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Trophic connections in Lake Superior Part I: The offshore fish community

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ABSTRACT

Detailed diet linkages within the offshore (>80 m bathymetric depth) food web of Lake Superior are currently not well identified. We used analyses of fish stomach contents to create an empirically based food web model of the Lake Superior offshore fish community. Stomachs were collected seasonally (spring, summer, and fall) from nine offshore locations in 2005, using bottom and midwater trawls. In total, 2643 stomachs representing 12 fish species were examined. The predominant fish species collected were deepwater sculpin (*Myoxocephalus thompsonii*), siscowet (*Salvelinus namaycush siscowet*), kiyi (*Coregonus kiyi*), and cisco (*Coregonus artedi*). *Mysis diluviana* was the most common prey item, indicating that changes in *Mysis* abundance could have a profound impact on the entire offshore food web. *Mysis* was the primary diet item of deepwater sculpin (≥53% by mass) and kiyi (≥96% by mass) regardless of depth or season. The invasive *Bythotrephes* was an important diet component of the pelagic cisco in summer and fall. Deepwater sculpin were the primary diet item of siscowet (≥52% by mass), with coregonines appearing in the diet of larger (>400 mm) siscowet. Non-metric multidimensional scaling analysis indicated that there were no statistically significant seasonal or site-specific differences in diets of deepwater sculpin, cisco, or kiyi. Site was the primary structuring factor in siscowet diets. Generally, in Lake Superior, the diet items of the dominant offshore species did not appear to be in danger from those types of major ecological shifts occurring in the lower Laurentian Great Lakes.

Introduction

In Lake Superior, an empirical lake-wide analysis of the ecological linkages of the offshore food web does not exist. Although Lake Superior has 5000 km of coastline (Chen et al., 2001), approximately 80% of the lake is classified as offshore (>80 m depth), and this deepwater habitat is an important component of the lake ecosystem (Horns et al., 2003; Matheson and Munawar, 1978). Zooplankton and fish from the coastline areas of Lake Superior have been routinely sampled for decades (Gorman et al., 2009; Gorman and Hoff, 2009), but offshore areas have received far less attention (Hansen, 1994; Stockwell et al., 2006). The offshore pelagic fish community is presently dominated by native cisco (*Coregonus artedi*) and kiyi (*Coregonus kiyi*) (Stockwell et al., 2006, 2010; Yule et al., 2008). The benthic fish community is dominated by the deepwater sculpin (*Myoxocephalus thompsonii*), and the dominant piscivorous fish is the siscowet (*Salvelinus namaycush siscowet*), the deepwater morphotype of lake trout (*S. namaycush;* Scott and Crossman, 1973; Goetz et al., 2010).

Food webs describe direct biological linkages and are thus a first step in identifying energy flow between different areas in a lake (Evans et al., 1987; Kitchell et al., 2000). For example, comprehensive offshore Lake Superior diet information could address possible diet overlap between deep and shallow water species such as coregonines or lake trout morphotypes. Such information would improve the ability to predict how perturbations of different prey groups might impact fish species, both directly and indirectly (*sensu* Kitchell et al., 2000). Definition of linkages of the relatively intact native fish community of Lake Superior could also provide information essential to rehabilitation of native species in the other Great Lakes. Rehabilitation of native fishes is especially relevant given the recent changes in the deepwater food webs of Lake Huron (Riley et al., 2008), Lake Michigan (Bunnell et al., 2006, 2009), Lake Ontario (Mills et al., 2003) and Lake Erie (Dermott and Kerec, 1997; Munawar et al., 2005). However, the majority of past Lake Superior diet studies have not attempted to define the ecology of the entire community, but instead focused on single or limited numbers of species in the nearshore zone of the lake (e.g., Bailey, 1972; Dryer et al., 1965; Dryer and Beil, 1968; Fisher and Swanson, 1996; Ray et al., 2007). Research on deepwater species such as siscowet rarely collected fish from bathymetric depths greater than 100 m until recently (Negus et al., 2007; Ray et al., 2007;

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Sitar et al., 2008). Selgeby (1988) examined sculpin food habits in Lake Superior in both nearshore and offshore areas, but sampled only in a limited region. Diet studies that have examined multiple species (e.g., Anderson and Smith, 1971; Johnson et al., 2004; Negus et al., 2008) have been geographically limited to specific regions such as western Lake Superior. Thus, the ecological linkages of much of the deep, cold-water offshore community need better definition.

To address the current gap in knowledge of offshore trophic relationships, we analyzed the diet composition of the offshore Lake Superior fish community from fish stomachs collected at multiple sites over three seasons. Our primary objective was to create an empirical model of the food web of the offshore fish community. Our secondary objective was to determine whether the offshore food web exhibited spatial and seasonal variation. Because of the cold-water conditions that prevail in offshore waters (Munawar and Munawar, 1978), we hypothesized that there would be no observable differences in fish diet composition within species across offshore sites or between seasons.

Methods

Field collections

Fish were collected from selected offshore areas across Lake Superior to capture spatial variability in diets (Fig. 1a). All offshore sites were randomly selected from a matrix of potential sites by the Canadian Department of Fisheries and Oceans. Average bathymetric depths at sites ranged between 85 and 305 m (Fig. 1b). Samples were collected during three discrete time periods: spring (May–June), summer (July–August), and fall (September–October) in 2005. All samples were collected by the research vessel *Kiyi*, operated by the United States Geological Survey, Great Lakes Science Center, in Ashland, Wisconsin.

Bottom trawl stations (all sites) were sampled both day and night with a 3/4 Yankee bottom trawl (11.9 m headrope, 15.5 m footrope, and 2.2 m wing lines having 13 mm cod-end mesh) (Stockwell et al., 2006). Midwater trawls (15.2 by 15.2 m at mouth having 13 mm cod-end mesh) were collected at night (all sites) in a stepped-oblique fashion above the bottom trawl path (see Stockwell et al., 2006 for details). Fish samples from each trawl tow were sorted by species. Species were subsampled if more than several hundred individuals were captured. At least 50 individuals from each species (if available) per trawl were tagged and frozen for diet analysis. Stomachs were later removed from the frozen samples and either preserved in ethanol or refrozen in individual bags before analysis. Collected fish species included: lean lake trout, siscowet, burbot (*Lota lota*), spoonhead sculpin (*Cottus ricei*), slimy sculpin (*Cottus cognatus*), deepwater sculpin, rainbow smelt (*Osmerus mordax*), ninespine stickleback (*Pungitius pungitius*), cisco, kiyi, and bloater (*Coregonus hoyi*).

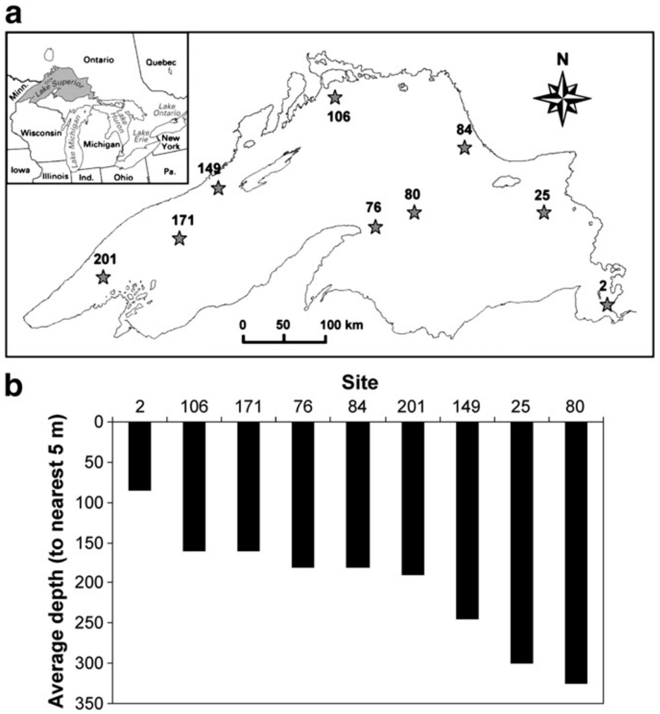

Fig. 1. Offshore sampling stations in Lake Superior, 2005 (a) and average bathymetric depths (b). Depths were rounded to the nearest 5 m. All sites were sampled once during spring, summer, and fall.

Diet analyses

Diet processing protocol was species dependent. Stomachs from piscivores (burbot, lean lake trout, and siscowet) were analyzed on an individual basis, because of small sample sizes. Stomachs from the planktivorous and benthivorous fishes, which were more abundant in our samples, were pooled by species prior to analysis in groups of 5 (deepwater sculpin) or 10 (all other species) per length bin. The length bins varied by species, ranging from 20 mm (all sculpin species, nine-spine stickleback, and rainbow smelt) to 30 mm (cisco, kiyi, and bloater). Stomachs were only pooled within individual trawls, and therefore were date- and site-specific.

Stomachs were dissected and contents were removed prior to analysis. Empty stomachs were recorded. Items retained in the gill rakers were not included. Piscivore stomachs were emptied into Petri dishes and diluted with 95% ethanol and water. Planktivore stomachs were opened under a dissecting microscope and analyzed for large invertebrates (*Diporeia* spp., *Mysis diluviana*, and *Bythotrephes longimanus*). Remaining stomach contents were diluted with water to a known volume and subsampled for smaller zooplankton. Contents were subsampled in 2-mL aliquots until either 10% of the diluted volume was sampled, or 100 individuals were identified.

For a stomach or pool of stomachs, 10 individuals per prey type (if available) were measured to the nearest mm, and the remaining individuals were counted. Stomach contents were classified as: *Mysis*, *Bythotrephes*, *Daphnia* spp., other cladocerans, calanoid copepods, cyclopoid copepods, *Diporeia*, ostracods, snails, sphaeriid clams, fish eggs, fish (to species when possible), and insects (to Order). *Mysis*, *Diporeia*, and *Bythotrephes* eyes and heads were counted if present, and assigned mean lengths and masses (Pothoven and Vanderploeg, 2004). *Bythotrephes* tail spines were not counted. For all prey species, if pieces of bodies were present, only the front half of the body was counted. If bodies were bent, straight line measurements were summed to obtain a total length. Zooplankton length was measured from the top of the head to the base of the caudal spine (the insertion of spines into the caudal ramus) or to the posterior end of the carapace (GLNPO, 2003). *Mysis* carapace length was measured from the anterior edge of the head to the cleft in the telson. *Bythotrephes* body lengths were measured excluding the caudal process. *Diporeia* were measured from the eye to the posterior edge of the telson.

Prey lengths were converted to dry mass (mg) using length-mass regressions from the literature (Tables 1 and 2 and references therein). To ensure consistency between invertebrate and fish masses, invertebrate dry masses were converted to wet masses prior to analysis. Conversion factors came from Juday and Birge (1927; *Mysis*), Cummins and Wuycheck (1971; *Diporeia*), Sage (1982; Insecta), Downing and Rigler (1984; zooplankton, fish eggs), Ross and Lima (1994; clams and snails), and Riccardi and Bourget (1998; isopods). Wet masses and counts per prey taxa from individual trawls were summed within season. These data were summarized as percentages