

**An Evaluation of the Importance of *Mysis relicta* to the Lake Superior
Fish Community**

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submitted to the faculty of the Graduate School
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by

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Abstract

Mysis relicta is a major prey item for many fish species in Lake Superior, However, its importance to an entire fish community as a whole has not been quantified. We describe seasonal prey selection of the major fish species collected across 18 sites in Lake Superior, and again at five locations in western Lake Superior in 2006 using a selection index (Chesson's Alpha). We also used bioenergetics models to estimate the consumption of prey items by the fish community at the same locations. Additionally, we modeled the production of *Mysis*, to evaluate this prey resource in terms of demand and supply. We found that rainbow smelt, kiyi, and bloater selected for *Mysis* over other prey items during all seasons, while lake whitefish only selected for *Mysis* in the spring and summer. Cisco selected for large zooplankton, while all three sculpin species exhibited neutral selection of prey items. Burbot and siscowet selected for deepwater sculpin and *Mysis* during all seasons, with juveniles showing a stronger selection for *Mysis* than did adults. *Mysis* was the most consumed prey item lakewide, with higher annual consumption offshore than nearshore. Predation on *Mysis* was mainly from rainbow smelt, bloater, and lake whitefish nearshore, and deepwater sculpin and kiyi offshore. Our estimates of *Mysis* production (supply) were higher than the consumptive demand by the fish community at nearly all locations, with this balance indicating stability in the food web. *Mysis relicta* was found to be a sought after prey item by many fish species, and is directly responsible in supporting the fish communities both nearshore and offshore. Thus, *Mysis* plays a pivotal role in the structure and function of the Lake Superior fish community.

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The Selection of Prey by the Lake Superior Fish Community

Introduction

Mysis relicta is a freshwater macroinvertebrate found in glaciated regions of North America and Europe (Balcer et al. 1984). It is an omnivore that feeds on phytoplankton, zooplankton, detritus, and benthos (Parker 1980, Grossnickle 1982, Branstrator et al. 2000, Johannsson et al. 2001). *Mysis* reside near the benthos during the day and migrate upward into the water column at night (Beeton 1960, Beeton and Bowers 1982, Gal et al. 1999, Jensen et al. 2009). The extent of this diel vertical migration (DVM) is mitigated largely by temperature and light (see reviews by Johannsson et al. 2003 and Gal et al. 2004). Their relatively large size, high energy content, and ability to couple benthic and pelagic habitats makes them an ideal food source for many planktivorous fish species (Wells and Beeton 1963, Anderson and Smith 1971, Owens and Dittman 2003, Pothoven and Vanderploeg 2004) and juvenile stages of piscivorous fishes (Dryer et al. 1965, Ebener 1995, Hudson et al. 1995, Fratt et al. 1997).

Although diet studies show *Mysis* to be an important prey item for many fish species, previous studies have generally described their relationship to a single fish species or multiple species with similar life histories. Less is known about their importance to entire fish assemblages. This is particularly relevant because *Mysis* are known to cause significant food web changes where they have been introduced (Lasenby et al. 1986; Spencer et al. 1991, 1999; Chipps and Bennett 2000). Moreover, recent

studies of the lower Great Lakes have shown decreases in *Diporeia* spp. abundances (Nalepa 1998, Dermott 2001, Pothoven et al. 2001, Hondorp et al. 2005); another important prey item to Great Lakes fishes. Decline in *Diporeia* abundance appears to increase consumptive demand on *Mysis* (McDonald et al. 1990, Pothoven et al. 2001, Owens and Dittman 2003, Hondorp et al. 2005), which may alter or disrupt food webs and cause fish community changes.

Of the Laurentian Great Lakes, Lake Superior has the least perturbed native fish community, including extant populations of cisco *Coregonus artedii*, kiyi *C. kiyi*, short-jaw cisco *C. zenithicus*, lake whitefish *C. clupeaformis*, deepwater sculpin *Myoxocephalus thompsoni*, and siscowet lake trout *Salvelinus namaycush* siscowet that have been extirpated (or are at remnant levels) in the lower Great Lakes. In addition, current populations of Lake Superior macroinvertebrates such as *Diporeia* and *Mysis* appear stable (Barbiero and Tuchman 2002, Scharold et al. 2004). Consequently, Lake Superior provides an opportunity to study the connectedness of *Mysis* to native fish communities in the context of a minimally disturbed food web

The objective of this study was to estimate prey selectivity by benthic and pelagic fish species in Lake Superior. Given the DVM behavior of *Mysis* across benthic and pelagic habitats, we expected *Mysis* to be an important prey item to many fish species. We also examined how fishes selected *Mysis* across seasons and bathymetry. Because *Mysis* abundance in Lake Superior is positively related to depth (Carpenter et al. 1974) with *Diporeia* showing an opposite pattern (Cook 1975, Auer and Kahn 2004, Auer et al. 2009), we expected selectivity of benthivorous fishes to vary by bathymetric depth. We

also expected that selection for *Mysis* will be higher for pelagic fish that undergo DVM because they are likely better at exploiting a migrating food source (Eshenroder and Burnham-Curtis 1999). We anticipate that selection for *Mysis* by piscivorous fishes will be stronger for juvenile life stages than for adults, as younger life stages typically consume smaller prey than adults because of size-selective predation (Ivlev 1961, Hrbáček 1962, Brooks and Dodson 1965).

Methods

Sample Design

Sampling was conducted at 9 nearshore and 9 offshore sites across Lake Superior in the spring (May-June), summer (July-August), and fall (September-October) of 2005 (Figure 1). Mean bathymetric depths at nearshore and offshore sites ranged from 15-91 m and 93-312 m, respectively. Five of those sites (3 nearshore, 2 offshore) in the western arm of Lake Superior were re-sampled in spring, summer, and fall of 2006 to provide estimates of inter-annual variability.

Fish Sampling

Benthic fish were collected at night and during the day (where feasible) at each station with a 3/4 Yankee bottom trawl (11.9 m headrope, 15.5 m footrope, and 2.2 m wing lines) with 89 mm and 64 mm stretch mesh with 13 mm at the cod end. Bottom trawls were towed at 3-4 km/hr across contour at nearshore locations and along contour at offshore locations. Pelagic fish were collected at night with a midwater trawl (Gourock

Trawls, Ferndale, WA, USA) measuring 15.2 x 15.2 m in width and height with a tapered stretch mesh of 152 mm at the mouth to 13 mm at the cod end. Midwater trawls started at a headrope depth of 5 m and were towed in a stepped-oblique fashion (Kirn and LaBar 1991) down the water column in 10-15 m increments to a maximum headrope depth of 80-95 m with equal amounts of time sampled at each depth stratum. Trawling methodology in nearshore and offshore areas are described by Stockwell et al. (2006, 2010). Sampling gears used to collect fish during each sampling event are listed in Table 1-1. All fish collected in trawls were identified to species, measured and weighed on ship. Sub samples of at least 50 fish per species (where possible) from each sampling event were immediately frozen to preserve stomach contents.

Stomachs were later removed from fish in the lab and either preserved in 70% ethanol or frozen. Stomachs from burbot *Lota lota* and siscowet lake trout were analyzed individually, whereas 5-10 individuals from each of the other species were pooled in 20-30 mm length bins and analyzed in aggregate from each sampling event. All macro-invertebrates (*Mysis*, *Diporeia*, *Bythotrephes longimanus*) found in stomachs were identified and counted under a dissecting microscope. The remaining stomach contents were diluted to a known volume and sub sampled with multiple 1-ml Hensen-Stemple Pipets until 10% of the sample or 100 individuals were counted. Up to 10 individuals of each prey species per stomach were measured. Detailed diet results are reported elsewhere (Gamble et al. in review). We combined diet information across length bins from each fish species at each sampling event. Empty stomachs and prey items that made up < 1% numerically of a species diet were removed from our analysis. Sample sizes of fish stomachs, and sizes of those fish used in our analysis are given in Table 1-2.

Hydroacoustics

To estimate pelagic fish density (fish/ha), a hydroacoustic unit was deployed concurrently while midwater trawling. Acoustic data were collected using a Biosonics (Seattle, WA, USA) DT-X digital echosounder equipped with either a 120 kHz or a 70 kHz split beam transducer with a nominal beam width of 6.7° and 5.3° respectively. The transducer was mounted on a 1.2 m long tow body and deployed 1 m below the surface. Acoustic pulse duration was set at 0.4 ms. Pulse frequency was set at 5 pings/sec for transects with depths less than 70 m and, 3 pings/sec for transects with 70-150 m depths, and 1-2 pings/sec for transects deeper than 150 m. Echo integration data were collected using a threshold of -75 decibels. Routine standard target calibration tests were performed using a 33-mm Tungsten carbide calibration sphere. Calibration results were always within 1.2 decibels (dB) of the theoretical target strength of the sphere (-40.5 dB). Acoustic data were processed with Ecoview post-processing software (version 3.10.132.06 SonarData Ltd, Tasmania, Australia). A line 0.2 m above the lake bottom was defined on echograms using an Echoview algorithm. Any anomalies in bottom tracking were eliminated by visually inspecting each echogram, and manually redefining the bottom line where needed. During rough sea conditions, a surface line was added between 2-5 m below the surface to prevent integration of surface noise when measuring fish acoustic backscattering.

Acoustic data were processed with Ecoview post-processing software (version 4.1 SonarData Ltd, Tasmania, Australia). A line 0.2 m above the lake bottom was defined on echograms using an Echoview algorithm. Any anomalies in bottom tracking were

eliminated by visually inspecting each echogram, and manually redefining the bottom line where needed. Sometimes during rough sea conditions, a surface line was added between 2-5 m below the surface to prevent integration of surface noise when measuring fish acoustic backscattering. A mark threshold of -65 dB was applied to the SV echogram before estimating area backscattering to exclude macro invertebrate targets (i.e., *Mysis*).

The density of fish in the water column was estimated by:

$$\text{Fish density (fish/ha)} = (\text{ABC} / \sigma_{\text{bs}}) * 10000$$

Where ABC or the area backscattering coefficient equals $10^{\text{SV}/10} * T$, where sv is the mean volume backscattering strength of the cell and T is the mean thickness of the cell; σ_{bs} is the mean backscattering cross-section of the average size fish in the cell (i.e., $\sigma_{\text{bs}} = 10^{(\text{TS}/10)}$ where TS is the mean target strength in decibels (db); and 10000 is the number of square meters in a hectare (Parker-Stetter et al. 2009). We used the single-target detection criteria and the single-target detection parameters presented in Yule et al. (2006) to estimate the mean TS. Total fish density was then allocated to size classes by the number of targets within three size categories (small, medium, large) which ranged from < -35.6 dB, -35.6 to -32 dB, > -32 dB in TS respectively (Hrabik et al. 2006; Stockwell et al. 2006, 2007, 2010; Yule et al. 2006, 2008). Acoustic fish densities of each size range were then apportioned to species based upon size and composition of fish collected in concurrent midwater trawls (see Stockwell et al. 2010 for details).

Invertebrate Sampling

To estimate prey availability, collections of *Mysis*, zooplankton, and benthic invertebrates were made during each fish sampling event. Invertebrate samples were

collected at the midpoint of each trawl transect to best represent prey availability to the fish collected. *Mysis* were sampled at night with a 1 m² net (1,000 µm mesh tapered to 250 µm mesh with a 63 µm mesh bucket) towed vertically from two meters off the bottom to surface. The net was retrieved at 0.3 m / sec after a 30 second delay when the net reached the bottom to allow *Mysis* to redistribute in the water column. Four replicates were taken at each station and preserved in 8% sugared-buffered formalin. All *Mysis* were counted and the first 100 individuals per replicate were measured (tip of rostrum to cleft in telson). The four replicates were then averaged to estimate mean density (# / m²) at each station during each season.

Zooplankton was collected with vertical net tows, in triplicate, during the day using a metered 0.5-m diameter net with 153-µm mesh. Tows were made from 100 m to the surface (or 2 m off the bottom at shallower sites). Stations deeper than 100 m also had a single stratified tow taken from 2 m off the bottom to 100 m to complete the water column profile. Contents from net tows were preserved with 8% sugared-buffered formalin with rose-bengal stain. Triplicate samples were pooled and split using a Folsom plankton splitter, with four stratified aliquots analyzed per sample. Subsampling methodology followed the U.S. EPA-GLNPO procedures (SOP-LG403, 2003). All crustacean zooplankton were identified according to Balcer et al. (1984) under a dissecting microscope. The first 20 individuals of each species were measured with a microscope mounted Leica digital camera. Zooplankton densities are reported in areal units (# / m²) to represent total zooplankton in the entire water column.

Benthic organisms were sampled with a Ponar dredge. Each “grab” sampled 0.046 m² of the sediments. Samples were taken in triplicate and the contents of each grab were elutriated and rinsed through a 500 µm mesh sleeve. Samples were preserved in 8% sugared-buffered formalin with rose-bengal stain and later identified and enumerated under a dissecting microscope. Replicates were analyzed individually and later averaged to estimate mean density (# / m²) at each station per season.

Data Analysis

Prey selection for each fish species was calculated using Chesson’s α (Chesson 1983). Selectivity for prey species i (α_i) was calculated by:

$$\alpha_i = \frac{\frac{r_i}{n_i}}{\sum_{j=1}^m \frac{r_j}{n_j}}$$

where r_i is the proportion of prey species i in a fish diet, n_i is the proportion of that prey species found in the environment, and m is the number of prey species. Values range from 0 (no selection) to 1 (complete selection of only one prey type). An α_i value of $1/m$ indicates neutral selection for a given prey type. Values higher or lower than $1/m$ indicate positive or negative selection, respectively. We calculated prey selection for pelagic fishes (rainbow smelt, bloater, kiyi, and cisco), benthic fishes (spoonhead sculpin *Cottus ricei*, slimy sculpin *Cottus cognatus*, deepwater sculpin, lake whitefish), and piscivorous fishes (burbot *Lota lota* and siscowet) for each station and season where caught. We also calculated prey selection for piscivorous fishes (burbot and siscowet) across size classes

as we expected prey selection to vary across fish lengths. Prey selection was not calculated for lean lake trout due to low sample sizes. We used a generalized linear model ($y = B_0 + \text{depth} + \text{season} + \text{depth} * \text{season}$), with season being a categorical variable, to determine if selection for *Mysis* or *Diporeia* changed across depths or seasons for each fish species. We used a Bonferroni correction to adjust for multiple comparisons with $\alpha = 0.005$. Two-sample t-tests were used to compare selection for *Mysis* between years 2005 and 2006 with $\alpha = 0.05$ using SAS statistical software (version 9.1, SAS Institute).

Results

Pelagic species

Rainbow smelt exhibited a strong positive selection for *Mysis* across all seasons, as the lakewide mean was found to be statistically positive during each season (Figure 1-2). Selection for *Mysis* by rainbow smelt did not change across seasons. Almost all (91%) stations where rainbow smelt were captured showed a positive selection for *Mysis* with many stations showing selection by rainbow smelt for *Mysis* alone (Table 1-3). Selection for *Mysis* by rainbow smelt did not change across depths.

Kiyi had the highest selection for *Mysis* when compared to other fish species examined. The lakewide mean was statistically positive across all seasons (Figure 1-2), with exclusive selection for *Mysis* in the spring at all stations (Table 1-2). No seasonal changes in the selection for *Mysis* by kiyi were found, with (93%) of stations where kiyi

were captured showed a positive selection for *Mysis* (Table 1-3). Furthermore, kiyi selection for *Mysis* was not affected by depth.

On average, bloater had a higher selectivity for *Mysis* than other prey items during each season. Bloater did, however, show positive selection for adult calanoid copepods and *Diporeia* in spring and *Bythotrephes* in summer and fall (Figure 1-2). Over half (58%) of the stations where bloater were captured showed a positive selection for *Mysis* (Table 1-3). However, the high variability in selection between sites created lakewide mean values that were not statistically different from neutral selection. Selection for *Mysis* changed (increased) with depth ($p = 0.001$) with absences of seasonal effects (Table 1-4).

Cisco showed marked changes in prey selection across seasons, exhibiting statistically significant positive selection for adult calanoid copepods in spring and *Bythotrephes* in summer and fall (Figure 1-2). *Mysis* was positively selected for at only a few locations where ciscoes were captured ($< 10\%$, Table 1-3). Furthermore, there were no changes in selection for *Mysis* across depths.

Benthic species

Spoonhead sculpin exhibited widely variable selection of prey items. Spoonhead sculpin selected for *Mysis* in spring, chironomids in summer, and *Diporeia* in fall (Figure 1-3). Lakewide and seasonal selectivity of these three prey items by spoonhead sculpin did not vary significantly from neutral selection, likely due to a high variability between stations. Positive selection for *Mysis* was found at 39% of sites where spoonhead sculpin were captured (Table 1-3). Selection for *Mysis* and *Diporeia* did not vary by depth.

Slimy sculpin selected for mayflies (Ephemeroidea) over all other prey items across all seasons (Figure 1-3), and showed positive selection for *Diporeia* in summer. Lakewide and seasonal averages were not statistically different than neutral selection for any prey type utilized by slimy sculpin. High variability between stations likely led to these findings. *Mysis* was only positively selected for at 13% of locations where slimy sculpin were captured (Table 1-3). Selection for *Mysis* and *Diporeia* did not vary across station depths.

Deepwater sculpin showed positive selection for clams in spring and summer, and *Diporeia* and *Mysis* in fall. However, lakewide means for these prey items were not statistically different from alpha neutral, and did not vary by season. There was a trend of decreasing selection for clams across seasons, with increasing selection for *Diporeia* and *Mysis*. *Mysis* was positively selected for at 34% of stations where deepwater sculpin were captured, many of which were from nearshore stations (Table 1-3). Selection for *Mysis* changed (decreased) with depth ($p < 0.001$), without any seasonal effects (Table 1-4). Selection for *Diporeia* did not change with depth, but there was some evidence that the slopes of the regression changed by season.

Lake whitefish selected for *Mysis* in spring, *Mysis* and clams in summer, and strongly selected for *Bythotrephes* in fall (Figure 1-3). Selection for *Mysis* decreased across seasons. However, this was not significant due to large variances between stations coupled with small samples sizes in summer and fall. We found positive selections for *Mysis* at 53% of the stations where lake whitefish were captured (Table 1-3). Selection of *Mysis* and *Diporeia* by lake whitefish did not vary by depth.

Piscivorous species

Burbot selected for *Mysis* and deepwater sculpin across all seasons, with rainbow smelt also being selected for in spring and *Diporeia* in summer (Figure 1-4). There were large differences in selection between stations, which created lakewide mean values that were not different across seasons or between prey types. In spite of this, the mean selection for *Mysis* by burbot increased across seasons, while selection for deepwater sculpin and rainbow smelt decreased (Figure 1-4). Burbot showed a positive selection for *Mysis* at 50% of the stations where burbot was captured (Table 1-3). Selection for *Mysis* and *Diporeia* did not change significantly across depths. Juvenile burbot (< 200 mm) selected for *Mysis* and deepwater sculpin, while larger burbot (200-400 mm) selected less deepwater sculpin (Figure 1-5). Selection for rainbow smelt increased with burbot size.

Siscowet selected for *Mysis* and deepwater sculpin during each season (Figure 1-4), with selection for deepwater sculpin being higher. To a lesser extent, coregonines (chiefly kiyi) were selected for in fall. There was a slight trend for siscowets to increase their selection for *Mysis* and decrease their selection for deepwater sculpin across seasons (Figure 1-4); however selection of prey did not vary significantly across seasons. We found siscowets to have a positive selection for *Mysis* at 52% of the sampling events (Table 1-3). Selection for *Mysis* and *Diporeia* did not change across depths. Juvenile siscowets (< 200 mm) positively selected for *Mysis* (Figure 1-5). As siscowets grew in size, selectivity of *Mysis* decreased while selectivity of larger prey items like deepwater sculpin and coregonines increased (Figure 1-5), evidence of an ontogenetic shift in prey selectivity.

Inter-annual variability

We compared the mean selection for *Mysis* pooled across seasons and stations in western Lake Superior (stations 139, 171, 172, 201, and 210; Figure 1-1) in 2005 and 2006, and found no differences in prey selection for any of the fish species examined (Figure 1-6; p-values ranged from 0.17-0.78). However, declines were noted for cisco and spoonhead sculpin between years. The higher selection for *Mysis* by cisco in 2005 can be attributed to the high summer value at station 172 (0.98) resulting from *Mysis* being found in two cisco stomachs. Spoonhead sculpin also showed a lower selection for *Mysis* in 2006, which may be a result of lower sample sizes in 2006. Prey selection for burbot and siscowet lake trout were unwarranted owing to extremely low 2006 sample sizes.

Discussion

Our results indicate that the fish community in Lake Superior is intimately connected to *Mysis relicta*. *Mysis* were important to both pelagic and benthic fish species, including planktivores and piscivores. Native fishes like kiyi, bloater, deepwater sculpin, lake whitefish, burbot, and siscowet were shown to utilize *Mysis* resources either by prey selection (present study) or from diet analysis (Gamble et al. in review). The link between *Mysis* and fish is important given that rehabilitation of native fishes in the Great Lakes is an important goal of the Great Lakes Fisheries Commission (GLFC 2001). These results emphasize the need to document and understand how current *Mysis* resources are being used in a minimally disturbed food web like Lake Superior. There have been changes in

benthic communities in the lower Great Lakes where macro-invertebrate prey resources like *Diporeia* have declined substantially, these having resulted in shifts in macro-invertebrate prey availability and dietary shifts towards *Mysis* supporting fish that formerly relied on *Diporeia* (Pothoven et al. 2001, Owens and Dittman 2003, Hondorp et al. 2005). However, the duration and sustainability of this increased predation upon *Mysis* is unclear.

Ecopath and Ecosim (EwE) simulations by Kitchell et al. (2000) suggested that rainbow smelt, deepwater sculpin, juvenile siscowet, and nearshore salmonids would all be negatively affected if *Mysis* were removed from the Lake Superior food web. The diet inputs used by Kitchell et al. (2000) had smaller proportions of *Mysis* to the diets of chubs (which grouped bloater and kiyi into one ecological entity), slimy sculpin, deepwater sculpin, and lake whitefish than used in our analyses. If *Mysis* currently make up a larger portion of diets, the effects of removing *Mysis* would be more pronounced to the fish community. However, certain fish species seem to exhibit plasticity in prey selection. If *Mysis* populations in Lake Superior were to decline in the same fashion as *Diporeia* in the lower lakes, would there be enough alternative resources to support the current planktivore community? In deep offshore waters, *Mysis* may be the only available prey in sufficient quantity to support benthic fish, leaving deepwater coregonines to either compete with sculpins near the benthos or higher in the water column with cisco.

Diel vertical migrations (DVM) of planktivores have been noted for rainbow smelt, kiyi, bloater, and cisco in Lake Superior (Heist and Swenson 1983, Hrabik et al. 2006, Yule et al. 2007, Ahrenstorff 2009, Stockwell et al. 2010). DVM behavior may be

a selected behavior trait to allow spatial overlap with a preferred prey species, as demonstrated for coregonids (Eshenroder and Burnham-Curtis 1999). Rainbow smelt are typically found in shallow nearshore areas with DVM made from the benthos to the thermocline (Heist and Swenson 1983), which maximizes their spatial overlap with *Mysis* during both photoperiods, and is consistent with the strong selection for *Mysis*. Kiyi exhibit a strong DVM pattern in offshore waters with 100-150 m vertical migrations from the benthos during daylight to the metalimnion at night (Ahrenstorff 2009, Stockwell et al. 2010), which leads to high spatiotemporal overlap with *Mysis*. Bloaters showed a lower selection for *Mysis* than rainbow smelt and kiyi, and exhibited diversity by also selecting for *Diporeia* and *Bythotrephes*. This is consistent with bloaters undergoing smaller DVM whereby they remain closer to the bottom at night (Brandt 1991, TeWinkle and Fleischer 1999, Yule et al. 2007). Cisco exhibited positive selection for adult calanoid copepods and *Bythotrephes* which are typically found high in the water column (Yurista et al. 2009), supporting the conclusions of Link (1996, 1998) that cisco are size-selective predators on zooplankton. Moreover, cisco are mainly pelagic and undergo a more limited DVM (Stockwell et al. 2010), thus their spatial overlap with *Mysis* is lower than that of kiyi.

Increases in cisco populations in the last few decades (Stockwell et al. 2009) and changes in species composition of deepwater ciscoes (Gorman and Todd 2007) favoring bloaters has likely led to increased predation upon large zooplankton (Link et al. 2004, Johnson et al. 2004). Flexibility in prey selection by bloater and cisco across seasons may indicate the ability to take advantage of large scale changes in prey resources, and the ability to co-exist with other coregonine forms like kiyi by selecting different prey items.

A shift in bloater abundance and range expansion was found in Lake Michigan following the decline of deepwater ciscoes from the 1900s to the 1950s (Smith 1964), which may be attributed to its flexibility in prey selection. However, changes in zooplankton communities by invasions of *Bythotrephes* may alter invertebrate communities (Foster and Sprules 2009) which may negatively impact planktivores.

Bythotrephes populations in Lake Superior are relatively low and more evenly distributed spatially compared to most of the lower Great Lakes (Barbiero et al. 2001). Stetter et al. (2004) modeled growth of rainbow smelt in Lake Erie that had consumed *Bythotrephes* and found they likely would have grown larger had they not accumulated indigestible spines in their stomachs. Slower growth rates of coregonines in Lake Maggiore, Italy, were found during months when consumption of *Bythotrephes* was high (Giussani and de Bernardi 1977). Conversely, Coulas et al. (1998) found no differences in growth between cisco that consumed *Bythotrephes* in Harp Lake, Ontario, and cisco in neighboring lakes that had not been invaded by *Bythotrephes*. Given that we show several Lake Superior fish species with positive selection for *Bythotrephes* (and consumed them in great numbers), investigations should be made to identify the impacts of *Bythotrephes* on the entire food web.

Benthic fish behave differently than pelagic fish because of their adaptations to habitats with lower light or complete darkness. For example, sculpins use proprioceptive mechanisms (Hoekstra and Janssen 1985) rather than vision to forage. Our findings show that all three sculpin species feed variably on food near the benthos, which is consistent with Kraft and Kitchell (1986) who suggested that sculpin were generally food limited.

Diet studies found that sculpins primarily feed during crepuscular periods, suggesting feeding may be enhanced when *Mysis* are active near the benthos (Brandt 1986, Selgeby 1988). Our study suggests that deepwater sculpin may not be able to prey on *Mysis* at greater depths, even though *Mysis* resources are more abundant. This may be due to *Mysis* being scattered throughout the deep hypolimnion, and not as close to the bottom as in nearshore areas (Beeton 1960, Bowers 1988, Gal et al. 2004), therefore decreasing their spatial overlap with deepwater sculpin.

Our estimates of prey availability for benthic fishes may be confounded by our methods for assessing the benthos and fish at the same location. Bottom trawl tows at nearshore stations were run across contour to get an integrated assessment of the fish, while the benthos was only sampled at the midpoint of the trawl transect. Because the abundance of benthic prey (primarily *Diporeia*) is greatly influenced by depth (Auer and Kahn 2004, Auer et al. 2009), our estimates of benthic prey may not be representative of densities over the entire trawl transect. For instance, burrowing mayflies (Ephemeroidea) were found in some slimy sculpin stomachs, but were not found in any of the benthos samples. This resulted in a very high selection for this prey item and likely confounded our selectivity estimates. Mayflies are typically found in shallow waters 1-8 m (Swanson 1999, Edsall et al. 2004) but our bottom trawl tows started at depths >15 m, suggesting fish moved across depths. Yule et al. (2008) found evidence that benthivores (spoonhead, deepwater sculpins and lake whitefish) moved across depth gradients between day and night in Lake Superior. There is a potential to compare isotopic signatures of prey items found in fish stomachs (i.e., *Diporeia*) to those found at different depths (see Sierszen et al. 2006) to assess depths where benthivores actually feed.

Diet compositions (Gamble et al. in review) in conjunction with our selectivity findings, show that *Mysis* and deepwater sculpin are more important to piscivorous fish like burbot and siscowet lake trout than previously thought (Negus 1995, Ebener 1995, Ray et al. 2007, Negus et al. 2008). This may be partly due to differences in piscivorous fish sizes captured using gill nets compared with trawling gear with the later gear being less size selective (Olin and Malinen 2003). Ray et al. (2007) found that siscowets selected for rainbow smelt in the spring, contrary to our findings, which may be attributed to higher densities of rainbow smelt during the 1980-2000 as compared to 2005-2006 (Gorman 2007).

Mysis were found at all 18 locations in Lake Superior and was the most prevalent prey item found in fish stomachs. Given the widespread use of *Mysis* as a prey resource, and the strong preference for them as prey by many of the dominant fish species, we feel that *Mysis* are vital to the Lake Superior fish community. This is further supported by the trophic position of *Mysis* in the Lake Superior food web, in which *Mysis* play an integral part of transferring energy from lower trophic levels (i.e., plankton, detritus) to fish production (Kitchell et al. 2000, Gamble et al. in review). Furthermore, we conclude that *Mysis* are a vital trophic vector in the Lake Superior food web and are deserving of continued monitoring to understand how this prey resource may change over time. Given the lack of historical data on *Mysis* abundance, we cannot infer the present strength of *Mysis* populations or the extent that the fish community is exhibiting top-down control upon *Mysis*. Additional research is needed to understand how perhaps the most important prey resource in Lake Superior is being utilized by the fish community in the terms of

supply and predator demand, which will provide invaluable insight into the stability of the ecosystem, and provide an enhanced understanding of the ecology of Lake Superior.

Table 1-1. List of trawling gears used to sample fish at each sampling event where DBT = day bottom trawl, NBT = night bottom trawl, and NMT = night midwater trawl.

Year	Station	Trawling Gear Used to Sample Fish		
		Spring	Summer	Fall
2005	2	DBT, NBT, NMT	NBT, NMT	NBT,NMT
	25	DBT, NBT, NMT	NBT, NMT	NBT,NMT
	76	DBT, NBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT
	80	DBT, NBT, NMT	NBT, NMT	NBT,NMT
	84	DBT, NBT, NMT	NBT, NMT	NBT,NMT
	101	DBT, NBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT
	106	DBT, NBT, NMT	DBT, NBT, NMT	NBT,NMT
	139	DBT, NBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT
	149	DBT, NBT, NMT	NBT, NMT	NBT,NMT
	171	DBT, NBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT
	172	DBT, NBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT
	174	DBT, NBT, NMT	NBT, NMT	NBT, NMT
	191	DBT, NBT, NMT	NBT, NMT	NBT, NMT
	201	DBT, NBT, NMT	NBT, NMT	NBT, NMT
	210	DBT, NBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT
	411	DBT, NBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT
	455	DBT, NBT, NMT	NBT, NMT	NBT, NMT
465	DBT, NBT, NMT	NBT, NMT	NBT, NMT	
2006	139	DBT, NBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT
	171	DBT, NBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT
	172	DBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT
	201	DBT, NBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT
	210	DBT, NBT, NMT	DBT, NBT, NMT	DBT, NBT, NMT

Table 1-2. The size range and sample size of each fish species (with prey in stomachs) used in the 2005 (lakewide) and 2006 (Western Lake Superior) selectivity analysis.

Species	Size Range (mm)	2005-Lakewide			2006-WLS		
		Spring	Summer	Fall	Spring	Summer	Fall
Rainbow Smelt	66-207	481	326	557	184	284	317
Kiyi	93-253	154	236	175	62	77	104
Bloater	88-306	113	217	188	41	60	11
Cisco	80-443	108	160	189	50	9	39
Spoonhead Sculpin	44-112	158	106	103	13	26	8
Slimy Sculpin	44-108	315	244	212	28	53	43
Deepwater Sculpin	44-152	511	296	292	116	135	91
Lake Whitefish	105-736	137	33	46	32	109	169
Burbot	140-730	17	13	7	na	na	na
Siscowet	81-771	73	50	19	na	na	na

Table 1-3. Seasonal prey selection for *Mysis* at each station (where captured) in 2005 by each fish species. Values range from 0-1 with neutral selection being 0.14 for siscowet, 0.17 for rainbow smelt, kiyi, and bloater, 0.20 for cisco, lake whitefish, burbot, and 0.25 for spoonhead, slimy and deepwater sculpins. Bold values represent positive selection, while asterisks (*) denote locations where a fish species was not captured.

	Station	210	172	174	191	139	101	411	455	465	2	106	171	76	84	201	149	25	80
	Depth	17m	26m	27m	29m	33m	37m	37m	81m	91m	93m	144m	151m	160m	186m	190m	246m	255m	312m
Rainbow smelt	Spring	0.99	1	0.44	0.99	0.99	0.99	0.88	0.99	0.09	0.71	*	*	*	*	*	*	*	*
	Summer	0.82	0.98	0	0.99	1	0.78	0.99	0.98	*	*	1	*	*	*	*	*	0.25	*
	Fall	0.72	0.84	0.99	0.92	0.21	0.92	0.98	0.92	0.82	0.98	0	*	*	*	0.99	0.40	1	*
Kiyi	Spring	*	*	*	*	*	*	*	*	*	*	1	1	1	1	1	1	*	1
	Summer	*	1	0	*	0.99	0.99	*	0.93	0	*	1	1	0.29	1	1	1	1	1
	Fall	*	*	*	*	*	*	*	1	*	1	0.91	0.81	0.95	0.99	1	0.31	1	1
Bloater	Spring	*	*	0.01	*	0.94	*	0	*	0.99	0.28	*	*	*	*	*	*	*	*
	Summer	0	*	*	0.78	0.79	0.1	0.01	*	1	*	*	0.99	*	*	*	*	*	*
	Fall	0.08	*	*	0.01	0	*	*	1	1	0.99	*	*	*	*	*	*	*	*
Cisco	Spring	0	0	0	0	0	0	0	*	0	*	0	*	*	0	*	*	*	*
	Summer	0	0.98	*	0.87	0	0.13	0	*	*	*	0.01	*	0	0	*	*	0	*
	Fall	0	*	0.69	0.01	0	0	0	*	*	0	0	*	*	0.19	0	*	0.17	0
Spoonhead Sculpin	Spring	0.90	*	0	0.76	0.95	0	*	0.61	0.66	0.14	0.22	*	*	0	*	1	*	*
	Summer	0.16	*	*	0.03	*	*	0	0.38	0.14	*	0.15	*	*	*	*	*	0	*
	Fall	0	*	0.40	0.08	0.51	0	*	0.74	0.82	0.12	0.01	*	0	*	*	*	*	*
Slimy Sculpin	Spring	0.75	0.57	0	0.03	0.40	0	0	0	0	0	*	*	0.01	*	*	*	*	*
	Summer	0	0	*	0	*	0.01	0.08	0	0	*	*	0	*	*	*	*	0	*
	Fall	0.28	0	0	0.01	0	0.06	0	0.24	0.01	0	*	*	0	*	*	*	*	*
Deepwater Sculpin	Spring	*	*	*	0.79	*	*	*	0.74	0.52	0.07	0.11	0.03	0.01	0	0.01	0	0.01	0.01
	Summer	*	0.07	*	0.52	*	0.79	0	0.94	0.83	*	0.03	0.02	0.18	0.01	0.01	0.02	0.01	0.01
	Fall	*	0.99	*	0	0.98	0.77	*	0.80	0.87	0.34	0.03	0	0.26	0.01	0.01	0.01	0.02	0.02
Lake Whitefish	Spring	*	*	0.29	*	0.96	0.99	*	0.85	0.06	*	*	*	*	*	*	*	*	*
	Summer	0.01	*	*	0.19	0.25	0.07	*	0.42	0.97	*	*	*	*	*	*	*	*	*
	Fall	*	*	0.14	*	0.02	*	*	*	*	*	*	*	*	*	*	*	*	*
Burbot	Spring	0.15	*	*	*	*	*	*	*	0	0.42	*	*	*	*	0	0	*	1
	Summer	0.51	*	*	0.01	0	0	*	0.33	*	*	*	*	*	*	*	1	*	*
	Fall	0.63	0.83	*	*	*	*	*	*	*	*	0.52	*	*	0.06	*	*	*	*
Siscowet	Spring	*	0	*	*	0	*	*	1	0.25	*	0.51	0.08	0.26	0.25	0	0	0	0
	Summer	*	*	*	*	0.74	0.44	*	*	0.04	*	0.30	0.17	0.63	0.25	*	0	0	*
	Fall	*	*	*	*	0	*	*	*	*	*	1	0.54	0.50	*	0	*	0	*

Table 1-4. Linear regression slopes and P-values for depth affects, and interactions between depth and season on the selection for *Mysis* and *Diporeia* by each fish species in 2005. Some regressions were omitted due to very small sample sizes of locations where *Diporeia* was consumed. Bold values represent significance.

	Selection for <i>Mysis</i>					Selection for <i>Diporeia</i>				
	Intercept	Slope	Depth P-value	Season P-value	Depth*Season P-value	Intercept	Slope	Depth P-value	Season P-value	Depth*Season P-value
Rainbow smelt	0.822	-0.001	0.172	0.995	0.462	na	na	na	na	na
Kiyi	1.028	0.001	0.193	0.530	0.435	na	na	na	na	na
Bloater	0.616	0.009	0.001	0.948	0.124	na	na	na	na	na
Cisco	0.112	-0.001	0.295	0.150	0.314	na	na	na	na	na
Spoonhead Sculpin	0.314	0.000	0.841	0.120	0.975	0.523	-0.001	0.484	0.214	0.828
Slimy Sculpin	0.402	-0.001	0.117	0.159	0.138	0.080	0.000	0.741	0.759	0.102
Deepwater Sculpin	0.474	-0.003	<0.001	0.441	0.673	0.550	0.001	0.103	0.049	0.007
Lake whitefish	1.410	0.005	0.173	0.090	0.133	0.563	-0.005	0.143	0.534	0.992
Burbot	0.824	0.011	0.224	0.280	0.067	0.062	-0.001	0.405	0.720	0.650
Siscowet	0.409	0.001	0.102	0.656	0.722	na	na	na	na	na

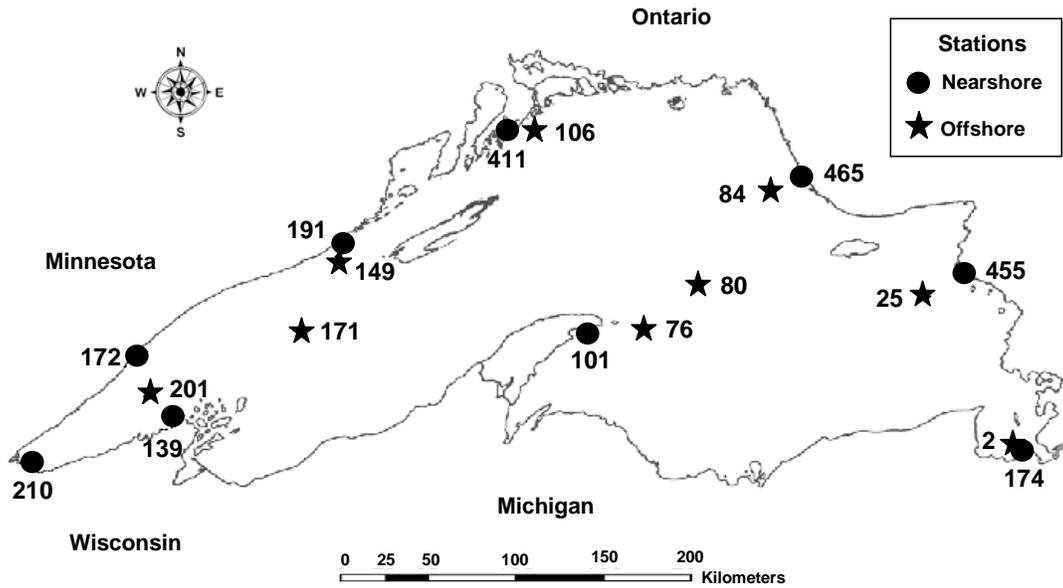


Figure 1-1. Locations of nine nearshore and nine offshore stations in Lake Superior sampled in the spring, summer, and fall of 2005. Five stations in western Lake Superior (139, 171, 172, 201, 210) were re-sampled during each season in 2006. Zooplankton, benthos, *Mysis*, and fish were concurrently collected during each sampling event.

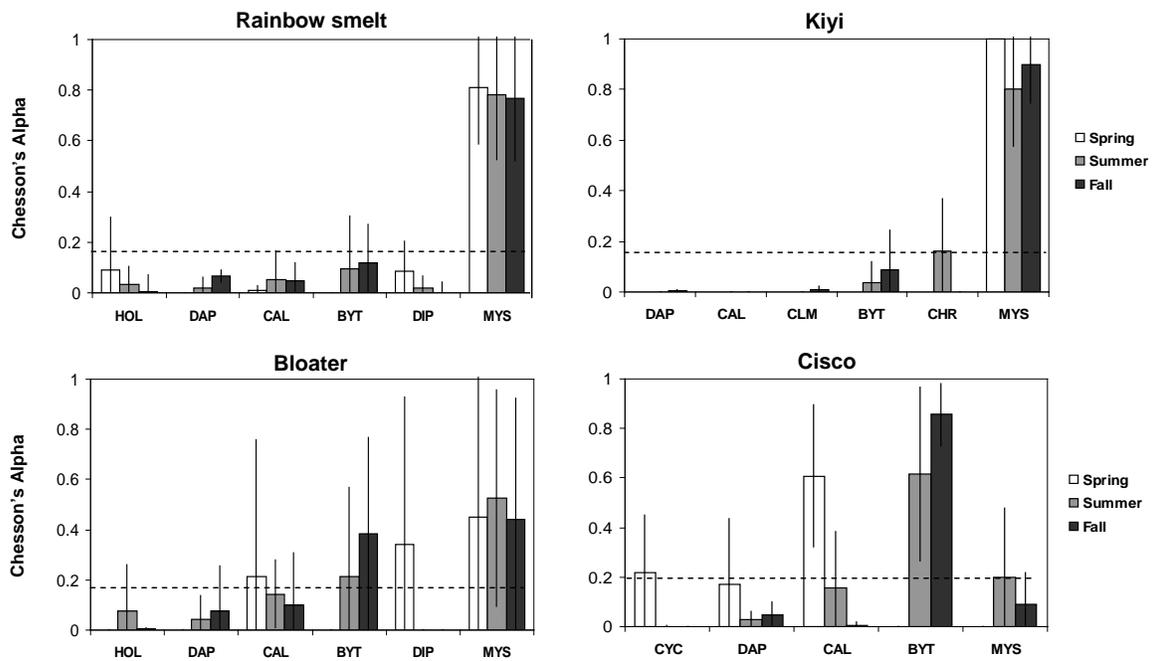


Figure 1-2. Seasonal prey selection by pelagic fish species averaged across all stations in 2005 from Lake Superior. Prey items are arranged according to size from left to right where HOL = *Holopedium gibberum*, CYC = adult cyclopoid copepods, DAP = *Daphnia* spp., CAL = adult calanoid copepods, CLM = clams, BYT = *Bythotrephes*, DIP = *Diporeia*, CHR = chironomid spp., and MYS = *Mysis*. Dashed lines indicate neutral selection. Vertical lines represent 95% CI's.

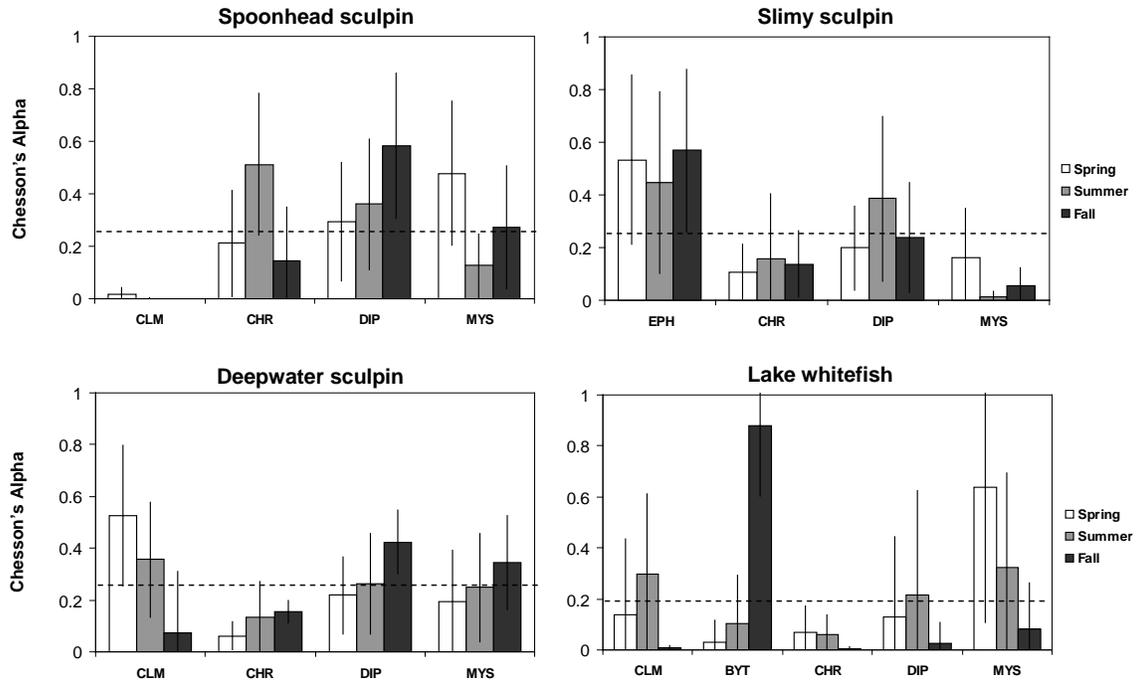


Figure 1-3. Seasonal prey selection by benthic fish species averaged across all stations in 2005 from Lake Superior. Prey items are arranged according to size from left to right where CLM = clams, EPH = ephemeroptera, BYT = *Bythotrephes* CHR = chironomid spp., DIP = *Diporeia* and MYS = *Mysis*. Dashed lines mark neutral selection. Vertical lines represent 95% CI's.

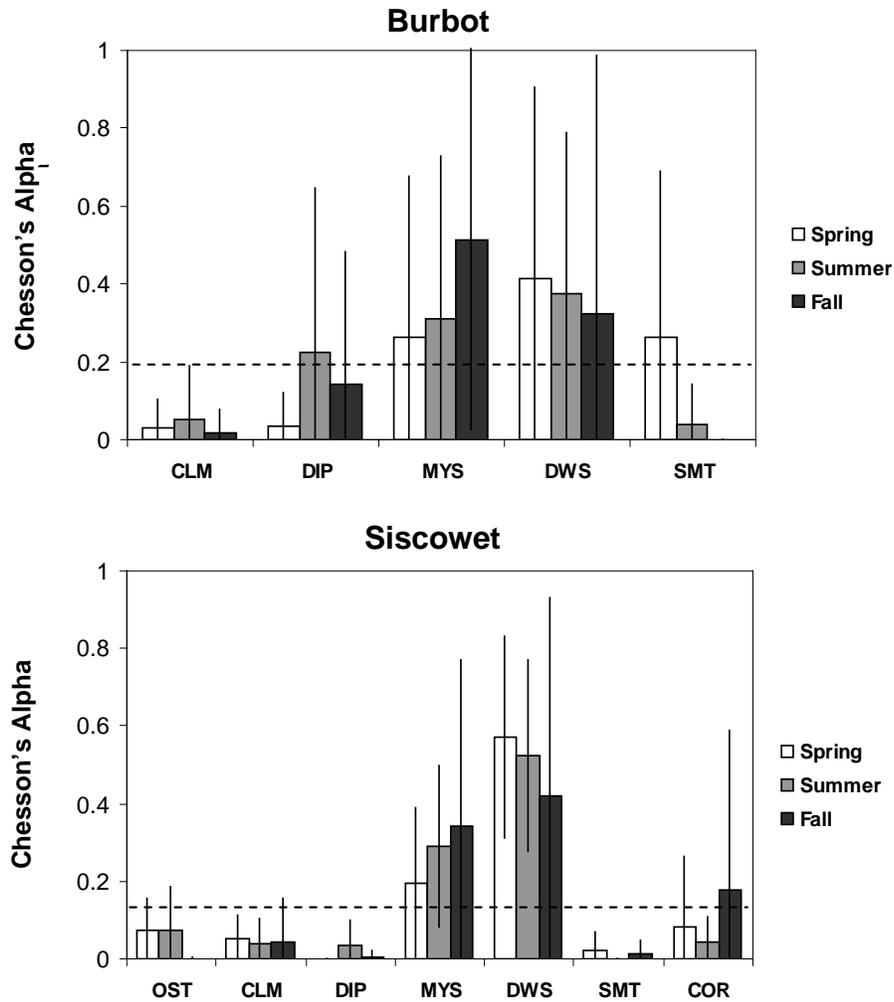


Figure 1-4. Seasonal prey selection by piscivorous fish species, averaged across all stations in 2005 from Lake Superior. Prey items are arranged according to size from left to right where OST = ostracods, CLM = clams, DIP = *Diporeia*, MYS = *Mysis*, SMT = rainbow smelt, and COR = Coregonines. Dashed lines mark neutral selection. Vertical lines represent 95% CI's.

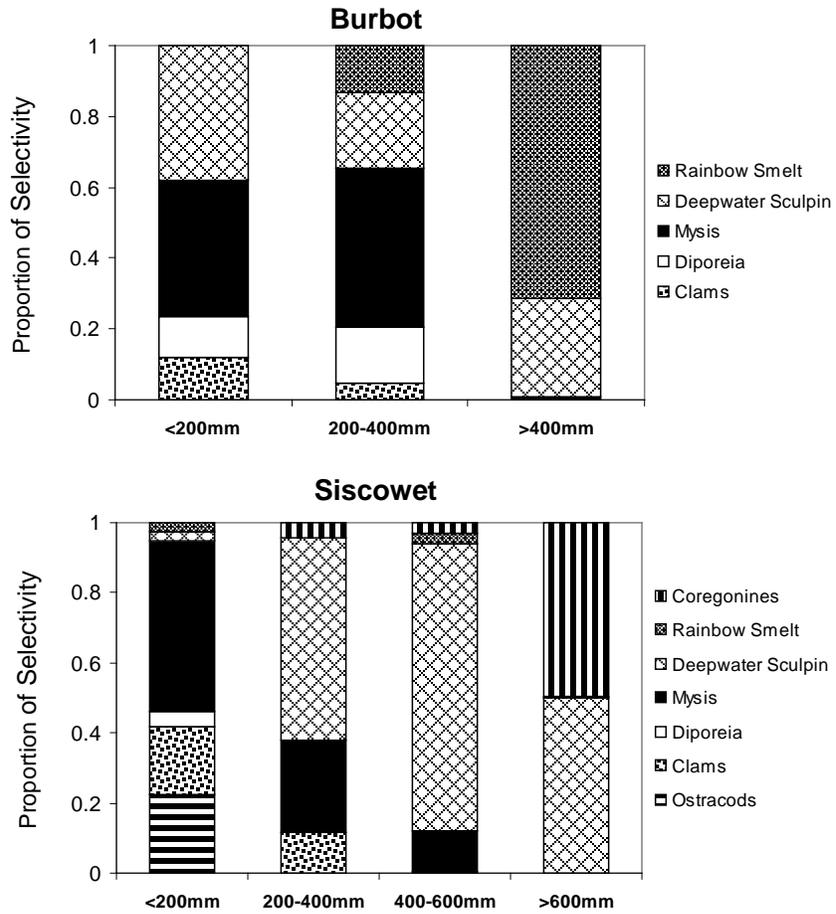


Figure 1-5. Proportional prey selection by piscivorous fish species across size bins, averaged across all stations and seasons in 2005.

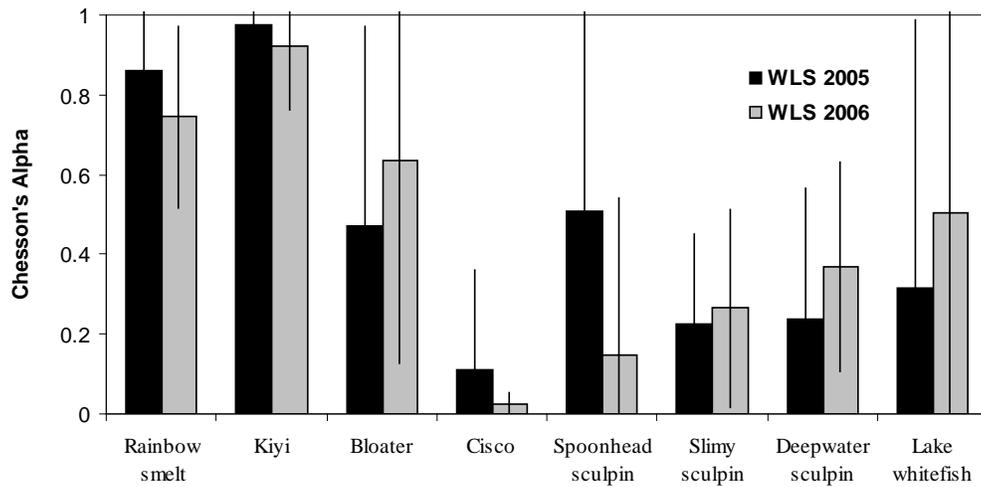


Figure 1-6. Mean selectivity for *Mysis* averaged across stations (139, 171, 172, 201, 210) and seasons in western Lake Superior, that was sampled in 2005 and 2006. Those stations are located in the Wisconsin and Minnesota waters of Lake Superior. Error bars are 95% CIs.

Consumption of Prey by the Lake Superior Fish Community: How Important are *Mysis relicta*?

Introduction

There is considerable interest in recovering and/or reintroducing native fishes such as cisco *Coregonus artedii*, deepwater ciscoes, deepwater sculpin *Myoxocephalus thompsoni*, and siscowet lake trout *Salvelinus namaycush siscowet* in the Great Lakes (Burkett et al. 1995, Great Lakes Fishery Commission 2001, Horns et al. 2003, Zimmerman and Krueger 2009). Many of the lower Great Lakes have experienced severe declines or extirpations of native fishes due to over-exploitation, invasions of exotic species, or habitat degradations (Eshenroder and Burnham-Curtis 1999). The Lake Superior fish community is largely comprised of native species, with many populations at or near historic levels (Bronte et al. 2003). A noteworthy exception is shortjaw cisco *Coregonus zenithicus*, which once supported a large commercial fishery, remains rare (Gorman and Todd 2007, Bronte et al. 2010). However, rehabilitations of lean and siscowet lake trout populations (Ebener 1995, Negus et al. 2008), coupled with changes in the prey fish community (Bronte et al. 2003, Gorman 2007) have created concerns about the predator-prey balance of the Lake Superior food web (Negus 1995, Johnson et al. 1998, Kitchell et al. 2000, Mason et al. 2005, Negus et al. 2008). Modeling efforts by Rand et al. (1995) found imbalances between consumption demands on *Mysis* and *Mysis* production in lakes Michigan (by alewife *Alosa pseudoharengus* and bloater *Coregonus*

hoyi) and Ontario (by alewife), and concluded that coarse spatial averaging may have led to these findings. Kitchell et al. (2000) also found imbalances between energy supply and demand, and suggested that spatial dynamics at local and regional scales may be an important component for resolving variability in food web dynamics. Some of the perceived imbalances, however, have been addressed through improvements in prey fish assessments, yielding higher prey fish densities likely closer to absolute (Stockwell et al. 2006, 2007; Yule et al. 2007, 2008, 2009).

Planktivorous and benthivorous fishes link primary and secondary production and detritus to predatory fishes (Johnson et al. 1998, Kitchell et al. 2000, Negus et al. 2008, Gamble et al. in review). In the Great Lakes many planktivorous fish species have been shown to govern the size and structure of invertebrate communities (McDonald et al. 1990, Johnson et al. 2004, Link et al. 2004, Hondorp et al. 2005). Because of severe declines in *Diporeia* populations in many of the lower Great Lakes (Nalepa et al. 1998, Dermott 2001), there is a great need to understand the interactions of fish and invertebrate populations (Pothoven et al. 2001, Hondorp et al. 2005). Pothoven and Vanderploeg. (2004) indicated that little work has been done relating the abundance of fish with *Mysis* distributions, with offshore *Mysis* consumers like deepwater sculpin ignored in most food web analyses (e.g., Brandt et al. 1991, Rand et al. 1995). Many investigators have recommended a closer examination of invertebrate populations with respect to the entire fish community at large spatial scales to advance understanding of the strength of linkages between trophic levels (Ney 1990, Rand et al. 1995, Johnson et al. 1998, Pothoven and Vanderploeg 2004, Mason et al. 2005). Not having current or

adequate information encompassing multiple trophic levels will hinder assessments of ecosystem health (Fabrizio et al. 1995).

Recent studies in Lake Superior encompassing multiple trophic levels (Harvey and Kitchell 2000, Kitchell et al. 2000, Gamble et al. in review, Isaac MS thesis chapter I) have suggested *Mysis relicta* is an important prey of fish. Kitchell et al (2000) suggested that changes to the invertebrate community (i.e., *Diporeia* spp. and *Mysis*) would cause major shifts in fish populations and alter the stability of the system. Ney (1990) implied that to understand system stability one must quantify the relationship between predator demand and prey supply (D:S). Recent D:S studies have been conducted on Lake Superior piscivores (Negus 1995, Mason et al. 2005, Negus et al. 2008) and some planktivores (Johnson et al. 1998), however, some of the most numerous fish (i.e., kiyi *Coregonus kiyi*, deepwater sculpin, lake whitefish *Coregonus culpeaformis*) that rely on *Mysis* (Anderson and Smith 1971, Hoff and Todd 2004, Gamble et al. in review, Isaac MS thesis chapter I) have not been formally examined.

This study addresses the informational gap that spans trophic levels at large spatial scales and attempts to quantify the importance of *Mysis relicta* to the fish community in terms of D:S. Our objectives are to 1) estimate consumption of prey by the fish community at 18 sites across Lake Superior with the use of bioenergetics models; 2) compare consumption estimates from 2005 and 2006 in the western arm of Lake Superior; 3) determine the contribution of *Mysis* as a prey resource to the fish community; 4) estimate *Mysis* production (supply) and compare with consumption (demand) by the fish community; and 5) evaluate if there are sufficient resources to

support rehabilitation of shortjaw cisco that is currently at a fraction of their former abundance in Lake Superior.

Methods

Bioenergetics Models

We used the Wisconsin bioenergetics models compiled by Hanson et al. (1997) to estimate consumption of prey by the major fish species in Lake Superior in 2005 and 2006. Eighteen locations distributed lakewide were sampled in 2005 and a subset of five locations in the western arm were resampled in 2006 (Figure 2-1). Fish density, size structure, diets, ageing structures, *Mysis* density and size structure, and temperature profiles were analyzed from these locations and used as inputs into bioenergetics models. The model parameters for rainbow smelt *Osmerus mordax*, bloater, lean and siscowet lake trout were taken from Fish Bioenergetics 3.0 (Hanson et al. 1997). We used the generalized coregonid model for cisco as described by Johnson et al. (1998), and made modifications to the respiration coefficient (RA) for this model (Madenjian et al. 2006) for lake whitefish. The bloater *Coregonus hoyi* model was used as a surrogate for kiyi as virtually no information regarding physiological parameters exist for this species. The Atlantic cod *Gadus morhua* model was adapted for burbot *Lota lota* following Rudstam et al. (1995). We reworked a deepwater sculpin model by Deboe (1994) to fit into the framework of the Hanson et al. (1997) software and then applied it to slimy sculpin *Cottus cognatus* and spoonhead sculpin *Cottus ricei* after a modification of the respiration coefficient to match those used by Johnston et al. (1991), Halfon et al. (1996), and Moss (2001).

All bioenergetics models included the inputs of predator and prey energy density, mortality rates, growth rates, body weight at age, age at maturity, spawning date, and percent of weight lost to spawning taken from lakewide means and published values. We used site specific diets, temperatures, and fish population metrics (density, age structure) as additional inputs into our models. Simulations were run over 365 days, starting on October 15 and ending the following year on October 14 for all fish species except for burbot and siscowet lake trout, which were simulated from May 15 to the following May 14. Starting dates were based on the availability of large sample sizes of fish collected for growth analysis in October 2005. Consumption was modeled for individual fish, which we scaled to density of age classes at each location modeled.

Growth and Weight-at-Age

We analyzed a subset of otoliths and scales (where possible) from each fish species collected from bottom and midwater trawls in 2005 and 2006. Otoliths were analyzed using the “crack and burn” methodology (Schreiner and Schram 2000), except for sculpin spp. which were cleared with a glycerol solution and directly read (Selgeby 1988). Scales were directly read under a dissecting microscope or microfiche. Both structures were analyzed from each individual fish when possible. Additional predatory fish (burbot, lean and siscowet lake trout) length at age data were used from 2005-2006 gill net surveys in the Apostle Islands region of Lake Superior (M. Seider, WI Department of Natural Resources, unpublished data), and adult cisco length at age data from 2006 spawning surveys in Wisconsin waters of Lake Superior (Yule et al. 2009). Mean length at ages were derived from fall caught fish, except spring data were used for

siscowet lake trout and burbot. Cursory length at age analyses showed no marked trends by location, therefore we pooled aged fish from all locations when creating growth models. The von Bertalanffy growth equation:

$$L_t = L_\infty (1 - \exp(-k \cdot (t - t_0)))$$

was modeled by estimating its parameters, where L_t = total length (mm) at age t (years), L_∞ = asymptotic length, k = Brody growth coefficient (per year), and t_0 = theoretical age at length 0. Residuals were calculated between our sample mean lengths at age and those predicted by the von Bertalanffy growth model, with iterations conducted until the residual sum of squares were minimized. Growth curves are shown for planktivores/benthivores and piscivores (Figure 2-2) with von Bertalanffy equation parameters listed in Table 2-1. We developed length-weight regressions (Table 2-2) to estimate fish weight (wet grams) for each age class based on 2005-2006 lakewide collections (Table 2-3).

Mortality Rates

We calculated annual instantaneous mortality rates (Z) from catch curves, by fitting a linear regression to the descending limb of the age distribution after a natural log transformation of our catch data (Ricker 1975). Estimates of Z for rainbow smelt, bloater, kiyi, cisco, spoonhead sculpin, slimy sculpin, and deepwater sculpin we calculated are presented in Table 2-1. We used published mortality rates for several demersal fish species when sample sizes captured from our trawling efforts were insufficient to construct catch curves. These include lake whitefish (Seider and Schram 2009), lean lake trout *Salvelinus namaycush* and siscowet (Negus et al. 2008), and burbot (Schram et al. 2006).

Predator and Prey Energy Density

Energy densities of predators and prey are summarized in Table 2-4. However, we used size-based predator energy densities reported in Fish Bioenergetics 3.0 when available. Modifications were made to the predator energy densities for lean and siscowet lake trout (Johnson et al. 1999), lake whitefish (Madenjian et al. 2006), and cisco (Vondracek 1996) in the bioenergetics model.

Spawning Parameters

Age at first maturation, spawning date, and the percent of body weight lost at spawning are summarized in Table 2-5 for each fish species. Reported fecundity values were averaged across both genders for each species.

Temperatures

Temperature profiles of the water column during each sampling event were measured with a bathythermograph (Sea-Bird Electronics, Inc. Bellevue, Washington) on each cruise. We used lake bottom temperatures as thermal inputs into bioenergetics models for benthic fish species (i.e., spoonhead sculpin, slimy sculpin, deepwater sculpin, lake whitefish, and burbot). Cisco, kiyi, and siscowet lake trout thermal occupancy were estimated using our water column temperatures with seasonal vertical trajectory profiles by Ahrenstorff (2009) accounting for time spent at each water column depth. We assumed that lean lake trout would follow a similar diurnal migration pattern as siscowet (i.e., spending night in warmer water temperatures) an assumption consistent with lean lake trout thermal occupancy reported by Ebener (1995). Temperature profiles for

rainbow smelt were estimated by averaging lake bed temperatures with temperatures of the metalimnion, as smelt typically inhabit these areas of the water column during the day and night respectively (Heist and Swenson 1983, Yule et al. 2007). Temperature profiles for bloater were estimated by averaging the temperatures of the hypolimnion as they typically do not migrate into the metalimnion (TeWinkle and Fleischer 1999, Yule et al. 2007). We modeled age 0 fish to inhabit the warmest waters achievable that did not exceed that species thermal preference (Lantry and Stewart 1993). Thermal inputs for each fish species were based on location and season specific data, and have been condensed (averaged across locations) for the sake of brevity (Table 2-6). We estimated winter temperatures to be 3°C at offshore locations, and 2.5°C at nearshore locations for all fish based on data compiled by Schneider et al. (1993) and Assel et al. (1994).

Diets

Location and season specific diet information from fish collected in bottom and midwater trawls were used as inputs into bioenergetics models, and are reported by Gamble et al. (in review) for nearshore and offshore locations. Diets for piscivorous fish (e.g., burbot, lean and siscowet lake trout) were pooled across locations (18) and years (2) and grouped into 200 mm size classes to better represent ontogenetic diet shifts. Because our sampling did not contain winter diet information, we averaged fall and spring diet compositions to estimate winter months, as done for coho salmon *O. kisutch* (Madenjian et al. 1998) and lake whitefish (Madenjian et al. 2006) in Lake Michigan.

Fish Density and Population Structure

Details of trawling methodology, acoustic sampling, and data processing for estimating densities of fish species are described by Stockwell et al. (2006, 2010). At each of the 18 locations in 2005 and 5 locations in the western arm in 2006, fish populations were assessed with a combination of day bottom trawl tows, night bottom trawl tows, and night midwater trawl tows. Hydroacoustic sampling was conducted concurrently with each trawl tow. Pelagic fish (rainbow smelt, kiyi, bloater, cisco) densities were calculated from night hydroacoustic assessments and concurrent midwater trawls. Benthic fish (spoonhead sculpin, slimy sculpin, deepwater sculpin, lake whitefish, burbot) densities were calculated from night bottom trawl tows. In some instances, night bottom trawl tows and acoustic data were not available and we relied on day bottom trawl density estimates. For these instances (rainbow smelt and bloater) day bottom trawl tows have been shown to adequately estimate the density of these prey fishes (Yule et al. 2007). Lake trout (lean and siscowet) density was measured by combining night bottom trawl tow estimates with pelagic acoustic estimates, as lake trout have been shown to occupy both benthic and pelagic habitats at night (Hrabik et al. 2006, Ahrenstorff 2009, Stockwell et al. 2010).

Acoustic data were processed with Ecoview post-processing software (version 4.1 SonarData Ltd, Tasmania, Australia). A line 0.2 m above the lake bottom was defined on echograms using an Echoview algorithm. Any anomalies in bottom tracking were eliminated by visually inspecting each echogram, and manually redefining the bottom line where needed. Sometimes during rough sea conditions, a surface line was added between 2-5 m below the surface to prevent integration of surface noise when measuring fish acoustic backscattering. A mark threshold of -65 dB was applied to the SV echogram

before estimating area backscattering to exclude macro invertebrate targets (i.e., *Mysis*).

The density of fish in the water column was estimated by:

$$\text{Fish density (fish/ha)} = (\text{ABC} / \sigma_{\text{bs}}) * 10000$$

Where ABC or the area backscattering coefficient equals $10^{SV/10} * T$, where sv is the mean volume backscattering strength of the cell and T is the mean thickness of the cell; σ_{bs} is the mean backscattering cross-section of the average size fish in the cell (i.e., $\sigma_{\text{bs}} = 10^{(TS/10)}$ where TS is the mean target strength in decibels (db); and 10000 is the number of square meters in a hectare (Parker-Stetter et al. 2009). We used the single-target detection criteria and the single-target detection parameters presented in Yule et al. (2006) to estimate the mean TS. Total fish density was then allocated to size classes by the number of targets within three size categories (small, medium, large) which ranged from < -35.6 dB, -35.6 to -32 dB, > -32 dB in TS respectively (Hrabik et al. 2006; Stockwell et al. 2006, 2007, 2010; Yule et al. 2006, 2008). Acoustic fish densities of each size range were then apportioned to species based upon size and composition of fish collected in concurrent midwater trawls (see Stockwell et al. 2010 for details). Because seasonal movements of fish in Lake Superior can be pronounced leading to highly variable density estimates across locations and seasons (Yule et al. 2009) we averaged each species density across seasons (spring, summer, fall) at each location to create a composite density representing the fish community at each location.

Length-age keys (midpoints of each age class from growth curves were applied to length-frequency distributions to construct densities of each species age class at each

location. Length-weight regressions (Table 2-2) were then applied to estimate cohort biomass (kg/ha) of each fish species at each location.

Mysis production

Quadruplicate *Mysis* samples were taken at night with a 1-m² *Mysis* net towed vertically from 2 m off the bottom to the surface, with contents preserved in 8% sugar-buffered formalin, while gravid females were preserved in individual tubes to facilitate fecundity analysis. *Mysis* from each sample were counted, with the first 100 individuals per sample measured to the nearest 0.1mm from the tip of rostrum to end of abdomen. Eggs were counted from brood pouches of gravid females to estimate production lost to eggs never reaching the first size class. We used a length-weight regression (USGS-Great Lakes Science Center-LSBS unpublished data) to convert *Mysis* lengths to dry mass. In depth methodology and results of *Mysis* sampling can be found in detail by Isaac and Stockwell (2010). *Mysis* production was estimated by using Menzies' (1980) modification of Hynes length frequency method outlined in Johannsson (1995);

$$\text{Production} = \sum_{j=1}^i (N_j - N_{j+1}) * (W_j W_{j+1})^{1/2} \text{ and } N_j = i * n_j * P_{ej} / P_{aj} * 365 / \text{CPI}$$

where i is the number of size categories, N_j is the number of *Mysis* that developed into size category j in a year, W_j is the mean weight of *Mysis* in the j th category, n_j is the mean number of *Mysis* in category j , P_{ej} is the estimated proportion of the life cycle spent in the j th category ($1/i$), P_{aj} is the actual proportion of the life cycle spent in the j th category, and CPI is the cohort production interval in days from hatching to reaching the largest size-class. Due to either very low densities or infrequent sampling of *Mysis* at four locations (84, 149, 201, 210) in 2005, we could not calculate production at those

locations. To estimate a production value, we took the average P:B ratio for the other locations in each depth strata, and applied that ratio to the standing stock of *Mysis* at that location. We then calculated lakewide production of *Mysis* by averaging the production values in each depth strata, and scaling to the area of that depth strata. We report annual *Mysis* production as wet weights (grams/m²/yr and kg/ha/yr), which were converted from dry weights (Downing and Rigler 1984).

Shortjaw cisco consumption

After calculating the consumption of *Mysis* by the fish community (demand), and the production of *Mysis* (supply) at each location, the difference in this *Mysis* budget was considered to be excess production (i.e., the amount of resources that could potentially be utilized by additional fishes). We used a bioenergetic model to estimate the consumption of *Mysis* by a theoretical shortjaw cisco population, by using the bloater bioenergetics model as a surrogate for shortjaw cisco, with dietary inputs of strictly *Mysis* (Anderson and Smith 1971, Turgeon et al. 1999, Hoff and Todd 2004), and the temperatures occupied, mortality rates, and life history traits borrowed from the bloater parameters described previously. We modeled locations in the 40-200 m depth range, as shortjaw cisco occupy this bathymetric depth (Koelz 1929, Hoff and Todd 2004, Gorman and Todd 2007). Growth rates, and population size structure of shortjaw cisco were obtained from a variety of sources (Koelz 1929; Van Oosten 1937; Hoff and Todd 2004; Gorman and Todd 2007; and O. Gorman USGS Lake Superior Biological Station, Ashland, WI unpublished data). After modeling the consumption of shortjaw cisco populations, we

were able to determine the density (#/ha) and biomass (kg/ha) of shortjaw that could be supported given the excess *Mysis* production at each location.

Results

Fish Populations

Average fish community biomass found at nearshore (12.0 kg/ha) and offshore (10.7 kg/ha) locations in 2005 were similar (Table 2-7). However, nearshore locations exhibited greater variability in biomass and species composition (Figure 2-3). Biomass at nearshore locations were typically composed of lake whitefish (26%), bloater (23%), cisco (22%) and rainbow smelt (9%). Offshore species composition was more homogenous, with biomass dominated by kiyi (31%) and deepwater sculpin (30%) (Figure 2-3). Biomass estimates for nearshore and offshore areas in 2005 were similar to that found in western Lake Superior in 2006.

Consumption Estimates

A total of 1,114 individual bioenergetics simulations were run to estimate annual consumption of prey for 2005 and 2006. The annual amount of prey consumed (mean \pm SE) by the fish community in 2005 averaged 64.4 ± 25.2 kg/ha at nearshore locations, and 44.2 ± 4.5 kg/ha at offshore locations (Figure 2-4). Consumption at nearshore locations was highly variable, with the dominant prey items being zooplankton (copepods and cladocerans) and *Mysis* consumed by planktivores like rainbow smelt, bloater, and

cisco (Figure 2-4). Consumption offshore was more uniform across locations with kiyi, deepwater sculpin, and cisco preying mainly on *Mysis* (Figure 2-4).

Estimated total annual consumption of prey at five locations in western Lake Superior was similar among years (Figure 2-5), with no significant changes in the average consumption of prey in western Lake Superior (ANOVA, $df = 8$, $p = 0.83$). However, there was an increase in consumption of *Mysis* and *Diporeia* at location 139, mainly due to increases in lake whitefish biomass from 23.7 kg/ha in 2005 to 67.8 kg/ha in 2006. Decreases in bloater, rainbow smelt, and burbot biomass led to lower consumption of cladocerans and fish at location 210 from 2005 and 2006.

Estimated annual consumption of *Mysis* was much higher offshore (30.0 ± 4.4 kg/ha) than nearshore (17.5 ± 8.8 kg/ha), with consumption arising from different fish species in each depth zone. Rainbow smelt, bloater and lake whitefish consumed *Mysis* nearshore, while deepwater sculpin and kiyi consumed *Mysis* offshore (Figure 2-6). *Mysis* comprised nearly 70% of the estimated prey consumed by fishes at offshore locations, making up greater proportion of the fish community diet with increasing depth (Figure 2-7).

We averaged our consumption estimates in the nearshore and offshore depth strata, and scaled up to the area of each depth strata, which yielded annual consumption rates of *Mysis* at $38,916 \pm 19,571$ metric tons (mt) in the nearshore waters and $179,583 \pm 26,330$ mt in the offshore waters. We combined our consumption rates to estimate the annual lakewide consumption, which we found was the highest for *Mysis* (218,499 mt)

followed by zooplankton (135,677 mt), fish (23,847 mt), *Diporeia* (22,679 mt), and other prey items (6,876 mt).

Mysis Production

Production estimates were comprised largely of the abundance and mass changes in the yearling cohort, which was easily tracked across seasons based on length frequency distributions, which yields production estimates that are relatively robust. Estimated *Mysis* production values ranged from 0.7-5.4 g/m²/yr with a mean of 2.6 g/m²/yr at nearshore locations. Production was much higher at offshore locations ranging from 3.6-18.1 g/m²/yr with a mean of 8.7 g/m²/yr (Table 2-8). Total annual production of *Mysis* in Lake Superior was 592,114 mt with nearly all (88%) of that production coming from offshore waters (521,138 mt).

Mysis Demand-Supply Relationship

Predation upon *Mysis* by the fish community was highest at offshore locations, and was attributable largely to kiyi and deepwater sculpin populations. However, *Mysis* production was also highest offshore. The demand-supply relationship was balanced at all offshore locations, indicating sufficient *Mysis* resources in offshore waters to support current fish populations (Figure 2-8). Estimated *Mysis* production at most offshore locations was 2-3 times higher than estimated consumptive demand, and much higher than consumption at the two deepest locations studied, which suggests *Mysis* may have a refuge from predation at these areas. At five nearshore locations *Mysis* production exceeded supply. However, the D:S relationship was not balanced at locations 174 in Whitefish Bay, 139 at Sand Island, and 210 near Duluth/Superior with consumption of

Mysis exceeding supply (Figure 2-8). Empirical D:S relationships are reported in Table 2-8. Estimated annual lakewide consumption of *Mysis* is 218,499 mt which is only about 40% of the estimated annual production (592,114 mt)..

Shortjaw cisco consumption

Consumption of *Mysis* by an individual shortjaw cisco was similar to that of the same sized kiyi, given the only differences used in the bioenergetics models were different growth rates, and could almost be thought of as modeling very large sized kiyi. We estimated how many shortjaw cisco could be added to fish populations if they utilized the remaining (excess) production of *Mysis*. On average, locations could support 93 shortjaw cisco per hectare (5.6 kg/ha), and ranged between 0-200 shortjaw cisco per hectare (0-12 kg/ha) among locations in the 40-200 depth range. These densities are a stark contrast to recent surveys that indicate shortjaw cisco density of less than two fish per hectare (Gorman and Todd 2007).

Discussion

Our consumption estimates are a direct reflection of planktivory and benthivory by fish populations in nearshore and offshore communities, with nearshore communities being composed mainly of rainbow smelt, bloater, cisco, and lake whitefish, which consume *Mysis* and zooplankton resources. Consumption of *Mysis* nearshore is relatively low compared to offshore. Consumption of zooplankton resources was directly linked to cisco abundance in both depth strata, however, cisco abundance has less influence on

Mysis consumption compared to other *Mysis* predators. Consumption of *Mysis* offshore was more than double than that observed nearshore, driven by high densities of kiyi and deepwater sculpin found offshore. Consumption of *Mysis* was less influenced by predatory fish like lean and siscowet lake trout similar to the findings of Negus et al. (2008) in western Lake Superior.

Our bioenergetics model inputs are relatively robust, with the majority drawn from empirical data collected at the same locations we modeled. The most sensitive parameter found from other studies have been the abundance of fish populations (Rand et al. 1995, Mason et al. 2005, Negus et al. 2008), which we assessed with multiple gears in an attempt to more accurately estimate both benthic and pelagic fish populations (Yule et al. 2008). Being able to model the fish community as a whole in Lake Superior with piscivores, planktivores, and benthivores provides an ecosystem approach absent in previous studies that did not account for benthivores (Johnson et al. 1998) or focused only on piscivores (Ebener 1995, Mason et al. 2005, Negus 1995, Negus et al. 2008).

Sampling each location multiple times a year yielded fish compositions and densities that are reflective of habitat use over a long time span, and provide accuracy in assessing fish populations that may not be captured with a single season survey like cisco or rainbow smelt (Mason et al. 2005; Stockwell et al. 2006, 2009; Yule et al. 2009), which are dominant members of the fish community. Other studies have implicated coarse spatial averaging as the principle mechanism for imbalances in demand-supply relationships (Rand et al. 1995, Kitchell et al. 2000, Mason et al. 2005, Negus et al. 2008). By deriving (empirically) fish population and size structure, diets, temperatures,

and *Mysis* populations at 18 locations in Lake Superior during three seasons in 2005 we were able to develop 18 comparisons of *Mysis* D:S.

We feel that our consumption estimates are conservative for zooplankton resources, as our models do not adequately represent larval fish or young of year cohorts because they have not recruited to trawling gear, which typically happens at age one. With variable populations of coregonids over time (Bronte et al. 2003, Mason et al. 2005, Hrabik et al. 2006, Stockwell et al. 2009) there may be extensive planktivory by coregonids at very early life stages, albeit during a short duration over the year with high mortality rates, that would contribute substantially to our consumption of zooplankton resources.

Johnson et al. (1998) estimated the consumption of *Mysis* in western Lake Superior in years 1978-1995 based on bioenergetics modeling of rainbow smelt, bloater and cisco populations and found the consumption of *Mysis* to range between 0.6 to 4.4 g/m² per year. Our mean average consumption of *Mysis* in western Lake Superior in 2005 was 3.7 g/m² per year and ranged between 0.5-8.7 g/m² per year while including other species known to prey upon *Mysis* like kiyi and deepwater sculpin. The consumption of *Mysis* found by Johnson et al. (1998) was primarily from rainbow smelt, which were much more abundant over that time series (2-3 times the biomass) than what is currently found in that region (Gorman 2007). Our consumption estimates for *Mysis* for Lake Superior, were much lower than reported in Lake Michigan (21.2 g/m²) and Lake Ontario (21.8 g/m²) by Rand et al. (1995).

The annual production values for *Mysis* we found in Lake Superior (0.1-18.1 g/m²) are somewhat lower than reported in Lake Michigan (11.3-21.3 g/m²) and Lake Ontario (2.3-22.2 g/m²) by Rand et al. (1995). This may be due to lower abundances of *Mysis* (Isaac and Stockwell 2010), or perhaps indicative of the lower productivity nature of the oligotrophic conditions in Lake Superior. Annual production to biomass ratios ranged between 2.2-3.2 in the other Great Lakes (Sell 1982, Rand et al. 1995, Johannsson 1995), similar to our average estimate of 3.6 for Lake Superior. Modeling *Mysis* production at numerous locations across Lake Superior likely provided robust estimates.

The two lowest production rates were found at shallow nearshore locations 210 (0.07 g/m²/yr) and 174 (0.11 g/m²/yr), and stemmed from incomplete size frequency distributions due to very low biomass of *Mysis* (0.02, 0.04 g/m² respectively), with some samples not collecting any *Mysis* at all. Due to the very low standing stock of *Mysis* at these locations, our production estimates are probably biased low, or a transport of *Mysis* into the area acting as a subsidy that supports fish consumption. Production values at location 139 are likely robust, as the *Mysis* population was adequately represented in abundance and size structure, with relatively high estimated production rates when compared to other nearshore locations (Figure 2-8). High abundances of lake whitefish in all three sampling seasons, was the primary cause of the high consumption estimates at that location. Our lake whitefish dietary information suggests that *Mysis* were the dominant prey item, however we are missing winter diet information that may have caused this imbalance in D:S, as populations of lake whitefish are continuous throughout all seasons and between both years. It has been suggested that winter diets of many benthivores (ie., lake whitefish) are dominated by eggs deposited by coregonids in

nearshore areas (Stockwell et al. in prep), which would reduce consumption estimates to levels that can be supported by *Mysis* production.

Unlike many other D:S relationships in the Great Lakes, we found that *Mysis* production exceeded consumptive demands by the fish community at almost all locations, indicating a surplus. This trend is important given that *Mysis* are a vital component in the Lake Superior food web (Harvey and Kitchell et al. 2000, Kitchell et al. 2000, Sierszen et al. 2006, Gamble et al. in review, Isaac MS thesis chapter I) supplying essential resources to prey fish and predators alike. In Lake Superior, the recovery of lean and siscowet lake trout populations has likely led to top-down control of prey fish, which has likely lowered planktivory upon *Mysis*. During the early 1970s, when rainbow smelt abundance was high and lake trout populations were relatively low, *Mysis* populations found by Carpenter et al. (1974) were much lower in nearshore waters than our current estimates measured under low smelt and high lake trout abundance (Bronte et al. 2003, Gorman et al. 2007). In contrast, offshore populations of coregonids, chiefly bloater and kiyi, have increased since the 1970s (Gorman and Todd 2007), albeit supported by the drastic decrease in the consumption of *Mysis* in nearshore areas as rainbow smelt populations declined, thus helping support siscowet lake trout populations that utilize coregonids as prey in offshore waters.

Increases in top-down controls on prey fish, may create excess *Mysis* production available to the fish community to the benefit of native fish species like shortjaw cisco that feed primarily on *Mysis* (Koelz 1929, Hoff and Todd 2004). However, competition among deepwater coregonids such as bloater and kiyi, have been implicated in impeding

shortjaw cisco forms in Lake Superior (Gorman and Todd 2007, Bronte et al. 2010) and in Lake Michigan (Smith 1964). Although our estimates of shortjaw cisco consumption are relative, owing to reliance on historic data and bioenergetics parameters not yet evaluated for this species, it provides valuable insight to the level of utilization of *Mysis* resources and the ability for a recovery of deepwater ciscoes. Our results imply that shortjaw cisco are presently not food limited, and we hypothesize that other factors such as low spawner biomass may be limiting shortjaw cisco expansion in Lake Superior.

Our work highlights the importance of understanding *Mysis* population dynamics over time. Our modeling work is a relative snapshot of the current state of the food web, which is subject to change because fish and invertebrate populations are temporally dynamic. Additional work to understand winter diets of benthic and pelagic fish, which utilize overwinter depositions of eggs as a resource, will help solidify our understanding of energy flow and fish consumptive demand with prey supply. Given the importance of *Mysis* in supporting the fish community in Lake Superior, reliance upon an outdated *Mysis* survey from 1971 to compare population changes in perhaps the most important prey resource is not encouraging, thus continued assessments are needed to describe temporal changes in *Mysis* populations and analyze the stability of the Lake Superior ecosystem.

Table 2-1. The von Bertalanffy growth equation parameters for each fish species, where L_{∞} = asymptotic length (mm), k = Brody growth coefficient (per year), t_0 = age (year) at length 0. Size ranges, sample sizes (N), and goodness of fit (R^2) measures are also shown. Instantaneous mortality rates (Z) developed from catch curves (present study unless otherwise indicated) are also shown are presented.

Species	Size-range (mm)	N	L_{∞}	k	t_0	R^2	Z
Bloater	91-295	123	344	0.126	-2.837	0.99	0.59
Burbot	156-778	79	783	0.147	0.407	0.93	0.43 ^a
Cisco	75-448	220	395	0.215	-1.659	0.94	0.29
Deepwater sculpin	25-150	112	298	0.074	-1.475	0.99	0.72
Kiyi	117-224	106	335	0.126	-2.319	0.99	0.42
Lake trout	58-967	210	863	0.130	-2.230	0.98	0.16-0.24 ^b
Lake whitefish	113-507	126	867	0.071	-2.271	0.99	0.29 ^c
Rainbow smelt	30-199	161	203	0.426	-0.634	0.97	0.83
Siscowet	52-782	141	986	0.043	-1.753	0.97	0.16-0.22 ^b
Slimy sculpin	25-99	96	251	0.079	-1.570	0.99	0.75
Spoonhead sculpin	25-101	104	259	0.066	-2.079	0.99	0.59

^aSchram et al. 2006

^bNegus et al. 2008

^cSeider et al. 2009

Table 2-2. Length weight regressions for the major fish species in Lake Superior. Lengths are in mm and wet weights are in g. Equations were developed from fish collected from Lake Superior during 2004-2006.

Species	Equation	N	R ²
Bloater	$\ln(\text{weight}) = -12.204 + 3.072 \cdot \ln(\text{length})$	779	0.98
Burbot	$\ln(\text{weight}) = -12.192 + 3.073 \cdot \ln(\text{length})$	164	0.97
Cisco	$\ln(\text{weight}) = -12.181 + 3.069 \cdot \ln(\text{length})$	1141	0.98
Deepwater sculpin	$\ln(\text{weight}) = -12.755 + 3.252 \cdot \ln(\text{length})$	1508	0.97
Kiyi	$\ln(\text{weight}) = -12.476 + 3.120 \cdot \ln(\text{length})$	1290	0.98
Lake trout	$\ln(\text{weight}) = -12.383 + 3.112 \cdot \ln(\text{length})$	286	0.99
Lake whitefish	$\ln(\text{weight}) = -12.627 + 3.159 \cdot \ln(\text{length})$	561	0.98
Rainbow smelt	$\ln(\text{weight}) = -13.613 + 3.315 \cdot \ln(\text{length})$	2664	0.98
Siscowet	$\ln(\text{weight}) = -12.329 + 3.103 \cdot \ln(\text{length})$	740	0.99
Slimy sculpin	$\ln(\text{weight}) = -12.801 + 3.344 \cdot \ln(\text{length})$	904	0.94
Spoonhead sculpin	$\ln(\text{weight}) = -12.218 + 3.159 \cdot \ln(\text{length})$	531	0.94

Table 2-3. Mean lengths (mm) and weights (wet g) at ages for each fish species used in bioenergetics models. Values are reflective of fall (October) fish, except for burbot and siscowet which are reflective of spring (May).

Age	Rainbow Smelt		Kiyi		Bloater		Cisco		Spoonhead sculpin		Slimy sculpin		Deepwater sculpin		Lake Whitefish		Burbot		Lean laketrout		Siscowet	
	Length (mm)	Weight (g)	Length (mm)	Weight (g)	Length (mm)	Weight (g)	Length (mm)	Weight (g)	Length (mm)	Weight (g)	Length (mm)	Weight (g)	Length (mm)	Weight (g)	Length (mm)	Weight (g)	Length (mm)	Weight (g)	Length (mm)	Weight (g)	Length (mm)	Weight (g)
0	48	0.5	na	na	104	7.8	119	11.9	33	0.3	29	0.2	31	0.2	130	16.1	na	na	25	0.1	na	na
1	102	5.6	115	10.3	132	16.5	172	37.3	48	0.9	46	1.0	50	0.9	181	44.1	66	1.9	127	14.8	110	9.5
2	137	14.9	141	19.5	157	28.1	215	74.1	61	2.1	62	2.7	67	2.5	228	90.9	164	32.6	217	78.0	146	23.2
3	160	24.9	164	31.2	180	42.1	250	117.4	74	3.9	76	5.5	84	5.2	272	158.7	249	117.5	296	204.9	182	45.2
4	175	33.5	185	44.9	199	57.9	278	162.8	85	7.0	89	9.3	99	8.9	313	248.5	323	259.5	365	394.4	215	76.7
5	185	40.1	203	60.0	216	74.7	301	207.0	97	9.6			113	13.7	351	360.2	386	450.1	426	637.1	248	118.4
6			218	75.8	231	91.9	319	248.0					126	19.6	387	493.1	441	676.0	479	920.3	279	170.7
7			232	91.9	245	109.3	334	284.8					138	26.5	420	646.0	488	923.8	526	1230.6	308	233.7
8			244	107.9	257	126.3	346	317.1					150	34.2	451	817.0	528	1181.5	567	1555.8	337	307.2
9					267	142.6	355	344.9							479	1004.4	563	1439.6	603	1885.7	364	391.1
10					276	158.2	363	368.4							506	1111.5	594	1690.7	635	2211.9	390	484.8
11					284	172.8	369	388.1									620	1929.8	663	2528.3	415	587.9
12					291	186.5	374	404.6									642	2153.6	688	2830.3	439	699.6
13							378	418.2									662	2360.2	709	3114.9	462	819.5
14							382	429.4									678	2548.9	728	3380.3	484	946.7
15							384	438.5									693	2719.7	745	3625.6	505	1080.5
16							386	446.0											759	3850.8	525	1220.3
17							388	452.1											772	4056.1	544	1365.2
18							389	457.1											783	4242.5	563	1514.5
19																			793	4410.9	581	1667.7
20																			802	4562.4	598	1823.9
21																			809	4698.3	614	1982.7
22																			816	4819.9	630	2143.3
23																			822	4928.5	645	2305.3
24																			827	5025.1	659	2468.1
25																			831	5111.0	673	2631.2
26																			835	5187.3	686	2794.2
27																			839	5254.9	698	2956.7
28																			842	5314.8	710	3118.3
29																			845	5367.7	722	3278.6

Table 2-4. Energy densities (J/g wet weight) of predator and prey species used in bioenergetics models.

Predator-Prey Species	Energy Density (J/g)	Source
Fish		
Bloater ^a	9879	Rottiers and Tucker (1982)
Burbot	5135	Johnson et al. (1999)
Cisco	6500	Pangle et al. (2004)
Deepwater Sculpin	5421	Rottiers and Tucker (1982)
Lake Whitefish ^b	9317	Madenjian et al. (2006)
Lean lake trout	7788	Johnson et al. (1999)
Rainbow Smelt	5000	As used by Negus et al. (2008)
Siscowet	10789	Johnson et al. (1999)
Slimy Sculpin ^c	5743	Rottiers and Tucker (1982)
Unidentified fish ^d	4435	Lantry and Stewart (1993)
Invertebrates		
<i>Bythotrephes</i>	1674	Lantry and Stewart (1993)
Chironomids	3134	Cummins and Wuycheck (1971)
Copepoda	3016	Cummins and Wuycheck (1971)
Cladocera	2412	Cummins and Wuycheck (1971)
<i>Diporeia</i>	4386	Gardner et al. (1985)
Fish eggs	5022	Lantry and Stewart (1993)
Mollusks ^e	2427	Schneider (1992)
<i>Mysis</i>	3537	Gardner et al. (1985)
Terrestrial Insects	3138	Lantry and Stewart (1993)

^a Value used for kiyi

^b Average value reported from Lake Michigan samples

^c Value used for spoonhead sculpin

^d A value of 6766 (average of rainbow smelt, deepwater sculpin, bloater, cisco) was used in the diets of burbot

^e Value was derived from *Dreissena polymorpha*

Table 2-5. The age at maturation, timing of spawning, and the % of weight lost to spawning by each fish species.

	Age mature	Spawning date	Weight lost at spawning	Sources
Bloater	3	February	10%	Dryer and Beil 1964, Rudstam et al. 1994
Burbot	5	March	11%	Baily 1972, Rudstam et al. 1995
Cisco	3	December	7.3%	Cahn 1927, Dryer and Beil 1964, Yule et al. 2006
Deepwater sculpin	3	January	12%	Bruch 1986, Selgeby 1988
Kiyi	2	December	10%	Koelz 1929
Lake trout	7	November	6.8%	Negus 1995, Negus et al. 2008
Lake whitefish	5	November	5.2%	Madenjian et al. 2006
Rainbow smelt	3	May	11.5%	Dryer and Beil 1964, Lantry and Stewart 1993
Siscowet	11	November	6.8%	Ebener 1995
Slimy sculpin	3	June	12%	Bruch 1986, Selgeby 1988
Spoonhead sculpin	3	May	12%	Bruch 1986, Selgeby 1989

Table 2-6. Mean water temperatures constructed from bathythermograph profiles used as thermal inputs into bioenergetics models. Data are averaged from all locations during each season and are shown for simplicity. Actual temperatures used were specific to the sampling event.

	Mean Water Temperatures (°C)			
	May	August	October	January
Bloater	3.9	7	7.9	2.6
Burbot	3.5	6	4.8	2.7
Cisco	3.6	6.6	8.5	2.8
Deepwater sculpin	3.4	4.8	4.6	3
Kiyi	3.4	5.6	7.2	2.8
Lake trout	3.9	9	9.4	2.5
Lake whitefish	3.9	7.2	6.6	2.5
Rainbow smelt	3.9	9.8	8.3	2.7
Siscowet	3.4	5.5	7	3
Slimy sculpin	3.5	5.6	5.5	2.5
Spoonhead sculpin	3.6	5.9	5.6	2.5

Table 2-7. Mean biomass (kg/ha \pm SE) of each fish species averaged across seasons at nine nearshore and nine offshore locations lakewide in 2005 and from three nearshore and two offshore locations in western Lake Superior in 2006. * denotes a biomass of zero indicating the species was not present. Otherwise, values showing 0.0 are biomass < 0.1kg/ha.

	2005-Lakewide		2006-Western LS	
	Nearshore	Offshore	Nearshore	Offshore
Bloater	2.7 \pm 1.5	0.1 \pm 0.1	0.6 \pm 0.3	0.1 \pm 0.1
Burbot	0.7 \pm 0.5	0.1 \pm 0.0	0.5 \pm 0.3	0.0 \pm 0.0
Cisco	2.7 \pm 1.5	1.8 \pm 0.4	2.3 \pm 0.9	1.7 \pm 0.3
Deepwater sculpin	0.0 \pm 0.0	3.2 \pm 0.8	*	2.8 \pm 2.3
Kiyi	0.2 \pm 0.1	3.4 \pm 0.7	0.0 \pm 0.0	4.5 \pm 2.2
Lake trout	0.8 \pm 0.3	0.0 \pm 0.0	1.0 \pm 0.6	0.0 \pm 0.0
Lake whitefish	3.1 \pm 2.6	0.0 \pm 0.0	22.6 \pm 22.6	0.0 \pm 0.0
Rainbow smelt	1.1 \pm 0.4	0.5 \pm 0.5	0.8 \pm 0.3	0.1 \pm 0.1
Siscowet	0.5 \pm 0.4	1.5 \pm 0.2	0.4 \pm 0.3	2.8 \pm 0.6
Slimy sculpin	0.1 \pm 0.0	0.1 \pm 0.1	0.0 \pm 0.0	0.0 \pm 0.0
Spoonhead sculpin	0.0 \pm 0.0	0.1 \pm 0.1	0.0 \pm 0.0	0.0 \pm 0.0
Total	12.0 \pm 4.5	10.7 \pm 1.0	28.2 \pm 23.0	12.0 \pm 0.8

Table 2-8. Summary of *Mysis* (wet weight) standing stock, annual production, consumption, and a demand-supply (D:S) relationship estimated from 2005 data. Standing stock values are reported in Isaac and Stockwell (2010). Weights were converted from dry to wet using a 1:6.25 ratio from Downing and Rigler (1984).

Station	Depth (m)	Standing Stock (g/m ²)	Annual Production (g/m ²)	Consumption (g/m ²)	D:S
210	17	0.02	0.07*	0.94	13.4
172	26	0.55	1.70	0.46	0.3
174	27	0.04	0.11	0.50	4.4
191	29	0.81	3.09	0.73	0.2
139	33	0.70	4.81	8.66	1.8
101	37	1.06	3.20	2.12	0.7
411	37	0.21	0.47	0.08	0.2
455	81	1.54	5.40	0.87	0.2
465	91	1.24	4.49	0.97	0.2
2	93	2.92	9.49	1.69	0.2
106	144	2.46	7.19	2.53	0.4
171	151	1.99	8.97	4.07	0.5
76	160	1.56	6.04	2.13	0.4
84	186	1.60	6.09*	5.55	0.9
201	190	2.04	7.75*	4.23	0.5
149	246	0.96	3.65*	2.66	0.7
25	255	4.20	18.10	1.82	0.1
80	312	2.69	10.92	2.24	0.2

* Production estimates that were found by applying a mean P:B ratio of 3.2:1 at nearshore locations or 3.8:1 at offshore locations to the standing stock.

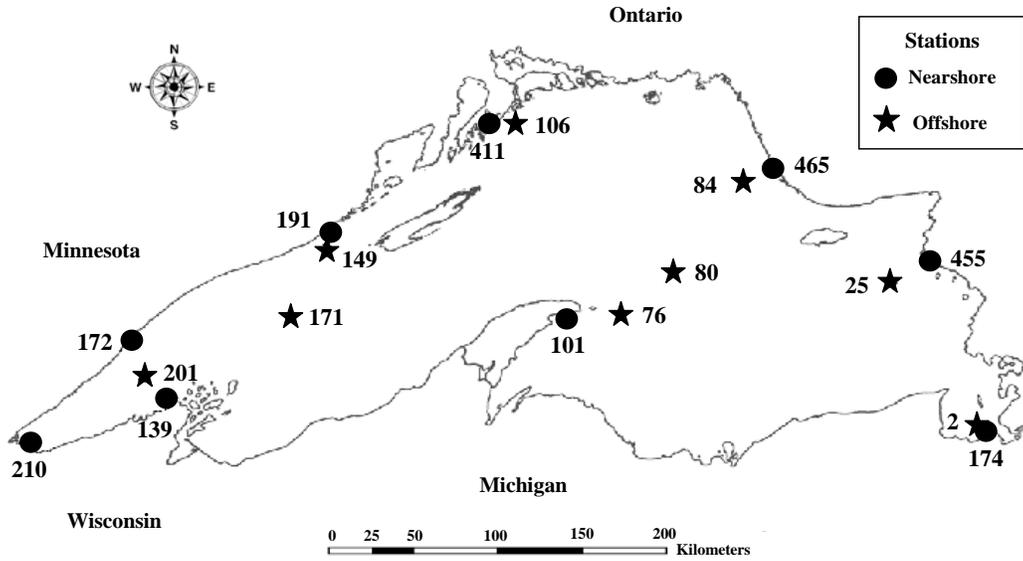


Figure 2-1. Locations of nine nearshore and nine offshore locations in Lake Superior sampled in 2005. In 2006 sampling was undertaken at locations 210, 172, 201, 139, and 171.

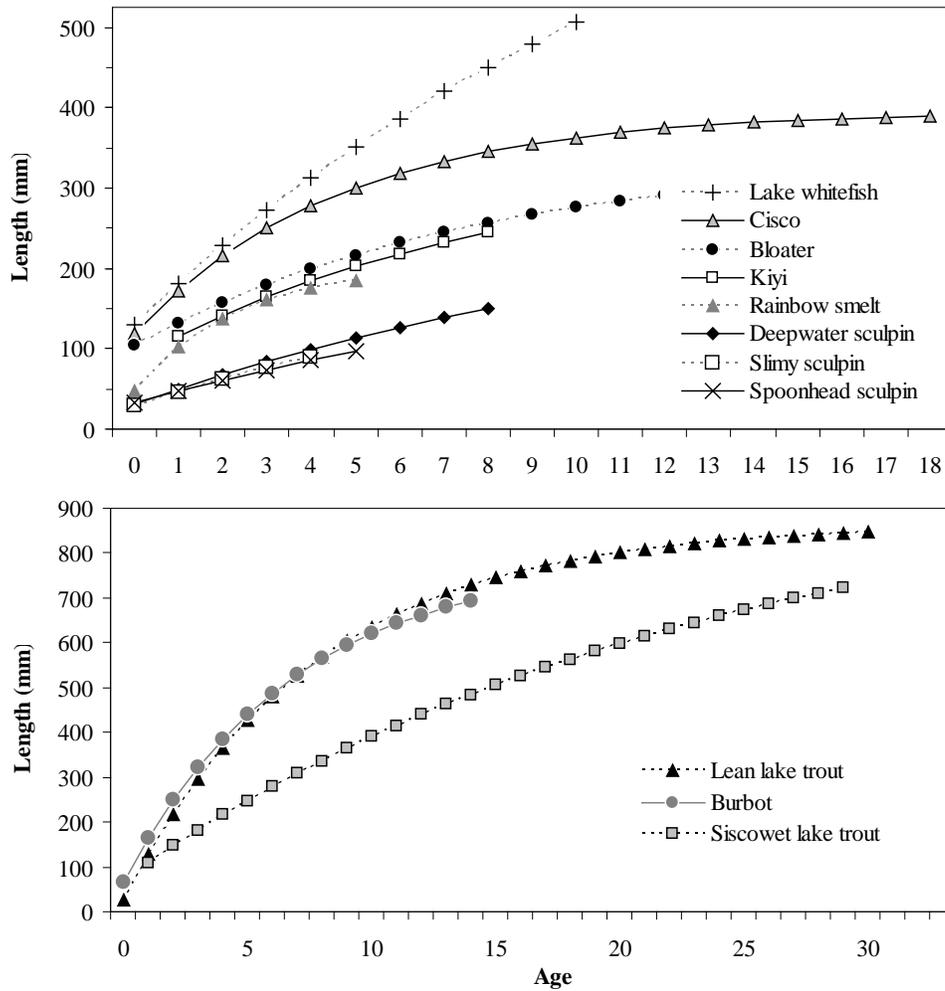


Figure 2-2. Von Bertalanffy growth curves for planktivorous and benthivorous (upper panel) and piscivorous fish species (lower panel) in Lake Superior derived from 2005-2006 age estimates. Von Bertalanffy growth equation parameters are provided in Table 2-1.

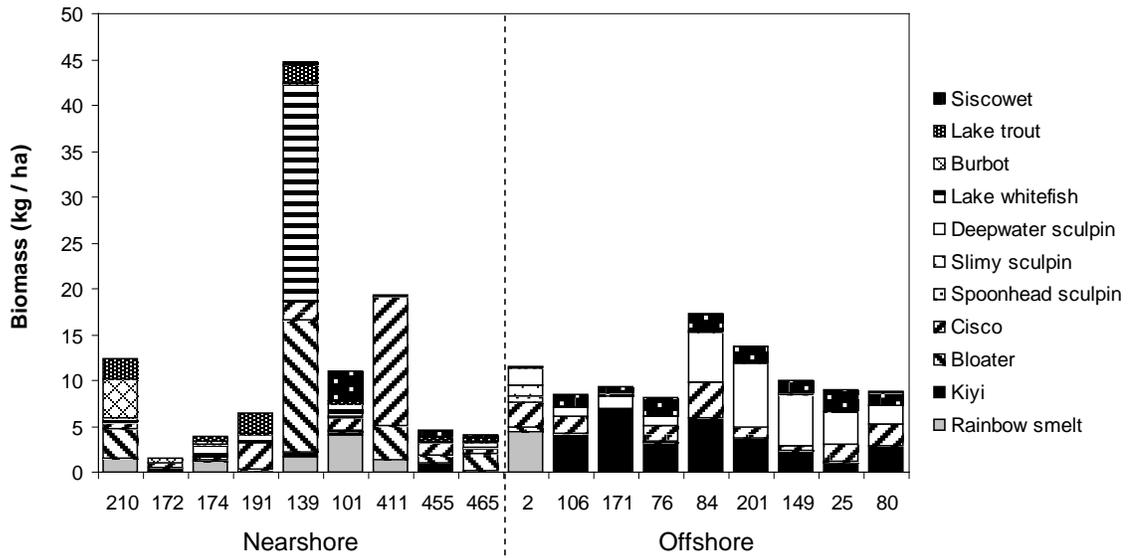


Figure 2-3. Biomass and species compositions of the fish community at nearshore and offshore locations sampled in 2005 from Lake Superior. Stations are arranged according to depth (shallow to deep).

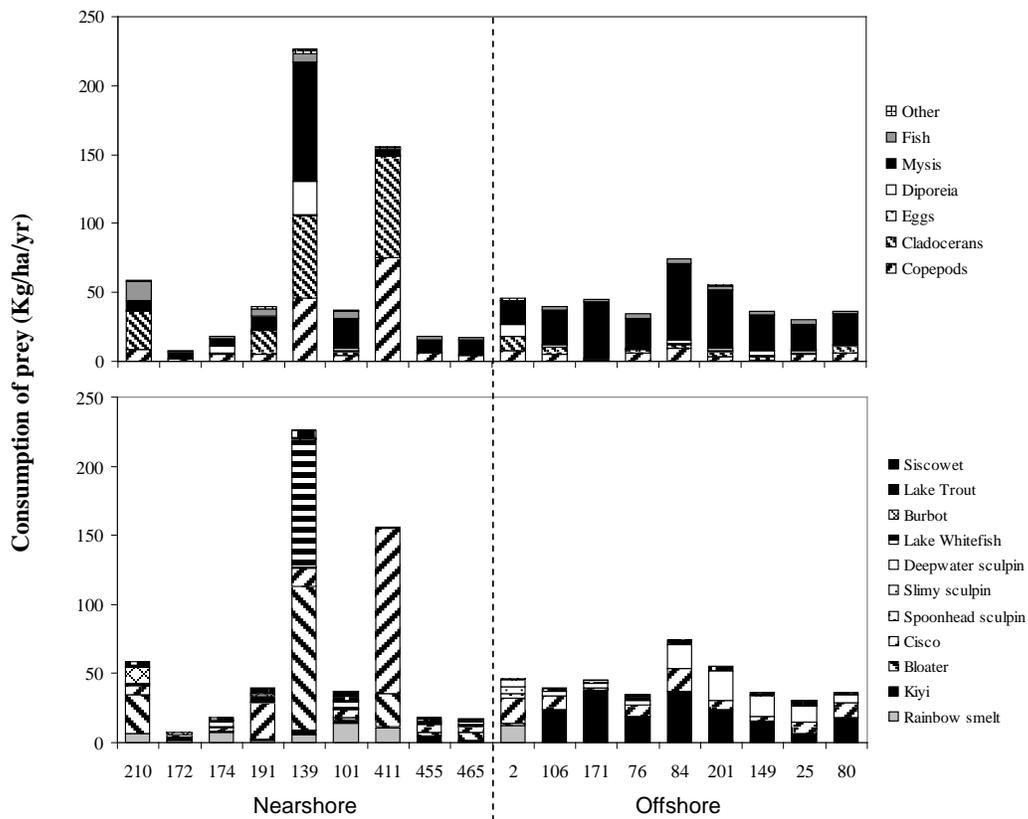


Figure 2-4. Annual consumption (kg/ha) of prey by the fish community (upper panel) and the annual consumption partitioned by the consumer (fish species) at each location (bottom panel) sampled in 2005. Stations are arranged according to depth (shallow to deep).

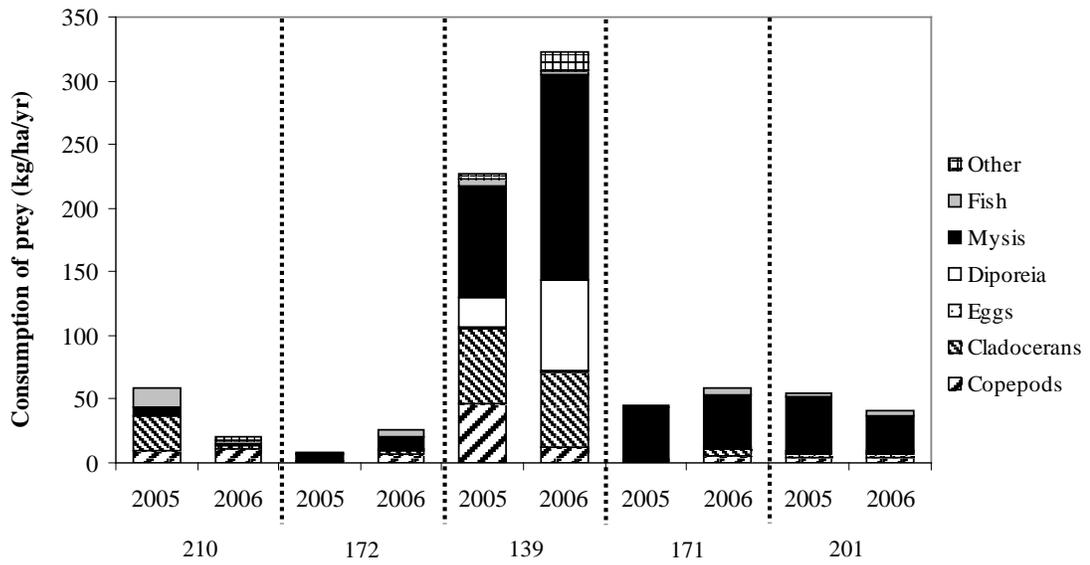


Figure 2-5. Comparison of consumption estimates by the fish community at five locations in western Lake Superior in 2005 and 2006. Stations are arranged according to depth (shallow to deep).

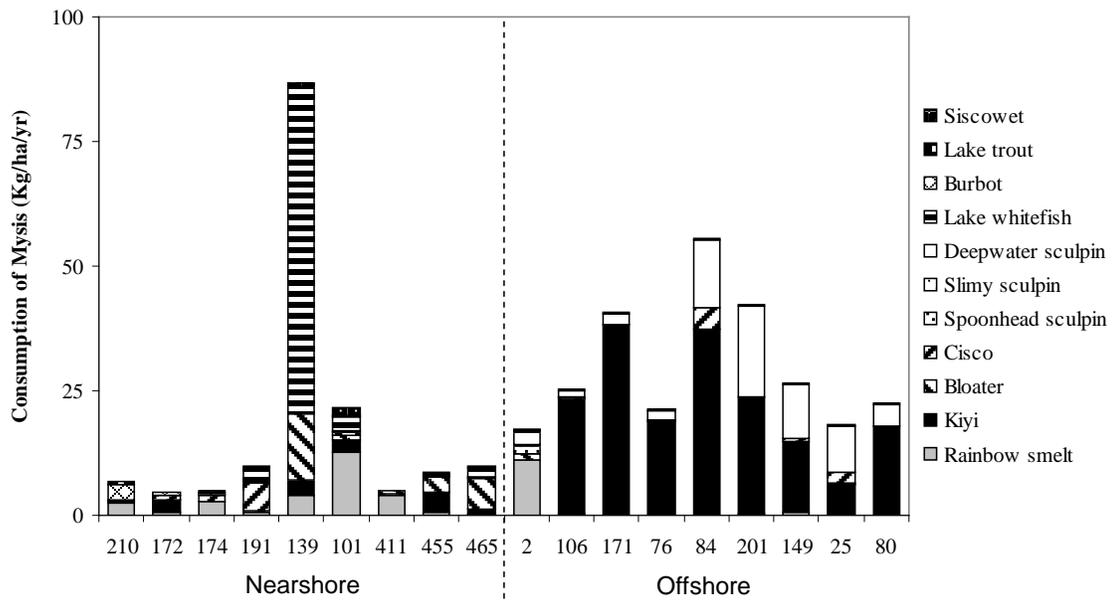


Figure 2-6. Annual consumption of *Mysis* by each fish species across locations in 2005.

Stations are arranged according to depth (shallow to deep).

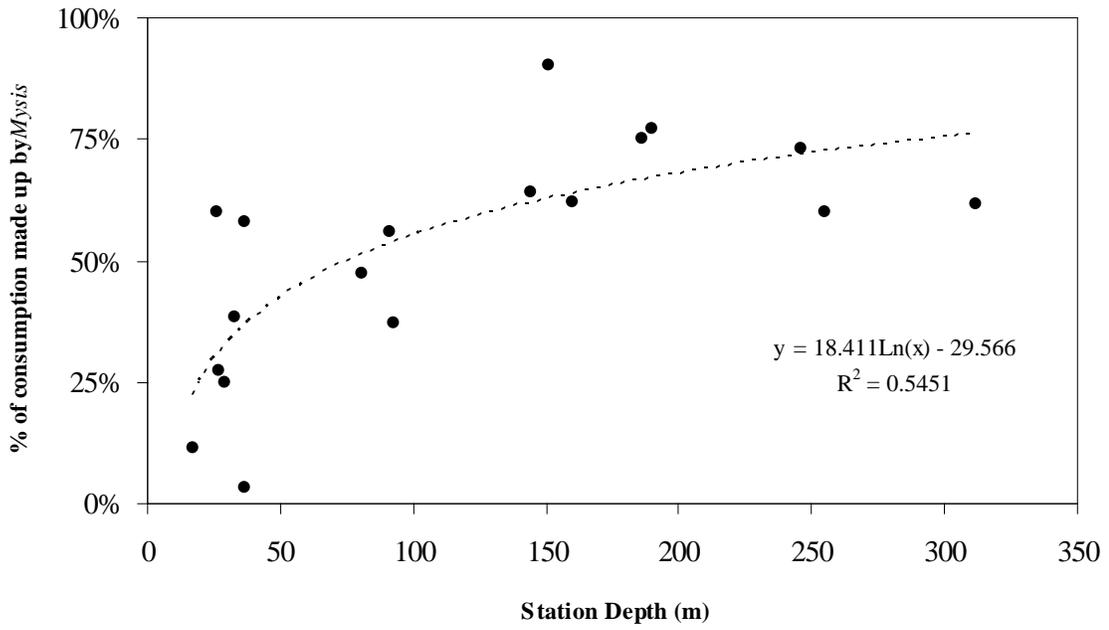


Figure 2-7. Consumption of *Mysis* as a percentage of total prey consumed by the fish community as a function of depth in Lake Superior.

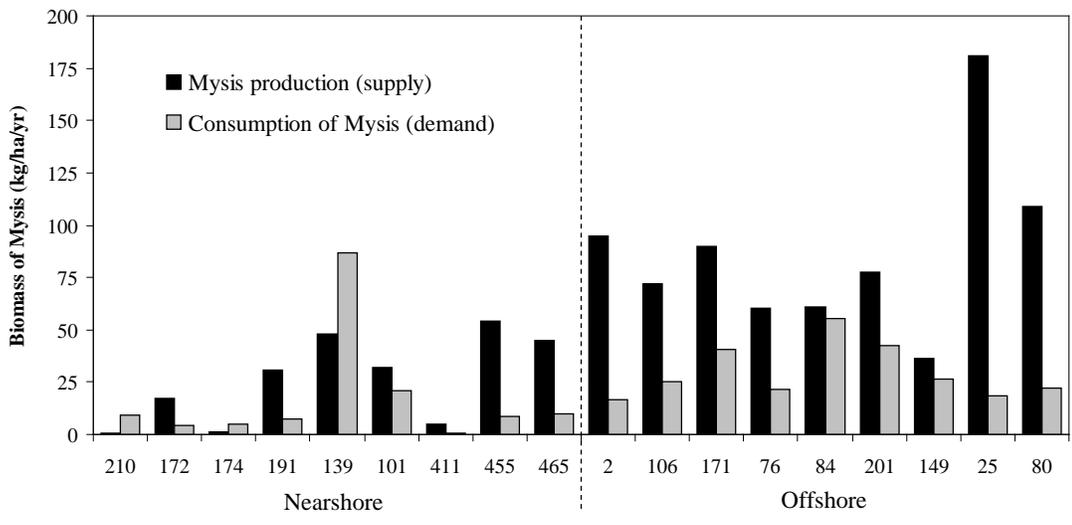


Figure 2-8. *Mysis* demand-supply relationship at each location modeled in 2005. Stations are arranged according to depth.

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