of mean seasonal temperature and sex, and sex and season of capture were included in the model. The relationship between average seasonal temperature of Lake Huron and condition factor (K) of juvenile sea lamprey was examined using a linear regression fit to K with mean seasonal water surface temperature, sex, season of capture, and year as fixed effects, and interaction effects of season of capture and sex, and seasonal mean temperature and sex. Tukey's HSD test was performed for means separation and group comparisons.

The sex by season of capture interaction, the sex by mean seasonal temperature interaction, and year were all statistically significant predictors of juvenile sea lamprey TL ($R^2 = 0.584$; $P < 0.05$). Total length varied significantly by sex in all months, except winter (Fig. 8). We expect length to vary by season and so those results are not reported or discussed. For the condition factor model, sex, season of capture, and year were significant ($R^2 = 0.054$; $P < 0.05$). Mean seasonal temperature was not a significant predictor of juvenile sea lamprey condition factor ($P = 0.72$). Our results show that K increases from spring to winter, and male juvenile sea lamprey have a significantly higher K value than females during summer and fall ($P < 0.05$, Fig. 9). Juveniles of either sex do not differ in mean K between spring and winter. Within each sex, condition factor is significantly different in all season comparisons, except for summer and fall (Fig. 9).

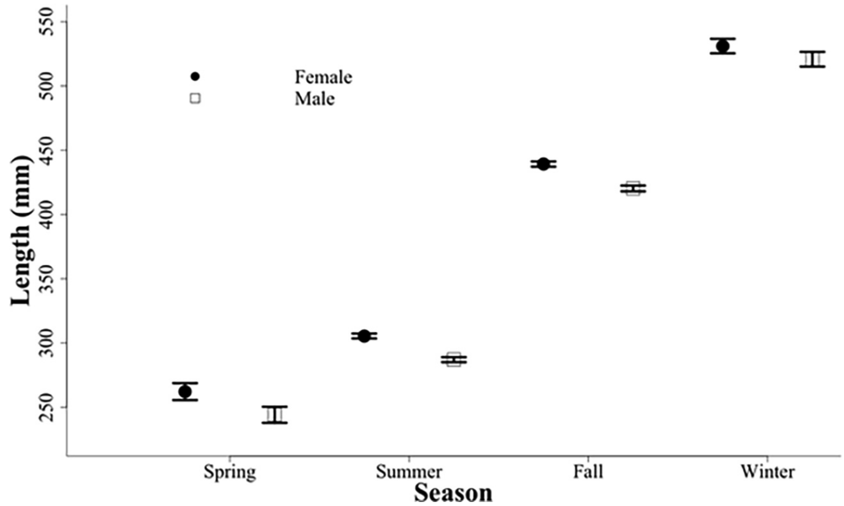

Fig. 8. Estimated average length of juvenile sea lamprey by sex and season. Females are black circles, males are hollow boxes. Error bars are the confidence intervals.

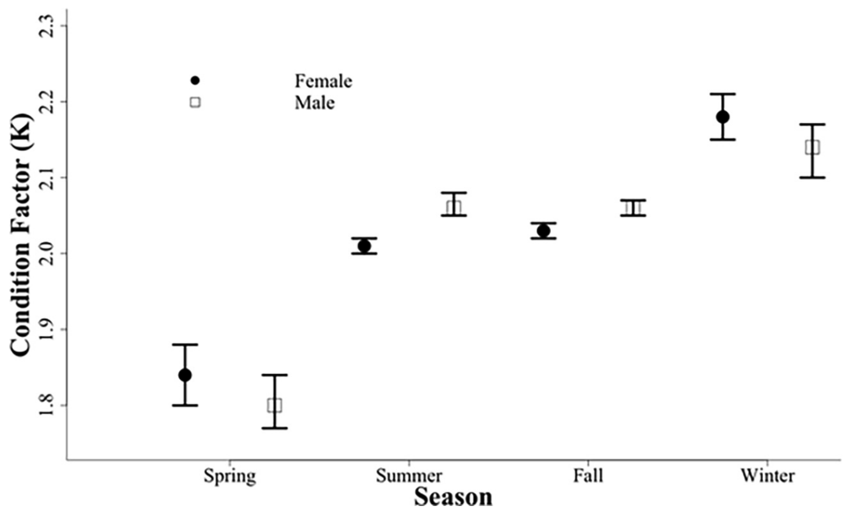

Fig. 9. Average condition factor of juvenile sea lamprey across seasons and between sexes. Females are black circles, males are hollow boxes. Error bars are the confidence intervals.

Water temperature in Lake Huron has a clear effect on juvenile sea lamprey growth (Bergstedt and Swink, 1995; Cline et al., 2014; Gambicki and Steinhart, 2017). Female juvenile sea lamprey are consistently larger than males, but average condition factor does not differ substantially between the sexes. However, condition factor does vary among seasons and is lowest in the spring. Juvenile sea lamprey exhibiting poorer condition in the spring is consistent with a prolonged fasting period during metamorphosis and the outmigration, and the depletion of lipid reserves stored during the larval life stage (Manzon et al., 2015). Females are consistently larger than male juveniles perhaps indicating that female larval sea lamprey initiate metamorphosis later than males, potentially not entering the lakes until one full year after males (Docker et al., 2019). Seasonal differences in condition factor between the sexes in summer and fall appear consistent with a later onset of sexual maturation in females, which rapidly increase oocyte size following entry into spawning tributaries (Docker et al., 2019).

Since 1980, the mean annual size of adult sea lamprey captured during the spawning migration in tributaries to Lake Superior has positively correlated with increasing surface water temperatures in the lake (Cline et al., 2014). A recent study found that surface water temperature in Lake Huron has increased significantly between 1948 and 2004, as it has in Lake Superior (Hume et al., 2021b). Predicting the effect of climate change on the management of sea lamprey has become an urgent concern (Gambicki and Steinhart, 2017; Lennox et al., 2020), and knowledge of how the juvenile life stage responds to this stress could help guide future decision making. Juvenile sea lamprey are hypothesized to feed at a greater rate in warmer water conditions (Swink, 2003), which could result in more frequent host attachments, higher mortality, and an overall greater increase in size during the juvenile period (Cline et al., 2014; Kitchell et al., 2014; but see Madenjian et al., 2003). The mechanism underpinning the positive relationship between water temperature and juvenile condition factor remains unclear and may stem from a greater number of optimal growing degree-days, improved host condition, broader thermal preferenda, or some mixture of these and other factors (Hume et al., 2021b). Regardless, our data appear to support a consensus that warmer waters will result in higher juvenile growth rates (Hansen et al., 2016; Lennox et al., 2020).

Distribution

- *Do male and female sea lamprey segregate during the juvenile parasitic phase?*

In the Great Lakes, juvenile sea lamprey have been captured from the surface to the deepest areas that have been fished, suggesting depth is not a constraint on distribution in this system (Johnson and Anderson, 1980). Typically, juveniles have been recovered from water <40 m deep because that is the strata commonly targeted by commercial fishers. However, we do not have any understanding of whether the sexes follow separate foraging strategies while in the lakes, a common ecological trait that can reduce within-species competition. Knowledge of sex-specific behaviors are important to accurately construct individual-based models of sea lamprey feeding (Madenjian et al., 2003).

To test for segregation between the sexes, we fit a linear mixed effects model with depth as the response variable, season and sex as fixed effects, and host family and fishery statistical district as random effects. We performed Tukey's HSD to test for differences within and between seasons. During spring, male and female juvenile sea lamprey were captured at similar depths (~30 m) but were found at different depths during other seasons ($P < 0.05$, Fig. 10). Females were captured at shallower depths in summer through winter compared to males (27.2, 25.6, 40.8 m compared to 28, 27.6, 42.4 m). In winter, both sexes were captured in deeper water compared to other times of year, by as much as 15 m. Male juveniles in the summer and fall were collected from similar depths, but all other comparisons of sexes between seasons were statistically significantly different ($P < 0.0001$).

Johnson and Anderson, (1980) hypothesized that male and female sea lamprey segregate into different habitats during the juvenile life stage and that this segregation develops in spring or early summer, with females found in deeper water and males shallower. Our data support the possibility of segregation between the sexes, but we found that it is females that were captured in shallower water, with both sexes then moving to deeper areas as the surface waters cool in fall-winter. Females may typically remain in shallower water to feed on different species than males, to take advantage of a more rapidly warming environment in the spring or mitigate energy expenditure prior to the spawning migration. Juvenile females in Lake Huron are larger than males (Fig. 8), which could be consistent with females tracking hosts or thermal preferenda for optimal growth. However, the magnitude of differences in depth between sexes is small and capture of juvenile sea lamprey is contingent on where fishery gears are set.

Sex ratio

- *Does juvenile sea lamprey sex ratio change through time?*

The sex ratio of juvenile sea lamprey in the Great Lakes appears highly variable, although data are scant (Docker et al., 2019). Potentially, the availability of hosts (abundance and community composition) could have influenced shifts in observed adult sea lamprey sex ratio during the juvenile life stage (Docker et al., 2019). As sea lamprey abundance increased in the Great Lakes, there were coincident declines in host abundance and adult sea lamprey body size, a relationship that was inverted as sea lamprey abundance decreased following onset of control (Marsden and Siefkes, 2019). Docker et al. (2019) speculate that female mortality rates during the juvenile stage may have increased as host abundance decreased, due to higher energetic costs associated with the maturation of ovaries. As hosts became more abundant, sea lamprey body size increased again and females became the predominant sex, suggesting female survival began to outstrip that of males. The proximate causes of these observed sex ratio shifts remain unknown. Here, we explore the shift in sex ratio of juvenile sea lamprey as they grow, as well as within and across years, to elucidate any consistent patterns.

Firstly, we plotted the proportion of female juvenile sea lamprey across 10 mm TL size bins (range = 112–630) to examine whether females became more abundant in the population as cohorts grew. To test for differences in sex ratio based on season of capture, length, and year, we fit a binomial generalized linear model with proportion female (sex) as the response variable and season of capture, length, and year as fixed effects and interactions between length and year, and length and season of capture. Year was treated as a categorical factor. We used Tukey's HSD test to detect differences between the seasons. We did not perform any post hoc analyses to detect differences between years due to the large number of comparisons with little interpretable meaning.

The effect of length, season of capture, year, and the two interaction effects (length and year, and length and season) were all statistically significant ($P < 0.05$; Fig. 11). The effect of total length was positive (mean = 0.001, SE = 0.0007). From visual inspection of Fig. 12 it is apparent that the proportion of female juvenile sea lamprey increased as body size (TL) increased. Juveniles < 360 mm

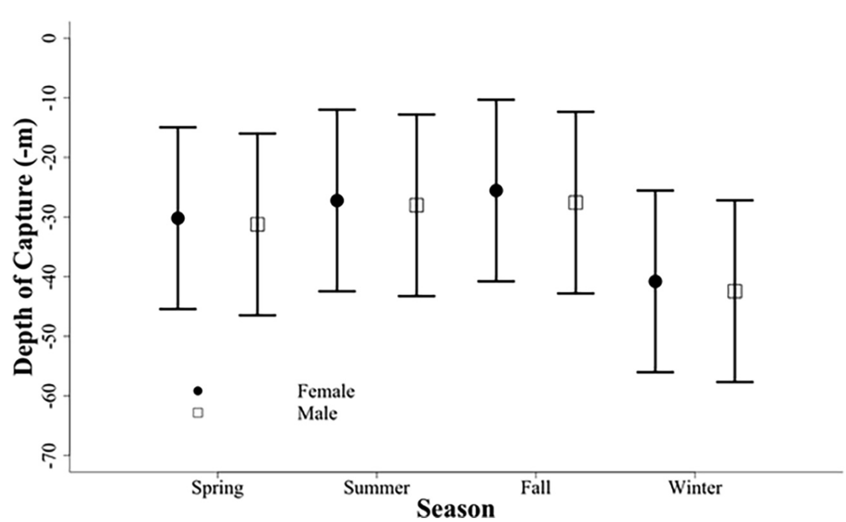

Fig. 10. Estimated depth of capture (-m) of juvenile sea lamprey by season and sex. Females are black circles, males are hollow boxes. Error bars are the 95% confidence intervals.

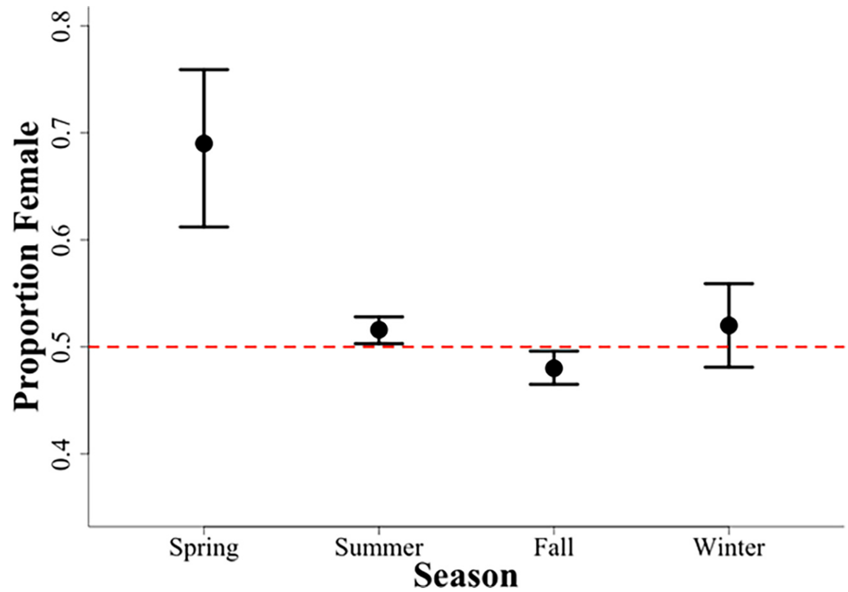

Fig. 11. Estimated proportion of juvenile sea lamprey population that is female by season. Error bars are 95% confidence intervals. Dashed line = 50%.

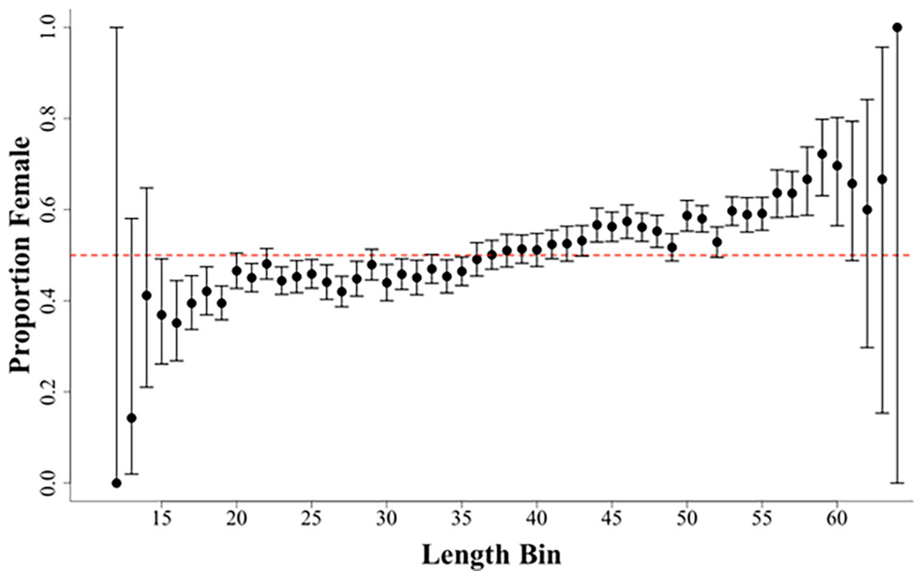

Fig. 12. Proportion female by total size of juvenile sea lamprey. Length bins were created by dividing TL by 10 and rounding the value to zero decimal places. Error bars are the 95% confidence intervals. Dashed line = 50%.

TL were male biased, and became increasingly female biased above this size. Conversely, as each year progresses female sea lamprey become less common in the juvenile population (Fig. 13). Juveniles were statistically more likely to be female in the spring vs all other seasons. The estimated proportion of females was significantly different for all season comparisons except fall and winter, and summer and winter ($P = 0.23$ and $P = 0.99$, respectively; Fig. 13). During spring, females comprised 0.69 of the population. This decreased to 0.51 in the summer, and 0.48 in the fall. When comparing sex ratio across years, males became the more common sex after 1996, before which the population was consistently female biased (Fig. 13).

Docker et al. (2019) concluded that, in general, male sea lamprey in the Great Lakes metamorphose, out-migrate, initiate and stop feeding earlier than females. This view is consistent with both our data showing larger proportions of females in larger size classes of juvenile sea lamprey, as well as our data on seasonal trends in sex ratio. Johnson and Anderson (1980) similarly presented data that suggests males are more frequently encountered in spring-early summer compared to late-summer or fall. The shift in sex ratio over the time series (1983 to 2017) is equally pronounced, but less simple to interpret. The St. Marys River, a connecting channel between Lakes Superior and Huron, has been the suspected primary producer of juvenile sea lamprey in Lake Huron since the 1980s (Young et al., 1996). In response to an explosion of the juvenile population in northern Lake Huron, itself probably responding to increased host abundance and better larval rearing conditions, an integrated control plan (trapping adults, sterile-male-release, and Bayluscide applications) was implemented in the St. Marys River in 1997 (Jones et al., 2015; Bravener and Twohey, 2016). Large Bayluscide treatments to target larvae occurred in 1999, 2010, and 2011, with smaller treatments occur-

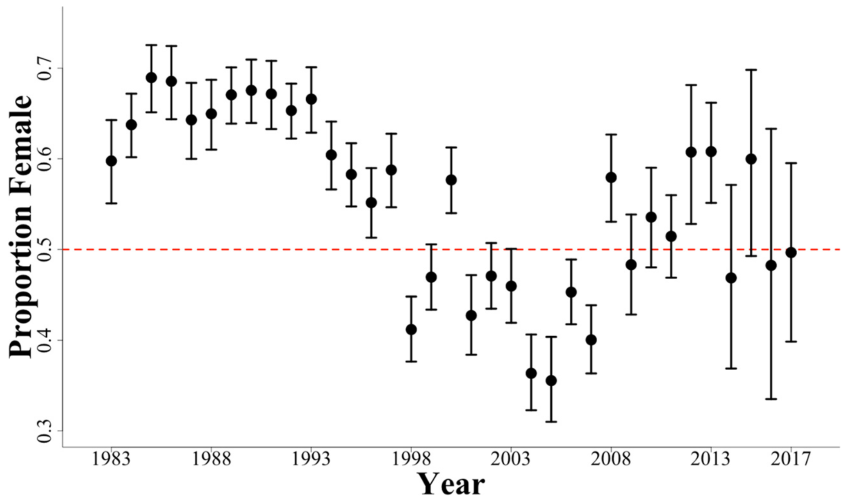

Fig. 13. Estimated proportion of juvenile sea lamprey population that is female from 1983 to 2017. Error bars are the 95% confidence intervals. Dashed line = 50%.

ring between 2005 and 2009 (Bravener and Twohey, 2016). The timing of the implementation of this integrated control program corresponds to the large-scale shift in sex ratio observed in the juvenile population. Prior to the first Bayluscide treatment (1999) juveniles were female-biased, suggesting female mortality may have been low at this time, and possibly responding to low density conditions in the St. Marys River, an increasing host population, or both (Docker et al., 2019). Pesticide applications are targeted toward removing larval populations the year before they are expected to metamorphose. Following the onset of Bayluscide treatments, juveniles became male-biased through most of the 2000s, which could support the hypothesis that female sea lamprey metamorphose later than males, and thus experienced proportionally higher rates of mortality due to pesticide applications in the St. Mary's River.

Management applications

At present, the SLCP uses two annual metrics to monitor sea lamprey abundance and damage in each of the Great Lakes: indices of adult sea lamprey abundance (Adams et al., 2021), and the number of sea lamprey-induced wounds per 100 lake trout (Treska et al., 2021). These metrics should be correlated and complement each other, assuming host abundance, host preference, and spawning stream preference is constant across years. However, in several Great Lakes these metrics are not correlated, and it is not clear why (GLFC annual report, 2018; Adams et al., 2020), although a recent analysis shows that mismatches may be related to prey switching by juvenile sea lamprey when certain hosts are at low abundance (Adams and Jones, 2021).

Captures of juvenile sea lamprey in the commercial fishery of northern Lake Huron could be useful for tracking changes in sea lamprey abundance and sea lamprey-induced damage to the fishery for three reasons: 1) corroborating trends observed in indices of adult sea lamprey abundance and wounding, 2) identifying localized areas of high sea lamprey abundance and wounding, due to management actions or a lack thereof, and 3) determining if host switching is occurring in northern Lake Huron. The first two will be examined briefly here; the third would require more information on host abundance (see *Host Selectivity*; Adams and Jones, 2021).

- *Corroborating trends in observed sea lamprey abundance and wounding*

Juvenile sea lamprey captures could be used to develop an index of juvenile sea lamprey abundance (catch-per-unit-effort, CPUE) to compare with the index of adult sea lamprey abundance. Adult index values are calculated annually using the sum of mark-recapture estimates in 5 – 7 trapped index streams per lake (Adams et al., 2021). This method of tracking adult abundance is used as a surrogate to estimate the population size of juveniles feeding within each lake (Mullett et al., 2003). Therefore, estimating the abundance of juvenile sea lamprey in each lake would be the most direct way of assessing the effectiveness of management actions. Researchers have previously attempted to develop estimates of juvenile abundance by conducting mark-recapture studies: once using recently metamorphosed individuals, and another using juveniles that were captured by the fishery (Bergstedt et al., 2003; Young et al., 2003). In both cases, abundance estimates of juvenile sea lamprey were nearly 10-fold greater than estimates of adult abundance and were considered unreliable because of suspected mortality of the marked population due to handling stress (Bergstedt et al., 2003). Here, we test the hypothesis that CPUE of juvenile sea lamprey by commercial fishers in northern Lake Huron is correlated with the index of adult sea lamprey abundance in Lake Huron (Adams et al., 2021).

Juvenile sea lamprey CPUE was calculated as the total number of juveniles collected in gillnets by participating commercial fishers, divided by the total km of gillnet set per night. Sea lamprey collected by anything other than gillnets (average of 4% of total catch year^{-1}) were not included. Fishers occasionally did not participate for the entire calendar year and in this case the effort or catch was subtracted. We fit a general linear model to adult sea lamprey abundance in Lake Huron with CPUE of juvenile sea lamprey, number of fishers in the fishery, and year as predictors. Year was included in the model to test for a year effect and number of fishers was included to account for the decrease in number of cooperating fishers in juvenile sea lamprey collections (Fig. 2a).

The results of our model suggest that CPUE of juvenile sea lamprey is a statistically significant predictor of adult sea lamprey abundance in Lake Huron ($P = 0.03$; Fig. 14). The effect of juvenile CPUE was positive, while the effect of number of fishers and year were both negative. These results support the hypothesis that the index of adult sea lamprey abundance accurately reflects the abundance of juvenile sea lamprey in Lake Huron. One advantage of evaluating CPUE of juvenile sea lamprey is that it can be calculated a year earlier than the adult index, providing an "early-warning" that could be used in situations where control barriers

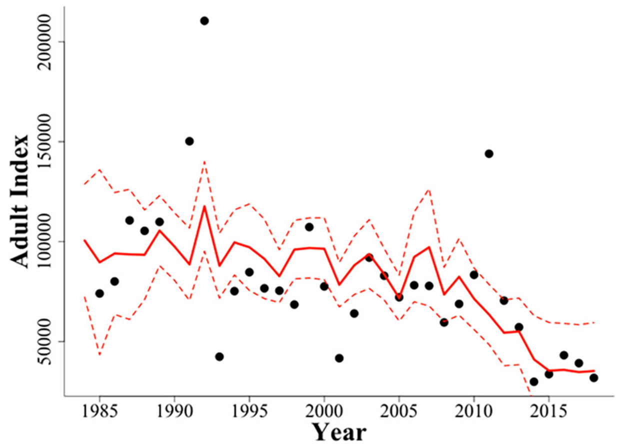

Fig. 14. Sea lamprey adult index of abundance by year. Solid line is the predicted fit of a general linear model for adult index with juvenile CPUE, number of fishers in the fishery, and year as predictors. Dashed lines are the 95% confidence intervals.

or traps are expected to function at lower efficiencies (e.g., high flows in spring, Hume et al., 2021b).

- *Identifying localized areas of high sea lamprey abundance*

Both the index of adult abundance and the index of juvenile abundance showed a marked decrease between 2011 and 2017, suggesting a dramatic change in the population of sea lamprey in northern Lake Huron (Fig. 3). The index of juvenile sea lamprey abundance has been an assessment metric for the St. Marys River control strategy since 1999 (Adams et al., 2003). The St. Marys River became a large contributor of juvenile sea lamprey to northern Lake Huron in the 1980s and 1990s (Schleen et al., 2003). Given its enormous size, the St. Marys could not be controlled using typical applications of the pesticide TFM (3-trifluoromethyl-4-nitro phenol) so alternative controls were devised and implemented. The plan began in the early 2000s with treatment of all high-density larval habitat with granular Bayluscide, followed by annual Bayluscide treatments of select high density larval habitat as well as annual trapping of adult sea lamprey and release of adult sterile male sea lamprey (Bravener and Twohey, 2016). Since 2012, the plan has included moderate levels of annual treatment with granular Bayluscide (300 ha year^{-1}) and no sterile male releases (Criger et al., 2021). Assessment of these control actions have been ongoing for 20 years and has considered the relative abundance of juvenile sea lamprey encountered by commercial fishers described here. Here, we test the hypothesis that the effectiveness of St. Marys River granular Bayluscide treatments can be assessed through changes in juvenile abundance in northern Lake Huron.

To evaluate the relationship between juvenile sea lamprey CPUE and the area treated with granular Bayluscide in the St. Marys River we regressed juvenile CPUE in year t with the area treated with granular Bayluscide in year t–1. We ignored sterile male release in the St. Marys as its effect on larval production was likely dwarfed by the effects of Bayluscide treatments (Jones et al., 2015). We found a negative relationship between juvenile CPUE in year t and the area treated with granular Bayluscide in year t–1; however, this relationship was not statistically significant ($P = 0.208$). Furthermore, the area treated with granular Bayluscide in year t–1 was a poor predictor of CPUE ($R^2 = 0.032$).

Support for the hypothesis that the effectiveness of granular Bayluscide treatment in the St. Marys River can be assessed through juvenile sea lamprey abundance in northern Lake Huron is lacking. However, our analysis does not account for community changes in the fishery or increased pesticide applications elsewhere in northern Lake Huron that could have altered juvenile abundance. Treatment effort generally increased between 2005 and 2010, punctuated by large scale pesticide applications to several tributaries in northern Lake Huron including the St. Marys River in 2010–11. Wild lake trout recruitment also took hold in northern Lake Huron after 2005 (Lake Huron Commercial Fishing Summary, 2020). Thus, while the juvenile index does provide a reflection of sea lamprey in this area, there are confounding factors obscuring the relationship with changing control strategies on the St. Marys River.

The CPUE of juvenile sea lamprey abundance could be useful for evaluating if recent delays in pesticide treatment of major tributaries to northern Lake Huron have resulted in increased juvenile sea lamprey abundance. Specifically, the Garden and Mississagi Rivers can produce millions of sea lamprey larvae and both flow into the North Channel. These rivers have been treated with TFM every 3–4 years since the 1960s, with no more than 4 years between treatments. However, in recent history, treatments have been postponed due to concerns surrounding non-target effects of pesticide application; the Garden River was overdue for treatment from 2015 to 2019 (last treated in 2014) and the Mississagi River was overdue from 2017 to 2018 (last treatment in 2013). Therefore, changes in juvenile sea lamprey CPUE since 2015 could reveal impacts of postponing pesticide treatments in the Garden and Mississagi Rivers and would be useful for managers and policy makers to consider during negotiations to access land to conduct treatments.

Given delays in pesticide treatment, we predicted that production of juvenile sea lamprey from the Garden and Mississagi Rivers increased since 2015 and that the increased production would be reflected in the CPUE of juvenile sea lamprey. We assumed that production of juvenile sea lamprey from the St. Marys River was stable from 2015 to 2019 because the total area of Bayluscide treated and estimates of larval population have not changed substantially since 2015. Indeed, we found that CPUE of juvenile sea lamprey increased in 2016, 2017, and 2018. No statistical analyses were conducted due to low sample size. We expect severe impacts of the delayed pesticide treatments will result in continued increases in the juvenile CPUE in 2019 through 2021.

Research and outreach

Juvenile sea lamprey captured by the commercial fishery in northern Lake Huron have been a key component of the Sea Lamprey Research Program (SLRP) as a supplier of live animals. Efforts to rear juvenile sea lamprey in the lab have been costly (many live hosts are required), inefficient (high mortality of sea lamprey; Swink, 2003; R. Bergstedt, retired, U.S. Geological Survey, personal communication, 2020), and pose ethical questions regarding animal care and use. Since 2010, live juvenile sea lamprey collected by commercial fishers have been used in 22 GLFC-funded research projects conducted by 13 different scientific teams. These projects have so far resulted in more than 35 peer-reviewed publications on a wide range of topics, including: the sub-lethal effects of sea lamprey attachment to host fishes (Smith et al., 2016); the potency and specificity of sea lamprey chemosensory cues (Green et al., 2017; Scott et al., 2019; Buchinger et al., 2020; Suntres et al., 2020); and the movement and distribution of juvenile and adult sea lamprey in Lakes Huron and Erie (C. Holbrook, U.S. Geological Survey, personal communication 2020).

Juvenile sea lamprey captured by commercial fishers are also a key component of the sea lamprey education and outreach program. The GLFC and its partners from U.S. Fish and Wildlife Service, Fisheries and Oceans Canada, and U.S. Geological Survey use live sea lamprey during outreach events (e.g., regional sport shows, school visits, fishing tournaments), media interactions (e.g., television shows, newscasts, and print media), at professional aquariums (e.g., Chicago's Shedd Aquarium and Toronto's Royal Ontario Museum), and during visits to members of Congress and Parliament. During the fall, winter, and spring, juvenile sea lamprey procured by commercial fishers in northern Lake Huron are the best display specimens for events because they are large, often in good condition, and are tolerant of transport and handling. Since 2007, live sea lamprey have been used in over 175 events and been viewed in person by millions of people. Therefore, live sea lamprey are useful for educating the public on the importance of the Great Lakes fishery, the threat of invasive species, and specifically the success and need for ongoing sea lamprey control.

The number of live juvenile sea lamprey procured for research and outreach has decreased nearly 90% since 2010. From the year 2000 to 2010, 1500 – 3000 live juvenile sea lamprey were procured each year, but from 2010 to 2018 that number has declined to less than 300 per year. Declines are attributed to fewer commercial fishers and more effective sea lamprey control in northern Lake Huron.

Conclusion

The dataset explored herein represents only a part of the total wealth of data available regarding juvenile sea lamprey in northern Lake Huron, and it is out of the scope of this contribution to examine in detail every possible aspect of their ecology or management applications. In asking of the data a specific set of questions spanning a range of topics our aim is to highlight how such data can be useful in revealing patterns that could be explored in greater detail using hypothesis-based approaches. For example, do juvenile sea lamprey exhibit specialist feeding strategies within a broader generalist approach by the population and what would that mean for tracking wounding on lake trout alone? What impact could larger juvenile sea lamprey have on their hosts because of a warming lake, and should the sexes be considered independently in feeding models? Do female sea lamprey metamorphose one year later than males and could this be incorporated in control strategies to reduce reproductive potential or uncertainty? These are a few examples of synergizing basic and applied approaches to sea lamprey management that could be directed at the juvenile life stage and supported by this type of dataset (e.g., Hume et al., 2021a).

Although incidental captures by commercial fishers can shine some light into the "black box" of the parasitic phase of the sea lamprey life cycle, this is not full-strength sunlight. Due to the inherent biases and limitations associated with a targeted fishery compared to random sampling, conclusions drawn from such data must be interpreted with caution. However, if juvenile sea lamprey collections continue, they can improve basic knowledge of juvenile ecology and guide future research, assist tracking sea lamprey abundance in Lake Huron in conjunction with adult indices, support research requiring live juveniles as experimental subjects, and increase awareness of the sea lamprey control program in the Great Lakes via outreach events. The cost of collection efforts remains relatively low, and most of this cost directly benefits a fishery negatively impacted by sea lamprey parasitism. Juvenile sea lamprey are inherently difficult to study and knowledge gains have been slow relative to other life stages. Despite being the cause of damage to the Great Lakes fishery, much remains to be learned about sea lamprey during their time in open water.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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