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Spatial and Ontogenetic Variability of Sea Lamprey Diets in Lake Superior

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ABSTRACT. *Invasive sea lamprey* (Petromyzon marinus) *remain an important source of fish mortality in the Laurentian Great Lakes, yet assessing their impact is hindered by lack of quantitative diet information. We examined nitrogen and carbon stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) of sea lamprey and host species in six ecoregions of Lake Superior, mainly in 2002–2004. Data implied that most sea lamprey fed primarily on upper trophic level species, including forms of lake trout* (Salvelinus namaycush)*. However, in Ontario waters, particularly semi-enclosed Black Bay, sea lamprey relied heavily on lower trophic levels, such as coregonines (*Coregonus *spp.) and suckers (*Catostomus *spp.). Sea lamprey $\delta^{15}N$ and $\delta^{13}C$ generally increased with sea lamprey size, implying dependence on higher trophic levels later in life. Most parasitic sea lamprey that we captured were attached to either lean lake trout (35% of observed attachments), lake whitefish (*Coregonus clupeaformis*; 25%), or cisco (*C. artedii*; 25%); the latter sea lamprey were typically < 15 g. Survey- and fishery-dependent wounding rate data compiled from 1986–2005 suggest that lean and siscowet lake trout were selectively parasitized by sea lamprey, which is consistent with our stable isotope data. Our results largely support the notion that lake trout are the principal host species in Lake Superior. However, stable isotope evidence that sea lamprey feed at lower trophic levels in some regions argues for comprehensive monitoring of sea lamprey impacts throughout the fish community in systems that sea lamprey have invaded.*

INDEX WORDS: *Sea lamprey, stable isotope analysis, lake trout, food web structure, invasive species, impact assessment.*

INTRODUCTION

Despite aggressive control measures in place since the mid 1900s, sea lamprey (*Petromyzon marinus*) remain an important source of mortality for many fishes of the Laurentian Great Lakes (Christie and Goddard 2003). Since radiating throughout the Great Lakes in the first half of the 1900s, sea lamprey contributed to large-scale declines in lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), burbot (*Lota lota*), suckers (*Catostomus* spp.), and many other species (Lawrie 1970, Christie 1974, Smith and Tibbles 1980). Sea lamprey control programs, particularly the application of chemical lampricides in nursery streams starting in the 1960s, reduced sea lamprey to ~10% of their peak abundance (Smith and Tibbles 1980), but they have persisted in all five lakes. Their role in the fish community remains evident: since the late 1990s sea lamprey-induced mortality has exceeded fishing mortality for lake trout in Lakes Superior, Huron, and Michigan (Sitar *et al*. 1999, Heinrich *et al*. 2003, Woldt *et al*. 2006). A recent study concluded that sea lamprey control in Lake Superior has been effective at reducing mortality only among small lake trout (Bronte *et al*. 2003).

During its 12- to 18-month parasitic phase, a Great Lakes sea lamprey may kill anywhere from one host (Bence *et al*. 2003, Madenjian *et al*. 2003) to tens of hosts (Jorgensen and Kitchell 2005).

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Quantifying sea lamprey impacts is a top management priority (Stewart *et al.* 2003), but doing so is contingent upon properly estimating sea lamprey diets and host survival rates. Previous sea lamprey impact estimation models have generally featured simulations in which sea lamprey feed only on lake trout or other salmonines (e.g., Kitchell 1990, Koonce *et al.* 1993, Madenjian *et al.* 2003, Jorgensen and Kitchell 2005). This perspective has a reasonable basis: lake trout were the first species to collapse when sea lamprey abundance peaked in the Great Lakes during the mid-1900s (e.g., Christie 1974). Sea lamprey preferentially target larger hosts (Farmer and Beamish 1973, Swink 1991, Bence *et al.* 2003), and lake trout are among the largest fishes in the system. In addition, lake trout are frequently observed with one or more fresh or healed sea lamprey wounds. However, sea lamprey are known to feed on other hosts (Lawrie 1970, Christie 1974, Smith and Tibbles 1980). Clearly, comprehensive sea lamprey damage assessments must account for mortality on all hosts, not just salmonines, and that in turn requires quantitative descriptions of sea lamprey diets. Unfortunately, dead hosts tend to sink (Bergstedt and Schneider 1988, Schneider *et al.* 1996), and conventional stomach content analysis is difficult to conduct on parasitic-phase sea lamprey because they consume mainly blood, not whole fish. Direct assessment of sea lamprey diets is therefore difficult.

An alternative means of inferring sea lamprey diets is through stable isotope analysis. Stable isotopes of elements such as carbon and nitrogen are well-established tracers of trophic linkages in food webs (Peterson and Fry 1987). Levels of heavy stable isotopes in an organism's tissues are expressed as standardized ratios, according to the equation:

$$\delta^n X = \left(\frac{R_{sample}}{R_{standard}} - 1 \right) \cdot 1000 \qquad (1)$$

where R is the ratio of heavy to light isotope of element X in a tissue sample or a certified reference standard, and $\delta^n X$ is expressed in ‰. The stable isotope ratios of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) can yield, respectively, information about a consumer's trophic level and its base of production. The $\delta^{15}N$ signature reflects trophic position because the differential assimilation rates of the heavy and light isotopes result in a strong shift (trophic fractionation) in the $\delta^{15}N$ of newly assimilated tissue relative to diet. Nitrogen fractionation in consumer muscle tissue generally causes a 2 to 4‰ increase relative to diet (Vander Zanden and Rasmussen 2001). By comparison, $\delta^{13}C$ generally experiences minor trophic fractionation (~0.5‰; Vander Zanden and Rasmussen 2001). Thus, a consumer retains a carbon signature similar to that of its diet and to the production sources (e.g., nearshore vs. offshore, pelagic vs. benthic) that ultimately support it (Hecky and Hesslein 1995).

In order to better characterize sea lamprey diets in space and time, we examined $\delta^{15}N$ and $\delta^{13}C$ of muscle tissue from post-larval, parasitic, and spawning sea lamprey from several regions of Lake Superior. We compared their stable isotope ratios to those of blood from several possible host species. Our goal was to answer the following questions: 1) do sea lamprey stable isotope ratios vary temporally, reflecting ontogenetic changes in sea lamprey diets; 2) do sea lamprey stable isotope ratios vary spatially, reflecting regional differences in host preference and/or community structure; 3) do sea lamprey stable isotope ratios imply a more diverse diet than just lake trout, the top salmonine predator in Lake Superior; and 4) are sea lamprey stable isotope ratios consistent with the feeding patterns implied by studies of wounding rates? If sea lamprey production is shown to be dependent on a greater-than-expected diversity of hosts, we will know that economic injury models of sea lamprey also must be diversified to account for mortality of hosts besides lake trout. Furthermore, if the isotopic relationship between sea lamprey and hosts is shown to vary from site to site, we must consider whether injury models should be run at regional (rather than whole-lake) scales.

MATERIALS AND METHODS

Study Sites

We examined sea lamprey and host fish stable isotope ratios from six ecoregions (ER) and one isolated bay (Black Bay, or BB) of Lake Superior (Fig. 1). We defined these areas based on their distinct physical and ecological characteristics. In brief, ER 1 and 2 are areas that are relatively shallow (< 100 m) and feature one or more major semi-enclosed bays; their fish communities are dominated by coregonines and catostomids. ER 3 and 4 represent more open-lake regions on either side of the Keweenaw Peninsula; they are largely over 100 m in depth and their fish communities have a greater proportion of lean and siscowet lake trout than ER 1 and 2. ER 5 is the region around the Apostle Islands and has notably high concentrations of forage fish and exten-