GREAT LAKES FISHERY COMMISSION

2004 Project Completion Report[1]

Compilation and analyses of Lake Superior Salmonine Diets: a Multi-Agency Collaboration

Thomas R. Hrabik[2] , Bradley Ray[2,6] , Donald R. Schreiner[3], Mark P. Ebener[4] and Owen Gorman[5]

[2]Department of Biology, 211 Life Science, 10 Univ. Dr., Duluth, MN 55812

[3]Department of Natural Resources, 5351 North Shore Drive, Duluth, MN 55804

[4] Chippewa Ottawa Resource Authority, 179 W. Three Mile Road, Sault Ste. Marie, MI 49783

[5] USGS Great Lake Science Center, Lake Superior Biological Station, Ashland, WI 54806

[6]Current Address: College of Natural Resources, 100 Cheatham Hall, Blacksburg, VA 24060

November, 2004

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Summary:

The objective of this project was to compile salmonine diet and forage fish information collected by tribal, state and federal agencies in Lake Superior. The data allowed analyses of spatial and temporal variability of prey composition, predator diet characteristics and selectivity as well as a summary diet database for use by other investigators. In Lake Superior, substantial changes in the forage fish community have occurred since the most recent diet analysis of salmonine predators in 1987. We expected that predator diet characteristics also changed between 1987 and 2001. Our primary expectation was that the diet content of salmonine predators was influenced by the numerical proportion prey species available at their location. Our approach to examining this expectation was taken in two steps.

In our initial step, we examined the spatial variability in numerical proportion prey fish composition within and among years to determine whether large, spatially contiguous of the lake shared similar prey communities. Variability in prey fish composition among collection sites and among years at the same site was high in most cases indicating local sampling site characteristics most likely determine prey fish composition. This suggests that analyses of predator selection should be conducted at the finest scale of resolution possible. Furthermore, we detected a consistent decrease in the abundance of common prey fish over the period of study suggesting that predator demand may be reducing the available forage.

Our second step was to meld numerical proportions of prey fish at each location with predator diet information from the same area to examine spatial and temporal trends in prey selection by each abundant predator species. We found that

rainbow smelt are positively selected by lean lake trout in most areas of Lake Superior. However, an analysis of selection by lean lake trout indicates that preference for smelt has decreased in recent years and selection for coregonines is increasing. This trend may be associated with the apparent decrease in rainbow smelt in most areas of the lake. Also, small siscowet (<600mm) appeared to select for rainbow smelt, particularly late in the period of study. However, large siscowets (>600mm) showed neutral selection for smelt as well as positive selection for coregonines and sculpin. Diet overlap between lake trout and siscowet, when averaged across all years was under 50%. However, between 1992 and 2001 there was a significant increase in the dietary overlap of these species and overlap exceeded 60% after 1992. The tendency for commonality in diet choices by siscowets and lake trout late in the record is likely associated with the apparent decrease in the abundance of prey fish observed in most areas of the lake. Furthermore, prey fish surveys in 2003 suggest that the abundance smelt continues to decline. Taken together, these results suggest a need for a comprehensive analysis of predatory demand across wide areas of the lake.

Spatial and Temporal Variability in Lake Superior Prey Fish Composition, 1986-2001

Abstract: We analyzed 16 years (1986-2001) of bottom trawl data from at least 51 locations around Lake Superior in each year to identify spatial and temporal variability in the prey fish composition of Lake Superior. Our objectives were to: 1. identify whether prey species composition exhibited clustering over relatively wide spatial areas, and 2. to identify whether there was significant temporal variability in prey species abundance and composition from 1986-2001. Discriminant function analysis and cluster analysis were used to determine if broad areas could be used to classify the prey fish community spatially. Our results indicate that prey communities are highly variable among sites in close proximity to one another. Spatial analysis of prey fish composition in spring bottom trawl data from 1986-2001 showed few consistent west-east or north-south spatial patterns. Temporal analysis of prey fish abundance showed a decrease in abundance for the four most abundant prey fish in many areas of Lake Superior from 1986-2001. 175 of 216 comparisons within grid cells indicated negative time trends in abundance, with 48 indicating strong negative trends. The results suggest that increasing lake trout and siscowet populations are placing higher predatory demand on the prey fish community in recent years. Continued predation pressure may shift prey species to one dominated by native coregonines. This composition may represent a more natural state for lake trout, which demonstrate the highest growth and production when their diet is contains native coregonines.

Introduction

Lake Superior is the largest body of fresh water in North America and lies at the head of the Saint Lawrence River Drainage (Lawrie and Rahrer 1973). Lake Superior is an oligotrophic lake characterized by low mean temperature, dissolved solids, and sparse phytoplankton populations resulting in high water clarity (Busiahn 1990). About 80% of Lake Superior is deeper than 70 m where the deepwater fish species begin to dominate the community (Busiahn 1990).

The fish community of Lake Superior was historically dominated by lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), lake herring (*Coregonus artedii*), deepwater ciscos (*Coregonus* spp.), sculpin (*Cottidae* spp.), suckers (*Catastomidae* spp.), and burbot (*Lota lota*) (Hansen 1994; Kitchell et al. 2000). Habitat degradation, fishing and interactions with exotic species led to the decline of several native species including shortjaw cisco (*Coregonus zenithicus*), lake sturgeon (*Acipenser fluvescens*) and brook trout (*Salvelinus fontinalis*). Furthermore, the Lake Superior fish community now contains many exotic species, including sea lamprey (*Petromyzon marinus*), rainbow smelt (*Osmerus mordax*), Eurasian ruffe (Gymnocephalus cernuus), round goby (*Neogobius melanostomus*), white perch (*Morone americana*) and naturalized, self-sustaining populations of Pacific salmon (*Oncorhynchus* spp.). These and other introductions, either intentional or accidental, will continue to change the Lake Superior food web. The result is a fish community that may differ from the native fish community that existed prior to European settlement.

Exotic fishes are usually generalists and are able to colonize disturbed systems and dominate fish communities (Dove 1998). The introduction of exotic

species into North America began in the late 1600's (Crossman 1991). These introductions include 25 non-indigenous fish species in the Laurentian Great lakes (Mills et al. 1993). By the 1950's excessive fishing and interactions between native and exotic species caused the collapse of lake trout, lake herring, and deepwater cisco populations in the Great Lakes (Hile et al. 1951; Jensen 1978; Coble et al. 1990). In Lake Superior, declines in lake herring and other coregonines were concurrent with increases in commercial fishing and exotic rainbow smelt populations, which first appeared in the lake in the 1940's (Christie 1974; Crossman 1991). Sea lamprey were first reported in Lake Superior in 1945 (Applegate 1951) and contributed greatly to the decline of lake trout and other native species prior to sea lamprey control efforts.

A primary objective of the Great Lakes Fishery Commission (GLFC) for Lake Superior is the rehabilitation of native fishes including lake trout and native coregonine populations to maintain a predator-prey balance that would allow normal growth of lake trout (Hansen 1990). Sea lamprey control, reduced fishing, and stocking efforts marked the beginning of a large-scale restoration of lake trout in the 1950's (Hansen et al. 1995). The restrictive management of lake trout populations allowed inshore lake trout abundance to increase ten-fold between 1961 and 1971 (Hansen 1994), although densities remained well below historic levels. Continued recovery of lake trout in the 1970's was slow due to reduced stocking and ineffective control of fishing (Hansen 1994). By 1989 lake trout populations increased to approximately half of the GLFC target level, 4 million pounds of sustained annual yield from naturally reproducing stocks (Busiahn 1990; Hansen 1990). Despite this

apparent recovery, lake trout populations were still supported largely by stocking in many areas (Hansen 1994). Furthermore, control efforts reduced sea lamprey populations by 90%, but a significant portion of lake trout mortality was still attributable to sea lamprey (Hansen 1994). Management agencies around the lake are continuing to implement commercial harvest quotas and sea lamprey control that will likely allow lake trout to recover to historic levels. However, to effectively manage increasing lake trout populations, diet content and prey selectivity by predator fish must be determined.

Determining whether sufficient prey fish resources exist to support predator demand is important for effectively managing fish communities. Lake Superior now supports wild lake trout populations that have reached or exceeded historic levels in some locations (Wilberg et al. 2003); this likely increased the demand on prey fish. Two recent analyses have suggested that demand by salmonine predators exceeded the prey supply in western Lake Superior (Negus 1995; Ebener 1995). Although salmonine growth rates and size at age have declined (Johnson et al. 2001), hydroacoustic estimates indicate that there were sufficient prey resources to balance estimated predator consumption (Mason et al. *in review*). Determining if the supply of prey fish in Lake Superior is adequate to support the increasing predator populations is needed to maintain the rehabilitated populations of lake trout.

Lake herring have been the principle species supporting commercial harvest in Lake Superior since 1908 (Anderson and Smith 1971). Prior to their collapse in the 1960's due to over fishing of discrete spawning stocks (Selgeby 1982); lake herring were the major component of the prey supply available to predatory species (Dryer et

al. 1965). Lake herring abundance and recruitment remained low in the 1970's (MacCallum and Selgeby 1987). However, by the 1980's and 1990's recovery of lake herring was underway due to several large reproductive events (Selgeby et al. 1994). Although commercial harvest increased during this recovery period, catches remained below historic levels due to state, provincial and tribal regulation of the harvest (Bronte et al. 1996). Effective management for the recovery of native species in the lake requires an analysis of the spatial and temporal variability in prey fish community structure and food web dynamics. This process must begin with an analysis of the state of prey fish populations within the lake and the associated linkages to predator use.

The objectives of this study were to analyze yearly bottom trawl data collected at consistent locations throughout Lake Superior to 1. identify whether prey species composition exhibited clustering over relatively wide geographic areas, and 2. identify whether significant temporal changes in prey species abundance and composition occurred between 1986-2001. We hypothesized that prey species would show significant spatial patterning or clustering if the characteristics of relatively large regions of the lake determined composition. Alternatively, if local site characteristics were driving prey composition, we expected to observe site specific variability in prey fish composition. Furthermore, we hypothesized that the increase in lake trout and siscowet populations would have a negative influence on the abundance of prey species. Our approach was two fold. First, we examined prey fish composition among survey locations to identify whether large, spatially contiguous areas contained similar prey communities. We then analyzed temporal trends within

spatial areas that allowed the identification of changes in the abundance of prey fish available to predators between 1986 and 2001. To address the first objective, we analyzed bottom trawl information on prey fish compiled by the Ashland USGS Great Lakes Science Center (GLSC) at various scales of spatial resolution to determine if prey fish composition was related to broad spatially defined areas. We then analyzed temporal variability within spatially defined areas to determine general trends in the abundance of prey species important to predatory species.

Methods

The USGS performs yearly spring (April-June) bottom trawl surveys at various locations in Lake Superior using standard methodology (Hoff and Bronte 1999). Data were compiled from bottom trawl surveys performed by the USGS on an annual basis from 1986-2001. The number of bottom trawl samples completed in each year ranged from 51 (1986) to 87 (Table 1). The bottom trawls were completed during daylight hours (usually between 0900 and 1600 hours), when fish are congregated at the bottom of the lake. Sampling was performed with a bottom trawl (Yankee bottom trawl, 12-m head rope) towed cross-contour starting at depths <15 m at nearshore to 100 m at the offshore terminus of the tow. All fish captured were identified to species, counted and measured.

To evaluate the level of spatial variability in the prey species composition, we analyzed information on proportional abundance as a function of sampling location and number of each fish caught. The fish caught in each trawl were assigned to one of seven prey fish categories that included: burbot, coregonines, rainbow smelt, salmonines, sculpin, sticklebacks, and a miscellaneous category that included

alewife, suckers, perch, minnows, bass, and walleye. From this set of information, the numerical proportions of each species were calculated for each spatial location. These proportions were then statistically analyzed using SAS (SAS 1999) and S-PLUS (S-plus v. 6.1 Insightful Inc.) to evaluate the level of spatial variability exhibited by prey fish communities.

The spatial variability in prey composition was analyzed using two methods, linear discriminant function analysis and cluster analysis to determine if broad spatial areas could be identified. First a linear discriminant function analysis was performed to determine if prey community composition corresponded to pre-existing “eco-regions” (Gorman, personal communication) (Figure 1 and Appendix 1).
The discriminant function analysis allowed assignment of a sample location to classes or eco-regions based on the numerical proportion of each prey fish group using Mahalanobis distance as the measurement for distance. This procedure was repeated for each yearly observation, after which percentages of stations misclassified were computed. In addition, a city-block method cluster analysis was used to cluster the sites into seven clusters (SAS 1999). The city block method uses the absolute value as a measure for the distance matrix (e.g. Schoener 1970) with bottom trawl sites grouped based on Euclidean distance. This process was performed using all stations for a single year and then compared across years to identify if clusters were consistent through time. The purpose of this analysis was to identify areas of Lake Superior that could be grouped based on similar prey fish composition.

If non-significant patterns were detected in the discriminant function analyses and cluster analyses, patterns were observed at a finer spatial resolution. We would then examine trends spatially by 10 x 10 km grid cells (statistical grid system) (Figure 2) to identify if consistent patterns in species composition were related to geographic location within the lake. We used the statistical grid system for Lake Superior to group sites on a finer spatial resolution for further prey fish analyses. The spatial variability in numerical proportions for the seven prey species groups was examined. A spatial indicator variable was used to describe locations in terms of shoreline distance from Duluth, MN, in order to examine spatial variability of the prey fish composition. 95% confidence intervals were estimated using the t-distribution. Significance of west-east trends over space was estimated using generalized additive models (GAM) (S-plus v. 6.1 Insightful Inc.). In addition, we analyzed for differences in the prey fish by separate analysis for the north and south shores respectively. GAMs have additive terms like linear (regression) models, but the terms are obtained using nonparameteric scatterplot smoothers, which allow the data to suggest nonlinearities (Hastie 1992). The GAMs reported here were fitted using cubic splines in Splus® 6.1 (S-plus v. 6.1 Insightful Inc.). The use of grid cells would help identify spatial and temporal differences more precisely.

This level of spatial resolution was also used to identify temporal trends. Year to year variability was analyzed for the four most abundant prey fish groups (rainbow smelt, coregonines, sculpin and sticklebacks) within the finest resolution, statistical grid cells, using linear regression analysis. This was done to identify trends in prey fish abundance over spatial areas between 1986 and 2001.

Results

Spatial Variability in Prey Fish Composition

Eco-regions did not provide adequate, consistent classifications of the prey fish community using spatial analysis. The discrimination function analysis on the eco-regions yielded a range of misclassification rates between 0.5699 and 0.8525 for each year (Table 2). The cluster analysis grouped similar areas based on the proportion of each species in the prey fish community. However, this analysis did not cluster areas that were spatially contiguous. Therefore, we used the finest spatial resolution attainable, which was the pre-established statistical grid system, and included groupings of sample locations within 10 x 10 km grid cells.

Prey fish composition exhibited a high degree of spatial variability among sampling sites located around Lake Superior (Figure 3). The abundance of rainbow smelt and coregonines was variable along both west-east and north-south spatial vectors. Analyses of grid cells suggested some general patterns; however, these patterns were inconsistent among years. The level of spatial variability was high within each year and among years. The generalized additive model (GAM) of prey fish species on the south shore of Lake Superior indicated significant spatial trends for sculpin and sticklebacks (Figure 4). GAMs showed that salmonines are found in similar proportions across Lake Superior. Furthermore, sculpin were found in a larger proportion in the eastern side of the lake then in the rest of the lake, while sticklebacks were found in similar proportions on both the eastern and western sides of the lake and lower proportions in the central portion of the lake. There were two prey species that had a significant relationship with the distance from Duluth, on the

north shore (Figure 5). Salmonines were found in higher proportions in the western arm then the rest of the lake, while rainbow smelt on the north shore represented higher proportions in the central portion of Lake Superior before decreasing in the proportion east and west.

Temporal trends in prey fish abundance.

The most numerically abundant fish caught by the bottom trawls in 1986-2001 was rainbow smelt (42%) followed by coregonines (39%, Table 1). Temporal trends of abundance for each species within grid cells indicated a general trend suggesting a decrease in prey abundance that was consistent across prey fish groups. Rainbow smelt, coregonines, sculpin and sticklebacks declined in abundance in most areas of Lake Superior between 1986 and 2001 (Figure 6). There was no significant increase of coregonines or sculpin in any grid cell. Coregonines declined in 43 of 48 locations with 11 of these locations showing a significant (p-value <.05) decline. Furthermore, a decline in sculpin abundance was identified in 40 of 48 locations, ten of which indicated significant trends. Both rainbow smelt and sticklebacks showed a significant increase at one location. However, rainbow smelt showed significant declines at 14 locations, while sticklebacks declined significantly in five locations.

Discussion

Spatial variability in Lake Superior prey fish composition was high and did not offer a grouping scheme that consistently captured the variability observed. The pre-established eco-regions were not at a resolution fine enough to accurately portray the prey fish community of Lake Superior. These results suggest that local site

characteristics influence prey composition in bottom trawl samples. Similarly, Johnson et al. (in press) found that there was high spatial variability in fish community composition occurring within areas of “eco-regions” of Lake Superior. Furthermore, the high spatial variability in fish composition in geographically small areas resulted in weak clustering. Taken together, these results indicate that prey fish composition at any sampling location may be driven by local environmental conditions and habitat characteristics. In addition, temporal variability in prey fish abundance in Lake Superior suggests an overall decrease in prey species over the period of study. The decrease in the abundance of prey species important to predators was consistent across spatial areas and indicates a response to increased predation rates exerted by increasing lake trout and siscowet populations

Spatial Variability in Prey Composition

Spatial analyses at a spatial resolution of the 10 x 10 km indicates weak patterns in several prey groups exist in both west-east and north-south directions. However, these patterns were exceedingly variable suggesting that grouping estimates of prey fish abundance to achieve lake wide patterns in prey fish community dynamics across time may be more appropriate. Spatial patterns were not consistent enough to allow broader categorization of areas and the pattern may be related to the large scales represented by Lake Superior, changing environmental characteristics at spatial locations through time, and the movement of fish among spatial areas of the lake. The high amount of spatial variability in prey composition indicates that the finest level of spatial resolution possible should be used when comparing diet information to prey composition in each year. This approach would

likely reduce the potential error in estimating prey selection by predators associated with aggregating samples among areas with vastly different prey composition.

Temporal variability in Prey Fish Abundance

Rainbow smelt were numerically the most abundant prey fish in Lake Superior. In many locations rainbow smelt were higher in abundance than other prey groups. However, rainbow smelt are declining in abundance in many areas of Lake Superior. This decline appears to have begun in 1978, despite periodic strong year classes of rainbow smelt (Bronte et al. 2003). Bronte et al. (2003) attributed the decline in rainbow smelt to predation by lake trout that consume large rainbow smelt (>120 mm) (also see Conner et al. 1993).

The abundance of native coregonines also declined between 1986 and 2001. The rate of decline appears to be lower than the rate of decline of rainbow smelt at many locations, and may be due to relatively low levels of reproductive success (recruitment) early in the record. Lake herring recruitment between 1978 and 1999 was sporadic, with only five significant year classes produced (Bronte et al. 2003). Another possible mechanism contributing to low recruitment of coregonines may be the high proportional abundance of rainbow smelt which may have had a negative effect on lake herring populations (Hrabik et al. 1998) by consuming larval herring (Selgeby et al. 1978). Predation pressure from the increasing siscowet and lean lake trout populations is likely linked to the observed declines in coregonine abundance.

Sculpin and sticklebacks declined in abundance between 1986 and 2001. However, sticklebacks exhibit lesser declines when compared to other abundant prey fish between 1986 and 2001. However, the maximum length observed has declined

since 1982, which could implicate predation as the primary cause for the decline of sticklebacks as well as the decline in sculpin abundances (Bronte et al. 2003).

The increasing lake trout populations will continue to place a high demand on the prey fish community. The continued predation pressure will likely keep the abundance and biomass of prey species at or below levels observed in this study, as indicated by the low occurrence of large rainbow smelt, sticklebacks, and sculpin in bottom trawls samples (Bronte et al. 2003). However, the change in the composition of prey fish to one dominated by coregonines may represent a more natural state for native predators and allow a more stable balance between predator and prey populations in Lake Superior. Furthermore, lake trout exhibit the highest growth rate when their diet contains a high proportion of coregonines (Mason et al. 1998). Lake Superior management agencies should continue to emphasize restoration of the native fish community. These findings show a shift from a prey community dominated by rainbow smelt to one with equal or higher proportions of native species suggesting that the restoration of the native community is underway. These findings, when coupled with information on predator diet characteristics and selectivity offer insight into the mechanisms underlying the observed changes and implicate predation by recovering lean lake trout and siscowet populations.

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Table 1. The number of each prey species caught and the number of bottom trawls completer in each year of the study.

Year	#of trawls	Burbot	Coregonid	Rainbow smelt	Salmonid	Sculpin	Stickleback	Other fish
1986	51	29	17646	16407	223	1735	2272	952
1987	53	26	10248	16021	183	1946	3383	521
1988	53	8	10424	10922	211	952	1658	1144
1989	76	27	40816	32291	268	1747	8486	3371
1990	81	25	58479	27419	206	1803	6217	1345
1991	83	32	49897	19120	199	2494	4285	2227
1992	85	32	26636	15692	248	3071	10001	1283
1993	86	27	16980	26065	269	2320	4049	2120
1994	87	19	16013	20230	373	2497	6930	1484
1995	87	20	12095	38062	435	2971	7306	1333
1996	87	27	7694	22050	374	3060	7600	1365
1997	84	14	5465	24127	345	1411	7708	2813
1998	87	13	8115	17691	353	1253	4414	757
1999	78	6	10300	12621	145	592	5215	1564
2000	81	5	9218	15678	200	2010	1897	3252
2001	82	14	10164	17783	324	1538	6912	2298

Table 2. Misclassification rates from discriminant function analysis of eco-regions.

Year	Misclassification Rate
1986	0.7464
1987	0.5699
1988	0.6379
1989	0.8356
1990	0.7791
1991	0.8483
1992	0.8525
1993	0.704
1994	0.6874
1995	0.7431
1996	0.6628
1997	0.6383
1998	0.6964
1999	0.8125
2000	0.76
2001	0.7861

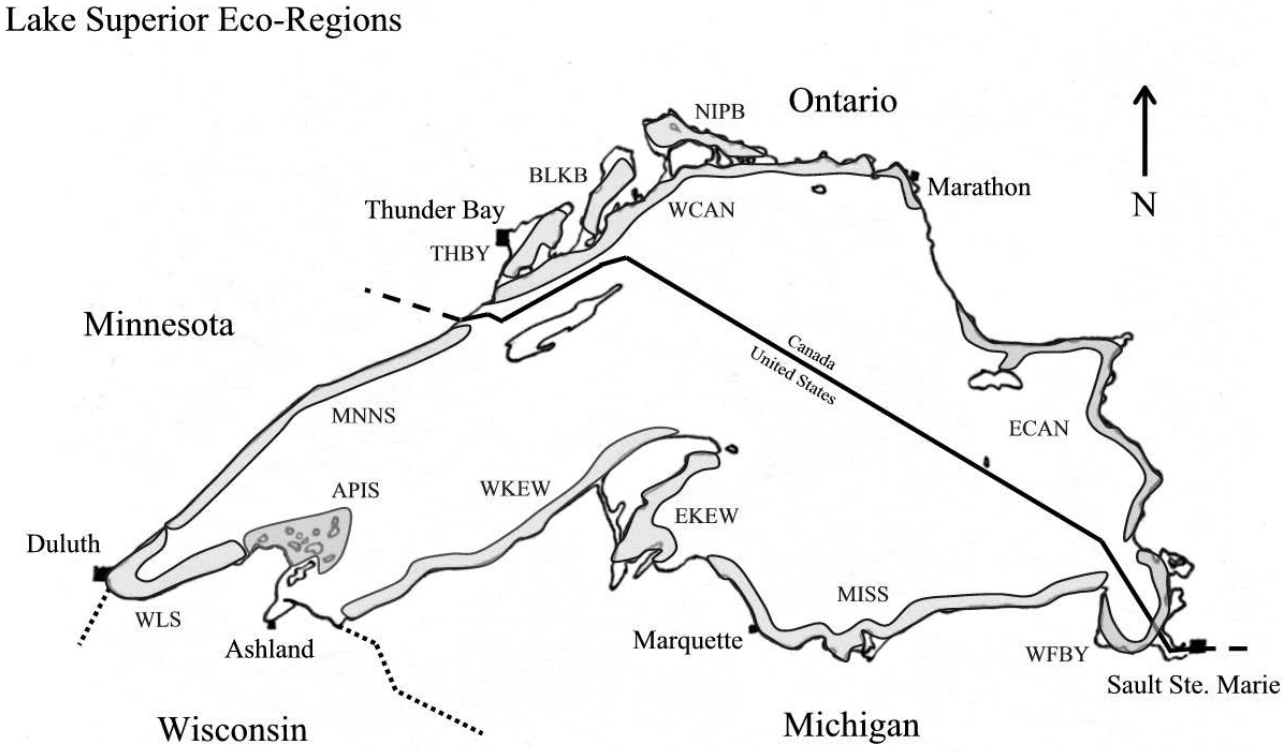

Figure 1. A map showing the location of ecoregions defined for Lake Superior.

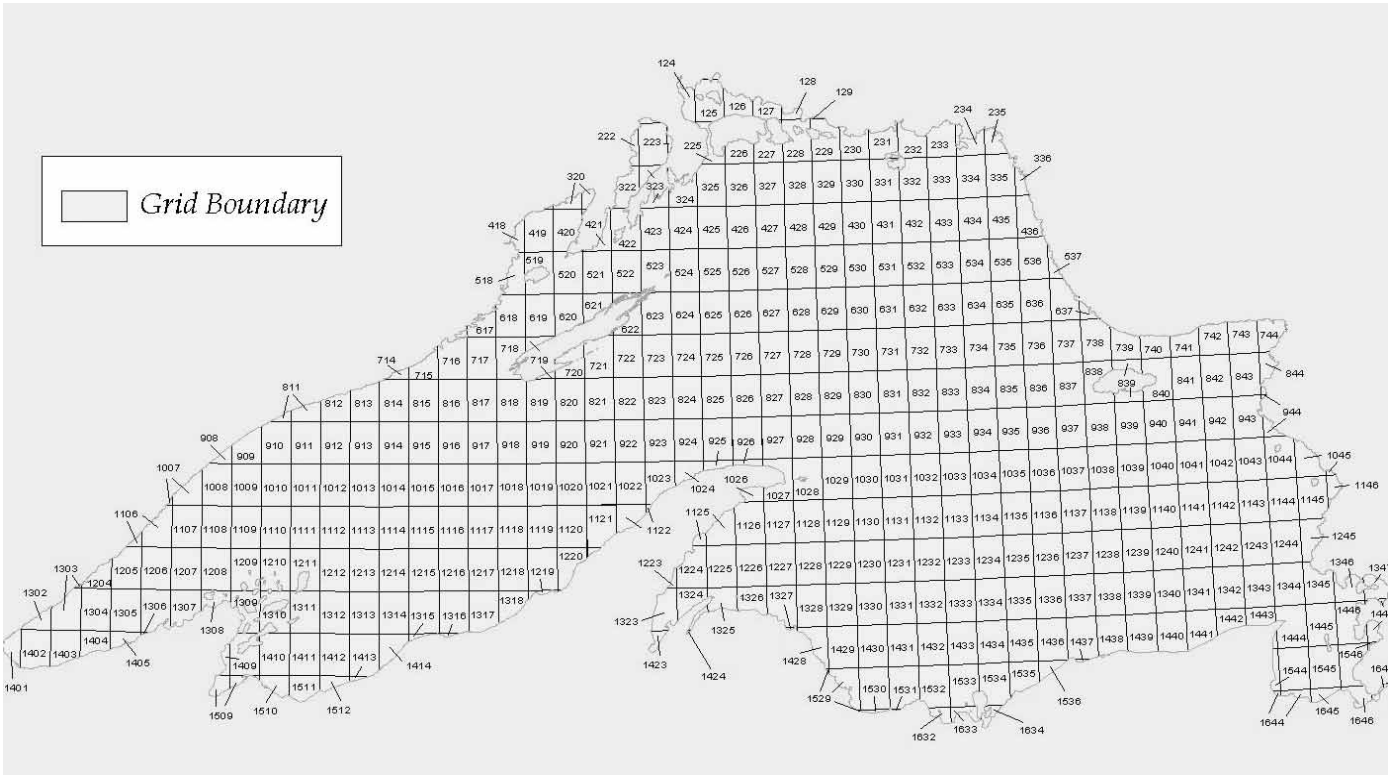

Figure 2. Map showing the statistical grid system in Lake Superior.

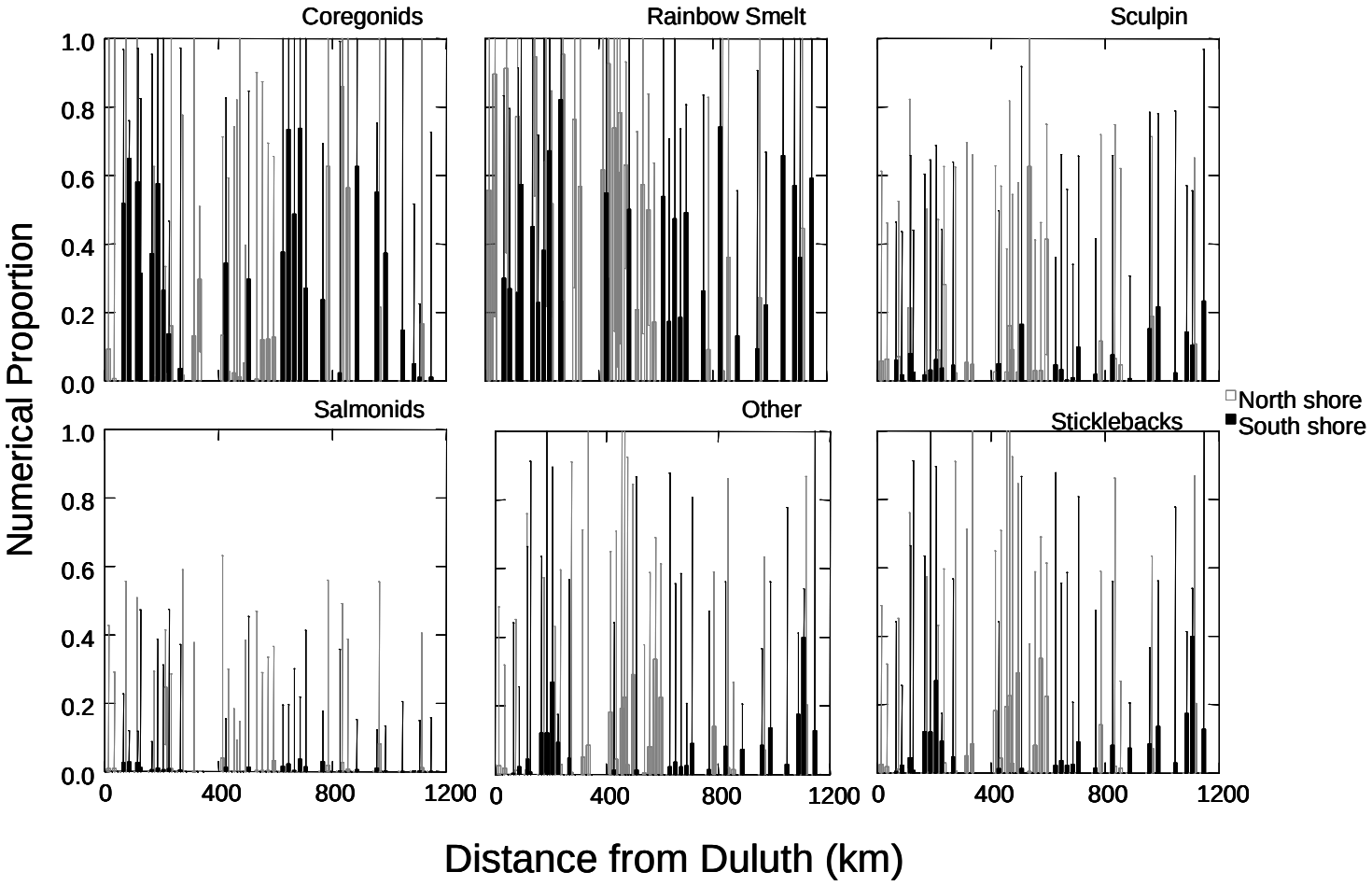

Figure 3. Numerical proportions of spring bottom trawl catches on north and south shorelines between 1986-2001 across Lake Superior, including 95% confidence intervals about the mean.

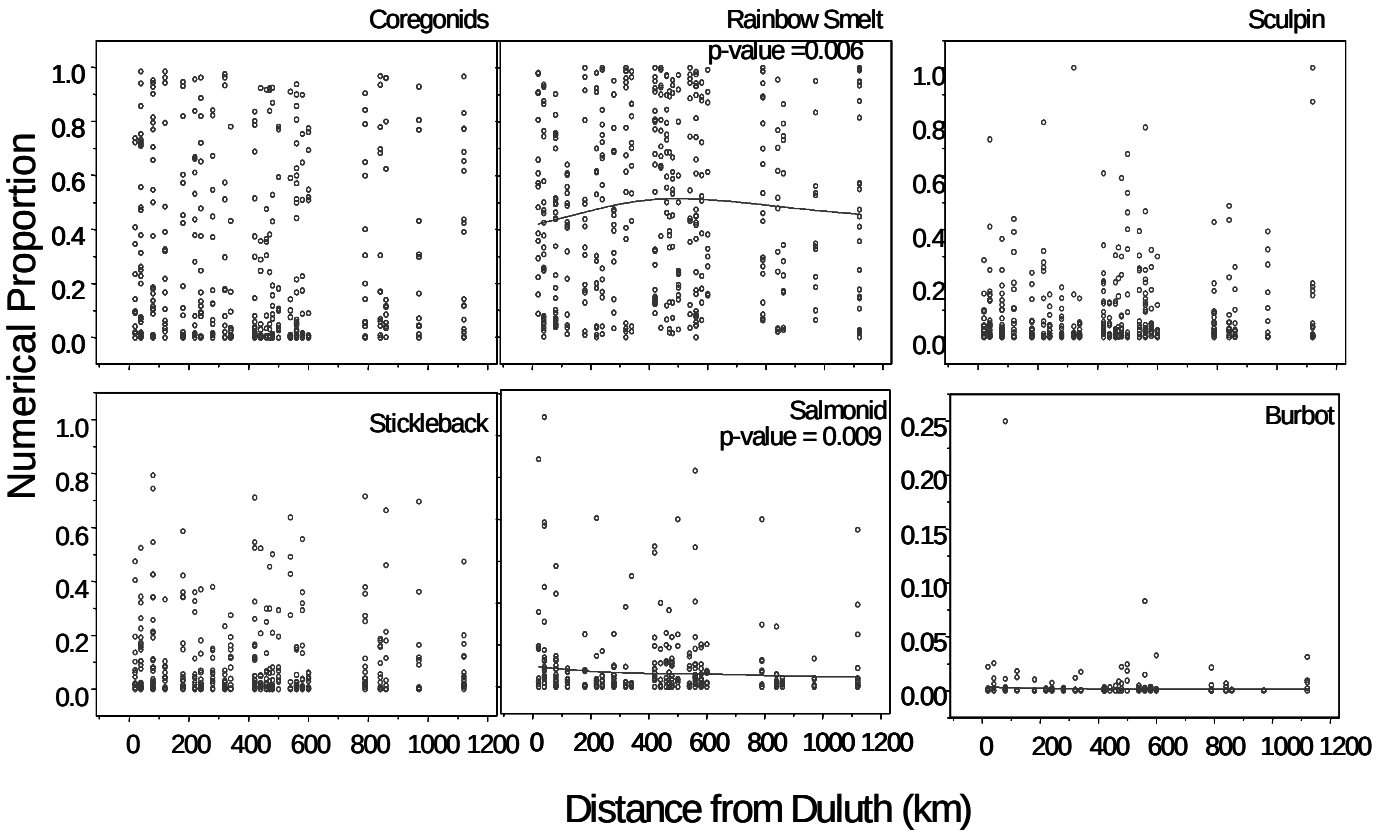

Figure 5. Numerical proportion of prey species at each location across the north shore of Lake Superior and the fitted cubic spline, generalized additive model.
Curves from cubic spline are shown only where p <0.05.

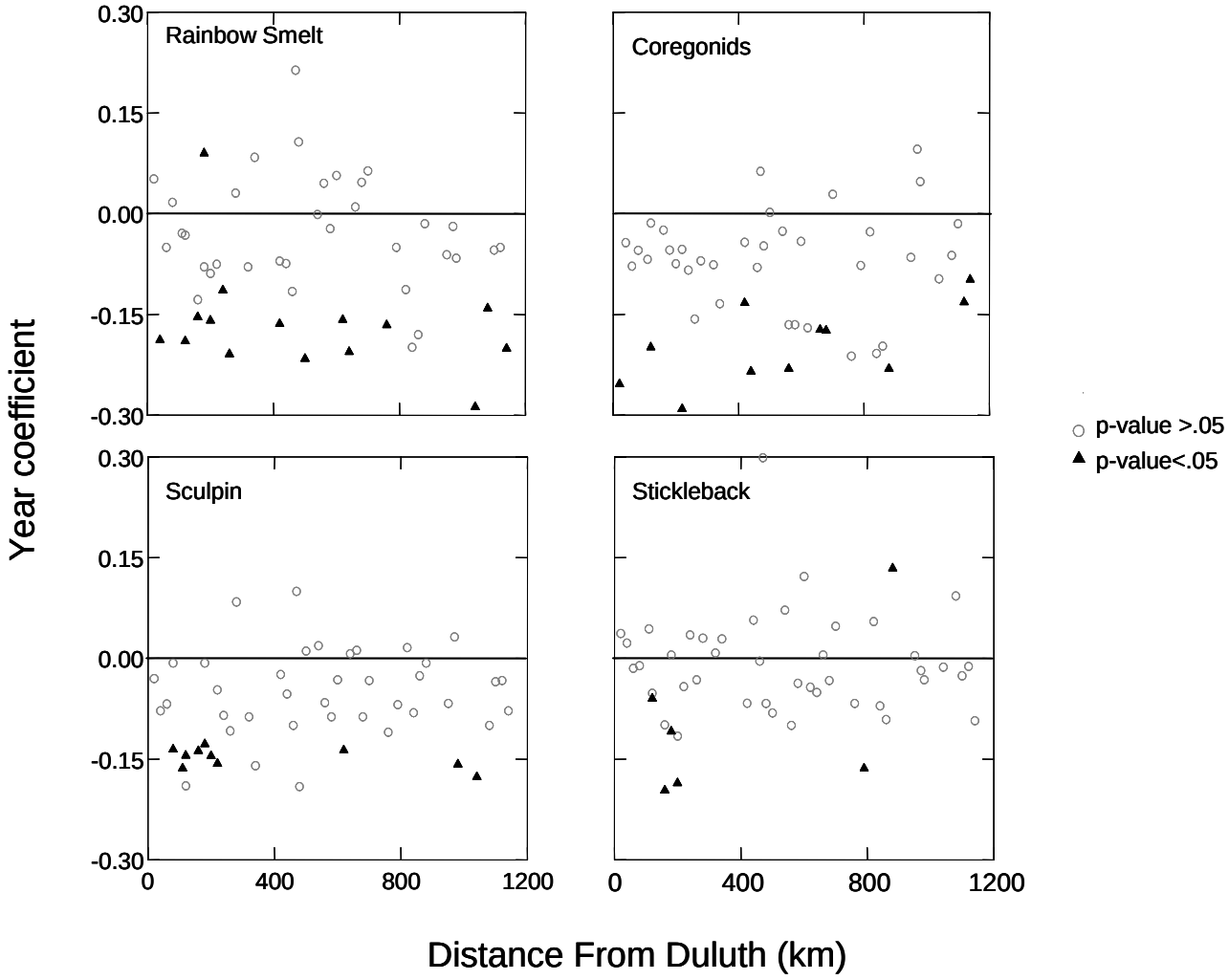

Figure 6. Year coefficients from regression analysis of prey species trends in Lake Superior by grid cell.

Appendix 1 Description of Lake Superior Eco-Regions

WLS- Western Lake Superior. This ecoregion consists of low-slope sandy shore areas west of the Apostle Islands (Squaw Point, Wisconsin) region around the western end of Lake Superior to the mouth of the Big Sucker River, Minnesota. Maximum depth is approximately 60 m in the nearshore area (<5 km from shore).

MNNS- Minnesota North Shore. This ecoregion consists of steep-slope granitic and basaltic rocky shore areas northeast of WLS from Two Harbors up to Wauswaugoning Bay, Minnesota. Maximum depth exceeds >100 m within 5 km of shore.

WCAN- Western Canada. This ecoregion consists of steep to moderate slope granitic and basaltic rocky shore areas from Cloud Bay to Heron Bay, Ontario. Maximum depth typically exceeds 100 m within 5 km of shore.

ECAN- Eastern Canada. This ecoregion consists of moderate slope granitic rocky shore areas from Otter Island to Alona Bay, Ontario. Maximum depth typically reaches 100 m within 5 km of shore.

WFBY- Whitfish Bay. Nearshore areas in this ecoregion are dominated by low-slope sandy shorelines. The region ranges from Pancake Point in Canadian waters to Whitefish Point in U.S. waters. Maximum depth reaches approximately 60 m within 5 km of shore.

MISS- Michigan South Shore. Nearshore zones in this area are dominated by low-slope sandy shorelines but steep rocky areas occur in the vicinity of Grand Island. The region ranges from Crisp Point west of Whitefish Point to Big Bay, Michigan. Maximum depth typically exceeds 60 m within 5 km of shore.

EKEW- Eastern Keweenaw. Nearshore zones in this area are dominated by low-slope sandy and rocky shorelines and but some steep slope areas occur inside Keweenaw Bay in the vicinity of Sand Bay. The region ranges from Huron Bay to Bete Grise near the tip of the Keweenaw Peninsula, Michigan. Depths typically exceed 100 m within 5 km of shore.

WKEW- Western Keweenaw. Nearshore near the north end of the Keweenaw Peninsula are steep and rocky, exceeding 100 m depth within 5 km. Nearshore areas west of Upper Entry are dominated by sandy low-slope shorelines, and depths rarely exceed 60 m within 5 km of shore. The region extends from Eagle River to Little Girls Point, Michigan.

APIS- Apostle Islands. Nearshore areas in this archipelago consist of a mix of low-slope sandy shorelines and moderate slope sandstone shorelines. Maximum depths range from less than 60 to more than 100 m within 5 km of shore.

ISRO- Isle Royale (not shown in figure). Nearshore waters of the largest island in Lake Superior are typically rocky, steep, and complex. Very difficult to find trawlable areas. Maximum depths typically exceed 100 m within 5 km of shore.

THBY- Thunder Bay. Nearshore areas in this large bay consist of low and moderate slope shorelines. Maximum depths range from less than 60 to more than 100 m within 5 km of shore.

BLKB- Black Bay. Nearshore areas in this large bay consist of low slope shorelines where maximum depths are typically less than 50 m within 5 km of shore.

NIPB- Nipigon Bay. Nearshore areas in this large bay consist of low and moderate slope shorelines. Maximum depths range from less than 50 to more than 100 m within 5 km of shore.

Spatial and temporal variability in Lake Superior salmonine predator diet characteristics and selectivity

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Abstract: We evaluated diet characteristics of 18,246 trout and salmon collected over 16 years (1986-2001) in Lake Superior. Our results indicate that rainbow smelt were the most abundant prey item both by number as well as biomass followed by coregonines. We estimated prey selectivity of lake trout and siscowet for a subset of the dataset by linking the numerical proportions of prey species from bottom trawl surveys to predator diet information at many locations around Lake Superior in each year. Lean lake trout and siscowet positively selected for rainbow smelt at many locations. However, lake trout selection for coregonines has increased in recent years. This trend is concurrent with a decrease in prey selection by lake trout for rainbow smelt. In addition, selection for rainbow smelt by small siscowet has increased in recent years. This trend underlies an apparent increase in diet overlap between siscowet and lean lake trout in recent years. These results indicate that rainbow smelt remain an important prey species in Lake Superior despite recent declines in their abundance. Combined, these results suggest that the increasing siscowet population may be placing greater demand on prey resources utilized by lake trout in recent years. This study contributes a synthesis of predator diet characteristics that will be useful in future bioenergetic and ecosystem models of Lake Superior that address the supply-demand debate.

Introduction

Fishing pressure, food web changes, and introduction of sea lamprey (*Petromyzon marinus*) have caused significant changes in lake trout (*Salvelinus namaycush*) populations of the Laurentian Great Lakes since the early 1900's. As a result, lake trout populations were essentially extirpated from all the Great Lakes by the mid 1900's (Christie 1974). The primary objective of the Great Lakes Fishery Commission (GLFC) is to restore the native fish community of Lake Superior to abundances that occurred prior to sea lamprey population increases (Busiahn 1990). Rehabilitation efforts to restore lake trout populations in Lake Superior include sea lamprey control, fishery closures, and stocking programs (Hansen et al. 1995). Lake trout have responded to these efforts with increased natural reproduction (Selgeby 1995) and Lake Superior now supports wild lake trout populations that have reached or exceeded historic levels in some locations (Wilberg et al. 2003).

Lake trout in Lake Superior exhibit a variety of phenotypes. The two dominant phenotypes are lean lake trout (*S. namaycush namaycush)* and siscowet lake trout (*S. namaycush siscowet*). The lean lake trout typically inhabits near-shore areas of the lake and has increased in abundance in recent years. The deepwater form or "siscowet" lake trout is also increasing in abundance and is placing an increasing demand on prey fish resources (Harvey et al. 2003). The increased abundance of siscowet lake trout has initiated efforts to accurately and comprehensively estimate their demand on the Lake Superior prey fish community.

Historically, the diet of lake trout was dominated by native coregonines (Dryer et al. 1964). However, as the prey fish community shifted from coregonines to a

community dominated by exotic rainbow smelt (*Osmerus mordax*), lake trout diets also shifted to rainbow smelt (Selgeby 1982). Recently, coregonines have increased in abundance and have become the most abundant planktivore in many locations in Lake Superior (Hansen 1994). However, through the 1980's, lake trout diets contained up to 90% rainbow smelt, despite declines in rainbow smelt abundance. Given the increasing trends in coregonine abundance, the high predation rate on rainbow smelt suggests that salmonine predators positively selected for rainbow smelt (Conner et al. 1993).

Siscowets are now the most abundant predator species in Lake Superior (Ebener 1995). However, the siscowet phenotype does not have the commercial value of lean lake trout due to its high fat content (Kitchell et al. 2000). Furthermore, siscowets generally inhabit waters greater than 80 m in depth and feed primarily on deepwater coregonines (e.g. bloater (*Coregonus hoyi*) and kiyi (*Coregonus kiyi*)) and deepwater sculpin (*Myoxocephalus thompsoni*) (Conner et al. 1993; Harvey and Kitchell 2000). However, siscowets have been reported to make foraging bouts in near shore waters where lean lake trout feed (Harvey et al. 2003). This tendency could impose a constraint on lean lake trout population recovery in some regions of Lake Superior. Therefore, there is a need to analyze the diet characteristics of both lake trout phenotypes to identify the extent of dietary overlap.

Analyzing the diet characteristics of lean and siscowet lake trout required a synthesis of existing fish data sets from agencies surrounding Lake Superior. This analysis is consistent with the mission of the Great Lakes Fishery Commission, and the goals of the Joint Strategic Plan for the Management of Great Lakes Fisheries.

Activities that allow the many agencies involved with analysis and management of the Lake Superior food web to collaborate within and across management units and jurisdictions are essential for development of the best management strategies. A comprehensive analysis of predator diet characteristics is essential to the continued success of the lake trout restoration program, particularly since the most recent synthesis of salmonine diet information is now over a decade old (Conner et al. 1993). Synthesis of salmonine diet information is essential to accurately assess prey selection and determine the importance of each prey fish species to an increasing lake trout population. Discerning spatial differences in prey selection by lean lake trout and siscowet is also important because spatial differences in lake trout diet composition in Lake Superior may be related to changes in the prey fish composition from north to south (Bronte et al. 1994). Spatial patterns in predator diet occur in Lake Michigan (Miller and Holey 1992) and Lake Huron (Diana 1990), however, no published studies have examined lake wide trends of spatial and temporal differences in Lake Superior salmonine diets. The objectives of this study were three fold: 1) to combine USGS spring bottom trawl data on prey fish with lake wide predator diet data collected during the same season to determine prey selectivity of Lake Superior predators; 2) to assess potential overlap in prey use among the predators; and 3) to identify spatial and temporal changes in prey selection since 1986. We used spatial data sets of prey fish characteristics and diet information compiled annually from 1986-2001 to address our objectives.

Methods

Salmonine diet data were collected yearly by tribal, provincial, and state agencies around Lake Superior during gill net assessments from 1986 to 2001. All agency data were combined into a database and locations of net collections were georeferenced. The combined database consisted of 18,246 non-empty diet samples for individual predators. Each entry contained information on the time and location of capture, the length and weight of each predator, and the length, weight and number of each prey type. The prey items were grouped into seven categories that included burbot, coregonines, rainbow smelt, salmonines, sculpin, sticklebacks, and other, which included alewife, suckers, perch, minnows, bass, and walleye. Unidentified prey items were removed from further analysis. In addition, the USGS collected yearly prey fish abundance with bottom trawls at consistently sampled locations around Lake Superior from 1986 to 2001. These abundance data were used to identify the appropriate spatial scale for the predator diet analyses. This data set was also used to estimate prey selectivity.

We used numerical proportions of prey species and diet proportions of predator species caught in proximity to calculate prey selectivity and predator size selectivity of six prey categories: burbot, coregonines, rainbow smelt, salmonines, sculpin and stickleback (e.g. Hrabik et al. 2001). We calculated prey selection for individual lean and siscowet lake trout caught in gill nets between April and June from 1986 to 2001. This represented 36.7% of all the diets in the database. We used Chesson's (1983) index of prey selection, α, to estimate predator selectivity. We calculated α for individual predators and determined 95% confidence intervals for

each year from 1986 to 2001. Variation in prey selection of different sized predators was also determined using Chesson's index of selection. Since few fish < 400 mm were collected each predator species was separated into two size categories (<600 mm, and >600 mm) (Table 1). This was done spatially and temporally for lean and siscowet lake trout at each location when diet information existed for more than five individual predators.

We examined spatial and temporal variation in diet selection for lean and siscowet lake trout. The shoreline distance from Duluth, MN was estimated for each sample site where prey and predator information existed. We used a Generalized Additive Model (GAM) to determine if significant variability in prey selectivity was explained by geographic location along both the north and south shorelines of Lake Superior. We fit GAMs using cubic splines in Splus® 6.1 (S-plus v. 6.1 Insightful Inc.) that identify nonlinearities (Hastie 1992) to determine if spatial patterns in prey selection existed.

We used predator diet information from all records to estimate dietary overlap between predator species in Lake Superior. To do so, we used Shoener's (1970) index to estimate diet overlap on a lakewide basis. Schoener's index was computed for all predator species from all locations in all years when sample sizes were greater than 10. In addition, we used linear regression analysis to assess the time trend in dietary overlap between lean and siscowet lake trout, for which we had adequate samples, from 1992 to 2001. Years prior to 1992 were not used due to a small sample size (< 10) of siscowets.

Results

Rainbow smelt dominated the diets of salmonine predators in Lake Superior geographically and through time (Figure 1). Coregonines, sculpin and sticklebacks were also abundant in predator diets (Figure 1). Conversely, salmonines, burbot and other species were minor components of predatory salmonines diet.

Prey Selectivity and Predator Size

Rainbow smelt were the most common diet item of large and small lean lake trout, followed by coregonines, sculpin and stickleback. Small (<600mm) and large (>600mm) lean lake trout fed selectively on rainbow smelt. All sizes of lean lake trout showed variable selection for coregonines (Figure 2). All sizes of lean lake trout showed negative or neutral selection for sculpin and sticklebacks with the exception of two locations where positive selection for sticklebacks was observed (Figure 3). However, when combined into lake wide averages, all sizes of lean lake trout selected for rainbow smelt and fed on coregonines in proportion to their abundance and negatively selected for sculpin and stickleback (Figure 4). Small siscowets positively selected for rainbow smelt in 40% of the locations (Figure 2) but large siscowets showed neutral selection for rainbow smelt at 80% of the locations.

Siscowet prey selection was related to the size of the individual fish. Small siscowets positively selected rainbow smelt at 80% of the sampling sites. Coregonines, however, were positively selected by small siscowets at only 10% of the locations (Figure 5). Small siscowets positively selected for sticklebacks at 33% of the locations while large siscowets showed neutral selection for sticklebacks at 40% of the locations (Figure 6). Large siscowets showed neutral selection for

rainbow smelt at all but one location. Large siscowets exhibited positive selection for coregonines at 40% of the locations. Small siscowets positively selected for sculpin at 40% of the locations and large siscowets showed positive selection for sculpin at 50% of the locations (Figure 6). However, when aggregated, each size category of siscowets showed neutral selection for sticklebacks (Figure 4).

Prey selection by large and small size classes of lean and siscowet lake trout were also examined through time. While selection for rainbow smelt remained positive throughout the record, selection for this species appears to have declined since 1995 for large and small lean lake trout (Figure 7). Large lean lake trout showed negative or neutral selection for coregonines through 1996. However, lake trout show positive selection for this prey category since 1997 (linear regression p-value < 0.001) (Figure 7). All sizes of lean lake trout exhibited negative selection for sculpin. Selection for sculpin appeared more negative later in the record (linear regression p-value < .02, Figure 8), while a trend towards neutral selection for sticklebacks was apparent later in the record (linear regression p-value < 0.05, Figure 8).

Selection by siscowets for rainbow smelt increased over the study period, while selection for coregonines did not change through time (Figure 9). Small siscowets showed an increase in selection for sculpin from negative selection to neutral selection over time. However, large siscowets showed neutral selection for sculpin through time, with the exception of 1999 (Figure 10). In general, siscowets showed neutral selection for sticklebacks across all years (Figure 10).

Overall trends in prey selection by predator species

There was no consistent pattern in the prey selectivity by lean and siscowet lake trout over spatially defined areas of Lake Superior (Figures 11 and 12). However, siscowets were rarely collected on the north shore. Generally, both lean and siscowet lake trout positively selected for rainbow smelt (Figure 13). Lean lake trout showed significant positive selection for coregonines at 15%, neutral selection at 28% and negative selection at 56% of the locations (Figure 11). Siscowet showed significant positive selection for coregonines at 20%, neutral selection for coregonines at 20% and negative selection at 60% of the locations (Figure 12).

Both lean and siscowet lake trout showed neutral selection for coregonines on a lake-wide basis (Figure 13) Furthermore, lean lake trout showed negative selection for burbot at 95% of the locations, salmonines at 88% of the locations, sculpin at 81% of the locations, and sticklebacks at 81% of the locations (Figure 11). Siscowets tended to show positive selection for sculpin throughout the lake (Figure 13), negative selection for salmonines and neutral selection for burbot and sticklebacks (Figure 13).

Prey selection by lake trout and siscowets did not show significant spatial patterning. This allowed temporal analysis of lake-wide estimates in prey selection for each species. Lean lake trout show significant positive selection for rainbow smelt in each year between 1986 and 2001 (Figure 14). However, the magnitude of selection for smelt appears to be declining in recent years. Furthermore, selection for coregonines has increased from negative selection in 1986 to neutral selection in 2001 (p-value < 0.001). Lean lake trout negatively selected sculpin, sticklebacks,

salmonines, and burbot throughout the record. However, lean lake trout selection for sticklebacks increased from negative to neutral selection by 2001 (p-value<0.02).

Patterns in siscowets selection were more variable than those observed for lean lake trout. Prey selection by siscowets for rainbow smelt appeared to increase from 1986 to 2001 (Figure 15). Furthermore, siscowet showed positive selection for sculpin prior to 1994. However, neutral selection for this prey item occurred by 2001. Siscowets showed neutral or negative selection for salmonines and burbot over all years; a pattern similar to that observed for lean lake trout.

Diet Overlap

Diet overlap between lean lake trout and siscowets was approximately 50% over all years of the study. However, the commonality in diet choices by lean lake trout and siscowets has increased significantly in the later years of the record (p-value <.01) (Figure 16). Since 1998 the overlap between lean lake trout and siscowets has exceeded 60%. In addition, lean lake trout and coho salmon showed a high degree of diet overlap (80%), however sample size of this species in the database was small (n=12). Diet overlap between siscowet and walleye (65%) and lake trout and intermediate morphotypes of lake trout were also high (62%). However, predator sample sizes were low with the exception of lean and siscowet lake trout.

Discussion

The diet of predatory salmonines in Lake Superior remains dominated numerically and in weight by rainbow smelt. The selection of smelt by increasing predator populations has likely resulted in high mortality and led to the observed

decline of rainbow smelt in Lake Superior (Bronte et al. 2003). Trends in prey selection indicate that lean lake trout and siscowet exhibit positive selection for rainbow smelt. The consumption of coregonines, however, appears to be increasing in proportion to their numerical abundance and this change is associated with declines in smelt abundance.

Size specific prey selection by lean lake trout

Lean lake trout of all sizes showed positive selection for rainbow smelt throughout Lake Superior. Vander Zanden et al. (2000) found no difference between body size and the trophic position and lake trout. Lake trout appear to consume a wide range of prey sizes and are opportunistic feeders. Busiahn (1985) posited that lake trout grow more rapidly when lake herring dominate the diet. Gape limitation may offer a mechanism to explain why small lean lake trout positively selected for rainbow smelt. Small Lean lake trout did not show positive selection for coregonines, although lean lake trout >400 mm may consume the larger coregonines at a lower frequency (Mason et al. 1998). Predator avoidance capabilities of the co-evolved coregonines may influence lean lake trout diet selection (Mason et al. 1998). Unlike rainbow smelt that may remain motionless in the water, a behavior that apparently decreases encounter rates with predators, coregonines are active swimmers (Savitz and Bardygula 1989). However, coregonines are able to avoid capture by predators about 60% of the time, while once detected rainbow smelt can be captured with ease (Savitz and Bardygula 1989). The behavioral differences between coregonines and rainbow smelt may at least partially explain the tendency for positive selection by lake trout for smelt and the neutral selection for coregonines.

Lean lake trout prey selection

Conner et al. (1993) showed that rainbow smelt was the dominant prey item by weight in the diet of lean lake trout throughout the year. However, while selection for smelt remains positive, there appears to be a decline in the level of selection for rainbow smelt by lake trout since 1986. Rainbow smelt have been declining in abundance since 1995 (Gorman et al. 2004) and are less abundant in deep water areas. Furthermore, lean lake trout shift their diet to coregonines in Minnesota waters when they move to deeper water in the fall (Ostazeski et al. 1999). The increase in the selection for coregonines over time is likely related to the decrease in the abundance of rainbow smelt in recent years. The decline in coregonine abundance over the same time period was slight when compared to that observed for rainbow smelt. The overall decline in the abundance of all prey species may have simply increased the number of coregonines encountered by lake trout relative to other species. The decrease in overall prey abundance may not affect lean lake trout consumption rates (Eby et al. 1995). However, Stewart and Ibarra (1991) showed that the decline of the principal prey of Lake Michigan salmonines caused a 25% decline in the average weight of sport caught fish. Although Lake Superior has the lowest growth rates for lake trout and the lowest prey densities of any of the Great Lakes (Eby et al. 1995), further decreases in prey fish abundance may cause a rapid decrease in the growth rate of lake trout. Examination of the demand placed on forage fish and the supply available may clarify this possibility.

Size specific prey selection by Siscowets

Siscowet prey selection varied depending on the size of each fish. Our findings are similar to those reported by, Ostazeski et al. (1999) who found that coregonines were the most important prey item for larger, adult fish, while sculpin are the most important for smaller siscowets. However, small siscowets appear to be selectively feeding on rainbow smelt. This also suggests a trophic linkage between siscowets and lean lake trout by the use of near shore prey items (Harvey et al. 2003). Our results are consistent with the hypothesis that siscowets, particularly those <600 mm, rely on near shore prey communities for up to 25% of their production until they reach large sizes (Harvey et al. 2003).

Siscowet prey selection

Siscowets showed positive selection for sculpin and rainbow smelt in many areas of Lake Superior. Ostezeski et al. (1999) found that siscowets utilized sculpin more so than did lean lake trout. However, selection for sculpin by siscowets has declined since 1986. This decline the selection of sculpin may be related to the recent decline in biomass of sculpin (Bronte et al. 2003) and underlie the observed increase in selection for rainbow smelt. Siscowets showed an increase in selection for rainbow smelt over a period where selection on rainbow smelt by lean lake trout decreased. This shift from neutral selection to positive selection of rainbow smelt may be related to the increased siscowet population size (e.g., Kitchell et al 2000). The increasing siscowet population may be expanding as density dependence becomes a factor in deepwater areas. Furthermore, the observed differences between prey selection by siscowets and lean lake trout are likely due to the greater depths inhabited by siscowets (Ostazeski et al. 1999). However, as siscowet populations

continue to increase, there may be more demand placed on resources used by lean lake trout.

Diet Overlap

The increase in prey selection by siscowets for rainbow smelt has lead to significant dietary overlap between the two major phenotypes of lake trout. We found the proportional overlap to be approximately 50% between the two phenotypes over all years and other studies have suggested that diet overlap between the two species may not be ecologically significant (e.g. Harvey and Kitchell 2000; Bronte et al. 2003; Harvey et al. 2003). However, given the relatively recent increases in siscowet abundance, and the observed trend toward a higher level of overlap between the two forms, competition between lean and siscowet lake trout may be increasing. We observed overlap in diet of lean and siscowet lake trout exceeding 80% in 2000 and 2001. Dietary overlap of this magnitude is consistent with the hypothesis that the increasing siscowet populations may be exploiting prey used by lean lake trout. Given the recent evidence that prey supply may be at or near predator demand in areas of Lake Superior (Mason et al. *in review*), siscowets may be decreasing the production of lean lake trout through exploitation competition. Although sample sizes were low, there was a substantial overlap between coho salmon and lean lake trout, which is similar to previous findings (Conner et al. 1993; Ostazeski et al. 1999). However, stable isotope analysis suggested that Pacific salmon occupy a lower trophic level than native predators (Harvey and Kitchell 2000) suggesting that competition with coho is unlikely to influence lean lake trout. Furthermore, coho

salmon consume substantially less biomass on a lake wide basis than both siscowet and lean lake trout (Ebener 1995).

Conclusions

Rainbow smelt, although declining, remain the largest component and most preferred prey species for both lean and siscowet lake trout. These findings indicate that should both populations continue to increase, exploitation competition may limit the production of lean lake trout. However, there has not been extensive sampling of siscowets in Lake Superior, and the number of samples represented in this analysis was substantially lower than that of lean lake trout. Larger samples of the diet characteristics of Pacific salmon and siscowets are needed to assess the potential dietary overlap and potential impacts on the economically important lean lake trout. These estimates of consumption rates on the efficiency of transfer among trophic levels may be used in bioenergetics models to assess the potential for further lake trout recovery.

Combined, these patterns suggest that lean and siscowet lake trout are influencing prey fish populations and are likely the source of the observed declines in prey fish abundance. Increased demand, in turn, appears to have influenced the diet characteristics and prey selection of each. Predation by the two phenotypes of lake trout may be causing a shift in the planktivore composition, which was previously dominated by exotic planktivores, to one dominated by native planktivores through selective predation. Restoration of native planktivore communities are likely facilitated by restoring native predator populations, which has been observed in other systems (Krueger and Hrabik *in review*). Although coregonine populations have shown a

decrease in recent years, the ability of these species to avoid predation by lake trout may bode well for management objectives focused on the restoration of the native fish community. However, should lake trout populations continue to increase and commercial harvest on coregonines continues, coregonine populations may continue to decline. These findings may serve as a reference for management agencies to set harvest restrictions on coregonines to maintain an adequate supply for the increasing predator populations. Generally, however, our findings suggest that the prey fish community of Lake Superior may be returning to a more natural state and that the recovery has likely been facilitated by selective predation by the increasing predator populations.

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Table 1. Number of lake trout caught <600 mm and >600 mm in each year

	Siscowet		Lean	
year	<600 mm	>600 mm	<600 mm	>600 mm
1986	--	--	101	51
1987	--	--	128	44
1988	--	--	112	46
1989	--	--	72	43
1990	1	--	57	35
1991	3	--	399	123
1992	8	4	449	165
1993	1	2	293	170
1994	4	3	274	160
1995	21	15	572	267
1996	70	2	260	184
1997	13	10	317	154
1998	19	11	186	72
1999	11	2	264	81
2000	74	32	657	277
2001	42	24	159	54
total	267	105	4300	1926

Table 2. Mean diet overlap between predators in Lake Superior between 1986-2001. Abbreviations indicate Lake trout (LT), siscowets (FT), burbot (BB), walleye (WAE), coho, (COS) and northern pike (NOP).

	LT	FT	HAT	BB	WAE	COS	NOP	count
LT	1							16339
FT	0.491636	1						1445
HAT	0.351832	0.619582	1					259
BB	0.277192	0.483837	0.414967	1				101
WAE	0.466979	0.651416	0.30868	0.262154	1			54
COS	0.799337	0.293068	0.206012	0.095945	0.309524	1		12
NOP	0.061389	0.082721	0.048423	0.062376	0.198148	0	1	10

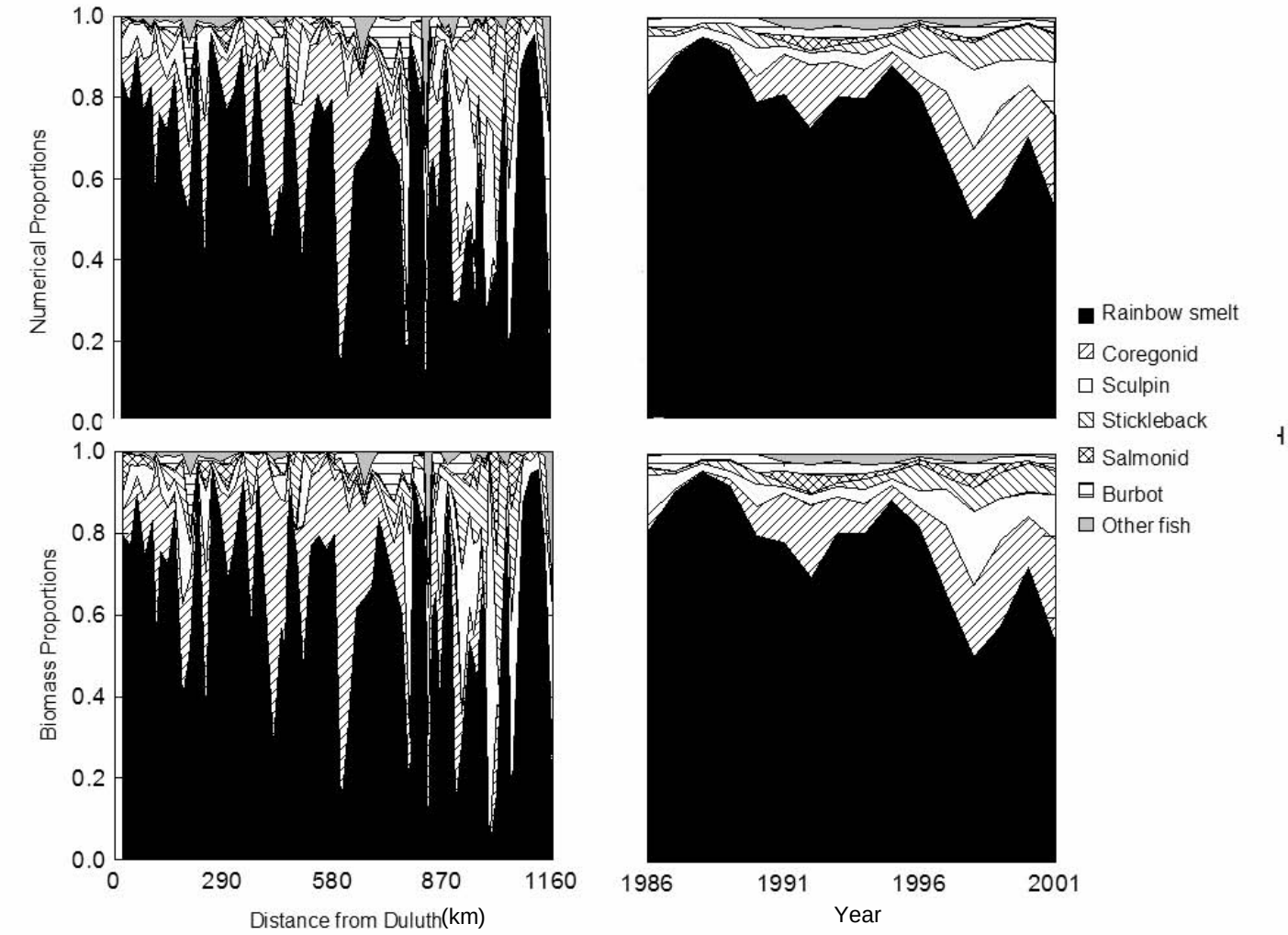

Figure 1. Proportions of prey fish items in predator diets. Panel figures represent: a) numerical proportions across space in Lake Superior, b) lakewide estimates of numerical predator diet proportions from 1986-2001, c) biomass proportions across space in Lake Superior, d) lake wide biomass proportions from 1986-2001.

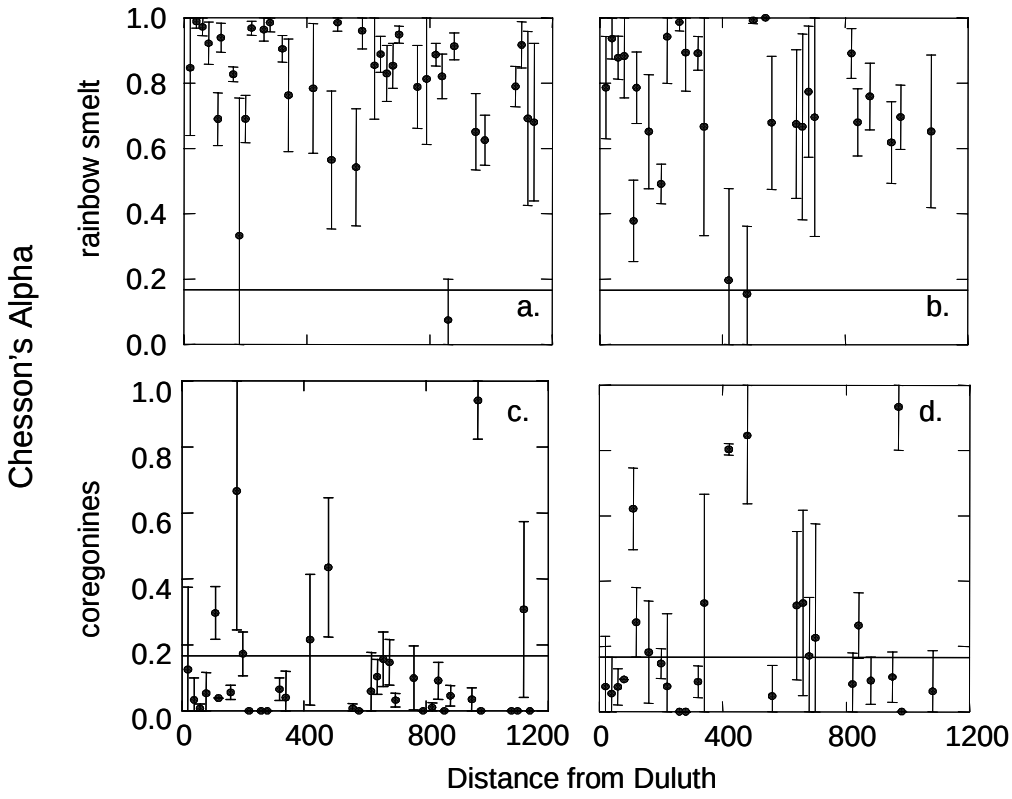

Figure 2. Prey selection averaged over years in different spatial areas of Lake Superior by different size classes of lean lake trout. Panel figuresrepresent prey selection by: a) <600 mm lean lake trout for rainbow smelt b) >600 mm lean lake trout for rainbow smelt c) <600 mm lean lake trout for coregonines and d) >600 mm lean lake trout for coregonines. Error bars represent 95% confidence intervals about the mean.

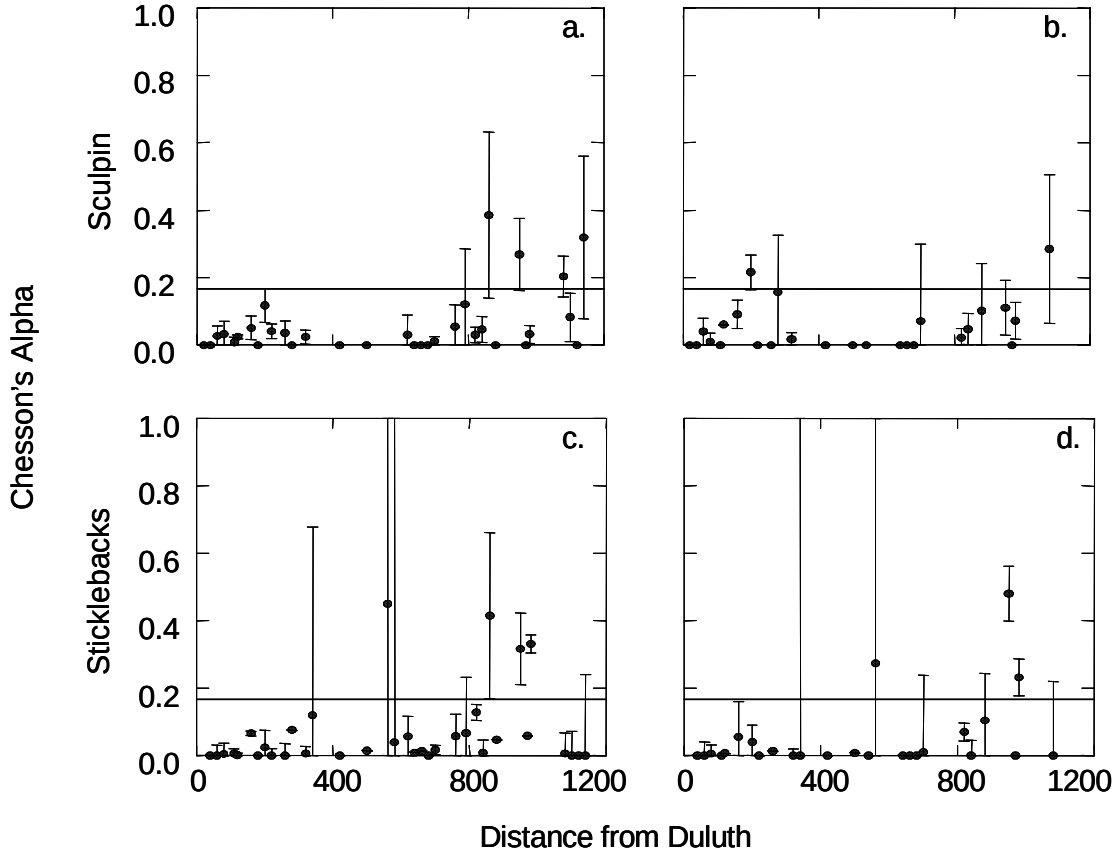

Figure 3. Prey selection averaged over years in different spatial areas of Lake Superior by different size classes of lean lake trout. Panel figures represent prey selection by: a) <600 mm lean lake trout for sculpin b) >600 mm lean lake trout for sculpin c) <600 mm lean lake trout for sticklebacks and d) >600 mm lean lake trout for sticklebacks. Error bars represent 95% confidence intervals about the mean.

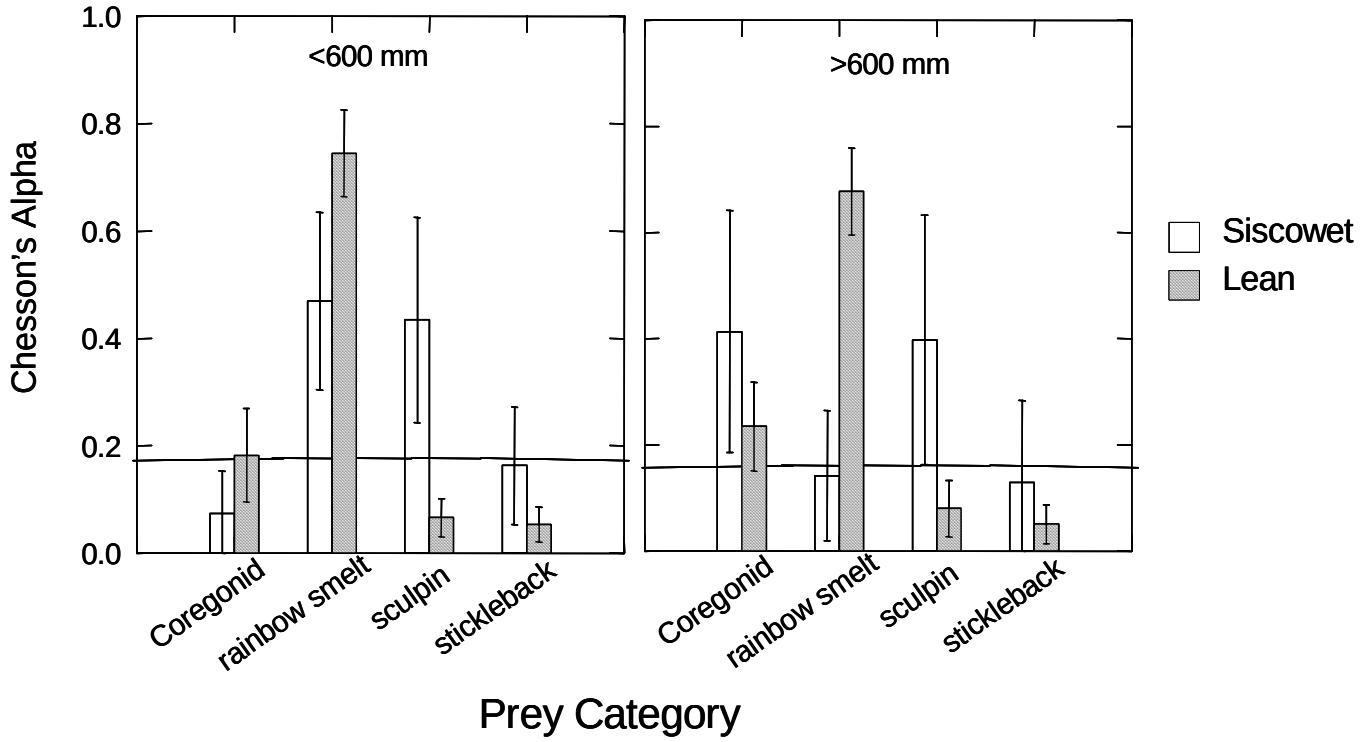

Figure 4. Lake wide estimates of prey selection by lean lake trout and siscowets of different sizes for each prey species. Error bars represent 95% confidence intervals about the mean.

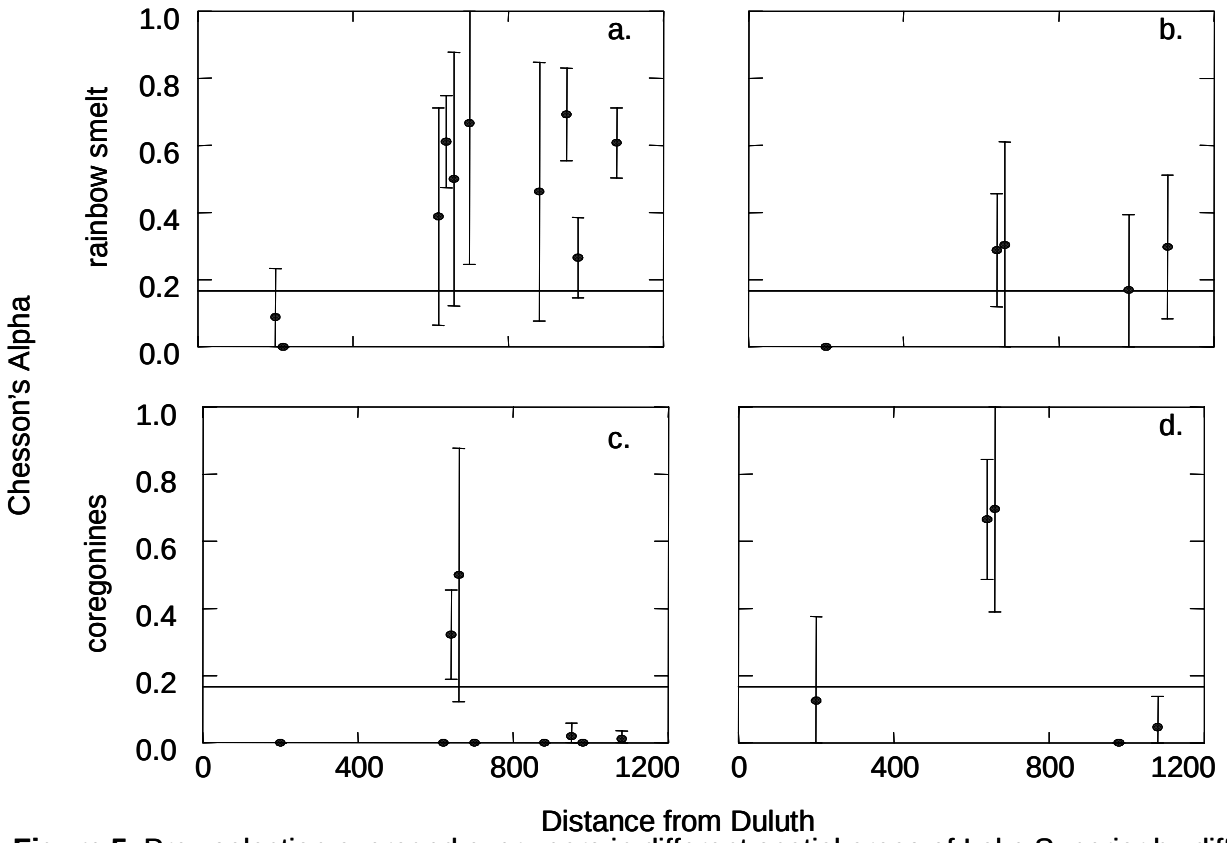

Figure 5. Prey selection averaged over years in different spatial areas of Lake Superior by different size classes of siscowets. Panel figures represent prey selection by: a) <600 mm siscowets for rainbow smelt b) >600 mm siscowets for rainbow smelt c) <600 mm siscowets for coregonines and d) >600 mm siscowets for coregonines. Error bars represent 95% confidence intervals about the mean.

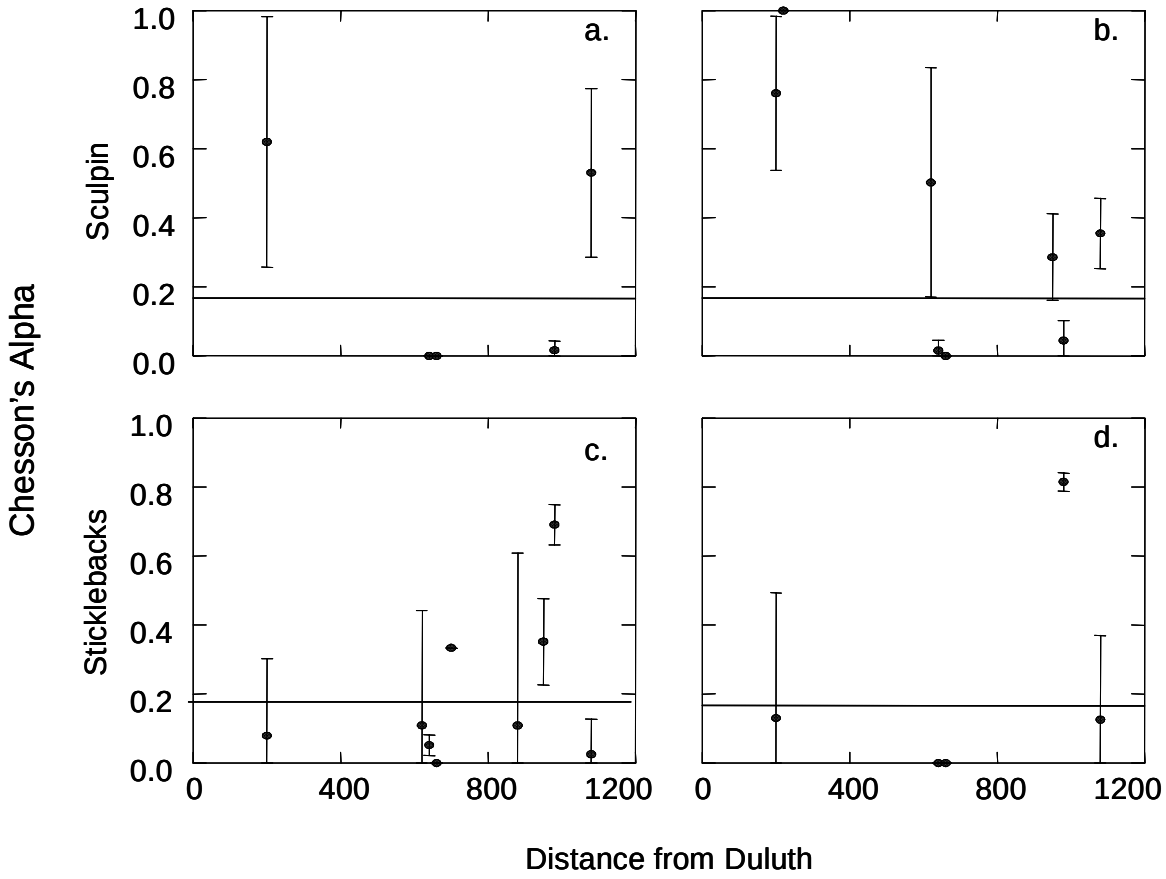

Figure 6. Prey selection averaged over years in different spatial areas of Lake Superior by different size classes of siscowets. Panel figures represent prey selection by: a) <600 mm siscowets for sculpin b) >600 mm siscowets for sculpin c) <600 mm siscowets for sticklebacks and d) >600 mm siscowets for sticklebacks. Error bars represent two 95% confidence intervals about the mean.

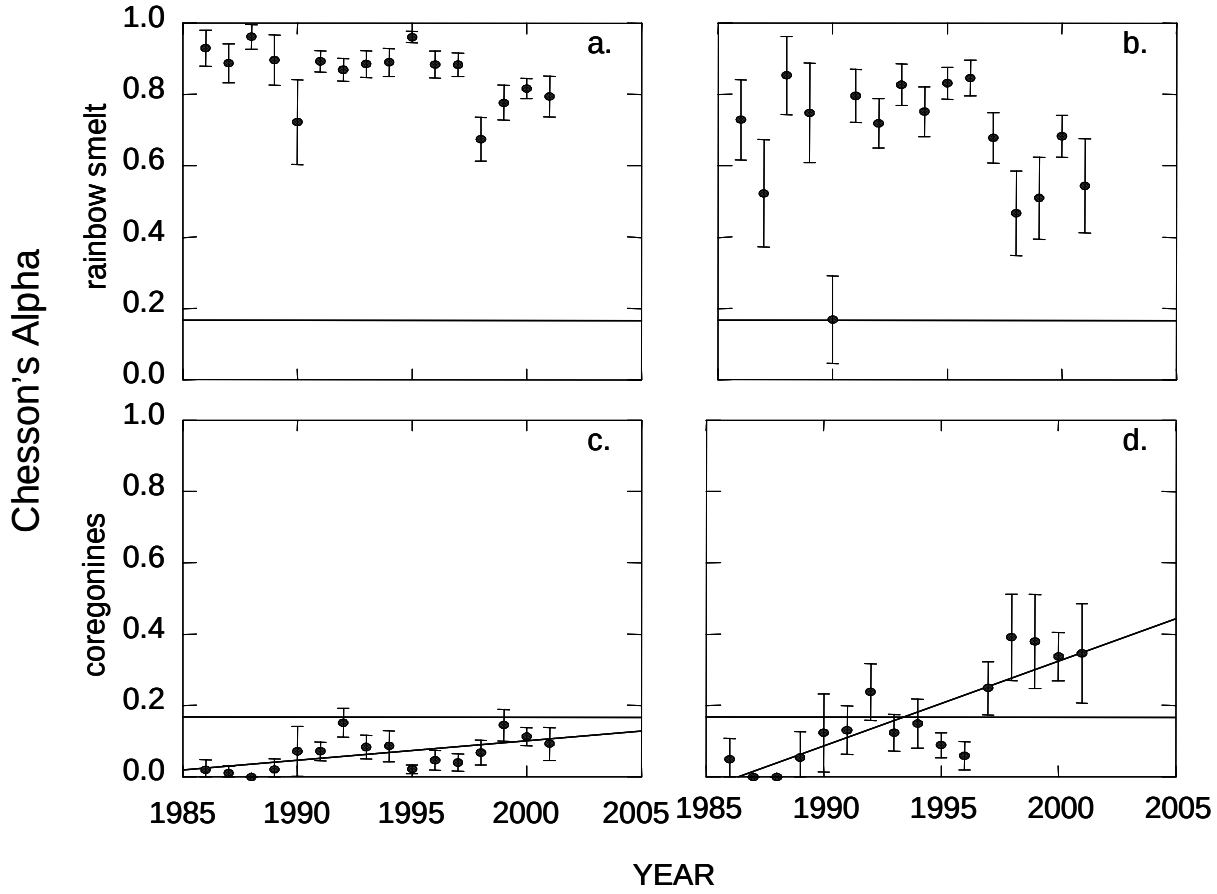

Figure 7. Yearly estimates of prey selection by different size classes of lean lake trout from 1986-2001. Panel figures indicate prey selection by: a) <600 mm lean lake trout for rainbow smelt b) >600 mm lean lake trout for rainbow smelt c) <600 mm lean lake trout for coregonines and d) >600 mm lean lake trout for coregonines. Error bars represent 95% confidence intervals about the mean.

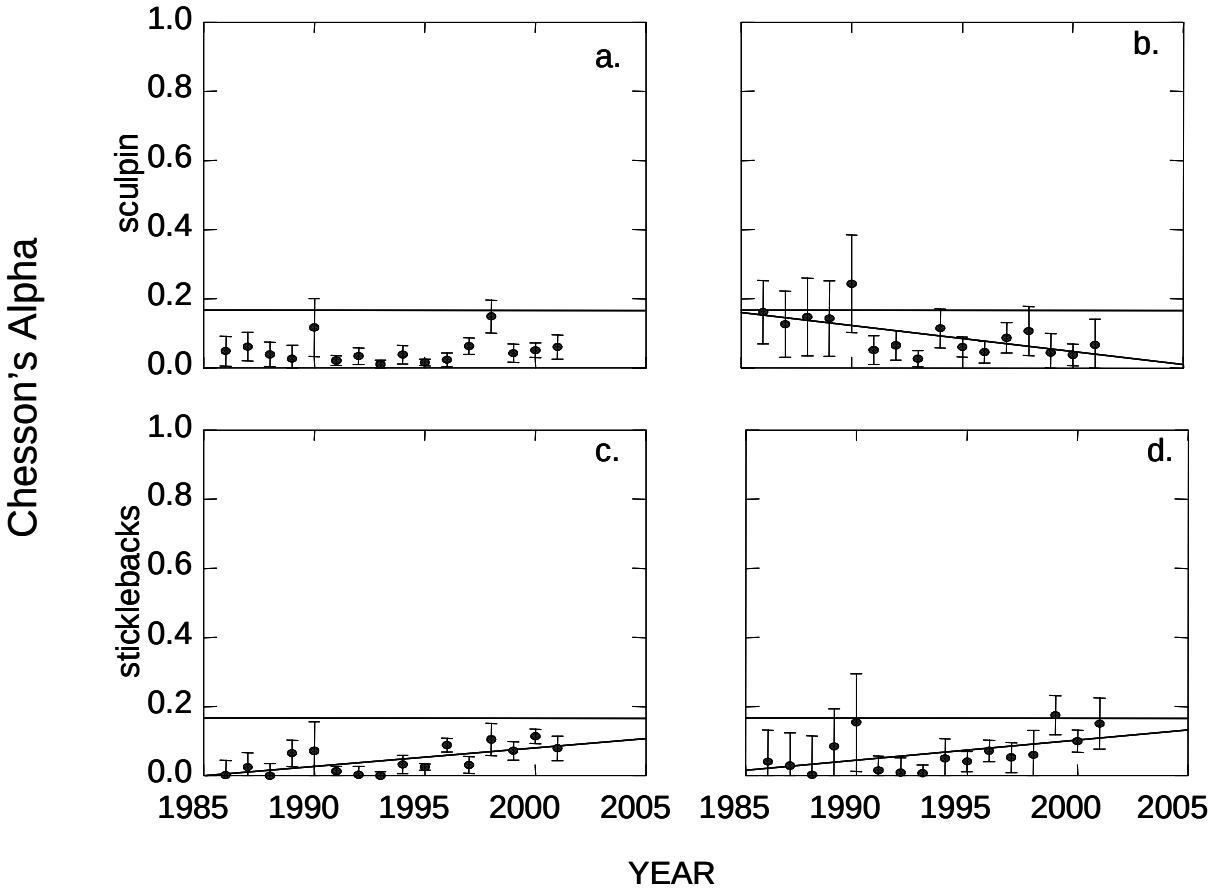

Figure 8. Yearly estimates of prey selection by different size classes of lean lake trout from 1986-2001. Panel figures indicate prey selection by: a) <600 mm lean lake trout for sculpin b) >600 mm lean lake trout for sculpin c) <600 mm lean lake trout for stickleback and d) >600 mm lean lake trout for stickleback. Error bars represent 95% confidence intervals about the mean.

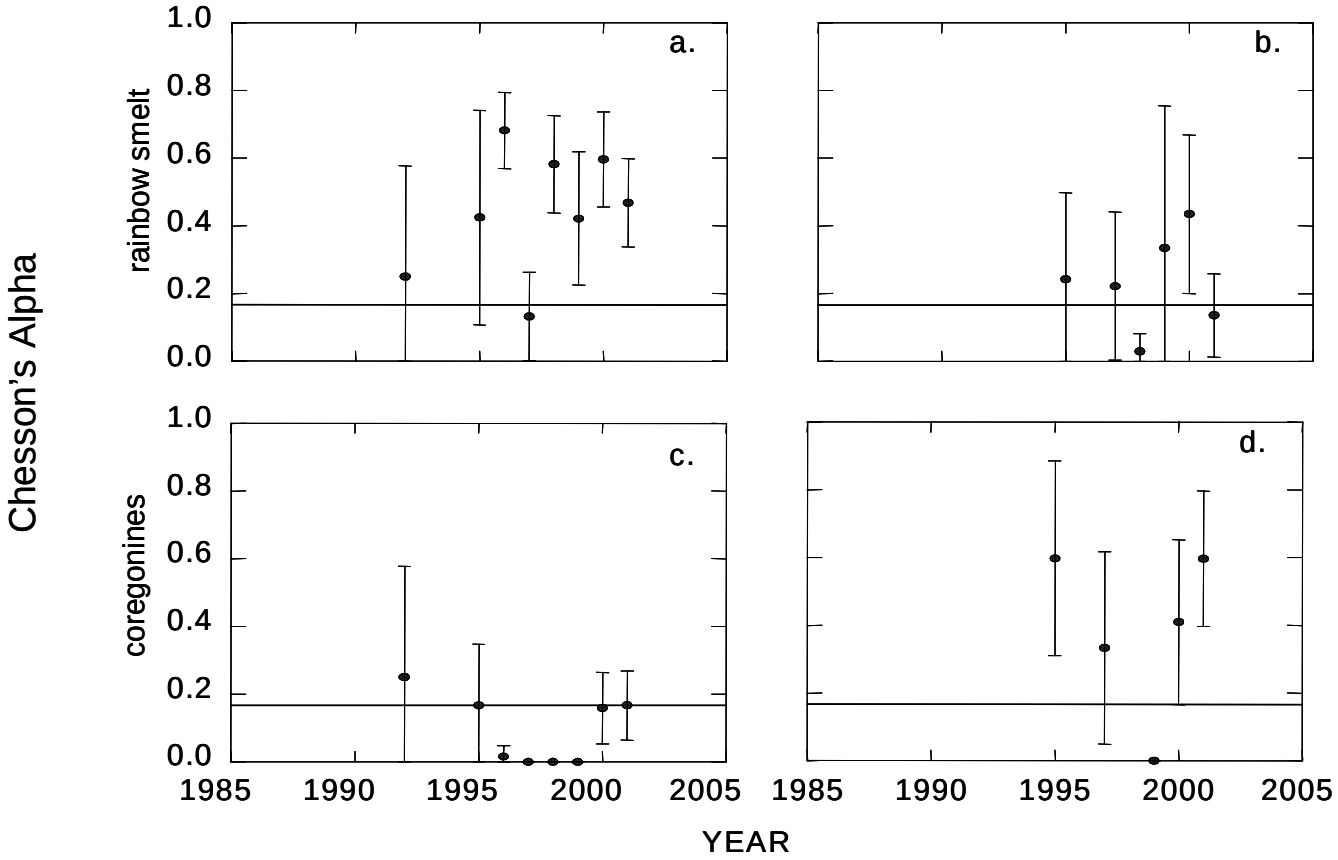

Figure 9. Yearly estimates of prey selection by different size classes of siscowet from 1986-2001. Panel figures indicate prey selection by: a) <600 mm siscowet for rainbow smelt b) >600 mm siscowet for rainbow smelt c) <600 mm siscowet for coregonines and d) >600 mm siscowet for coregonines. Error bars represent 95% confidence intervals about the mean.

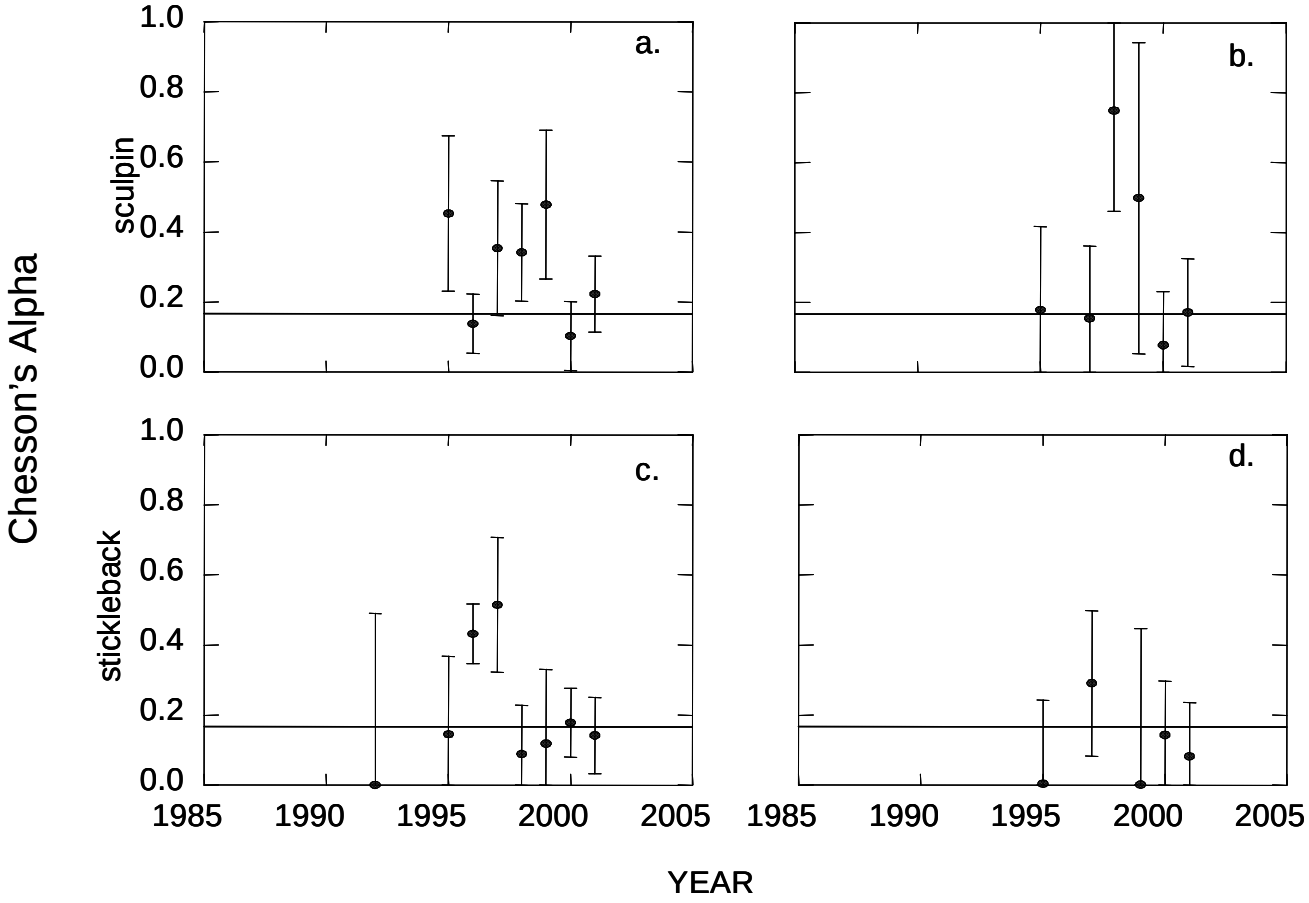

Figure 10. Yearly estimates of prey selection by different size classes of siscowet from 1986-2001. Panel figures indicate prey selection by: a) <600 mm siscowet for sculpin b) >600 mm siscowet for sculpin c) <600 mm siscowet for stickelback and d) >600 mm siscowet for stickleback. Error bars represent 95% confidence intervals about the mean.

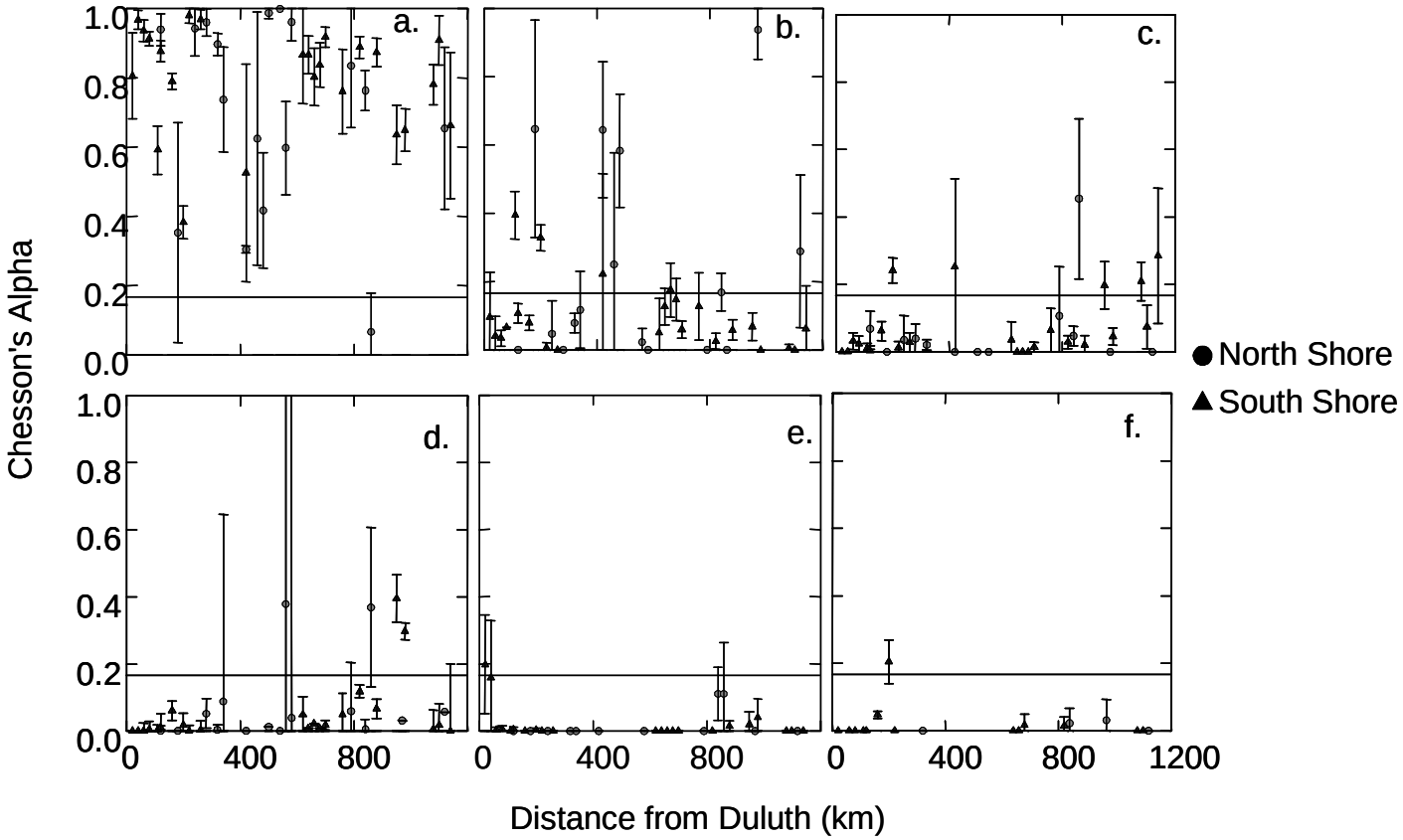

Figure 11. Estimates of prey selection by lean lake trout of all sizes averaged across all years for rainbow smelt, b) coregonines, c) sculpin, d) sticklebacks, e) salmonines and f) burbot in Lake Superior between 1986 and 2001. Error bars indicate variation at the same location among years and represent 95% confidence intervals about the mean for each location.

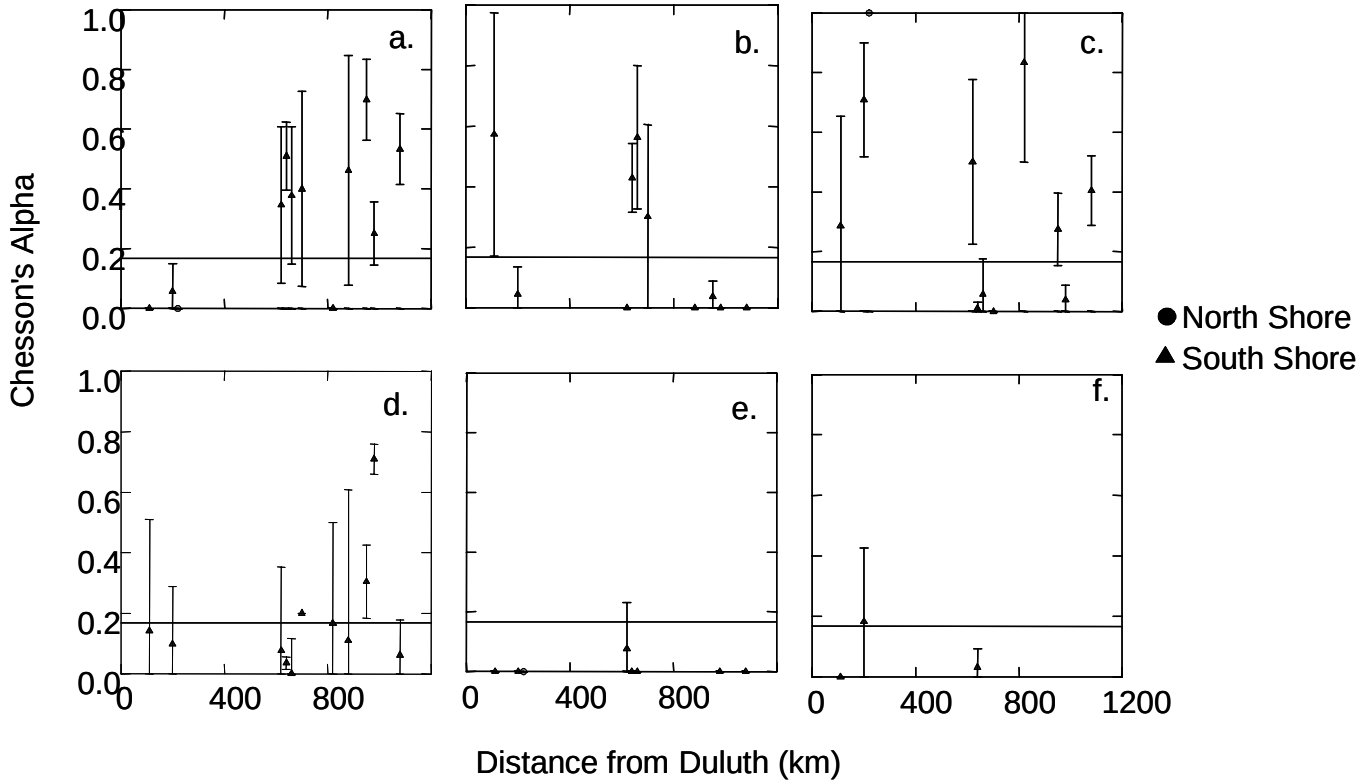

Figure 12. Estimates of prey selection by siscowet of all sizes averaged across all years for a) rainbow smelt, b) coregonines, c) sculpin, d) sticklebacks, e) salmonines and f) burbot in Lake Superior between 1986 and 2001. Error bars indicate variation at the same location among years and represent 95% confidence intervals about the mean for each location.

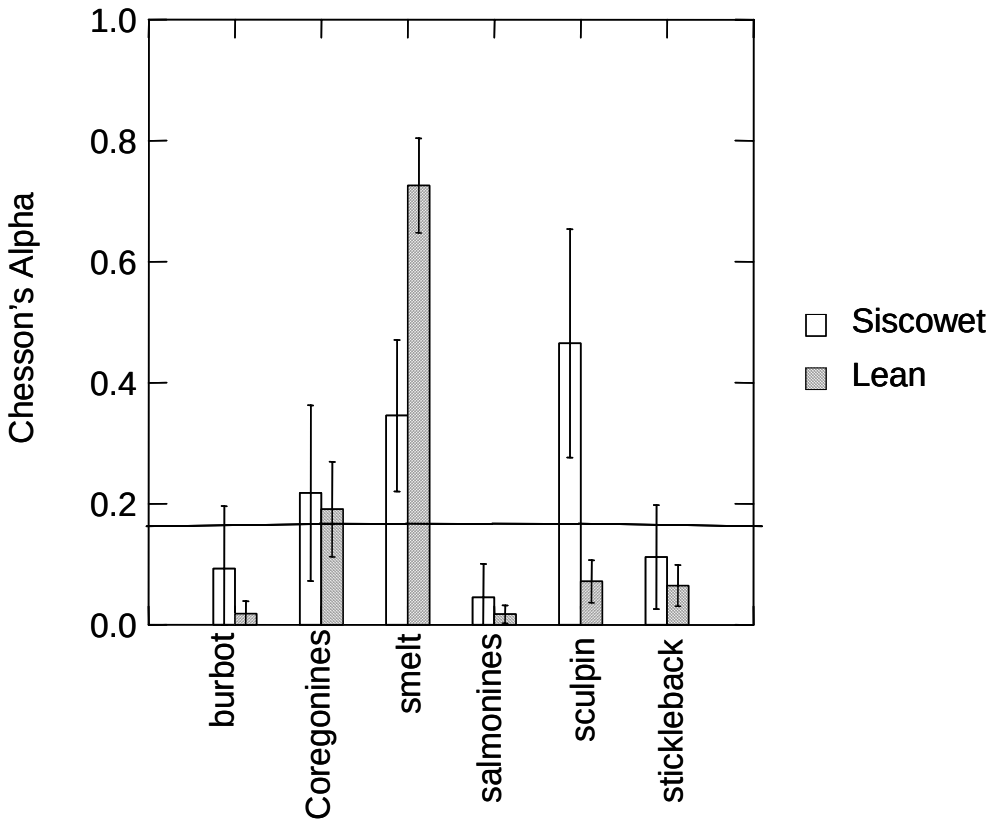

Figure 13. Lake wide estimates of prey selection by lean lake trout and siscowets of all sizes for each prey species. Error bars represent 95% confidence intervals about the mean.

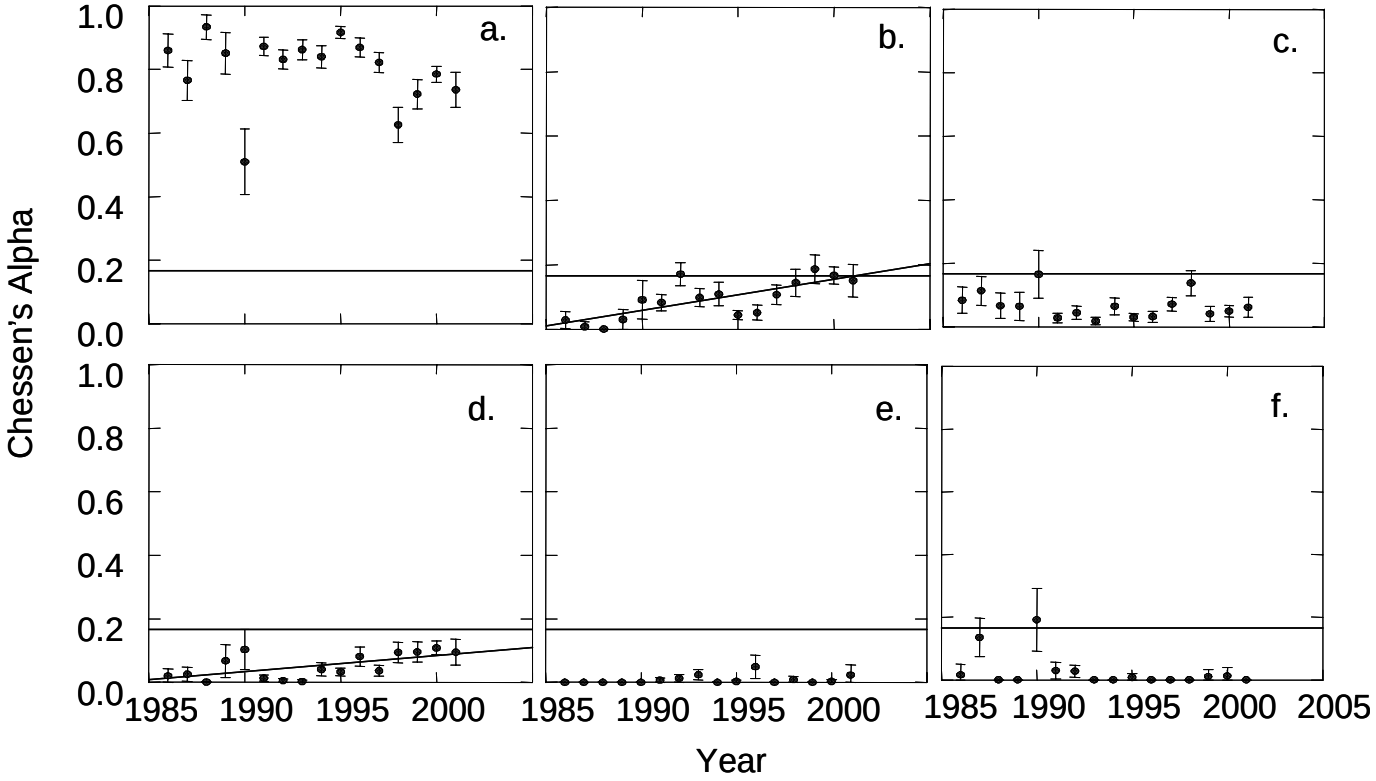

Figure 14. Yearly estimates of prey selection by lean lake trout for a) rainbow smelt, b) coregonines, c) sculpin, d) sticklebacks, e) salmonines and f) burbot averaged across spatial areas of Lake Superior between 1986 and 2001. Error bars represent 95% confidence intervals about the mean.

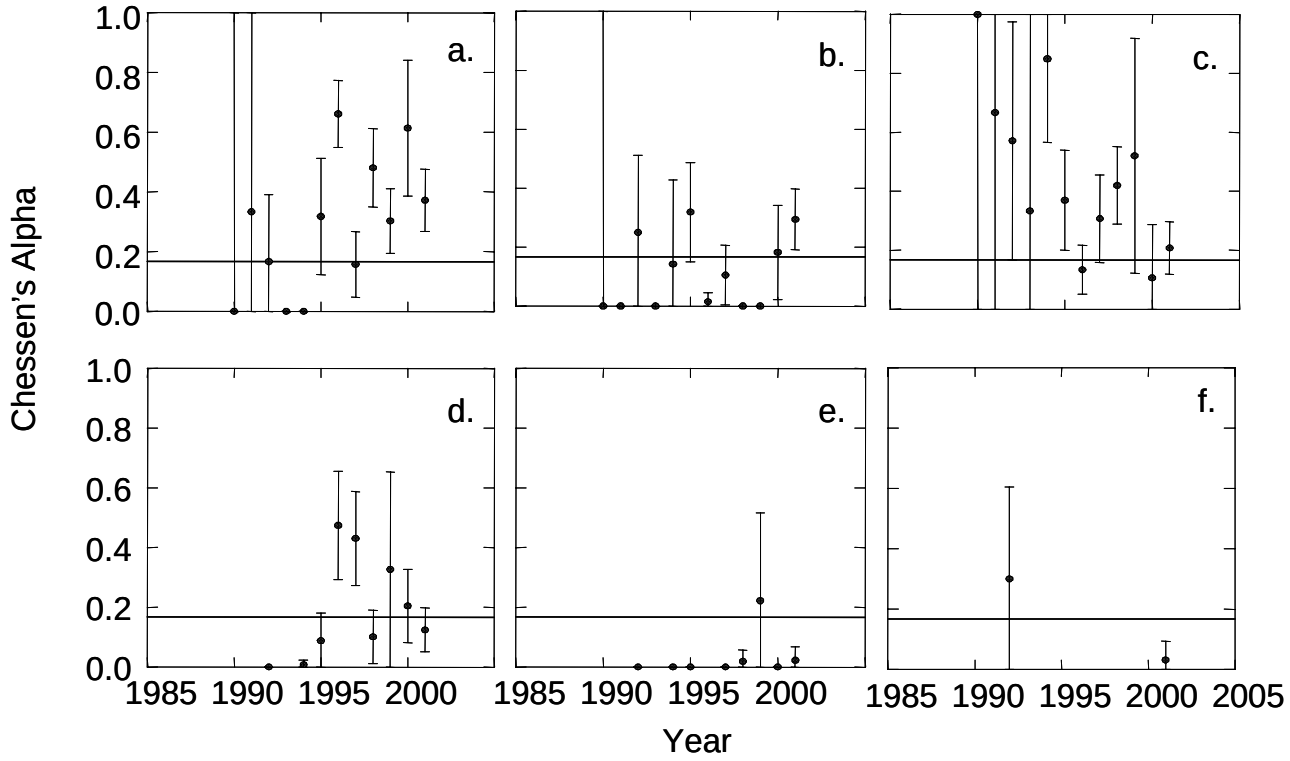

Figure 15. Yearly estimates of prey selection by siscowet for a) rainbow smelt, b) coregonines, c) sculpin, d) sticklebacks, e) salmonines and f) burbot averaged across spatial areas of Lake Superior between 1986 and 2001. Error bars represent 95% confidence intervals about the mean.

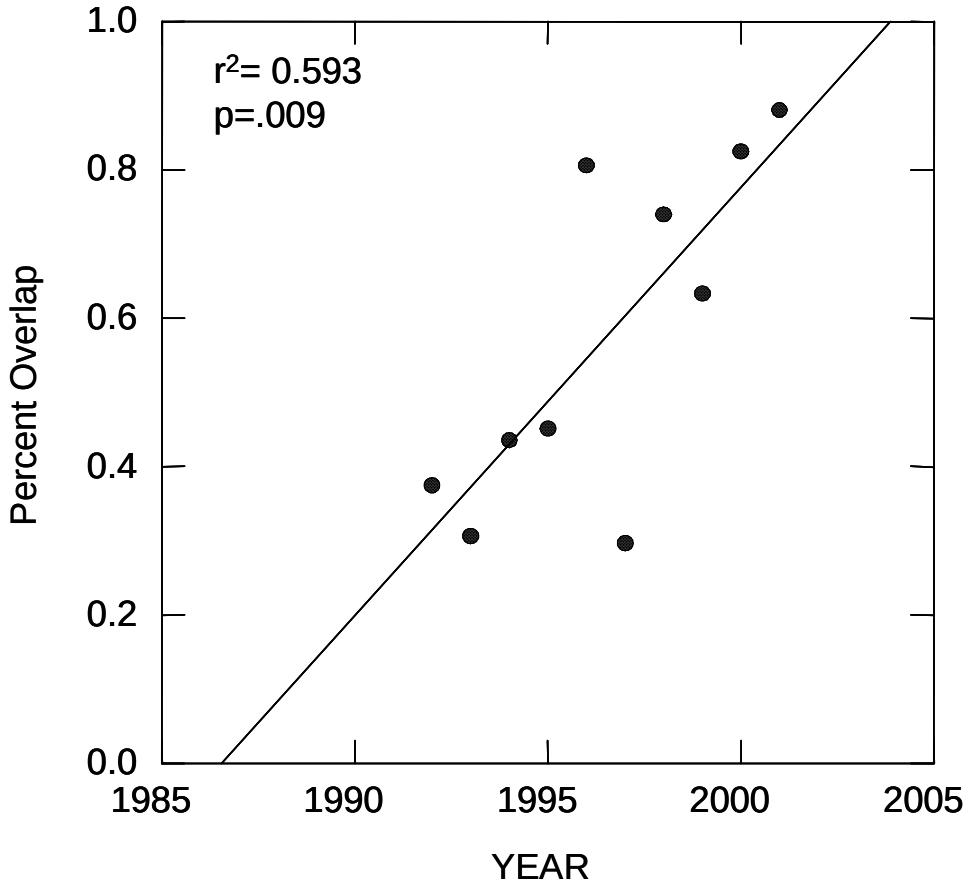

Figure 16. Yearly estimates of dietary overlap between lean lake trout and siscowet lake trout between 1992 and 2001.

Acknowledgements

We thank all of the research staff and technicians from the Minnesota, Wisconsin and Michigan Department of Natural Resources. We acknowledge the significant effort that Steve Schram from the Wisconsin Department of Natural Resources, Shawn Sitar from the Michigan Department of Natural Resources, Bill Mattes from the Great Lakes Indian Fish and Wildlife Commission, Mike Petzold from the Ontario Ministry of Natural Resources, and Scott Koproski from the Bay Mills Indian Community put forth in the transfer of data.