Growth potential, host mortality and size trends of the parasitic–phase of the sea lamprey, Petromyzon marinus, in Lake Superior

by

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ABSTRACT

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Jeffrey C. Jorgensen

Under the supervision of Professor James F. Kitchell

at the University of Wisconsin Madison

Successful colonization by exotic species can have significant effects on ecosystems. The Lake Superior fish community changed dramatically after the successful colonization of the sea lamprey (*Petromyzon marinus*). Its invasion, along with overharvest, were responsible for the near extirpation of the native top predator in Lake Superior, the lean lake trout (*Salvelinus namaycush*). Efforts to control the sea lamprey to low abundance levels, combined with hatchery supplementation of lean lake trout and fishing regulations, have successfully restored and maintain lean lake trout at or near their historical abundance. During the period of lean lake trout recovery, systematic annual stocking of Pacific salmon (*Oncorhynchus* spp.) and other sport fishes began to provide additional fishery opportunities and increase economic activity in the lake basin. Pacific salmon stocking has also provided sea lampreys with alternative hosts and, along with them, the potential for very different growth trajectories. I used bioenergetics modeling to exam-
ine the potential for sea lamprey growth, and to project host size thresholds of survival based on blood removal by feeding sea lampreys. Sea lampreys were able to attain larger sizes feeding on Pacific salmon, which occupied a warmer thermal niche than lean lake trout. The proportion of maximum consumption ($P$ value) was higher for sea lampreys of an equivalent weight that fed only on lean lake trout compared to those that fed only on Pacific salmon as hosts. The size threshold for host survival increased dramatically with sea lamprey size. The overall high $P$ values of larger sea lampreys suggested that (1) they utilized warmer water hosts, (2) the model was incorrectly parameterized, or (3) they spent more than one summer as parasites. Though there is no direct empirical evidence, the results here suggest that larger sea lampreys may spend more than one summer as parasites. I also examined sea lamprey size trends, and constructed models of sea lamprey size in relation to salmonid ($S. namaycush$ and $Oncorhynchus$ spp.) stocking using a Bayesian model averaging technique. Sea lamprey size has increased by nearly 30 g in the period after the control program began. I found that size was mostly strongly related to lean lake trout stocking rates lagged by 3, 9, 11, and 13 years, and Pacific salmon stocking rates lagged 4 years. These regressors were significant features among the models with the highest posterior probabilities. One year ahead weight prediction estimates ranged from 190 g to 205 g, with approximate 95% prediction intervals from $\pm 6.4$ g to $\pm 12.5$ g. Sea lamprey size was more strongly related to lean lake trout, but Pacific salmon was also important. There may be a tradeoff for managers trying to achieve the fish community objectives for Lake Superior: by maintaining a healthy Pacific salmon fishery, managers may be subsidizing sea lamprey size, which, in turn, can cause higher host mortality.
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Chapter I:
Thesis Introduction

Ecologists commonly examine animal growth and diet, and how one affects the other. Often of interest is the scope for growth of the predator, and the prey needed to sustain that growth (e.g., Kerfoot and Sih 1987). In the following chapters, I address these questions for landlocked Lake Superior sea lamprey: How much prey, which prey types, what is the growth potential with respect to prey types, and how has growth changed over time? What are the ecological effects of a size increase, and how might management practices influence size?

Why is it important to ask these questions about sea lampreys? What makes them so special? The sea lamprey invaded the Great Lakes early in the last century, perhaps by the late 1930s in Lake Superior (Heinrich et al. 2003). The subsequent decline of commercially important fishes spurred action by Canadian and U.S. authorities to jointly restore and manage the fish resources of the Great Lakes. A binational agreement established the sea lamprey control program in the 1950s which today is implemented by the Ontario Ministry of Natural Resources (OMNR), the Department of Fisheries and Oceans (DFO), and the U.S. Fish and Wildlife Service (USFWS). In the beginning, electrical and low head mechanical barriers erected in tributaries known to contain significant populations of sea lampreys captured migrating animals and prevented them from reaching spawning grounds. Later, managers employed the use of weirs with portable traps on known sea lamprey spawning streams, and regularly applied chemi-
cals (3-trifluoromethyl-4-nitrophenol) to tributary waters to remove sea lamprey larvae, called ammocoetes (Applegate et al. 1961; Smith and Tibbles 1980; Heinrich et al. 2003). These and other ongoing efforts successfully control sea lampreys to perhaps 10% of their historical abundance in Lake Superior (Heinrich et al. 2003).

Thus, the sea lamprey numbers are suppressed. Is their suppression enough to mitigate their deleterious effects on host species? What characteristics of Great Lakes sea lamprey life history are important in understanding host damage and how are these characteristics different than their ocean-going anadromous conspecifics? Sea lampreys exhibit a semelparous life history. Anadromous sea lampreys spend their parasitic phase of life in the ocean (perhaps 24–48 months), spawn in coastal freshwater tributaries, and die shortly thereafter. Their eggs, which they deposit in nests (redds) during spawning, hatch after a few weeks into plankton feeding larvae, called ammocoetes, that remain for an undetermined period, but typically about 4 years, before transforming into the parasitic form and migrating to the ocean (Beamish 1980). Sea lampreys in the Great Lakes utilize the lakes' host resources in lieu of an ocean migration, and are thought to spend less time in the parasitic phase, about 12–20 months or one summer (Applegate 1950; Smith 1971), than anadromous sea lampreys. Newly transformed parasites grow substantially during their parasitic phase, by as much as $20 \times$ their larval size (about 10 g), or more. Parasitic sea lampreys attach to the sides of fishes with their oral disc and use a rasping tongue to bore a hole into the host's body to obtain bodily fluids (Lennon 1954; Hardisty and Potter 1971). Sea lampreys have been known to feed on most of the larger fishes found in Lake Superior (Farmer and Beamish 1973), and they appear to prefer relatively larger hosts over smaller hosts if given a choice (Swink 1991,
Salmonid species are among the largest pelagic fishes found in Lake Superior (Table 1), and of these lean lake trout are hypothesized to be the preferred hosts of sea lampreys (Johnson and Anderson 1980; Swink 2003).

There appears to be a long-term increase in Lake Superior sea lamprey size (Jorgensen, Chapter III), which has the potential of increasing host mortality. Larger sea lampreys remove more blood from hosts than smaller sea lampreys, which influences the size of hosts capable of surviving sea lamprey feeding. In Chapter II, I examine the growth potential of sea lampreys and host mortality as a function of increasing sea lamprey size and host type. In Chapter III, I use Bayesian model averaging to examine how sea lamprey size relates to salmonid stocking, and to determine the potential drivers of the long-term size increase. In Chapter IV, I summarize the findings and propose some policy recommendations that may mitigate the size increase.
REFERENCES


Table 1: Larger salmonids of Lake Superior.

<table>
<thead>
<tr>
<th>Species name</th>
<th>Common name</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Coregonus artedii</em></td>
<td>lake herring</td>
</tr>
<tr>
<td><em>C. clupeaformis</em></td>
<td>lake whitefish</td>
</tr>
<tr>
<td><em>Oncorhynchus kisutch</em></td>
<td>coho salmon</td>
</tr>
<tr>
<td><em>O. mykiss</em></td>
<td>steelhead</td>
</tr>
<tr>
<td><em>O. tshawytscha</em></td>
<td>chinook salmon</td>
</tr>
<tr>
<td><em>Salmo salar</em></td>
<td>Atlantic salmon</td>
</tr>
<tr>
<td><em>Salmo trutta</em></td>
<td>brown trout</td>
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<tr>
<td><em>Salvelinus fontinalis</em></td>
<td>brook trout</td>
</tr>
<tr>
<td><em>Salvelinus namaycush</em></td>
<td>lake trout</td>
</tr>
<tr>
<td><em>Salvelinus fontinalis × Salvelinus namaycush</em></td>
<td>splake</td>
</tr>
</tbody>
</table>
Chapter II:

Host size threshold for survival and growth potential of sea lampreys

(*Petromyzon marinus*) in Lake Superior

ABSTRACT

Landlocked Lake Superior sea lampreys (*Petromyzon marinus*) cause a significant yet uncertain amount of direct mortality on host species. I used bioenergetics modeling to examine the scope of the size of hosts vulnerable to death as a consequence of daily host blood volume loss due to sea lamprey feeding. I accounted for the bimodal migration timing of newly transformed parasitic sea lampreys, which spent 12 (spring migrants) or 17 months (fall migrants) as parasites, and simulated sea lamprey growth through a range of observed adult spawner weights (100 g to 400 g). Spring migrants attacking lean lake trout (*Salvelinus namaycush*) were capable of feeding rates that could kill hosts up to 2.0 kg. The size of hosts vulnerable to death during the seasonal peak was lower for fall migrants (1.8 kg). Spring migrants at their peak consumption feeding on Pacific salmon (an amalgam of coho, *Oncorhynchus kisutch*, and chinook, *O. tshawytscha*, salmon, and steelhead, *O. mykiss*) were capable of feeding rates that could kill hosts up to 2.0 kg, and fall migrant feeding rates could kill hosts as large as 2.8 kg. Fall migrants that switched from lean lake trout to Pacific salmon were capable of feeding rates that could kill hosts up to 2.8 kg. The differences in host size survival were due to the feeding rate, a temperature–dependent function, and the warmer thermal niche occupied by Pacific salmon. *P* values (proportion of maximum consumption) depended on the length
of the parasitic phase and the thermal niche of hosts. Sea lampreys that spent two summers as parasites (24 or 29 months as parasites) had markedly lower $P$ values than one-summer parasites due to the longer time period in which to grow to the same size, and readily attained sizes observed in adult anadromous sea lampreys. Two-summer parasites’ feeding rates were capable of killing lean lake trout and Pacific salmon hosts ranging in size from 3 kg to over 5.5 kg. The maximum upper limit number of 2 kg hosts killed by one-summer parasites in the range of observed spawner sizes was perhaps 20, and the maximum upper limit of fishes killed by two-summer parasites was higher by $3\times$. Though there is no direct empirical evidence, these results suggest that a fraction of larger sea lampreys might be spending more than one summer as parasites.

INTRODUCTION

Interactions between predators and their prey have important feedbacks, which govern the size, shape, morphology, behavior, and survival of each other (e.g., Alcock 2001). Host–parasite interactions are linked in a similar manner, and their interactions can take several forms. In the case of landlocked Great Lakes sea lampreys (*Petromyzon marinus*), they can take the form of an ectoparasite that inflicts nonlethal wounds during the course of feeding, or a predator that removes enough host fluids to cause death directly or through secondary infection (Parker and Lennon 1956; Hardisty and Potter 1971; Farmer and Beamish 1973; Farmer 1980; Swink 2003).

The successful invasion of the sea lamprey in Lake Superior contributed significantly to the decline of the historically dominant native top predator, the lean lake trout (*Salvelinus namaycush*; Smith 1971; Laurie and Rahrer 1972; Smith and Tibbles 1980). The sea lamprey is thought to have invaded Lake Superior from the lower Great Lakes in the
late 1930s and was well established lake-wide about ten years later (Smith and Tibbles 1980; Heinrich et al. 2003). Through chemical treatments of tributaries, mechanical and electrical barriers, and traps, sea lampreys in Lake Superior have been reduced and are controlled to about 10% of their historical abundance (Smith 1971; Smith and Tibbles 1980; Heinrich et al. 2003). Lake trout were nearly extirpated in Lake Superior before the sea lamprey control program began. The largest sea lamprey spawning streams were treated in the western arm of Lake Superior beginning in the late 1950s and early 1960s, and the control program was expanded eastward into Wisconsin and Michigan tributaries. The control effort has widened and now encompasses each of the Great Lakes. Lake trout in Lake Superior have since recovered to near historical levels because of successful sea lamprey control efforts, stocking, and fishery regulations (Lawrie and Rahrer 1972; Lawrie 1978; Hansen et al. 1995; Kelso et al. 1996; Bronte et al. 2003; Wilberg et al. 2003).

Although controlled to a fraction of their historical abundance, sea lampreys have increased in size during the period of recovery (Figure 1; and, described in detail in Jorgensen, Chapter III). For example, the mean weight of sea lampreys for the period 1999–2003 ($\bar{x}=200.9$ g, n=3,607) was larger than from the period 1961–1965 ($\bar{x}=173.5$ g, n=74,954; USFWS, unpublished data). Great Lakes landlocked sea lampreys are considerably smaller than their anadromous conspecifics. Anadromous (sea–run) spawning sea lamprey observed sizes can reach 1 kg, which is as much as 4× the typical size of landlocked sea lampreys in the Great Lakes (Beamish 1979, 1980; Yergeau 1983; Stier and Kynard 1986; Halliday 1991; Dempson and Porter 1993). Thus, Lake Superior sea lampreys’ spawning size is a fraction of their potential for growth.

One reason cited for the difference in size between anadromous and landlocked sea
lampreys is that anadromous sea lampreys are believed to spend more than one year at sea before reaching sexual maturity (Hardisty and Potter 1971; Beamish 1980). Investigators have hypothesized that landlocked Great Lakes sea lampreys spend only one summer as parasites (Applegate 1950; Parker and Lennon 1956; Hardisty and Potter 1971; Smith 1971; Johnson and Anderson 1980; Bergstedt and Swink 1995). Duration of the parasitic phase in the Great Lakes appears to be variable, since transformation to the parasitic phase and migration to the lake to feed occur over several months. Sea lampreys migrating lake-ward leave their natal streams and larval state to become parasites (Manion and Stauffer 1970). Their migration timing is bimodal, one peak in the fall and another in the spring (Applegate 1950; Applegate and Brynildson 1951; Applegate 1961; Davis 1967). Host type, abundance, and preference, as well as annual temperature cycles and host thermal preferenda are different for anadromous and landlocked sea lampreys, all of which could lead to variations in life history characteristics.

Whatever the causes of the changes in Lake Superior sea lamprey size and life history from their anadromous conspecifics, they have important consequences on their host species. Larger sea lampreys are more fecund (Applegate 1950; Manion and Hanson 1980), and likely have higher survival to reproduction given the energy requirements of finding a tributary, swimming to suitable habitat in the tributary and spawning, a period when no feeding occurs (Hardisty and Potter 1971; Beamish 1979). Food requirements are higher for larger sea lampreys, and feeding rates have direct effects on host survival (Farmer et al. 1975, 1977; Kitchell 1990). Significant blood removal weakens the host, and can result in host death if the rate of blood removal exceeds the capacity of the host to replenish it (Farmer et al. 1975).
In this chapter, I address the following questions related to host death caused by blood removal by sea lampreys: (1) What is the size threshold of host survival under different sea lamprey feeding rates and size trajectories; (2) How do host death threshold sizes differ for hosts occupying different thermal niches; (3) How might the host size survival threshold change if sea lampreys switch to different host fishes; and, (4) How do the size thresholds of host survival change due to feeding by sea lampreys that spend two summers as parasites and may grow to larger adult sizes?

Some aspects of these questions have been addressed by other workers through direct laboratory experimentation and/or modeling (Farmer and Beamish 1973; Farmer et al. 1975; Lett et al. 1975; Farmer et al. 1977; Kitchell and Breck 1980; Cochran and Kitchell 1989; Kitchell 1990; MacKay 1992; Madenjian et al. 2003). None has explicitly considered the bimodal sea lamprey migration timing and its implications for the length of the parasitic phase, incorporated host species switching, nor extended projections of host size death thresholds caused by the feeding of two-summer parasites.

METHODS

Sea lamprey bioenergetics

To model growth and feeding rates of parasitic sea lampreys I used a bioenergetics model developed by Kitchell and Breck (1980). I fit models to observed growth and thus was able to estimate blood consumption necessary to reach spawner weights. I parameterized the model as implemented in Fish Bioenergetics 3.0 (Hanson et al. 1997), with one difference (Table 1). Recent laboratory studies by Cochran et al. (2003) indicated
that energy density for sea lampreys <119.5 g is described by following equation:

\[ \text{Predator Energy Density} = 951.3 \text{ cal} \cdot g_{\text{wet weight}}^{-1} + 3.489W, \]  
(1)

where \( W \) is the mass (g) of a sea lamprey. Once a sea lamprey reached the upper weight limit, predator energy density remained constant at 1368.6 cal-g\(^{-1}\)\( _{\text{wet weight}} \) (Table 1) thereafter. This was incorporated into the model for sea lampreys that exceeded this weight cutoff by using the second equation set (Hanson et al. 1997), which required setting the Beta2 parameter (the slope of the allometric function above the sea lamprey upper weight limit; Table 1) to a very small number because a zero value produced spurious results. Prey energy density (host blood) was assumed to have the same caloric value for all host species (3202 J-g\(^{-1}\)\( _{\text{wet weight}} \); Farmer et al. 1975; Kitchell and Breck 1980).

By fitting the model to growth, I was also able to estimate \( P \), the proportion of maximum consumption. \( P \) ranges from 0 to 1.0 (0 to 100%), where 0 means no feeding and 1.0 signifies a fish feeding at its maximum rate given its size and temperature (Hanson et al. 1997). I began sea lamprey growth simulations at the same initial weight, 10 g (Applegate 1950; Kitchell 1990; Madenjian et al. 2003), for newly transformed parasites and fit the model to adult spawner weights that ranged from 100 g to 400 g. This range of spawner sizes captured a large portion of spawner sizes observed for Lake Superior (Figure 2). In other simulations, the final end weights were allowed to exceed 400 g until \( P \) reached 1.0.

Proxies for sea lamprey thermal history were used in the model since actual thermal histories were not available. Sea lampreys likely spend much of their parasitic phase
attached to hosts, whose thermal histories and/or temperature preferenda are known. I used mean daily in situ temperatures recovered from Lotek thermal/depth archival tags planted in wild and hatchery-reared Lake Superior lean lake trout (Mattes and Madsen 2004). These temperatures ranged from 0.10 to 12.77 °C (Figure 3). Pacific salmon (an amalgam of chinook, *O. tshawytscha*, and coho, *O. kisutch*, salmon, and steelhead, *O. mykiss*) thermal histories were based on mean near-surface water temperatures (McCormick 1996) measured in the thirteen year period from 1980–1992, with modifications such that temperatures did not go below 3 or above 18 °C (Figure 4), and thus were representative of a hypothetical Pacific salmon thermal history in Lake Superior (Wisimar and Christie 1987; Christie and Regier 1988; Stewart and Ibarra 1991; Rand et al. 1993). For this study, I assumed that sea lampreys were always attached and feeding to the host species indicated and, therefore, experienced the temperature of that host’s thermal niche.

To incorporate the bimodality of newly transformed parasitic sea lampreys I ran separate bioenergetics models for spring and fall migrants. Migrants began feeding either in the fall (22 November) or spring (1 April), and ceased feeding by spring of the next year (1 April), about six weeks before the beginning of the spawning run (Applegate 1950; Johnson and Anderson 1980). Thus, sea lampreys were parasitic for 12 and about 17 months, which included one summer as parasites (Applegate 1950; Parker and Lennon 1954; Applegate 1961; Johnson and Anderson 1980; Bergstedt and Swink 1994). I also ran simulations to model growth over two summers, the lower estimate of the hypothesized duration of the parasitic phase of anadromous sea lampreys, which corresponded to 24 and about 29 months as parasites.
Prey switching

Previous modeling efforts of parasitic sea lamprey growth have focused on one host species throughout the growth period, although sea lampreys are known to feed on most large fishes. The duration of attacks by sea lampreys declines with an increase in sea lamprey size (Lennon 1954; Parker and Lennon 1956). A parasitic sea lamprey likely feeds on many different hosts before reaching reproductive maturity; there is an inevitable switch from one host to another. In some of the simulations I assumed that sea lampreys switched from one host species to another at a distinct time during the growth simulations. I restricted these simulations to fall migrants only, and determined switching time based on host movements. In these simulations they began feeding on lean lake trout, coincident with the fall spawning season when lean lake trout are in shallow waters, and then switched at day 58 (18 January) to feeding on Pacific salmon thereafter (Figures 3 and 4). Prey energy density was assumed to be the same for both species, and that switching to a new host species did not affect daily feeding rates. Thus, species switching only affected the temperatures experienced by sea lampreys.

Host size survival threshold

I based the calculation of host mortality on the rate of host blood removal (sea lamprey feeding rate) by finding a threshold of host survival size below which death occurred as a consequence of blood loss (Farmer et al. 1975; Kitchell 1990). Blood removal was calculated from sea lamprey feeding rates, which were estimated on a daily time step. The lethal rate of daily blood removal was based on the experiments of Farmer et al. (1975, 1977), who estimated that a daily blood removal rate of 10% of the total amount of blood available was lethal to the host. Using this lethal blood removal rate, host size
death threshold is expressed by the following equation:

\[
HSDT = FR \cdot \frac{1000 \text{ } g}{4.04 \text{ } g},
\]

where \( HSDT \) is the host size threshold for survival (expressed in g), \( FR \) is the daily blood ration or sea lamprey feeding rate (g·d\(^{-1}\)), multiplied by the reciprocal of the percent blood by body weight of a 1000 g host, 4.04%. The percent blood of a fish by body weight was the mean value of studies for salmonids cited by Olson (1992), and from Bushnell et al. (1998). For this study I illustrated the impact of a single feeding sea lamprey on a host, although multiple wounds are frequently observed on a host. One could adjust (2) for multiple feeding bouts on the same host by multiplying the equation by the number of simultaneously feeding sea lampreys on a host.

**RESULTS**

There was a strong seasonal pattern of increase in the sea lamprey feeding rate, and hence, size threshold of host survival. The strong peak, evident in all the modeling scenarios, occurred in the fall when lake water temperatures inhabited by fishes were the highest. The start of the increase in host size death threshold occurred when waters began to warm, typically between early to mid–June, and the crest of the peak occurred in the fall, usually late September to mid–October. As discussed below, the shape and size of the host size survival thresholds varied with the duration of parasitic phase and with host species.

*Spring migrants, one summer parasites*

Spring migrants that spent 12 months as parasites and that utilized only lean lake
trout as hosts were able to achieve a potential maximum weight of 248 g (proportion of maximum consumption, $P=1.0$; Figure 5). Mean weight for sea lampreys in 2003 (203 g; Figure 1) corresponded to a $P$ value of 0.91 feeding only on lake trout for the entire 12 month parasitic phase (Figure 5). Hosts $\leq 1.2$ kg were vulnerable to death during the seasonal feeding rate peak by sea lampreys reaching the maximum weight. The seasonal peak of the host size death threshold occurred at approximately day 200 (17 October).

Spring migrants that fed only on Pacific salmon had lower $P$ values than those that fed only on lean lake trout at comparable sizes, and were able to grow to a larger maximum size. These sea lampreys were able to achieve a maximum potential weight of 369 g ($P=1.0$; Figure 6), which was 49% larger than sea lampreys feeding only on lean lake trout. Sea lampreys that reached the mean 2003 mean spawner weight had a $P$ value of 0.77. Hosts $\leq 1.8$ kg were vulnerable to death by sea lampreys reaching the maximum size. Day 175 (22 September) was the seasonal peak of the host size death threshold.

*Fall migrants, one summer parasites*

Sea lampreys that spent 17 months as parasites feeding only on lean lake trout were able to achieve a maximum potential weight of 360 g ($P=1.0$; Figure 7). This was slightly less than spring migrants feeding only on Pacific salmon, and 45% larger than spring migrants feeding only on lean lake trout hosts. The mean weight achieved by sea lampreys in 2003 required a $P$ value of 0.77 (Figure 7). Hosts $\leq 1.6$ kg were subject to the threat of death during the seasonal feeding peak. Although these sea lampreys migrated about 5 months before the spring migrants feeding on lake trout, the peak of the size threshold of host survival was similar, 11 October (day 325).

Sea lampreys parasitizing only Pacific salmon hosts were able to achieve a maximum
potential weight of 501 g \((P=1.0; \text{Figure 8})\), a 39\% increase over the maximum weight achieved by fall migrants feeding only on lean lake trout hosts. Sea lampreys that reached the 2003 mean weight had a \(P\) value of 0.69. Even larger hosts (up to 2.6 kg) were vulnerable to death during the seasonal peak of the feeding rate. The peak of the host size threshold was roughly day 325 (11 October), which coincided with the peak date for sea lampreys feeding on lean lake trout.

*Host switching*

In simulations where sea lampreys switched from one host species to another they were parasitic for 17 months, began feeding on lean lake trout, and then switched on simulation day 58 (18 January) to Pacific salmon hosts thereafter. They were able to achieve a maximum potential weight of 506 g \((P=1.0; \text{Figure 9})\), which was higher than the maximum size achieved by sea lampreys feeding solely on either host species. Sea lampreys under this host regime achieved a \(P\) value of 0.68 when grown to the mean 2003 weight. Hosts \(\leq 2.6 \text{ kg}\) were vulnerable to death by sea lampreys that reached the maximum weight. The peak of the host size death threshold for these lampreys was approximately the earliest, about day 300 (16 September).

*Spring migrants, two summer parasites*

Spring migrants that spent two summers feeding only on lean lake trout (24 months as parasites) were able to achieve a maximum potential weight of 704 g \((P=1.0; \text{Figure 10})\). This was 184\% larger than one summer migrants utilizing the same host species. Sea lampreys required a \(P\) value of 0.61 to achieve the 2003 mean weight of 203 g, a 33\% drop from one summer spring migrants on the same host species. Hosts \(\leq 3.5 \text{ kg}\) were vulnerable to death at the peak of feeding by lampreys reaching the maximum weight.
The peak of the host size death threshold occurred at day 550 (2 October).

Two summer spring migrants that fed only on Pacific salmon achieved a substantially larger size than those feeding only on lean lake trout. For 24 month parasites, their maximum weight reached 980 g \( (P=1.0; \text{Figure 11}) \), a 39% increase from parasites feeding only on lean lake trout. This size increase was 166% larger than one summer spring migrants feeding on the same host species. Sea lampreys that grew to the mean 2003 weight had a \( P \) value of 0.56. Hosts \( \leq 5 \) kg were vulnerable to death during the peak feeding time by sea lampreys reaching the maximum size. The host size death threshold peaked at the same day as those feeding on lean lake trout, day 550 (2 October).

**Fall migrants, two summers**

Fall migrants that spent two summers as parasites (29 months) and that fed on lean lake trout grew to a maximum weight of 856 g \( (P=1.0; \text{Figure 12}) \), a 22% increase over spring migrants utilizing the same host species. The \( P \) value required to grow to the 2003 mean weight was 0.57. Hosts \( \leq 4 \) kg were susceptible to death at the peak of feeding. Fall migrants that fed exclusively on Pacific salmon grew to the largest size of any of the simulations. The largest grew to a maximum potential weight of 1135 g \( (P=1.0; \text{Figure 13}) \), which was 33% larger than two summer fall migrants feeding only on lean lake trout. These sea lampreys had the smallest \( P \) value, 0.53, of all the other simulations necessary to achieve the 2003 mean weight. Hosts \( \leq 5.5 \) kg, the largest of all the simulations, were vulnerable to death. The day the peaks of the host size death threshold occurred for both of these simulations were similar, at about day 675 (26 September).
DISCUSSION

There were strong seasonal effects of host mortality which corresponded to a pulse in the sea lamprey feeding rate, and these seasonal effects were consistent with empirical observations of sea lamprey growth, host wounding rates, and sea lamprey–induced mortality patterns (Applegate 1950; Spangler et al. 1980; Bergstedt and Schneider 1988; Bergstedt and Swink 1995). Lake water temperatures available to fishes are highest during the late summer–early fall period (Figure 3 and 4), and the sea lamprey feeding rate is a temperature–dependent function (Kitchell and Breck 1980; Hanson et al. 1997).

Adult spawner weights achieved by sea lampreys depended on the duration of the parasitic phase, migration timing, and host type. Fall migrants (17 and 29 month parasites) were able to attain larger spawning sizes than spring migrants (12 and 24 month parasites), regardless of host type. Parker and Lennon (1956) found in laboratory studies that the total growth of fall lake–ward migrants was greater than that of spring migrants. Fall migrants, despite over–wintering in the cold lake waters, spend a longer time as parasites, and thus have more opportunities to feed than spring migrants. Host type was also important. A sea lamprey feeding on lean lake trout required a higher $P$ value to reach the equivalent weight as a sea lamprey that fed on Pacific salmon over the same feeding period. The thermal niches occupied by these hosts were the drivers of the differences in sea lamprey growth. Sea lampreys at higher temperatures had lower $P$ values because estimates for $P$ are derived from the proportion of maximum feeding multiplied by the reciprocal of the temperature dependence function (Hanson et al. 1997). Thus, $P$ values are inversely related to temperature.

Sea lampreys in these simulations had high proportion of maximum consumption
values compared to other bioenergetics modeling of fish growth. There may be several causes for the high $P$ values. Spawning sea lampreys captured in 2003 included weights up to 400 g. The $P$ value necessary for modeled growth to reach the observed growth for that year, 203 g (Figure 1), was above 0.5 for all of the simulations, and more frequently above 0.7. These values were necessary for growth of the average size fish for that year. These values were high relative to bioenergetics models developed to model growth of other fishes (Stewart et al. 1983; Lantry and Stewart 1993; Rudstam et al. 1994, 1995; Negus 1995; Johnson and Martinez 2000), which are rarely above 0.6. Thus, sea lampreys larger than the mean weight in 2003 likely either (1) fed on host fishes with warmer water thermal histories than were used in this study, (2) the bioenergetics model was incorrectly parameterized, (3) spent more than 12–17 months (and more than one summer) as parasites, or (4) some combination of these.

Temperature is an important factor for growth. Thermal histories of Pacific salmon were warmer than those of lean lake trout in these simulations (Figure 3 and 4). The other Great Lakes serve as examples of increasing the availability of warmer water and raising the relative abundance of host species that inhabit those waters in Lake Superior. Sizes of sea lampreys in other Great Lakes are routinely 50 to 100 g larger than Lake Superior (e.g., GLFC Annual Reports, <www.glfc.org>), which is not surprising since it is the coldest of the five Great Lakes (see Assel et al. 1994). Sea lamprey temperature preferences appear to be closer to Pacific salmon than lean lake trout (McCauley et al. 1977; Wismar and Christie 1987; Bergstedt et al. 2003; Mattes and Madsen 2004), which should impart a lower $P$ value to sea lampreys feeding on warmer-water hosts.

Hosts that occupy warmer waters when they are available provide an opportunity for
sea lampreys to grow to larger sizes than cold-water hosts. The shift in $P$ values from sea lampreys growing to the mean 2003 weight utilizing lean lake trout hosts decreased when grown on Pacific salmon. Although size-selective, sea lamprey wounds have been observed on most of the larger fishes found in the Great Lakes (Parker and Lennon 1956; Farmer and Beamish 1973; Farmer 1980; Johnson and Anderson 1980; Spangler et al. 1980). Recent investigations of the Lake Superior food web suggested that sea lampreys may not be feeding exclusively on hosts at the highest trophic position, and that lower trophic position species such as suckers (family Castostomidae) and lake whitefish (*Coregonus clupeaformis*) may be important hosts for sea lampreys (Harvey and Kitchell 2000; Harvey 2001; C. Harvey, pers. comm.). Host size thresholds of survival for fishes utilizing surface waters, whose thermal history was estimated using surface water temperatures that did not fall below 3 °C (Figure 4), were nearly identical to those of Pacific salmon. If these hosts are utilized to any extent by large sea lampreys, given their smaller size they would suffer the highest mortality rates and increase sea lamprey growth rates.

The high $P$ values could be the result of incorrect model parameterization or assumptions. Since the sea lamprey bioenergetics model was developed (Kitchell and Breck 1980) new information about predator energy density and host thermal histories have become available (Cochran et al. 2003; Mattes and Madsen 2004). Using model refinements in conjunction with laboratory studies of blood consumption and growth similar to Farmer et al. (1975) would further improve model inputs (Table 1). $P$ values determined from the original model calibration (Kitchell and Breck 1980), based on laboratory studies of Farmer et al. (1975), ranged from 0.45 to 0.65, the highest of which corresponded to sea lampreys feeding on lean lake trout in Lake Superior. Previous growth simulations were
run for 12 months only and started on 1 January (Kitchell and Breck 1980; Madenjian et al. 2003), and did not take into account the bimodal migration timing of transformed sea lampreys.

For comparison, I used Kitchell and Breck’s (1980) estimated thermal history for lean lake trout hosts to compare the percent change (\( \frac{\text{This study} - \text{K&B}}{\text{K&B}} \times 100 \)) in \( P \) values and total consumption with \( in situ \) lean lake trout temperatures for growth of the mean 2003 sea lamprey (203 g). I parameterized the model as per this study (Table 1), and growth was modeled for 12 and 17 months. \( P \) values increased by 21 and 16% for 12 and 17 month parasites, respectively, from the old to the new model, while total blood consumption decreased 12% for parasites of the same growth period (Table 2). Thus, the original model may have underestimated the proportion of maximum consumption and overestimated total blood consumption on lean lake trout. The discrepancies between the \( P \) values in this study and those of the earlier study suggest that perhaps the model parameters and assumptions about migration timing may need re-evaluation with more laboratory and field study.

Consumption and growth outputs from bioenergetics models are sensitive to changes in model parameters and data inputs. The results I obtained here are vulnerable to the same set of limitations of other such models (e.g., Ney 1993). As illustrated above, the model is highly sensitive to temperature. Several studies have shown that the activity multiplier can be highly variable, and also can have a strong effect on model estimates of growth and consumption (Boisclair and Leggett 1989; Boisclair and Sirois 1993). The activity multiplier in this study was assumed to be 1.5 (Table 1; Kitchell and Breck 1980), which is based on laboratory experiments of Farmer et al. (1977). The activity
multiplier’s *in situ* distribution in the Lake Superior sea lamprey population is probably highly variable, but it was probably not responsible for the discrepancy between observed growth and model predictions at maximum $P$ because when it was added to the sea lamprey model it minimally increased the potential for error in consumption estimates (Kitchell and Breck 1980). Although temperature, activity metabolism, and other parameters vary across individuals, I assumed that the parameters and input data represented the average sea lamprey and how changes in migration timing, host choices, and length of the parasitic phase could affect consumption and growth. Recent advances in the model’s parameters (predator energy density; Cochran et al. 2003) and data inputs (*in situ* lake trout thermal histories; Mattes and Madsen 2004) have presumably improved the model’s performance in estimating sea lamprey blood consumption (Ney 1993; Hansen et al. 1993), and, hence, host death size thresholds (Kitchell 1990).

A recent individual–based modeling approach suggested setting the $P$ value equal to 1.0 for sea lampreys <160 g, with an exponential decline thereafter (Madenjian et al. 2003). Optimal foraging theory suggests that animals strive to maximize food benefits while reducing the cost to obtain those benefits (e.g., Townsend and Winfield 1985). If sea lampreys follow this strategy, they should maximize host attachment time and minimize the search for new hosts (Cook and Cockrell 1978; Sih 1980; Cochran and Kitchell 1989). Sea lampreys have been observed attached to hosts without initiating feeding, and remained attached to the same host for long periods without inducing host mortality (Parker and Lennon 1956; Cochran 1984), which may suggest they are balancing the costs associated with finding a new host with the benefits of remaining attached to a host with some capacity to replenish its blood supply. The lower the sea lamprey:host weight
ratio, the longer a sea lamprey can remain attached and feed (Parker and Lennon 1956; Farmer et al. 1977; Swink and Hanson 1986, 1989; Swink and Fredricks 2000; Cockran and Kitchell 1989; Swink 1990, 1991, 1993, 2003). Thus, there may be some evidence for adjusting the $P$ value as Madenjian et al. (2003) suggest for smaller sea lampreys, though further laboratory validation similar to Farmer et al. (1975) is needed.

In any case, this analysis suggests that some fraction of Lake Superior sea lampreys have a longer parasitic phase than previously hypothesized. Though there is no direct evidence to support this (Bergstedt and Swink 1995), bioenergetics modeling suggests that it is plausible from a growth standpoint. The proportion of maximum consumption decreased the longer a sea lamprey spent as a parasite, and the warmer the host species’ thermal history. $P$ values decreased substantially as simulations increased in duration from one summer to two. The lowest $P$ values are more consistent with other bioenergetics model simulations of the growth of other Great Lakes fishes (Stewart et al. 1983; Lantry and Stewart 1993; Rudstam et al. 1994, 1995). Anadromous sea lampreys are hypothesized to have a parasitic phase about $2 \times$ the length of Great Lakes sea lamprey parasites, and they grow to about $3 \times$ (or more) their size (Beamish 1979, 1980; Vergeau 1983; Stier and Kynard 1986; Halliday 1991; Dempson and Porter 1993). The reasons for this are not known, but perhaps the energy requirements necessary for anadromous sea lamprey spawning in coastal rivers requires a higher buildup of biomass (Beamish 1979, 1980). Although only speculation, perhaps there are size–selective predatory pressures (e.g., Brooks and Dodson 1965) on anadromous sea lampreys in their oceanic parasitic phase which may cause an upward shift in the adult size distribution. Certainly, the thermal histories experienced by sea lampreys in the Atlantic Ocean are probably quite
different than landlocked sea lampreys, and sea lampreys in the Atlantic Ocean can attack very large hosts with enormous blood pools. Regardless, anadromous sea lampreys reveal the potential for growth of their landlocked conspecifics. Since their invasion into Lake Superior, landlocked sea lamprey growth has not reached its potential but a small fraction approach it (Figures 1 and 2). Parker and Lennon (1956) reported that three out of 22 sea lampreys grown in laboratory studies, although reaching sizes comparable to others that spawned, failed to reach sexual maturity after the usual parasitic-phase life cycle period. Two other studies documented captures of large, presumptively spawning weight, sea lampreys in the Great Lakes after the traditional spawning period was over (Moore et al. 1974; Bergstedt and Swink 1995). Setting $P=1.0$ for one summer parasites feeding exclusively on Pacific salmon still does not account for the largest sea lampreys observed. The overall high $P$ values for one summer parasites suggest that large sea lampreys are either extremely aggressive feeders, or that they spend more time as parasites to reach observed growth. Those observations, together with the results presented in this study, suggest that some fraction of sea lampreys have a longer parasitic phase than previously hypothesized.

The damage to hosts caused by sea lampreys is difficult to measure. Direct in situ host mortality as a consequence of parasitic feeding is elusive. The total pool of blood consumed by sea lampreys likely represents a considerable amount of fish killed. Recent estimates of sea lamprey-induced mortality on lean lake trout, based on wounding rates, suggest that the number of lean lake trout killed by sea lampreys is increasing (Ebener In prep). The maximum upper limit number of fishes killed by a sea lamprey is depicted in Figure 14, using total blood consumption divided by the amount of blood in a 2 kg
fish. These values are speculative estimates of the maximum possible number of fishes killed directly by feeding sea lampreys of differing growth trajectories, duration of the parasitic phase, and host type. Actual death rates depend on the hosts’ capacities to replenish the blood removed. Sizes of spawning Lake Superior sea lampreys are largely below 400 g, which suggests that up to 20 host fishes 2 kg in size could be killed by sea lampreys that spend one summer as parasites. A 203 g sea lamprey (the mean weight in 2003) feeding on lean lake trout (12 to 17 months as a parasite) and Pacific salmon (12 months) hosts could have potentially killed a maximum of 9–12 fishes. The number of fishes killed by a sea lamprey of the same size increases for parasites that switched from lean lake trout to Pacific salmon, or a 17 month parasite feeding on Pacific salmon. What is most striking is the increase in the maximum number of fishes that can be killed by large parasites spending more than one summer as parasites. Even at final weights between 100 and 400 g the number of fishes killed is about $3 \times$ the maximum upper limit killed by one summer parasites (Figure 14).

The research presented here suggests revisiting some of the sea lamprey bioenergetics parameters and assumptions. Further studies with thermal/depth archival tags implanted into sea lampreys, in conjunction with the stable isotope analysis of the Lake Superior food web (C. Harvey, pers. comm.), and sea lamprey statolith aging studies (M. Steeves, pers. comm.) will reveal more information about the length of the parasitic phase, host selection, and their potential for growth in Lake Superior.

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thermal history data. I thank M. Ebener (CORA), G. Christie (GLFC), R. Bergstedt, and B. Swink (USGS) for valuable discussions. I thank M. Henson and R. Kahl (USFWS, Marquette Biological Station, Marquette, Michigan, U.S.A.) for sea lamprey size data. Thanks to D. Sarker for developing the R lattice plotting functions and his assistance using them. C. Harvey, I. Kaplan and L. Schubert provided valuable comments on an earlier draft of this chapter. This research was supported in part by the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Sea Grant College Program award number NA16RG2257, the State of Wisconsin, and an Anna Grant Birge Memorial Award.
REFERENCES


Lett, P.F., F.W.H. Beamish, and G.J. Farmer. 1977. System simulation of the predatory activities of sea lampreys (Petromyzon marinus) on lake trout (Salvelinus namay-


Table 1: Inputs for sea lamprey bioenergetics modeling (Kitchell and Breck 1980; Hanson et al. 1997; Cochran et al. 2003). Energy densities are expressed in wet mass.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description and Equation</th>
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</thead>
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<td>$P$</td>
<td>Proportion of maximum consumption</td>
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<td>CQ</td>
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<td>Prey Energy Density</td>
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Table 2: Comparison of bioenergetics model outputs between the estimated Kitchell and Breck (1980; noted here by “KB”) thermal history for lean lake trout with *in situ* temperatures (Mattes and Madsen 2004). Model outputs are based on growth of the mean size lamprey, 203 g, in 2003.

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<th>P value</th>
<th>Total Blood Consumption (g)</th>
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<tr>
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<td><em>in situ</em></td>
<td>17 months</td>
<td>0.77</td>
<td>862.5</td>
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FIGURE CAPTIONS

Figure 1: Sea lamprey (*Petromyzon marinus*) spawner mean weights captured in U.S. tributaries to Lake Superior by mechanical and electrical barriers (○), and portable trap (●), for the period 1961–2003. Error bars represent ±1 standard error. The dot–dashed line (mechanical and electrical barriers) and solid line (portable traps) are local regression (loess) curves (span=0.6) of the size trends. Data courtesy of M. Henson, U.S. Fish and Wildlife Service, Marquette Biological Station (Marquette, Michigan, U.S.A.).

Figure 2: Size frequencies of spawning sea lamprey weights in Lake Superior for the period 1954–2003. Data courtesy of M. Henson, U.S. Fish and Wildlife Service, Marquette Biological Station (Marquette, Michigan, U.S.A.).

Figure 3: Thermal history of lean lake trout (*Salvelinus namaycush*) derived from Lotek thermal archival tags implanted in Lake Superior wild and hatchery reared fish *in situ* (Mattes and Madsen 2004). Mean temperatures (black dots) are bounded by ±1 standard deviation (gray bars).

Figure 4: Mean near–surface temperatures in Lake Superior (solid line) from the period 1980–1992 (McCormick 1996). Day 1 begins on 1 January. Dashed lines indicate upper and lower cutoff values for the constructed Pacific salmon thermal history.

Figure 5: Host size threshold of survival contour surface of spring migrating (12 months) parasitic sea lampreys grown to different spawning weights on lean lake trout hosts. Contour lines and colors represent host death threshold sizes (in g), and colors are indexed in the color key. Horizontal lines describing selected $P$ values (proportion of maximum consumption) are superimposed. Final weights achieved by sea lampreys with $P=1.0$
were 248 g. Sea lampreys that grew to 400 g had a $P$ value of 1.25. The mean sea lamprey size in 2003, 203 g, required $P$ to be 0.91.

**Figure 6:** Host size threshold of survival contour surface of spring migrating (12 months) parasitic sea lampreys grown to different spawning weights on Pacific salmon hosts. Contour lines and colors represent host death threshold sizes (in g), and colors are indexed in the color key. Horizontal lines describing selected $P$ values are superimposed. Final weights achieved by sea lampreys with $P=1.0$ were 369 g. Sea lampreys that grew to 400 g had a $P=1.04$. The mean sea lamprey size in 2003, 203 g, required $P$ to be 0.77.

**Figure 7:** Host size threshold of survival contour surface of fall migrating (17 months) parasitic sea lampreys grown to different spawning weights on lean lake trout hosts. Contour lines and colors represent host death threshold sizes (in g), and colors are indexed in the color key. Horizontal lines describing selected $P$ values are superimposed. Final weights achieved by sea lampreys with a $P$ value of 1.0 were 360 g. Sea lampreys that grew to 400 g had a $P$ value of 1.05. The mean sea lamprey size in 2003, 203 g, required $P$ to be 0.77.

**Figure 8:** Host size threshold of survival contour surface of fall migrating (17 months) parasitic sea lampreys grown to different spawning weights on Pacific salmon hosts. Contour lines and colors represent host death threshold sizes (in g), and colors are indexed in the color key. Horizontal lines describing selected $P$ values are superimposed. Final weights achieved by sea lampreys with $P=1.0$ were 501 g. The mean sea lamprey size in 2003, 203 g, required $P$ to be 0.69.

**Figure 9:** Host size threshold of survival contour surface of fall migrating (17 months)
parasitic sea lampreys grown to different spawning weights that switched host species. Sea lampreys switched on day 58 from lean lake trout to Pacific salmon. Contour lines and colors represent host death threshold sizes (in g), and colors are indexed in the color key. Horizontal lines describing selected $P$ values are superimposed. Final weights achieved by sea lampreys with $P=1.0$ were 506 g. The mean sea lamprey size in 2003, 203 g, required $P$ to be 0.68.

**Figure 10:** Host size threshold of survival contour surface of spring migrating (24 months, two summers) parasitic sea lampreys grown to different spawning weights feeding on lean lake trout hosts. Contour lines and colors represent host death threshold sizes (in g), and colors are indexed in the color key. Horizontal lines describing selected $P$ values are superimposed. Final weights achieved by sea lampreys with $P=1.0$ were 704 g. The mean sea lamprey size in 2003, 203 g, required $P$ to be 0.61.

**Figure 11:** Host size threshold of survival contour surface of spring migrating (24 months, two summers) parasitic sea lampreys grown to different spawning weights feeding on Pacific salmon hosts. Contour lines and colors represent host death threshold sizes (in g), and colors are indexed in the color key. Horizontal lines describing selected $P$ values are superimposed. Final weights achieved by sea lampreys with $P=1.0$ were 980 g. The mean sea lamprey size in 2003, 203 g, required $P$ to be 0.56.

**Figure 12:** Host size threshold of survival contour surface of fall migrating (29 months, two summers) parasitic sea lampreys grown to different spawning weights feeding on lean lake trout. Contour lines and colors represent host death threshold sizes (in g), and colors are indexed in the color key. Horizontal lines describing selected $P$ values are superimposed. Final weights achieved by sea lampreys with $P=1.0$ were 856 g. The
mean sea lamprey size in 2003, 203 g, required $P$ to be 0.57.

**Figure 13:** Host size threshold of survival contour surface of fall migrating (29 months, two summers) parasitic sea lampreys grown to different spawning weights feeding on Pacific salmon. Contour lines and colors represent host death threshold sizes (in g), and colors are indexed in the color key. Horizontal lines describing selected $P$ values are superimposed. Final weights achieved by sea lampreys with $P=1.0$ were 1135 g. The mean sea lamprey size in 2003, 203 g, required $P$ to be 0.53.

**Figure 14:** The maximum upper limit number of 2 kg fishes killed as a result of sea lamprey feeding on indicated hosts. Hosts are denoted by “PSH” (Pacific salmon hosts) and “LTH” (lake trout hosts), and the numbers following indicate the time, in months, spent as parasites. Lines extend to adult spawning weights by sea lampreys with $P=1.0$ or 400 g, whichever was higher. Dashed vertical lines at 100 and 400 g indicate the size range of adult spawner sizes in Lake Superior, and the dotted line shows the mean sea lamprey weight for 2003 (203 g).
Figure 1: Lake Superior sea lamprey sizes, 1961–2003.
Figure 2: Histogram of Lake Superior spawning sea lamprey size frequencies, 1954–2003

Min. = 20 g
Max. = 598 g
\( \bar{x} = 169.765 \) g
n = 218,685
Figure 3: Lean lake trout thermal profile from Lake Superior.
Figure 4: Mean Lake Superior surface water temperatures, 1980–1992.
Figure 5: Host size threshold of survival response surface for spring migrating (12 months) parasites feeding on lean lake trout hosts.
Figure 6: Host size threshold of survival response surface for spring migrating (12 months) parasites feeding on Pacific salmon hosts.
Figure 7: Host size threshold of survival response surface for fall migrating (17 months) parasites feeding on lean lake trout hosts.
Figure 8: Host size threshold of survival response surface for fall migrating (17 months) parasites feeding on Pacific salmon hosts.
Figure 9: Host size threshold of survival response surface for fall migrating (17 months) parasites that switched from feeding on lean lake trout to Pacific salmon hosts.
Figure 10: Host size threshold of survival response surface for spring migrating (24 months, two summers) parasites feeding on lean lake trout hosts.
Figure 11: Host size threshold of survival response surface for spring migrating (24 months, two summers) parasites feeding on Pacific salmon hosts.
Figure 12: Host size threshold of survival response surface for fall migrating (29 months, two summers) parasites feeding on lean lake trout hosts.
Figure 13: Host size threshold of survival response surface for fall migrating (29 months, two summers) parasites feeding on Pacific salmon hosts.
Figure 14: The number of 2 kg fishes killed as a function of sea lamprey spawner size, host type, and parasitic phase length.
Chapter III:

Sea lamprey (Petromyzon marinus) size trends in a salmonid stocking context in Lake Superior

ABSTRACT

Fish community objectives for Lake Superior include restoring the fish community so that it resembles its historical species composition yet allows for supplementation of naturalized populations of Pacific salmon (Oncorhynchus spp.). To achieve their objectives, managers strive to reduce the sea lamprey (Petromyzon marinus) to a level that causes insignificant (<5%) mortality of their prey species. While the focus has been on suppressing their numbers, which has been successful, their size has increased during the control period. I analyzed long-term trends of the mean weight of sea lampreys in Lake Superior and found a significant increase in sea lamprey weight in the period 1961–2003 (F=36.76, p<0.001, R²=0.473). A local regression (loess curve) fit revealed that sea lampreys had two significant size increase periods, from 1961 to the mid–1970s, and from the mid–1980s to 2003. I used Bayesian model averaging (BMA) to find the relationship between mean sea lamprey weight and the stocking of native lean lake trout (Salvelinus namaycush) and nonnative Pacific salmon. BMA identified 91 possible models, which indicated a high degree of model uncertainty. However, several regressors were significant features in many of the models. Sea lamprey weight was related to stocked lean lake trout lagged 3, 9, 11, and 13 years, and stocked Pacific salmon lagged 4 years. The posterior-weighted prediction estimate for the year 2004 mean weight was 195.4 g, ±9.0 g (1 SD).
While lean lake trout are important hosts, Pacific salmon also appear to be important in subsidizing sea lamprey diets. If sea lampreys can achieve larger sizes attached to Pacific salmon hosts, and in the process inflict more damage on hosts, there may be a tradeoff for managers in achieving the fish community objectives for Lake Superior.

**INTRODUCTION**

The fish community of Lake Superior has changed dramatically in response to fishery activities and the invasion of exotic species (Christie 1974; Bogue 2000). The historical abundance of the top predator in Lake Superior, lean lake trout (*Salvelinus namaycush*), was depleted by fishery exploitation and the successful colonization of the sea lamprey (*Petromyzon marinus*; Smith 1971; Smith and Tibbles 1980). By the late 1950s lean lake trout had been extirpated from all of the Great Lakes except the western arm of Lake Superior (Christie 1974; Lawrie 1978). In response to these and similar patterns of the decline of fishes in the other Great Lakes a binational program to control sea lampreys was implemented in the 1950s (Heinrich et al. 2003). U.S. and Canadian resource managers erected mechanical and electrical barriers on selected tributaries to prevent sea lampreys from reaching spawning grounds. At these sites, managers recorded biological characteristics, such as weight and sex.

Biological characteristics of sea lampreys have been used by investigators to infer information about lamprey and host abundance. Heinrich et al. (1980) attempted to couple the relative abundance of sea lampreys with weight over a long-term period. For each year in the period 1958–1978 they fit length–weight models, and from this they computed the weight at length corresponding to the average length of sea lampreys in the Great Lakes. Heinrich et al. (1980) found a significant positive correlation between
annual average sea lamprey weight with lake trout abundance the previous year in Wisconsin waters of Lake Superior. They also found a negative correlation between sea lamprey size and abundance. Thus, their analyses suggested some density dependence among sea lampreys for host resources: as sea lamprey abundance decreased, the size of sea lampreys increased; and, when more hosts were available, sea lamprey size increased. They concluded that three interrelated factors influenced sea lamprey size: (1) sea lamprey abundance; (2) the effectiveness of the sea lamprey control program; and, (3) the availability of preferred host species.

Most recently, Houston and Kelso (1991) assessed the relationship of sea lamprey biological characteristics and salmonid abundance. First, they described changes in biological characteristics over time. They reported that sea lamprey weight decreased through the 1950s, increased during the period 1962–1972, stabilized during the period 1973–1978, and increased in the period 1979–1987. They regressed two biological characteristics (weight and the percent males in the population) on three predictor variables separately: salmonid stocking (an aggregation of eight species), commercial salmonid catch, and sea lamprey relative abundance. For Lake Superior, Houston and Kelso (1991) found both sea lamprey weight and the percent of males in the population were significantly positively related to salmonid catch, but not to salmonid stocking. However, it is not clear how the aggregation of stocked salmonids were time–lagged to account for their growth necessary to become suitable hosts.

I had two objectives for this study. First, I analyzed long–term trends of sea lamprey weight in Lake Superior, which included data collected subsequent to the last trend analysis. Second, I employed Bayesian model averaging to select a subset of models
that related sea lamprey weight to the stocking of lean lake trout and Pacific salmon in Lake Superior. My research questions were: (1) What are the long–term trends in sea lamprey size; (2) How is salmonid stocking related to sea lamprey size; and, (3) What size forecasts can be made based on past stocking efforts?

**METHODS**

_Data_

The USFWS maintains a database at the Marquette Biological Station (Marquette, Michigan, U.S.A.) that contains biological characteristics of adult spawner sea lampreys caught by electrical and mechanical barriers as well as portable traps in U.S. tributaries to Lake Superior (Figure 1A). Since the early 1950s, personnel have annually recorded weight of a subsample of sea lampreys caught at each location. Subsample sizes of measured fish were larger in earlier years (1000’s) than later years (100’s). Though not every tributary was sampled each year, the 25 tributaries in the data set span the length of the southern shore of Lake Superior, from western Wisconsin to the eastern edge of Michigan’s Upper Peninsula. Sea lampreys can move long distances during their parasitic phase (Smith and Elliott 1952; Moore et al. 1974; Bergstedt et al. 2003) and there is no compelling evidence suggesting that they home to their natal streams (Applegate and Smith 1951; Bergstedt and Seelye 1995). Therefore, I assumed that sea lampreys caught in streams likely represent lake–wide independent random samples of spawning adults.

Sea lamprey collection methods included barriers (electrical and mechanical) and portable traps. The different fish capture methods may have had different size–selectivities, but the data do not contain enough overlapping years in which both barriers and portable traps were used to standardize size between collection methods. Thus, I ignored the
method of collection and combined measurements if multiple capture methods were used in the same year.

I obtained fish stocking records for Lake Superior from the Great Lakes Fishery Commission (GLFC), which maintains an internet–based searchable database (<www.glfc.org>). Records of fishes stocked in Lake Superior begin in 1950 and continue through 2002 (Figure 1B). Lean lake trout stocking began in 1950, and systematic stocking of Pacific salmon began in 1967. I define Pacific salmon here as an amalgam of chinook and coho salmon (*Oncorhynchus tshawytscha*, and *O. kisutch*) and steelhead (*O. mykiss*). I chose to use stocking rates since there are no historical long–term lake–wide abundance estimates of these fishes available.

**Modeling**

To accomplish the first goal of analyzing size trends of sea lampreys over time, I used two different procedures. I used weight as a measure of size (after Houston and Kelso 1991), and since there was no statistical difference in weight between males and females (*p*<0.05), I pooled data for both sexes. For size trend analysis, I limited the data to the period 1961–2003, the period after nearly full sea lamprey control efforts were in place (Heinrich et al. 2003). First, I fitted a simple least squares linear regression model of weight over time to describe the general trend. Second, I fitted a loess curve, a locally distance–weighted least squares polynomial regression (Venables and Ripley 2002), to capture both short– and long–term weight trends. I set the span (*α*, the percentage of data points used in the localized fitting, here equal to 0.6) such that the loess curve captured decadal trends without overfitting the data.

For the second goal of relating salmonid stocking to sea lamprey size, I used Bayesian
model averaging to select a subset of multiple linear regression models that related sea lamprey weight to salmonid stocking. The multiple linear regression models for relating sea lamprey weight to salmonid stocking were based upon the following conceptual framework:

\[
\text{sea lamprey weight today} = \text{previously stocked lake trout} + \text{previously stocked Pacific salmon} + \text{error},
\]

where the sea lamprey weight today is a function of salmonids stocked some number of years before present. In its general form (1) is represented by:

\[
W_t = \beta_0 + \sum_{i=1}^{m} \beta_{1i}LT_{t^*} + \sum_{j=1}^{n} \beta_{2j}PS_{t^*} + \varepsilon,
\]

where \(W_t\) represents mean lamprey weight in year \(t\), \(\beta_0\) is the intercept, \(LT\) and \(PS\) represent the number of time–lagged (by \(t^*\) years) stocked lean lake trout and Pacific salmon respectively, \(\beta_{1i}\) and \(\beta_{2j}\) are the regression coefficients of the stocked salmonid terms (\(LT\) and \(PS\)) included in the model and indexed by \(i\) and \(j\) (to \(m\) and \(n\) number of regressor terms), and the error is captured by \(\varepsilon\). Lake trout can live as much as 20 years or more (Martin and Olver 1980), while the Pacific salmon stocked in Lake Superior do not persist beyond about five years (Scott and Crossman 1973; Groot and Margolis 1991; Busby et al. 1996). In this modeling approach, the host species are time–lagged to account for growth needed to become eligible as preferred hosts. Thus, I considered lean lake trout lagged from 3 to 15 years and Pacific salmon lagged from 2 to 5 years as
potential predictors.

Given the uncertainty in the lagged terms to be included in the model and the potential for bias in traditional model selection methods (e.g., Olden and Jackson 2000), I employed Bayesian model averaging (BMA) to aid in model selection. This technique has been used extensively in recent years in many disciplines and applications, and its merits in an ecological context have been described in detail elsewhere (Volinsky et al. 1997; Hoeting et al. 1999; Fernández et al. 2001; Wintle et al. 2003). A concise summary follows. Using a traditional frequentist step-wise procedure to identify the “best” model, there are a potential of $2^k$ models to be evaluated, where $k$ is the number of potential predictor variables. Thus, the potential model space ($2^k$) can be quite large if $k=17$ potential regressors, as in this analysis. BMA assumes that because of model uncertainty there is not one “best” model; instead, multiple models may describe the relationship in the data with varying accuracy. BMA evaluates models in the $2^k$ model space and determines a posterior model probability, i.e., the probability of a model given the data or $\Pr(M_i \mid \text{Data})$, for each model selected based on certain criteria, where $M_i$ is the $i$th model from the model space. I used a uniform prior, meaning that each model was equally likely.

The criteria used for selecting models is based on two principles. First, when two nested models are compared and the simpler model is rejected based on its fit to the data, then all submodels of the simpler model are rejected. The second principle is based on “occam’s window,” which concerns a ratio of the posterior model probabilities (Madigan and Raftery 1994; Hoeting et al. 1999). It removes models based on the outcome of a posterior probability ratio, $\frac{\Pr(M_0 \mid \text{Data})}{\Pr(M_1 \mid \text{Data})}$, where $M_0$ is
the smaller model derived from $M_1$. If there is evidence for the smaller model then the larger model is rejected. If the evidence is inconclusive (i.e., ratio~1) then both models are kept. I set the criteria for accepting the larger model if the ratio was at least 1/20. These criteria identify a more parsimonious set of models and may improve predictive performance (Hoeting et al. 1999). I adapted the BMA function bicreg (Hoeting et al. 1997) for use in R (Ihaka and Gentleman 1996).

I used the models selected by BMA to find annual posterior–weighted estimates of mean sea lamprey weight, and to find the predicted year 2004 mean weight. I extracted annual fits and the 2004 mean weight predictions from each model and used the corresponding posterior model probabilities to weight these fits according to the following:

$$P_p(y | x, n_{models}) = \sum_{i=1}^{n} \phi_i P_{pi}(y_i | x_i, data), \tag{3}$$

where $P_p(y | x, n_{models})$ is the posterior–weighted estimation of weight, $P_{pi}(y_i | x_i, data)$ is the $i$th model’s prediction given the regressors (the $x_i$’s) in that model and the data, and $\phi_i$ is the $i$th model’s posterior probability.

RESULTS

Trends in sea lamprey weight fluctuated, but generally increased during the period 1961–2003. A linear fit to the data showed a highly significant increase in weight through the period 1961–2003 (Figure 2A). Weights increased by nearly 1 g·year$^{-1}$ during the period (Weight = 0.9681×Year; $F=36.76$, $p<0.001$, $R^2=0.473$). The loess curve of the mean weights increased from 1961 to the mid–1970s, leveled off, then decreased slightly during the early 1980s, and then increased from the late 1980s through 2003 (Figure 2A).
The two increases in weight roughly corresponded to time–lagged increases in lean lake trout and Pacific salmon stocking rates (Figure 2B).

Bayesian model averaging identified 91 models that explained the relationship between sea lamprey weight and salmonid stocking. The small differences between the models’ posterior probabilities indicated a high degree of uncertainty (Table 1; Wintle et al. 2003). The top 25 models, listed by the rank of their posterior probabilities, are shown in Table 1. The BMA analysis calculated the mean values of the coefficients across the 91 models, and their probabilities of not being equal to zero given the data (Table 2). The intercept was included in all models, and BMA indicated that $LT_{t-3}$, $LT_{t-9}$, $LT_{t-11}$, and $LT_{t-13}$ were important to sea lamprey weight based upon their high probabilities of not being equal to zero (Table 2). Other regressors that may have had an effect on weight included $PS_{t-4}$ and $LT_{t-7}$. These terms made up the components of some or all of the top five models with the highest posterior probability (Table 1). Also of note were $LT_{t-14}$, $PS_{t-2}$, and $PS_{t-5}$ that were included in some of the 91 models identified through BMA. Other coefficients also somewhat important were $LT_{t-8}$, $LT_{t-10}$, and $PS_{t-3}$. There were six other potential regressors which were considered in the model space, however the probabilities that these coefficient values were equal to zero was high (Table 2).

Using the models identified in BMA, I compared the averaged models’ fit to the observed mean sea lamprey weight (Figure 3) and used the posterior–weighted model predictions to estimate sea lamprey weight for one year ahead, 2004. The models’ fit followed the general trends of the observed data (Figure 3). Weight prediction estimates for 2004 from the 91 models ranged from 177.8 g to 212.6 g, with a raw (unweighted by
their posterior probability) mean of 196.4 g, ±9.0 g (1 SD), and the frequency distribution appeared to be slightly bimodal with peaks at about 187 g and 202 g (Figure 4). The posterior–weighted distribution of predictions for the year 2004 mean weight appeared more normal (Figure 5), and the posterior–weighted prediction estimate was 195.4 g.

DISCUSSION

The size of sea lampreys increased through the period from 1961 to 2003 (Figure 2A) and, in particular, size has increased during the period since the last study of size (Houston and Kelso 1991). This increase was observed despite the potential for size–selective differences in capture methods. Mean sizes obtained from mechanical and electrical barrier catches appeared to be larger than those from portable trap catches in years when the two collection methods overlapped (Figure 1A). Mean sizes after 1979 were exclusively based on portable traps which may underestimate mean sizes. Thus, the size increase trend may be more pronounced than that presented here.

The exception to the size increase trend that occurred from the mid–1970s to the early 1980s and the reasons for it are unclear. Stocking rates of lean lake trout declined from the late 1960s to the early 1970s, which might account for the size drop. However, Pacific salmon stocking increased during this period (Figure 2B), which might suggest that size should have increased. Lake trout catch per effort in Michigan waters of Lake Superior during the size decrease period suggests that lean lake trout were near pre–sea lamprey invasion and pre–overharvest abundance levels (Wilberg et al. 2003). There is some evidence that lamprey abundance may have been declining during this period (Heinrich et al. 1980). If size is a density–dependent characteristic in sea lampreys, then it should have increased in these years. Thus, this period represents an unexplained
anomaly in an otherwise long-term trend of increasing sea lamprey size.

Upon visual inspection, sea lamprey size peaks appeared to have some relationship with peaks in stocking events, offset by some number of years (Figures 2A and 2B). Bayesian model averaging revealed that, of the variables considered as potentially important to sea lamprey size, stocked lean lake trout lagged 3, 9, 11, and 13 years stand out as most important (Table 2). The coefficient for lake trout lagged 9 years had the highest probability of not being equal to zero (Table 2). Lake trout stocked in the current year are primarily from the previous brood year class. Thus, age 10 lake trout \((LT_t - 9)\) were important hosts for sea lampreys. Lean lake trout terms lagged more than 9 years may reflect the importance of recruits from stocked fish. As stocked fish mature and reproduce, their offspring grow and become potential host resources for sea lampreys. Significant long-lagged stocking terms may reflect a long interaction memory between sea lampreys and host species (Franklin 1989; Magnuson 1990). Age 4 lean lake trout \((LT_t - 3)\), which were also a significantly important regressor, are not likely the preferred hosts of large sea lampreys, but they may be very important to newly transformed sea lampreys and more abundant than older (larger) lean lake trout.

Age 5 Pacific salmon \((PS_t - 4)\) were also a significant regressor in many of the models (Tables 1 and 2), and appeared in three of the five models with the highest posterior probabilities (Table 2). Bayesian model averaging indicated that Pacific salmon lagged 4 (and to a lesser extent, 5) years may be important to sea lamprey weight. Stocked Pacific salmon predictors were composites of three species, two of which mature in about 2 years (chinook, coho) and another maturing in approximately 5 years (steelhead). Since the significant lag for Pacific salmon was 4 years, this indicated that chinook and coho
salmon, with a shorter life history, may not be as important to sea lamprey weight as the longer lived steelhead. However, chinook and coho recruits from naturally reproducing stocked fish might have contributed to the 4 year time lag significance.

Sea lamprey size information included 50 years of data, and stocking information has been tabulated for 54 years, but time lags and missing data removed years available for model fitting. For example, if sea lamprey weight in 1972 was related to lake trout stocked from 4 to 15 years and Pacific salmon stocked from 2 to 5 years before, the data available for model fitting would encompass the period from 1957 to present because of the time–lagged stocking data. However, because I included Pacific salmon stocking rates in model selection, which was systematically begun in 1967 and lagged up to five years, the earliest possible year for data analysis was 1971. This, coupled with the exclusion of years with missing data, restricted model fitting to the years where the predictors had overlapped data (32 years) and, thus, permitted only a one–step ahead (year 2004) forecast prediction of size.

There are other potential predictors that could have been used in model fitting; however, they would have imposed more restrictions on the analysis. For example, other regressors that express host abundance and community composition could have been used in model selection, such as commercial catch per effort (CPE) of salmonids. Although efforts to standardize CPE have been done for Michigan waters of Lake Superior (Wilberg et al. 2003), the models considered here would have required lake–wide CPE estimates given the assumption of opportunistic selection of streams by sea lampreys for spawning (Bergstedt and Seelye 1995). Future modeling would benefit from incorporating lake–wide CPE estimates since these figures more accurately reflect host availability
than stocking rates. The focus on stocking rates ignores differential survival of stocked cohorts and recruitment from naturalized and wild fishes. Sea lamprey abundance estimates could have also been used; however, reliable lake–wide estimates begin for the year 1980 (J. Adams, U.S.G.S., personal comm.) and would have reduced the number of years available for model selection. Focusing on salmonid stocking rates also ignores all the other potential known host species, such as siscowets (*Salvelinus namaycush* siscowet, a deepwater morphotype of lake trout), burbot (*Lota lota*), lake whitefish (*Coregonus clupeaformis*), herring (*C. artedii*), or suckers (family Castostomidae), of which there is very little or no long–term lake–wide data available.

Although the efforts to suppress sea lamprey abundance in Lake Superior and to restore the fish community have been largely successful, the size trend is alarming. Average adult spawning landlocked sea lampreys in Lake Superior are as little as one fifth the size of anadromous sea lampreys (Davis 1967; Beamish 1980; Yergeau 1983; Halliday 1991). If their anadromous conspecifics are indicative of the size potential of landlocked Great Lakes sea lampreys, they are capable of growing to sizes much larger than those attained since their invasion. Sea lampreys in Lake Superior are typically 50 to 100 g smaller than sea lampreys in the other Great Lakes (e.g., Great Lakes Fishery Commission Annual Reports, <www.glfc.org>). As sea lampreys grow to larger sizes, their increased fecundity could offset some of the benefits of sea lamprey control (Applegate 1950; Wigley 1959; Manion 1972; Manion and Hansen 1980; Houston and Kelso 1991). Larger sea lampreys consume more blood, have a higher feeding rate (Kitchell and Breck 1980; Kitchell 1990), and cause increases in the host size death threshold (Kitchell 1990; Jorgensen, Chapter III). In general terms, this sets the stage for decreases in the sur-
vival of host species (Farmer and Beamish 1973; Farmer et al. 1977; Kitchell and Breck 1980; Swink 1990, 2003) and increases in the host death threshold size (Kitchell 1990; Jorgensen, Chapter II). The size increase trend, coupled with lower growth rates of lake trout as their populations have recovered (Sitar et al. In Prep.), adds to the concern about lake trout mortality caused by to sea lamprey attacks.

What conclusions for management action can be drawn from sea lamprey size trends and the potential relationship it has with salmonid stocking? Among the goals set by Lake Superior stakeholders is to “rehabilitate and maintain a diverse, healthy, and self-regulating fish community, dominated by indigenous species and supporting sustainable fisheries,” and for naturally reproducing Pacific salmon to be supplemented “by stocking that is compatible with restoration and management goals for indigenous fish species” (Horns et al. 2003). Pacific salmon sport fisheries are an important economic activity for many communities that surround the Great Lakes, and stocking will likely continue in the future (Goddard 2002).

Managers are, however, re-evaluating stocking levels. They have reduced salmonid stocking because the lean lake trout has probably reached historical abundance levels and salmonid growth has slowed likely as a consequence of overstocking (Bronte et al. 2003; Wilberg et al. 2003). According to the modeling results presented here, stocking Pacific salmon may have had a significant effect on sea lamprey size (Tables 1 and 2). Sea lampreys are able to grow to larger sizes more easily feeding on Pacific salmon than lean lake trout (Jorgensen, Chapter II). The larger observed sizes of sea lampreys in the other Great Lakes (e.g., Great Lakes Fishery Commission Annual Reports, <www.glfc.org>) exemplify the effect of increasing the relative abundance of Pacific salmon in the Lake
Superior fish community: more opportunities for sea lampreys to reach larger sizes. Pacific salmon have established naturalized reproducing populations which without further supplementation from hatchery-reared fish would still likely support a sport fishery, although perhaps at a reduced level.

To mitigate the potentially damaging effects of salmonid stocking while trying to achieve their stated goals, managers should also focus on strategies that provide alternative hosts to deflect sea lamprey-induced mortality on lean lake trout and Pacific salmon. These alternative hosts should preferably be cold-water fishes that are undesirable commercially and recreationally, and that can sustain sea lamprey predation pressure without significantly altering their abundance or ecological roles in the fish community. Such a list of alternative host fishes could include siscowets and burbot. Currently, siscowets and burbot are at or near historically high densities (Bronte et al. 2003). These fishes could serve as buffers; siscowets very likely do now, given their high abundance and their observed sea lamprey wounding rates (Bronte et al. 2003). Thus, maintaining these species at their current abundance would provide alternative host opportunities for sea lampreys that inhabit the colder waters, and they could inhibit sea lamprey growth.

Any management action may have unintended or unpredictable consequences. The effects of decreased Pacific salmon stocking on Lake Superior sea lamprey size are not known. There is evidence that suggests sea lampreys cannot easily reach large sizes feeding only on lean lake trout (Jorgensen, Chapter II). However, the effect on sea lamprey weight from a shift in the salmonid community is unclear. A decrease in Pacific salmon stocking may have unintended consequences on the forage fish populations (Conner et al. 1993; Ebener 1995; Negus 1995; Kitchell et al. 2000). For example, Lake Superior
salmonid diets are dominated by the nonnative rainbow smelt (*Osmerus mordax*), and because Pacific salmon growth trajectories are faster than lean lake trout, a reduction in Pacific salmon may lead to a reduction in predation pressure on rainbow smelt. This could release rainbow smelt and lead to interspecific competition for zooplankton between rainbow smelt and juvenile lake herring (*C. artedii*), which could cause poor lake herring recruitment (Anderson and Smith 1971). Therefore, any management actions with respect to Pacific salmon reductions, therefore, must be carefully considered. Attention should first focus on current levels of Pacific salmon natural recruitment, which should then influence future stocking decisions.

The fish community objectives state that Pacific salmon should be supplemented to keep a healthy fishery and that sea lampreys should cause insignificant (<5%) mortality of their prey species (Horns et al. 2003). Nevertheless, a relationship exists between sea lamprey size and Pacific salmon. Thus, there may be tradeoff for managers trying to reach the goals for the Lake Superior fish community. By stocking Pacific salmon, managers may be unintentionally subsidizing sea lamprey production, achieving one goal at the expense of another.

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Table 1: The top 25 of 91 models, ranked by their posterior model probabilities from Bayesian model averaging of sea lamprey weight with salmonid stocking as predictors ($LT = \text{lean lake trout}, PS = \text{Pacific salmon}$), lagged from year $t$ by the number of years indicated.

| Model Rank | Intercept | $LT_{t-3}$ | $LT_{t-4}$ | $LT_{t-7}$ | $LT_{t-8}$ | $LT_{t-9}$ | $LT_{t-11}$ | $LT_{t-13}$ | $LT_{t-14}$ | $PS_{k-2}$ | $PS_{k-3}$ | $PS_{k-4}$ | $PS_{k-5}$ | Pr($M_j | \text{Data}$) |
|------------|-----------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|------------|----------------|
| 1          | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.04577       |
| 2          | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.03947       |
| 3          | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.03528       |
| 4          | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.03495       |
| 5          | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.03405       |
| 6          | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.02550       |
| 7          | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.02414       |
| 8          | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.02371       |
| 9          | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.02051       |
| 10         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01761       |
| 11         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01539       |
| 12         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01539       |
| 13         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01435       |
| 14         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01434       |
| 15         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01394       |
| 16         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01356       |
| 17         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01305       |
| 18         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01279       |
| 19         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01244       |
| 20         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01240       |
| 21         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01230       |
| 22         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01208       |
| 23         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01185       |
| 24         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01170       |
| 25         | ✓         | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | ✓          | 0.01133       |
Table 2: Bayesian model averaging intercept and coefficient mean values, and the probability averaged over 162 models of not being equal to zero.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean coefficient value</th>
<th>Standard error</th>
<th>Pr($\beta \neq 0$</th>
<th>Data)</th>
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Table 2: continued.

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FIGURE CAPTIONS

Figure 1: **A**) Mean sea lamprey weights (g) captured in U.S. tributaries to Lake Superior by mechanical and electrical barriers (○) and portable traps (●), with smoothed loess lines (mech./elect. barriers = dot dashed, portable trap = solid; span=0.6). Error bars represent ±1 standard error. **B**) Lean lake trout (\textit{S. namaycush}; solid line, +'s) and Pacific salmonids (\textit{O. tshawytsha}, \textit{O. kisutch}, \textit{O. mykiss} combined; dashed line), in millions of fishes stocked in Lake Superior.

Figure 2: **A**) Observed mean sea lamprey weights (g) derived from multiple capture methods (see text), with a linear trend line (dashed line; F=36.76, p<0.001, $R^2=0.473$) and a loess curve (solid). Error bars represent ±1 standard error. **B**) Stocking rates of lean lake trout (solid line, +'s) and Pacific salmon (dashed line) in millions of fishes.

Figure 3: Model fits (solid line) from Bayesian model averaging of sea lamprey weight and salmonid stocking, and observed sea lamprey weight (●). The year 2004 predicted weight (○) is bounded by ±1 standard deviation of the raw (non–posterior–weighted) predictions of 2004 sea lamprey mean weight.

Figure 4: Raw frequency distribution of year 2004 predicted mean sea lamprey weight, not weighted by their posterior model probabilities, from the 91 models selected by Bayesian model averaging.

Figure 5: Posterior–weighted frequency distribution of year 2004 predicted mean sea lamprey weight. Predictions are weighted by their posterior model probabilities, and the mean posterior prediction, $P_p$, is indicated by the dashed line.
Figure 1: Sea lamprey size and salmonid stocking in Lake Superior.
Figure 2: Standardized sea lamprey size and salmonid stocking in Lake Superior.
Figure 3: Bayesian model averaging fits to observed sea lamprey size.
Figure 4: Raw frequency distribution of Bayesian model averaging predictions of sea lamprey weight for 2004.
2004 predicted mean weights (g)

\[ 195.4438 = \sum_{i=1}^{n} \phi_{i} P_{p_{i}}(y|x_{i}) \]

Figure 5: Posterior–weighted frequency distribution of Bayesian model averaging predictions of sea lamprey weight for 2004.
In the years since the invasion of the sea lamprey in the Great Lakes, much has been learned about its biology, life history, and impact on the fish communities. Though there is still much more to learn, managers’ knowledge has been sufficient to develop and implement successful control procedures that maintain sea lampreys to a fraction of their historical abundance (Heinrich et al. 2003). The preceding chapters contribute to that understanding with a further examination of their impacts on host mortality, potential for growth based on host selection, and trends in sea lamprey size and their possible drivers.

The sea lamprey size increase has important implications. Larger sea lampreys are capable of killing larger hosts (Jorgensen, Chapter II). Sea lampreys are capable of achieving larger sizes feeding on hosts that occupy a warmer thermal niche. With the presence of Pacific salmon, opportunities exist for sea lampreys to grow larger. While there is no direct empirical evidence to support it, results of bioenergetics modeling suggest that large sea lampreys may be the result of feeding over two summers as parasites (Jorgensen, Chapter II). Sea lampreys achieving sizes comparable to their anadromous conspecifics can inflict substantially more damage.

Although we control sea lamprey abundance, we cannot directly control host choices made by sea lampreys and the subsequent host damage incurred. We can, however, change the host community composition. Sea lamprey growth is dependent upon several
factors, including host species types and their availability. Although lean lake trout stocking is very important to sea lamprey size, Pacific salmon stocking has an influential role (Jorgensen, Chapter III).

What recommendations for fishery managers can be drawn from this research? Although actions are directed at controlling the numbers of sea lampreys, managers should consider how fisheries policies affect sea lamprey size. Managers have taken the first step by re-examining the Pacific salmon fishery (Bronte et al. 2003) and lowering their stocking rates. Since Pacific salmon occupy a warmer thermal niche than lean lake trout (and most other large potential hosts), and their presence provides a size subsidy and the potential opportunity for sea lampreys to grow larger than without them. Second, managers should continue policies that maintain abundances of cold-water sea lamprey hosts. Sea lampreys feeding on fishes inhabiting colder waters, such as siscowets (Salvelinus namaycush siscowet, a deepwater morphotype of lake trout) and burbot (Lota lota), cannot easily grow to the larger sizes that are capable of inflicting significant host mortality (Jorgensen, Chapter II). Currently, these fishes are probably at or near historical abundance levels (Bronte et al. 2003). Therefore, any policies that maintain abundance levels of colder water hosts will aid in suppressing sea lamprey size increases. Third, expansion of the sterile male release program, which currently targets lotic areas difficult to treat with chemicals alone (Twohey et al. 2003), could address any fecundity (Applegate 1950; Wigley 1959; Manion 1972; Manion and Hanson 1980) and survivorship enhancements (Beamish 1979) imparted to sea lampreys as a result of size increases.

Sea lampreys are persistent pests that are not likely to be exterminated from the Great Lakes. The devastation of host fishes in the last century as a result of their invasion is a
reminder of the fate awaiting the fish community if the control program is scaled back. Yet, a danger still lurks in their capacity to increase in size and the potential damage large sea lampreys can inflict on their hosts. The tradeoffs of management actions and their ecological expression clearly call for continuing attention to the food web context required for effective restoration of the Lake Superior fish community.
REFERENCES


