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Bioenergetics Evaluation of the Fish Community in the Western Arm of Lake Superior in 2004

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Abstract.—Lake Superior's fish community continues to change as a result of the recovery of populations of lake trout *Salvelinus namaycush*, the naturalization of introduced salmonids *Oncorhynchus* spp. and *Salmo* spp., declines in the populations of rainbow smelt *Osmerus mordax*, and the fluctuating recruitment of cisco *Coregonus artedii*. This study used bioenergetics modeling of the dominant predator fish in the western arm of Lake Superior in 2004 to provide a comprehensive picture of the relationship between predator demand and prey fish availability. The results, presented for nearshore and offshore areas and three geographically distinct ecoregions, indicate that the western arm is at or near its carrying capacity for predators. Estimated predator demand was about one-half the annual biomass plus production of coregonines but exceeded the biomass plus production of rainbow smelt, possibly because of underestimates of this species in shallow areas and recent shifts in predator diets. Lean lake trout were responsible for most of the consumption of these prey fish, while the deepwater siscowet form ranked second. The commercial harvest of prey fish biomass was trivial compared with the consumption by predator fish. Chinook salmon *Oncorhynchus tshawytscha*, along with other nearshore potamodromous species, played minor roles in total consumption. Chinook salmon are an indicator of forage status, as they have responded to declines in the rainbow smelt biomass with a dramatic diet shift to ciscoes and a decline in weight at age since the early 1990s. Slightly reduced lean lake trout growth and density-dependent survival in some areas also indicate that competition for prey is intense. Because most of the predators in the western arm are wild fish, stocked predators no longer have a great impact on prey populations. Bioenergetics modeling of predator demand combined with hydroacoustic estimates of prey supply can be valuable for managing the fisheries of large lakes, allocating resources to various interest groups, and increasing basic understanding of lake production and community dynamics.

The Lake Superior fish community has been changing for more than a century, but the alterations have been most dramatic since the 1950s, when sea lampreys *Petromyzon marinus* invaded the lake, native populations of lake trout *Salvelinus namaycush* and cisco *Coregonus artedii* declined, introduced rainbow smelt *Osmerus mordax* became the dominant prey species, and several species of Pacific salmon *Oncorhynchus* spp. were introduced to enhance recreational fishing (Kitchell et al. 2000; Bronte et al. 2003; Ebener 2007; Gorman 2007). The recent rehabilitation of lake trout populations in much of Lake Superior, the naturalization of introduced salmonine species, and continued shifts in the abundance of forage species have raised concern that increased predation may

negatively impact the forage base. Heist and Swenson (1983) warned that rainbow smelt production was insufficient to support the commercial fishery and predator demand in the late 1970s, and dramatic declines in rainbow smelt abundance and survival appear to substantiate this prediction. Overstocking predators could result in a catastrophic decline in a primary prey stock (in our case, rainbow smelt), and a rapid switch to other prey species could similarly depress those populations (Stewart and Ibarra 1991).

The concept of limited productive capacity is difficult to convey to the public proponents of each predator species. Angling groups have opposed reductions in stocking and have promoted the simultaneous restoration of both native and nonnative species to historic high levels. This advocacy has only recently begun to falter based on evidence of poor survival of stocked fish and indications of inadequate forage for some species (Corradin 2004; Schreiner et

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al. 2006). Some of these same angler groups oppose the commercial harvest of prey fish, suggesting that food is being taken away from predatory game fish. The emergence of hydroacoustics as an effective tool for quantifying pelagic prey biomass and the application of bioenergetics modeling to predator species has facilitated the comparison of predator demand and prey supply. Thus, we can evaluate the capacity of Lake Superior to support current and potential abundances of wild, naturalized, and hatchery-reared predators, and removal of prey species by commercial harvest.

In a previous study, Negus (1995) applied bioenergetics models to fisheries data from Minnesota waters in 1989 to quantify predator consumption relative to prey supply. The Wisconsin bioenergetics model (Hanson et al. 1997) provided a straightforward format for compiling available data and integrating information to investigate various management or growth scenarios. Negus (1995) used simulation results to compare the relative impacts of predator consumption, commercial harvest, and sportfishing on the forage base. The results were compromised by a paucity of information, but the study nevertheless served to identify areas for future research. For example, the lack of adequate forage base estimates was used to justify hydroacoustic studies of forage populations in the western arm of Lake Superior (Johnson et al. 2004; Mason et al. 2005; Hrabik et al. 2006b).

Other data deficiencies identified by Negus (1995) have also been addressed, including diets of several species (Ray 2004) and thermal distribution of lake trout (Mattes 2004). Stocking of lean lake trout has been reduced or eliminated due to population rehabilitation (Schreiner and Schram 1997; Schreiner et al. 2006), and statistical catch-at-age models have been used to estimate lean lake trout abundance, mortality rates, and size at age (Bence and Ebener 2002; Schreiner et al. 2006; Linton et al. 2007). We have a greatly improved understanding of the ecological role of the fat (or "siscowet") form of lake trout in deepwater regions (Bronte et al. 2003; Hrabik et al. 2006a; Ebener 2007) and the size at age and mortality of potamodromous fishes (lake-dwelling species that spawn in streams; Halpern 2002; Schreiner et al. 2006; Minnesota Department of Natural Resources [MNDNR], unpublished data). Finally, research has revealed the high degree of naturalization of Chinook salmon *Oncorhynchus tshawytscha* (Jones and Schreiner 1997; Peck et al. 1999; Schreiner et al. 2006).

By incorporating recent data into the bioenergetics framework, we are able to revisit the earlier conclusions of Negus (1995), validate the predictive ability of the Wisconsin bioenergetics model (Hanson et al. 1997), and study community dynamics within Lake

Superior. Rand and Stewart (1998) undertook a similar comparison to evaluate shifts in the forage base and predator diets in Lake Ontario. While several other studies have modeled specific aspects of the predator and prey communities in Lake Superior (Ebener 1995; Mason et al. 1998; Kitchell et al. 2000; Harvey et al. 2003), sufficient new data on predator and prey populations have only recently become available to allow an updated study to parallel the earlier one by Negus (1995).

This modeling synthesis was designed to reveal the current status of predator-prey relationships in the western arm of Lake Superior, compare the relative importance of various predator species, and evaluate the current significance of stocking and harvest operations relative to prey fish production and predator consumption. Negus's earlier study (Negus 1995) was limited to primarily stocked fish in Minnesota waters of Lake Superior, but the present study includes both stocked and naturally reproduced predatory fish and encompasses the entire western arm of the lake, which comprises all of Minnesota and Wisconsin waters. Further, these waters include three ecoregions that encompass distinct habitats representative of much larger areas of Lake Superior. The specific objectives of this study were to (1) compile recent data on predator and prey species in the western arm of Lake Superior; (2) estimate predator demand by means of bioenergetics models and compare these estimates with estimates of available coregonine (including cisco, kiyi *C. kiyi*, and bloater *C. hoyi*) and rainbow smelt biomass; (3) compare the relative amounts of prey consumed by predators in nearshore and offshore areas and within three ecoregions of the western arm; (4) compare commercial, sport, and assessment harvests with predator consumption and available biomass of coregonines and rainbow smelt; (5) compare the consumption by stocked predators with that of naturally reproduced predators; (6) compare diets and lifetime consumption by individual fish and populations of each predator species; and (7) compare current estimates of predator consumption with those found in previous bioenergetics studies conducted in western Lake Superior.

Study Area

The western arm of Lake Superior includes both Minnesota and Wisconsin waters, and this region has been divided into three ecoregions based on habitat type (Figure 1; Table 1). The three ecoregions are similar to those used in hydroacoustic studies of the forage base (Johnson et al. 2004; Mason et al. 2005), except that this study included Minnesota and Wisconsin waters in their entirety, and divisions

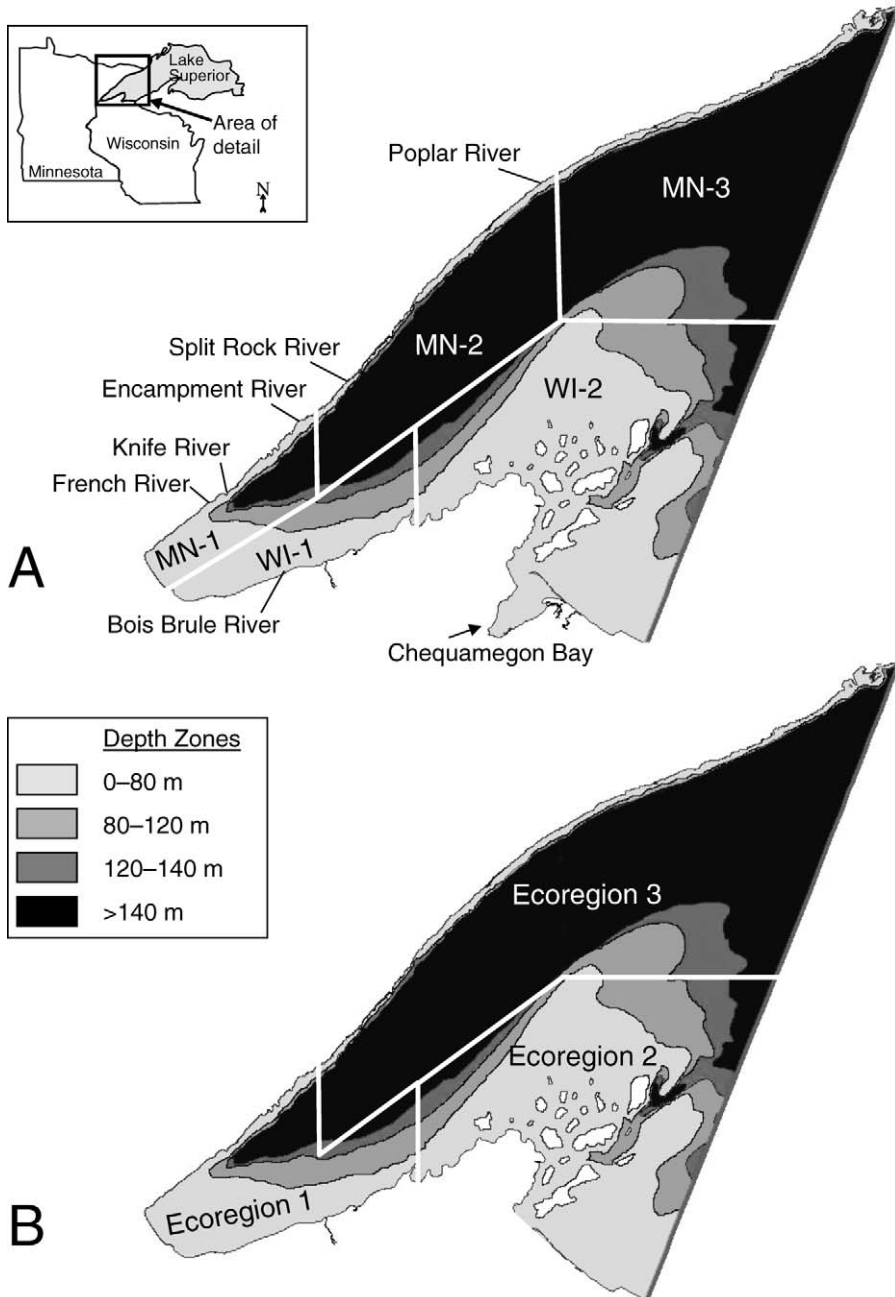


FIGURE 1.—Maps of the western arm of Lake Superior showing (A) Minnesota lake trout management zones MN-1, MN-2, and MN-3 and Wisconsin lake trout management zones WI-1 and WI-2 and (B) ecoregions 1–3 (see text for explanation). Chequamegon Bay was not included in the ecoregions studied. The management zones in Minnesota waters incorporate definitional changes in 2006 that reflect current and historic management practices. The bathymetric contours were supplied by the National Oceanic and Atmospheric Administration in November 2005.

TABLE 1.—Areas (km²) within the western arm of Lake Superior (Figure 1) calculated using ArcView GIS (ESRI 1996) software. Depth contours were taken from a map supplied by NOAA in November 2005. Surface areas within Minnesota management zones reflect 2006 boundary changes.

Management zone or ecoregion	Nearshore (depth <80 m)	Offshore (depth >80 m)	Total area	Percentage of western arm
MN-1	388	368	755	6.5
MN-2	127	1,950	2,077	17.8
MN-3	184	3,592	3,776	32.4
Minnesota total	699	5,910	6,608	56.7
WI-1	532	387	919	7.9
WI-2 ^a	2,662	1,467	4,130	35.4
Wisconsin total	3,194	1,855	5,049	43.3
Ecoregion 1 (western tip of lake)	920	755	1,674	14.4
Ecoregion 2 (Apostle Islands) ^a	2,662	1,467	4,130	35.4
Ecoregion 3 (north shore)	311	5,542	5,853	50.2
Western arm total ^a	3,893	7,764	11,657	100.0

^a Minus Chequamegon Bay and land areas of the Apostle Islands. Chequamegon Bay encompasses about 145 km².

between ecoregions incorporate the borders of lake trout management zones rather than the 100-m contour. Ecoregion 1, at the western tip of the lake, includes the cities of Duluth, Minnesota, and Superior, Wisconsin, and has the highest amount of development. This region has low-to-moderate slope and intermediate water temperatures and fish densities. Ecoregion 2 is the Apostle Islands area (excluding Chequamegon Bay) and includes the largest area of shallow water, warmer temperatures than the other ecoregions, and the highest fish densities. Ecoregion 3, located along Minnesota's steep, rocky north shore, represents the deep open lake and has low temperatures and fish densities. Chequamegon Bay was not included in this study because of its dissimilarity to the rest of the western arm and because that area was the focus of another bioenergetics study (Devine et al. 2005).

Methods

The Wisconsin bioenergetics model (Hanson et al. 1997) was used to model consumption based on the growth of the major predator species in the western arm of Lake Superior. The year 2004 was modeled, including extant year-classes of all major predators, both stocked and naturally reproduced. Predators included native species (lake trout [both the lean and siscowet forms], burbot *Lota lota*, and walleye *Sander vitreus*) and nonnative species (Chinook salmon, coho salmon *Oncorhynchus kisutch*, two migratory strains of rainbow trout *Oncorhynchus mykiss* [the naturalized steelhead strain and the Kamloops hatchery strain stocked in Minnesota], and brown trout *Salmo trutta*). The 80-m contour was used to distinguish nearshore and offshore communities (Harvey et al. 2003).

The model parameters for most predators came from Fish Bioenergetics 3.0 (Hanson et al. 1997). Additional parameters for lean lake trout and siscowets (Johnson

et al. 1999), brown trout (Hayes et al. 2000; Dieterman et al. 2004), and burbot (Rudstam et al. 1995; Johnson et al. 1999) were also used. The required inputs to the model included the abundance at age, mortality rate, weight at age, age of maturity, spawning date, average weight lost during spawning, diet, prey energy density, and temperature occupied for each predator species in each ecoregion.

We modeled only the time that each species spent in Lake Superior, omitting stream-dwelling periods for potamodromous species. For most species, the first simulation day was 1 June, and the final day was 31 May. Most migratory species enter the lake as smolts or are stocked about 1 June, and thus their predatory impact begins at that time. Age-0 lake trout simulations began on 1 July to correspond to the approximate start of exogenous feeding (Bronte et al. 1995; Hudson et al. 1995). Chinook salmon and coho salmon stop eating before fall spawning and die after spawning, so simulations ended on 15 September for age-5 Chinook salmon and 15 October for age-2 coho salmon.

The total consumption of coregonines and rainbow smelt by all predators was compared with the availability (i.e., the standing stock biomass estimated from summer hydroacoustic surveys, plus annual production derived from published production-to-biomass [*P:B*] ratios) of these prey categories in the western arm as a whole, in nearshore and offshore areas of the western arm, and in the three ecoregions. Consumption of prey fish by predators was also compared with the commercial, sport, and assessment harvests (i.e., fish captured in gill nets set by agency personnel and licensed netters to monitor prey populations). The lifetime levels of consumption of coregonines and rainbow smelt by individual predators and by populations of predators were compared to determine which species had the greatest impact on

these forage fish. Similar comparisons were made for total prey consumption by individuals and by populations of predators.

Detailed tables of model input data and data source descriptions are provided in Negus et al. (2007); general information is provided below.

Predator population abundance.—Predators in the western arm of Lake Superior in 2004 (Table 2) included naturally reproduced and stocked fish of each species. Most lean lake trout in Lake Superior are naturally reproduced, although some continue to be stocked as yearlings. The abundances of both populations were estimated with statistical catch-at-age models developed for three Minnesota lake trout management zones (MN-1, MN-2, and MN-3) and Wisconsin lake trout management zone WI-2 (Figure 1; Bence and Ebener 2002; Linton et al. 2007; M. Drake, MNDNR, personal communication). The abundances in Wisconsin lake trout management zone WI-1 were calculated using the densities in MN-1. The abundances of siscowets were estimated based on the ratios of siscowets to lean lake trout caught in assessment nets set in four depth zones (<73, 73–110, 110–146, and >146 m) in each of three locations (the deepest portion of MN-1, WI-1, and WI-2).

Estimates of potamodromous predator populations were based on annual harvests as determined by creel surveys and the numbers returning to fish traps in Minnesota's French and Knife rivers; Wisconsin's Brule, Flag, Cranberry, Sioux, and Onion rivers; and Wisconsin's North Fish, Whittlesey, and Pikes creeks (MNDNR and Wisconsin Department of Natural Resources [WIDNR], unpublished file data). Percent survival at each age was applied to the numbers stocked to determine the numbers at age within each management zone, and these estimates were expanded to include wild fish based on the percentage of stocked fish (identified by fin clips) in the total population (Negus et al. 2007). Population estimates within each management zone were combined to represent appropriate ecoregions (Figure 1).

Chinook salmon are stocked as age-0 fingerlings in May and June. They smolt and migrate to the open lake within a few days or weeks and live in Lake Superior for 3 to 5 years before returning to streams to spawn and die in September and October. However, nearly 95% of Chinook salmon in Minnesota waters are now wild fish (Schreiner et al. 2006), and at least 76% of those in management zone WI-2 are also wild (Peck et al. 1999; Ebener 2007). Coho salmon have become naturalized in Lake Superior and are no longer stocked in the western arm. They spend 16–18 months in streams, smolt and migrate to Lake Superior in spring,

and spend 18–20 months in the lake before returning to spawn and die in November. Populations of potamodromous rainbow trout in the western arm include naturalized steelhead that reproduce in the wild and are supplemented by fry, fingerling, and yearling stocking, and the Kamloops hatchery strain that is stocked as fin-clipped yearlings in Minnesota waters. Simulations of unclipped rainbow trout began with age-2 fish because most steelhead that survive to adulthood smolt at this age. Brown trout are stocked in Wisconsin waters, but survival of the stocked fish is very low, and at least 95% of the brown trout in the western arm are wild fish.

Burbot abundance was estimated at 100,000 in WI-2 (Schram et al. 2006) and expanded to 200,000 fish age 1 and older in the western arm. Numbers in each ecoregion were estimated by applying equal densities per unit of surface area (including nearshore and offshore waters). The primary stock of walleyes in the western arm spawns in the St. Louis River estuary, and population estimates were made in 2002 (Negus et al. 2007; WIDNR, unpublished data).

Mortality rates.—Mortality rates for lean lake trout (Table 2) were derived from statistical catch-at-age models developed for Minnesota waters and the Apostle Islands region of Wisconsin (Linton et al. 2007; M. Drake, personal communication). Mortality rates for siscowets were assumed to equal the natural mortality plus sea lamprey mortality rates in the lean lake trout model. Mortality rates for Chinook salmon, coho salmon, rainbow trout, brown trout, and walleyes were calculated from catch curves derived from creel census and trap return data (Negus et al. 2007). Burbot mortality was estimated by Schram et al. (2006).

Weights at age.—The weights at age of most predators (Table 2) came from unpublished MNDNR and WIDNR data (Negus et al. 2007); those for burbot came from Schram (1983) and Schram et al. (2006) and those for walleyes from Mayo et al. (1998).

Age of maturity, spawning date, and weight lost during spawning.—Spawning data are summarized in Table 3. This information represents an average for each species, taking into account both genders and variation in rates of development. Because Chinook salmon and coho salmon die after spawning, spawning weight loss is not included in the models of these species.

Predator diets and prey energy densities.—Most diet information came from the MNDNR Lake Superior Fisheries office (unpublished data) and Ray (2004) (Figure 2; see also Negus et al. 2007). All predator diet files were based primarily on data collected during the spring and summer and were modified for fall and winter to reflect seasonal

TABLE 2.—Mean weight (*W*; g) at age, abundance (*N*), and annual mortality (*A*) of predator species modeled in the western arm of Lake Superior in 2004. The mortalities listed for each species reflect the values for ecoregion 1. Predator abundances and mortalities in each ecoregion are available in Negus et al. (2007). For unclipped steelhead, weight at age varied by ecoregion (*W1*, *W2*, *W3* for ecoregions 1, 2, and 3 respectively).

Age (years)	Lean lake trout (wild) ^a			Lean lake trout (stocked) ^a			Siscowet			Chinook salmon			Coho salmon		
	<i>W</i>	<i>N</i>	<i>A</i>	<i>W</i>	<i>N</i> ^b	<i>A</i>	<i>W</i>	<i>N</i>	<i>A</i>	<i>W</i>	<i>N</i>	<i>A</i>	<i>W</i>	<i>N</i>	<i>A</i>
0	0.02	6,295,476	0.897				0.02	20,432,275	0.898	6	423,259	0.995			
1	41	644,046	0.151	41	27,226	0.148	5	1,729,044	0.150	300	24,469	0.380	35	114,011	0.850
2	105	546,938	0.151	105	22,461	0.148	45	1,469,466	0.150	1,240	33,237	0.300	620	22,802	0.900
3	170	464,475	0.157	170	21,887	0.149	59	1,248,866	0.150	2,550	24,540	0.480	1,307		
4	362	391,674	0.158	362	20,883	0.153	125	1,061,538	0.155	4,100	10,671	0.800			
5	663	305,393	0.167	663	5,507	0.168	200	899,549	0.163	5,500	3,020	0.990			
6	910	338,428	0.189	910	4,075	0.185	250	755,499	0.172	5,500					
7	1,234	285,522	0.209	1,234	2,957	0.204	290	627,957	0.169						
8	1,600	202,370	0.229	1,600	17,017	0.229	350	519,632	0.186						
9	1,836	151,682	0.233	1,836	14,931	0.251	430	423,684	0.197						
10	2,100	144,276	0.238	2,100	13,987	0.260	500	340,599	0.203						
11	2,400	112,971	0.247	2,400	7,026	0.302	600	272,059	0.212						
12	2,695	76,382	0.237	2,695	15,162	0.317	700	218,651	0.213						
13	2,960	47,265	0.243	2,960	4,322	0.285	800	173,106	0.218						
14	3,213	30,794	0.248	3,213	4,231	0.286	950	136,475	0.221						
15	3,390	22,202	0.254	3,390	3,487	0.290	1,070	107,595	0.233						
16	3,543	16,582	0.253	3,543	2,399	0.305	1,210	83,729	0.226						
17	3,620	12,389	0.253	3,620	1,668	0.303	1,355	65,667	0.226						
18	3,732	9,100	0.251	3,732	674	0.277	1,540	51,515	0.226						
19	3,780	6,261	0.250	3,780	363	0.255	1,700	40,424	0.225						
20	3,861	2,850	0.250	3,861	4,802	0.257	1,900	31,730	0.225						
21							2,100	24,913	0.225						
22+							2,300 ^c	86,396	0.224						
Total age 1+															
Western arm		3,811,600			195,065			10,368,095			95,937			136,813	
Ecoregion 1		675,797			149,250			1,220,915			73,476			32,312	
Ecoregion 2		2,689,258			0			5,486,660			8,790			93,571	
Ecoregion 3		446,545			45,815			3,660,521			13,671			10,930	

^a Lean lake trout in ecoregion 2 were modeled with higher weights at age after age 15, reaching 4,400 g at age 22.

^b Numbers of stocked lean lake trout following initial stocking mortality.

^c Siscowets were modeled up to age 25+, reaching 3,270 g at the end of their 25th year.

^d Values apply to all three ecoregions together.

availability of diet items. Rainbow smelt are a favored diet item and are most vulnerable in spring, when they congregate in shallow nearshore areas, but consumption of this species was greatly reduced in other seasons. The different species of coregonines and sculpins (slimy sculpin *Cottus cognatus* and deepwater sculpin *Myoxocephalus thompsoni*) consumed by lean lake trout and siscowets reflect their different habitats and had different energy densities (Table 4). The indigestible portion of the diet was assumed to be 3.3% for fish and 10% for invertebrates (Stewart et al. 1983).

Temperatures.—The temperatures used in the simulations reflected species’ preferences coupled with the available temperature ranges within each ecoregion (Table 5; Negus et al. 2007). For example, thermal distribution recorded using archival tags implanted in lean lake trout in Lake Superior (Mattes 2004) provided monthly mean temperatures for lean lake trout in ecoregion 2, which were modified for ecoregions 1 and 3 based on available temperature ranges. Thermal stratification in nearshore areas of

Lake Superior provided a range of temperatures from June through November, but nearly uniform cold temperatures occurred from about December through May, so all nearshore salmonines were assumed to occupy similar temperatures during the coldest months.

Nearshore and offshore distributions.—The distributions of predator populations were categorized as “nearshore” or “offshore,” the 80-m depth contour being used as the dividing line. Lean lake trout primarily occupy water less than 80 m in depth, and siscowets primarily occupy areas deeper than 80 m (Becker 1983; Bronte et al. 2003), but distributions within ecoregions were modified based on assessment netting done at various depths by MNDNR and WIDNR. Burbot populations were assumed to distribute evenly in nearshore and offshore areas. Potamodromous species were assumed to occupy the nearshore zones for this study, based on their thermal and diet preferences, although they are sometimes found in the upper 80 m of offshore waters. For the purposes of this study,

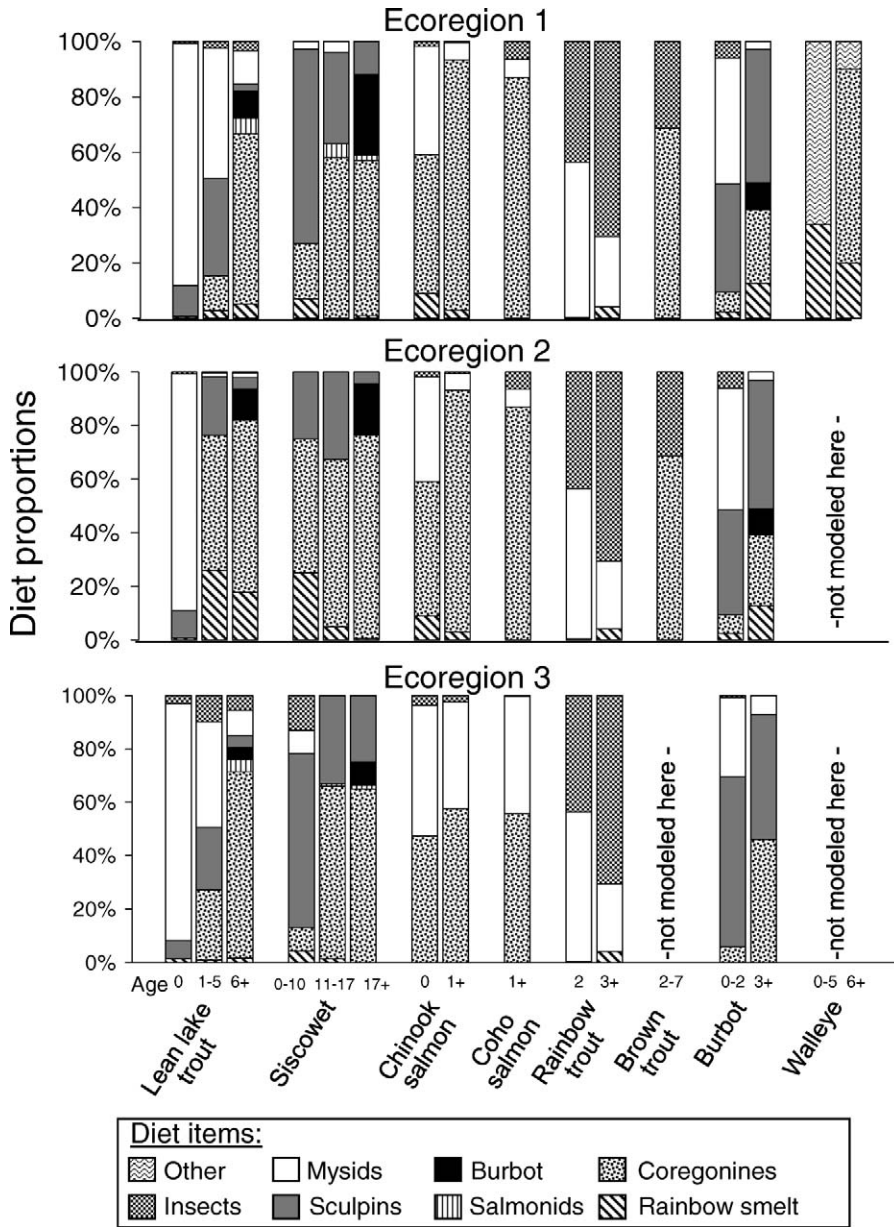


FIGURE 2.—Annual proportions of diet items in bioenergetics simulations of predator fish cohorts. Diets also varied seasonally (Negus et al. 2007). The coregonines consumed by lean lake trout were ciscoes, those consumed by siscowets were kiyis and bloaters, and those consumed by burbot were assumed to be one-half ciscoes and one-half kiyis and bloaters. The sculpins consumed by lean lake trout were slimy sculpins *Cottus cognatus*, those consumed by siscowets were deepwater sculpins *Myoxocephalus thompsonii*, and those consumed by burbot were assumed to be one-half slimy sculpins and one-half deepwater sculpins. The “other” prey category consists of warmwater fishes consumed by walleyes at the mouth the St. Louis River near Duluth, Minnesota.

Results

Prey Consumption versus Availability

Based on bioenergetics modeling, we estimate that predators consumed about 44% of the available

coregonines in the western arm of Lake Superior in 2004 (Figure 3A). They consumed 68% of the available coregonines in nearshore waters (Figure 3B) and about 28% in offshore waters (Figure 3C).

TABLE 4.—Energy densities (J/g of wet weight) of prey species.

Prey species	Energy density	Reference
Burbot	5,135	Johnson et al. (1999)
Coregonines ^a		
Cisco	~6,500	Pangle et al. (2004)
Bloater	9,879	Rottiers and Tucker (1982)
Insects (aquatic and terrestrial)	3,138	Lantry and Stewart (1993)
Other small fish		
Bluegill <i>Lepomis macrochirus</i> ^b	4,186	Kitchell et al. (1974)
Dace <i>Phoxinus</i> spp. ^c	5,006	Hanson et al. (1997)
Yellow perch <i>Perca flavescens</i>	5,700	Adults: Hartman and Margraf (1992)
	2,512	Larvae and juveniles: Post (1990)
Ruffe <i>Gymnocephalus cernuus</i>	4,843	Mayo et al. (1998)
Salmonines, small	5,442	Stewart (1980)
Sculpins ^d		
Slimy sculpin	5,743	Rottiers and Tucker (1982)
Deepwater sculpin	5,421	Rottiers and Tucker (1982)
Rainbow smelt	5,000	Intermediate value from Foltz (1974), Rottiers and Tucker (1982), and Rand et al. (1994) used in this study
Zooplankton <i>Mysis relicta</i>	3,537	Gardner et al. (1985)

^a Values for ciscoes were used in the lean lake trout diets, the values for bloaters in the siscowet diets, and a mean value in the burbot diets.

^b Value used for black crappie *Pomoxis nigromaculatus* in the walleye diet.

^c Value used for spottail shiner *Notropis hudsonius* and emerald shiner *N. atherinoides* in the walleye diet.

^d Values for slimy sculpin were used in the lean lake trout diets, values for deepwater sculpin in the siscowet lake trout diets, and a mean value in the burbot diets.

Estimates of rainbow smelt consumption exceeded estimates of available biomass in both nearshore and offshore waters. Predators consumed about 57% of the available coregonine biomass in ecoregion 1, 70% in ecoregion 2, and 15% in ecoregion 3 (Figure 4). Estimates of rainbow smelt consumption exceeded estimates of available biomass in ecoregions 2 and 3. Coregonine biomass in the western arm was greater

and constituted a larger portion of the prey base than rainbow smelt biomass. These two prey categories made up about 55% of the total prey biomass consumed by all predator species (Table 7; Figure 5).

Relative Consumption by Predator Species

In the western arm, lean lake trout were the primary consumers of rainbow smelt and coregonines, and

TABLE 5.—Water temperatures (°C) used in bioenergetics simulations of predators in three ecoregions of Lake Superior. The preferred temperatures of the species were used when available in the environment.

Month	Lean lake trout			Siscowet	Chinook salmon			Coho salmon			Rainbow trout (steelhead and Kamloops strains)			Brown trout		Burbot ^a			Walleye ^b
	1	2	3		1	2	3	1	2	3	1	2	3	1	2	1	2	3	1
Jan	2.2	2.5	2.8	3.2	2.2	2.6	3.0	2.2	2.6	2.8	2.2	2.6	2.8	2.2	2.6	2.2	2.6	2.8	2.2
Feb	1.5	1.0	2.2	2.7	1.5	1.1	2.5	1.5	1.1	2.2	1.5	1.1	2.2	1.5	1.1	1.5	1.1	2.2	1.5
Mar	1.3	0.4	1.6	2.4	1.3	0.3	2.0	1.3	0.3	2.0	1.3	0.3	2.0	1.3	0.3	1.3	0.3	1.6	1.3
Apr	2.0	1.4	2.0	2.2	2.0	1.4	2.0	2.0	1.4	3.0	2.0	1.4	3.0	2.0	1.4	2.0	1.4	2.0	3.0
May	3.4	3.4	3.0	1.5	3.4	3.4	3.0	3.4	3.4	3.0	3.4	3.4	3.0	3.4	3.4	3.4	3.4	3.0	7.7
Jun	5.4	6.0	3.5	3.0	5.4	6.0	4.0	6.0	6.0	4.0	6.0	6.0	4.0	5.5	6.0	5.4	5.4	3.5	11.5
Jul	8.2	7.9	4.0	3.8	9.5	9.5	5.0	10.0	10.0	5.0	10.0	10.0	5.0	10.0	10.0	8.5	8.5	4.0	13.8
Aug	8.3	8.0	5.5	3.8	11.5	12.0	7.0	12.0	14.0	7.0	12.0	12.0	7.0	12.0	12.0	10.0	10.0	5.5	16.8
Sep	8.2	8.5	6.0	4.0	11.5	12.0	8.0	14.0	15.0	8.5	13.5	13.5	8.5	13.0	13.0	10.0	10.0	6.0	13.1
Oct	7.9	8.5	6.7	4.0	7.9	7.9	8.0	8.0	8.0	7.0	8.0	8.0	7.0	8.0	8.0	7.9	7.9	6.7	8.5
Nov	5.6	6.9	5.5	4.0	5.6	5.6	6.0	6.0	7.1	5.5	6.0	7.1	5.5	6.0	7.1	5.6	5.6	5.5	4.0
Dec	3.8	4.7	3.9	4.0	3.8	3.8	4.0	3.8	4.9	3.9	3.8	4.9	3.9	3.8	4.9	3.8	3.8	3.9	3.8
Mean	4.8	4.9	3.9	3.2	5.5	5.5	4.5	5.9	6.2	4.5	5.8	5.9	4.5	5.7	5.8	5.1	5.0	3.9	7.3

^a Temperatures shown were used for adult burbot. Juveniles were modeled by using 12°C in August and September, 9°C in October, and 7°C in November.

^b Ecoregion 1.

TABLE 6.—Biomass (*B*) and production (*P*) (metric tons) of prey species in the western arm of Lake Superior in 2004. Data for Ecoregions 1 and 3 are averages of hydroacoustic estimates from 2003 to 2005 (Hrabik et al. 2006 and unpublished data). Data for Ecoregion 2 are from nearshore hydroacoustic estimates collected in this region in 2004, along with offshore estimates from contiguous areas in management area MN-3 (Hrabik et al., unpublished data).

Area of Lake Superior	Coregonines		Rainbow smelt	
	<i>B</i>	<i>B</i> + <i>P</i>	<i>B</i>	<i>B</i> + <i>P</i>
Entire western arm				
Ecoregion 1	1,900	2,645	40	115
Ecoregion 2	4,415	6,132	135	391
Ecoregion 3	5,413	7,563	15	43
Minnesota waters	6,258	8,752	32	92
Wisconsin waters	5,471	7,587	157	457
Western arm total	11,729	16,339	189	549
Nearshore areas (<80 m deep)				
Ecoregion 1	1,230	1,700	32	94
Ecoregion 2	2,795	3,864	133	386
Ecoregion 3	556	763	1	2
Minnesota waters	1,075	1,500	14	42
Wisconsin waters	3,507	4,827	152	440
Western arm total	4,582	6,327	166	482
Offshore areas (>80 m deep)				
Ecoregion 1	671	945	7	21
Ecoregion 2	1,620	2,268	2	5
Ecoregion 3	4,857	6,800	14	40
Minnesota waters	5,183	7,252	17	50
Wisconsin waters	1,964	2,761	6	17
Western arm total	7,147	10,013	23	67

siscowets were the second-largest consumers (Table 7; Figure 5). Chinook salmon and walleyes were each responsible for about 4% of the total rainbow smelt plus coregonine consumption. The nonnative predators modeled in this study were responsible for 7% of the total consumption of rainbow smelt plus coregonines. Rainbow trout were the third highest consumers in terms of total prey, although a high percentage of their diet consisted of insects and invertebrates that contain less energy and more indigestible material than do prey fish (Table 7). In all nearshore areas, lean lake trout were the primary predators, and the relative importance of other predator species varied by ecoregion. Based on the assumed distribution of nonnative potamodromous predators, their predatory impact was confined to nearshore waters in this study. In all offshore areas of the western arm, siscowets were the dominant predators followed by lean lake trout; burbot played a relatively minor role (Table 7; Figure 6).

In ecoregion 1, lean lake trout were the primary predators of coregonines, while Chinook salmon, walleyes, and siscowets were roughly equal and of secondary importance. Walleyes were the primary consumers of rainbow smelt (Figure 5). Within ecoregion 2, lean lake trout were the primary predators,

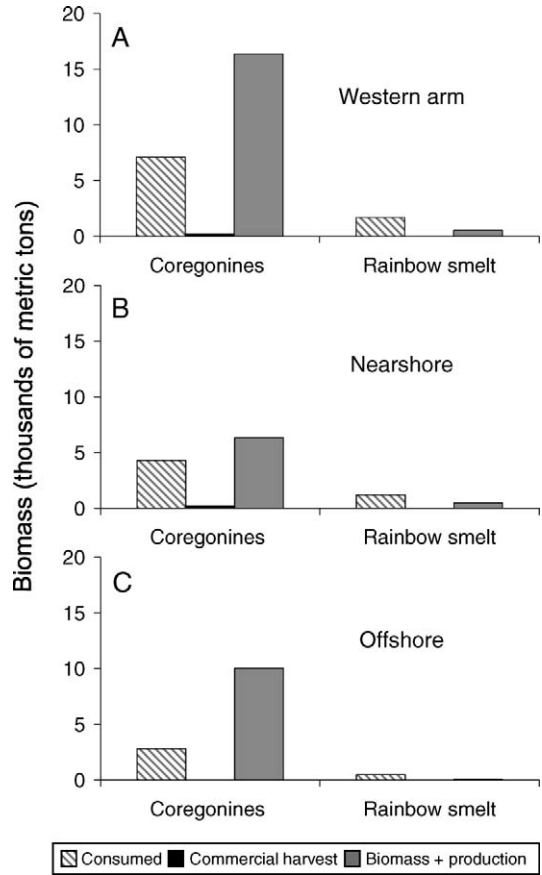


FIGURE 3.—Biomass of coregonines and rainbow smelt consumed by predator fish, harvested commercially, and available (standing stock plus annual production) in 2004 in (A) the western arm of Lake Superior, (B) nearshore areas only (<80 m), and (C) offshore areas only (see Figure 1).

followed by siscowets; other species were responsible for less than 6% of the total consumption. In ecoregion 3, siscowets were the primary predators, followed by lean lake trout.

Commercial, Sport, and Assessment Harvests

Commercial fishers harvested less than 2% of the available coregonine biomass and less than 1% of the rainbow smelt biomass in the western arm (Figure 3A). Our modeling suggests that the loss of coregonine and rainbow smelt biomass from commercial fishing is trivial compared with losses from predator consumption. The commercial harvest was assumed to occur nearshore, where the impact on local coregonines increased slightly to 4% of the available biomass (Figure 3B). The sport and assessment harvests of rainbow smelt and coregonines were also trivial, far

below 0.01% of the total predator consumption or available biomass.

Consumption by Stocked Predators

Stocked fish in the western arm (which include some lean lake trout, Chinook salmon, rainbow trout, brown trout, and walleyes) were responsible for 6% of the total consumption of rainbow smelt and coregonines in 2004 (Table 7). Lean lake trout were the primary predators among stocked fish, and most of the stocked lake trout inhabited Minnesota waters.

Predator Diets and Consumption Rates

The lean lake trout consumed more coregonine biomass than rainbow smelt biomass, but their diverse diet included mysids, sculpins, burbot, and other taxa as well (Figure 6). Siscowets, rainbow trout, and walleyes also had diverse diets and were not as heavily dependent on coregonines or rainbow smelt (Figure 6). In contrast, the Chinook salmon diet lacked diversity and was heavily dependent on coregonines (Figure 6). While the coho salmon diet also lacks diversity during the 18–20-month lake phase of their lives, they spend the first half of their lives in streams consuming primarily insects and invertebrates.

As individuals, Chinook salmon consumed more rainbow smelt and coregonines per unit time than any other predator, but walleyes and lean lake trout consumed a greater total amount if they survived 13 or 16 years, respectively (Figure 7A). Individuals of all the potamodromous species consumed more total prey per unit time at younger ages than the longer-lived species (Figure 7B). However, populations and not individual fish impact prey resources, and the more abundant lean lake trout and siscowets dominate the consumption of either prey aggregate (Table 7).

Discussion

Predator Consumption versus Prey Availability

Bioenergetics estimates of prey consumption by predators reveal that the biomass of coregonines is adequate to support the estimated populations of predator species in the western arm of Lake Superior (Figures 3, 4). However, predation pressure is high, especially in nearshore regions where 50% or more of the available coregonines may be consumed annually. Predation pressure is highest in ecoregions 1 and 2, which contain the greatest amount of nearshore area. Ecoregion 3 had higher coregonine abundances and lower predator biomass density and is dominated by deep offshore water, creating a potential refuge for prey. Hrabik et al. (2006b) demonstrated that large ciscoes (>150 mm) and kiyis and bloaters (>120 mm) were abundant in the offshore waters of ecoregion 3,

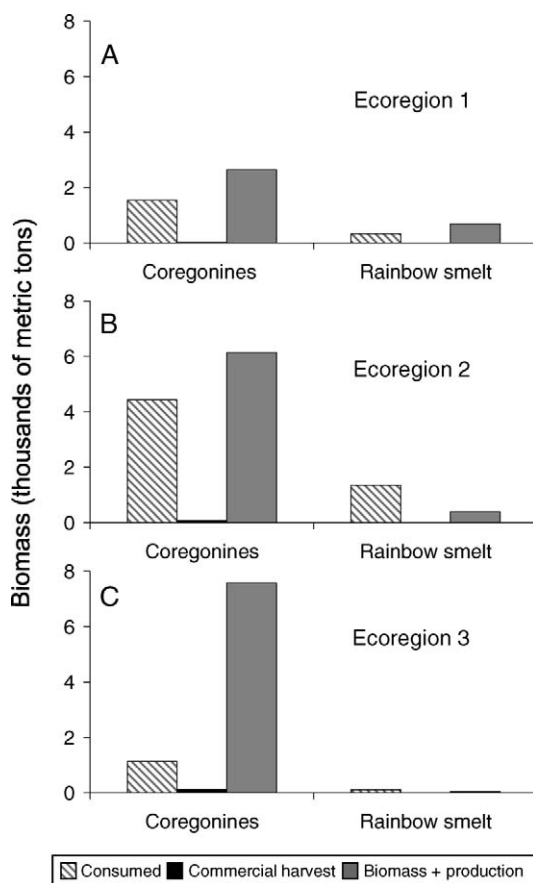


FIGURE 4.—Biomass of coregonines and rainbow smelt consumed by predator fish, harvested commercially, and available (standing stock plus annual production) in 2004 in (A) ecoregion 1, (B) ecoregion 2, and (C) ecoregion 3 in the western arm of Lake Superior (see Figure 1).

suggesting better survival. In contrast, estimates of rainbow smelt consumption exceeded available supplies in ecoregions 2 and 3 (Figure 4), but rainbow smelt population estimates were so low that small variations in simulated predator diet could produce consumption estimates that exceeded availability.

Ciscoes reach a much larger size than rainbow smelt in the western arm (495 mm versus 210 mm; MNDNR assessments, 2006), but their large size may provide only a limited refuge from predation. Diet studies in Minnesota waters have shown that large lake trout will consume coregonines as large as 50% of their total length (MNDNR, unpublished data), and in 2006, ciscoes up to 460 mm total length were found in the stomachs of lean lake trout, although most prey fish consumed were smaller. At about age 10, lean lake trout become large enough to consume spawning-size ciscoes (>305 mm), which dominated total cisco

TABLE 7.—Consumption (metric tons) in 2004 by major predators in the entire western arm of Lake Superior, nearshore areas, and offshore areas (divided at the 80-m contour). The values for rainbow smelt and coregonines are followed by percentages of each item consumed by each predator species. Prey species abbreviations are as follows: RBS = rainbow smelt, COR = coregonines, SAL = salmonines, BUB = burbot, SCU = sculpins, MYS = mysids, and INS = insects.

Species	RBS	COR ^a	SAL	BUB	SCU ^b	MYS	INS	Total by predator	% of total predator consumption
Western Arm totals									
Lean lake trout	1,080 (64)	4,018 (56)	81	520	786	889	128	7,502	47
Siscowet	395 (23)	2,277 (32)	15	87	2,119	200	198	5,290	33
Chinook salmon	11 (1)	381 (5)	0	0	0	54	4	450	3
Coho salmon	0 (0)	132 (2)	0	0	0	13	11	156	1
Rainbow trout	55 (3)	0 (0)	0	0	0	661	1,221	1,938	12
Brown trout	12 (1)	23 (<1)	0	0	0	0	10	45	<1
Burbot	5 (<1)	30 (<1)	0	4	79	40	3	162	1
Walleye	133 (8)	254 (4)	0	0	0	0	0	388	2
Total	1,693 (100)	7,115 (100)	96	611	2,984	1,858	1,575	15,931	100
Stocked fish only	40 (2)	266 (4)	18	29	45	353	515	1,267	8
Nearshore areas of the western arm									
Lean lake trout	897 (75)	3,080 (72)	45	168	278	399	53	4,920	57
Siscowet	86 (7)	413 (10)	1	9	212	20	20	761	9
Chinook salmon	11 (1)	381 (9)	0	0	0	54	4	450	5
Coho salmon	0 (0)	132 (3)	0	0	0	13	11	156	2
Rainbow trout	55 (5)	0 (0)	0	0	0	661	1,221	1,938	22
Brown trout	12 (1)	23 (1)	0	0	0	0	10	45	1
Burbot	3 (<1)	9 (<1)	0	0	7	5	0	25	<1
Walleye	133 (11)	254 (6)	0	0	0	0	0	388	4
Total	1,198 (100)	4,293 (100)	46	178	497	1,152	1,319	8,682	100
Stocked fish only	35 (3)	163 (4)	1	392	483	716	858	2,650	31
Offshore areas of the western arm									
Lean lake trout	183 (37)	938 (33)	36	352	508	490	75	2,582	35
Siscowet	310 (63)	1,863 (66)	15	85	2,065	196	195	4,730	64
Burbot	2 (<1)	21 (1)	0	1	71	36	1	131	2
Total	495 (100)	2,822 (100)	51	438	2,644	722	271	7,443	100
Stocked fish only	5 (1)	102 (4)	4	4	7	36	8	166	2

^a The coregonines consumed by lean lake trout were ciscoes, those consumed by siscowets were kiyis and bloaters, and those consumed by burbot were assumed to include 50% ciscoes and 50% kiyis and bloaters.

^b The sculpins consumed by lean lake trout were slimy sculpins, those consumed by siscowets were deepwater sculpins, and those consumed by burbot were assumed to include 50% of each sculpin species.

biomass in 2003 (86%) and 2004 (68%; Hrabik et al. 2006b). Just 2% of the ciscoes captured in the commercial fishing nets and MNDNR assessment nets in 2006 exceeded the 460 mm length found in lean lake trout stomachs.

Our estimates of the consumption of rainbow smelt exceeded those of supply (standing stock plus production), which is clearly not the case. This discrepancy has five possible explanations: (1) the predator diet information for all seasons was incomplete; (2) predator population estimates were inaccurate; (3) prey population estimates were inaccurate; (4) predators, prey, or both moved between or beyond ecoregion boundaries and between nearshore and offshore areas; and (5) prey production was underestimated owing to inaccurate *P:B* ratios. Each of these explanations will be discussed in more detail below.

Incomplete diet information would overestimate the consumption of one prey type while underestimating that of other prey. The diet information for this study came primarily from samples taken from 1996 to 2001.

While some modifications were made to the 2004 diets based on known rainbow smelt population declines and occasional stomach samples examined by MNDNR, it is probable that we overestimated the rainbow smelt proportions in the diets of lean lake trout, siscowets, rainbow trout, and walleyes in 2004. Diet information for all predator fish during fall is limited and for winter is unavailable. More frequent monitoring of diets of all dominant predators on a seasonal basis will capture shifts in dietary preference resulting from changes in available forage and therefore improve our bioenergetics estimates.

Obtaining accurate estimates of predator abundance and mortality remain one of the greatest challenges for fishery managers. Substantial resources are directed toward obtaining estimates of lean lake trout abundance, and population parameters are under constant revision based on creel data, assessment netting, and improvement to stock assessment models. Absolute abundance of other predators is less well known.

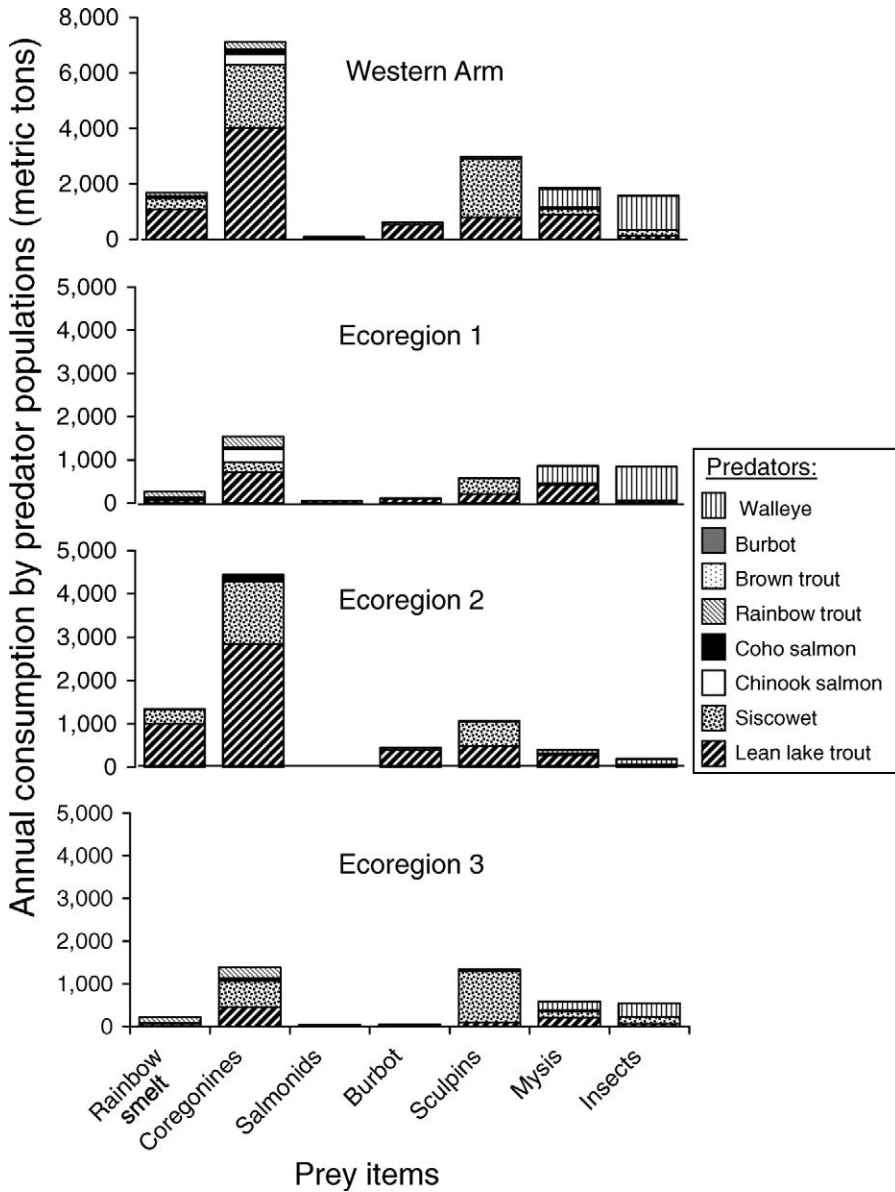


FIGURE 5.—Consumption of prey items by predator populations in 2004 in the entire western arm of Lake Superior and each of three ecoregions. Detailed information on prey consumption in each ecoregion and the nearshore and offshore areas of each ecoregion can be found in Negus et al. (2007).

Continued investment in these analyses for all species will improve future estimates of predator demand.

Spatial and temporal influences can greatly affect hydroacoustic estimates (Yule et al. 2007), and rainbow smelt probably use depths shallower than those surveyed acoustically. Hydroacoustic surveys of prey populations conducted by Yule et al. (2008) in October and November 2006 produced higher coregonine and rainbow smelt density estimates in the western

arm than the surveys conducted from July to September 2003–2005 (Hrabik et al. 2006b) referenced in this study. The higher 2006 densities are the combined result of a large 2003 year-class of ciscoes, slightly increased densities of rainbow smelt in 2006 (Geving 2007), and nearshore concentrations of spawning coregonines in the fall. Use of the 2006 estimates would resolve the rainbow smelt predator demand or prey availability discrepancy and slightly reduce the

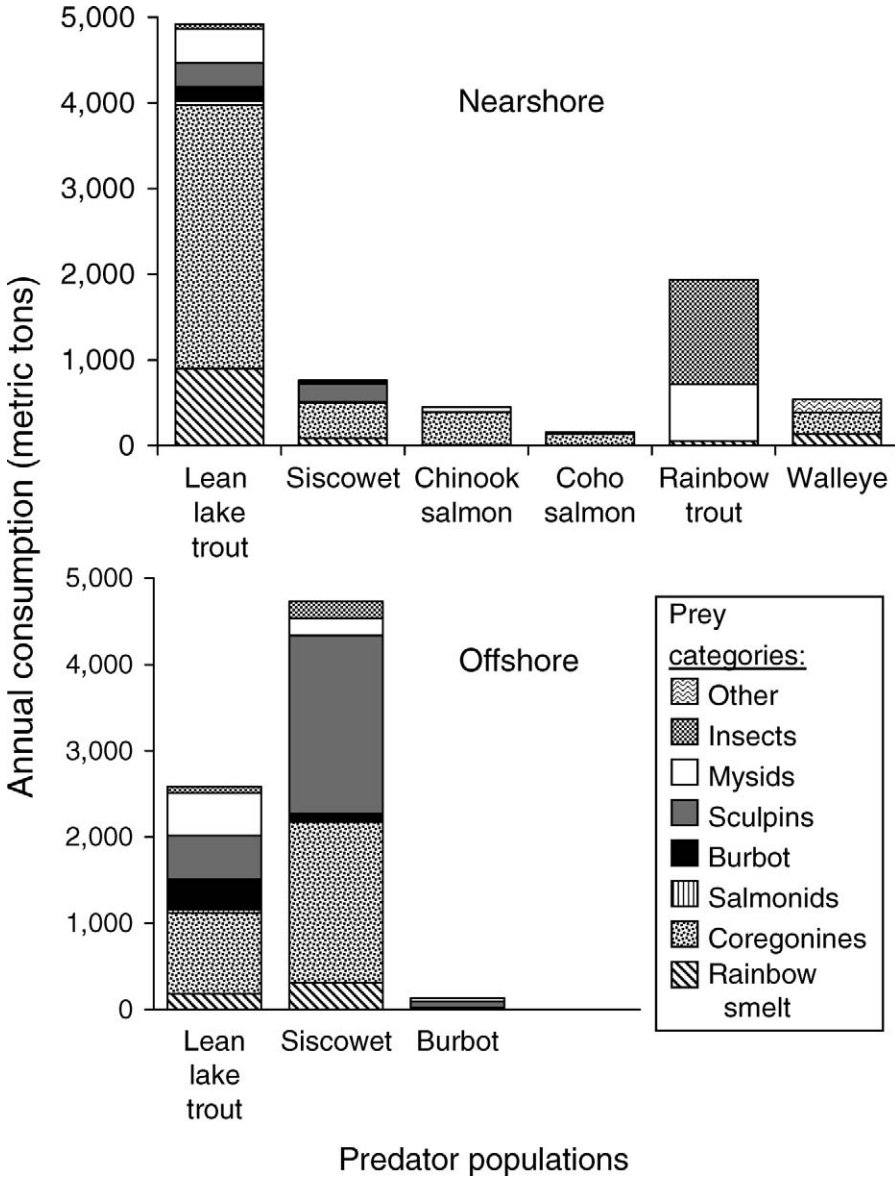


FIGURE 6.—Consumption of prey items by predators in nearshore and offshore areas of the western arm of Lake Superior. The consumption by brown trout (45 metric tons) and burbot (25 metric tons) has not been plotted on the nearshore graph owing to the low values involved.

heavy predation pressure on coregonine populations we observed.

Vertical migration and movement between ecoregion boundaries can occur on a daily basis and for different life stages of predators. Siscowets, for example, generally live in water deeper than 80 m (Becker 1983; Bronte et al. 2003) but are known to forage near the surface or in shallower water (Hrabik et al. 2006a). Stable isotope analyses of lean and siscowet

lake trout in western Lake Superior suggest that these strains feed in similar locations at young ages (Harvey et al. 2003). Chinook salmon stocked in each jurisdiction surrounding Lake Superior have been recaptured in every other jurisdiction (Peck et al. 1999), and rainbow trout are known to stray widely (Negus 2003). Therefore, an improved understanding of the proportional distribution of predators and prey between habitats throughout the year would further

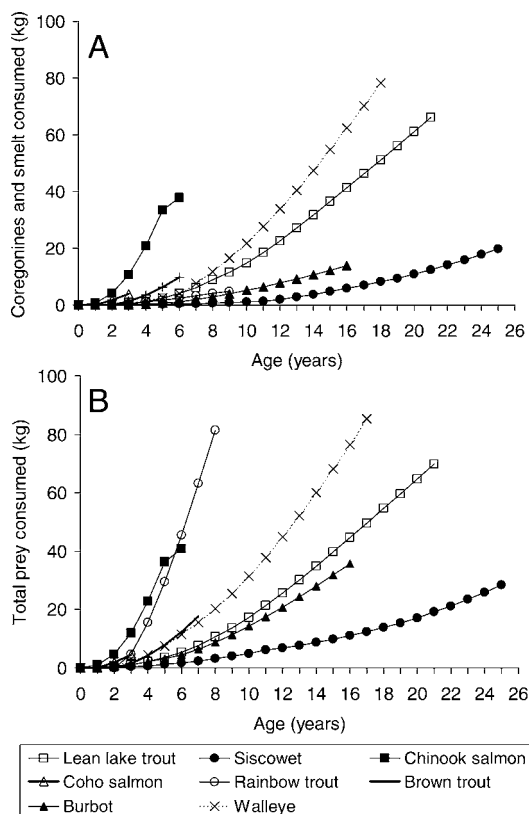


FIGURE 7.—Cumulative consumption of (A) coregonines and rainbow smelt and (B) all prey items by individual predator fish (lean lake trout, coho salmon, burbot, siscowets, rainbow trout, walleyes, Chinook salmon, and brown trout) over their life spans.

improve our estimates of predator demand relative to prey supply.

The $P:B$ ratios reported in the literature are variable (e.g., Lantry and Stewart 1993; Kitchell et al. 2000; Cox and Kitchell 2004), and because they are used to calculate prey availability from the standing stock, they play a critical role in our interpretation of predator-prey interactions. The most recently published $P:B$ ratios that we used were the basis of a whole-lake ecosystem mass balance (Ecopath) model (Cox and Kitchell 2004).

Relative Consumption by Predator Species

Lean lake trout were the primary consumers of coregonines and rainbow smelt in this study, and siscowets played a secondary role. Other studies have demonstrated that siscowet and lean lake trout have minimal dietary overlap (Harvey and Kitchell 2000). Consumption by siscowets was considerably less than that predicted by Ebener (1995), but he used an older

set of model parameters, and the waters he modeled had more siscowets per unit area, a higher growth rate was used, and the modeled diet consisted of more coregonines and fewer sculpins. The western arm contains about 33% nearshore water (<80 m deep), offering less habitat for deep-dwelling siscowets than does Lake Superior as a whole (only 22% nearshore water), so the impact of this form in the western arm may be less than that lakewide (Bronte et al. 2003).

Negus (1995) cautioned that the bioenergetics models do not account for fish behavior, and reduced prey availability may not equate to reduced rations for both lean lake trout and Chinook salmon if lake trout are more efficient predators. Lake trout are able to sustain high predation rates at low prey densities, so reduced availability of prey would have less effect on lake trout feeding preference (Eby et al. 1995) such that the composition of their diverse diet may not reflect changes in relative abundance of the various items (Stewart and Ibarra 1991). Indeed, lean lake trout diets in the western arm of Lake Superior have changed only slightly since 1989. The major change is a higher reliance on coregonines by older fish. During this same period, wild lean lake trout populations have increased through natural reproduction to levels that justified a reduction or cessation of stocking in most areas of the lake (Schreiner and Schram 1997; Bronte et al. 2003; Ebener 2007). Within the western arm, only in ecoregion 2 did lean lake trout show some decline in growth rates between 1981 and 2003, although abundance of lean lake trout was high enough in four out of five management zones (MN-1, MN-3, WI-1, and WI-2) to cause density-dependent survival (Corradin 2004).

In contrast, since 1989, Chinook salmon growth has decreased significantly (Figure 8). This coincides with a decline in rainbow smelt populations (Gorman 2007) and a shift in the major component of their diet from rainbow smelt to coregonines, for which competition is high, especially in nearshore areas. Despite high levels of stocking, returns of spawning Chinook salmon to the French River in Minnesota showed a precipitous decline from more than 1,600 fish in 1986 to 25 fish in 2001, although summer angler harvest rates have remained fairly constant (Schreiner et al. 2006). Most of the Chinook salmon in the western arm are now wild fish, and the minimal influence of stocking on population abundance led to the discontinuation of Chinook salmon stocking in Minnesota waters after 2006. Elsewhere in the Great Lakes basin, Chinook salmon are exhibiting a similar pattern of declining growth rates and condition, lower survival, and a diet shift in response to major declines in alewife *Alosa pseudoharengus*, suggesting insufficient forage as a

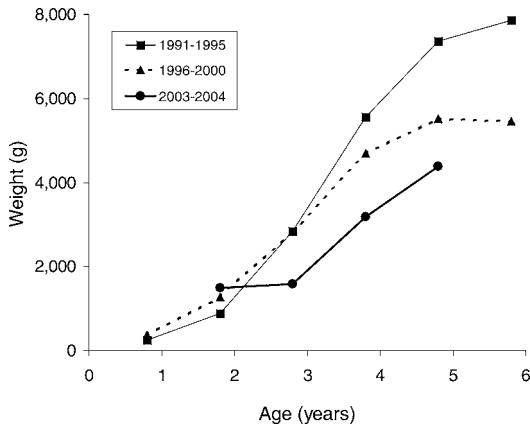


FIGURE 8.—Mean weight at age (g) of Chinook salmon returning to spawn in the French River, Minnesota, in 1991–1995, 1996–2000, and 2003–2004.

mechanism (Stewart and Ibarra 1991; Rand and Stewart 1998; Ebener 2005; Holey and Trudeau 2005).

The impact on the forage base by all the introduced potamodromous predators was small relative to that of lean lake trout and siscowets, which are native to Lake Superior. The preference of both forms of lake trout for colder temperatures and their lower and slower individual consumption of prey fish, slow growth, and efficient foraging behavior despite fluctuations in the prey base all indicate that this species is well adapted to the challenging habitat of Lake Superior.

Commercial, Sport, and Assessment Harvests

The commercial harvest of rainbow smelt and coregonines in the entire western arm is minor, and the low harvests by both sport anglers and assessment fishers are insignificant compared with the total consumption by predator fish and the total available biomass of prey fish. Because commercial harvest is concentrated nearshore in areas where predation pressure is already high and the harvest season typically corresponds with prespawning or spawning for rainbow smelt and coregonines, the local impacts on their populations are greater than the overall totals imply. This situation emphasizes the critical need for regular hydroacoustic monitoring of prey populations and bioenergetics evaluation of predator impacts.

Comparison of Current Study with Previous Bioenergetics Studies

This bioenergetics study of the western arm of Lake Superior provides a more complete estimate of consumption by predators and a more coherent overview of predator–prey relationships than previous studies. The consumption estimates obtained in this

study fell within the same order of magnitude as those reported in previous bioenergetics analyses in western Lake Superior (Ebener 1995; Negus 1995); the variations are due to the numbers of species modeled and updated population, growth, and diet information. The combined consumption estimates of coregonines and rainbow smelt in Minnesota waters in 2004 declined 39% from the 1989 estimates (Negus 1995), primarily owing to a 40% reduction in the estimated numbers of age-1+ lean lake trout and Chinook salmon and lower modeled growth rates for these species in Minnesota waters in 2004. The predictions of Negus (1995) that lake trout might be better able to survive fluctuations in the forage base as a result of their efficiency at capturing prey fish at low densities and their natural adaptation to the oligotrophic environment of Lake Superior, while Chinook salmon populations might suffer under those circumstances, were validated with the current study.

One obvious advantage that this study has over previous bioenergetics studies is that the prey estimates were based on hydroacoustic sampling. The earlier studies by Ebener (1995) and Negus (1995) demonstrated large discrepancies between predator consumption and prey availability. Both of the earlier studies relied on estimates of forage fish derived from daytime bottom trawl surveys conducted annually in May–June, which have since been shown to greatly underestimate pelagic prey fish, especially ciscoes, compared with surveys conducted with night midwater trawls and hydroacoustic gear (Stockwell et al. 2006; Yule et al. 2007).

Management Implications

This study suggests that the western arm of Lake Superior is at or near its carrying capacity for predators. Lake trout rehabilitation has progressed, but we should be attentive to signs of inadequate forage, such as reduced growth rates or lower population abundance, especially in ecoregions 1 and 2 where lean lake trout densities are highest. Chinook salmon could be considered an indicator species that demonstrates early warning signs of reduced forage, although this species plays a less significant role than that of lake trout in the total fish community. The diet shift and declining growth rates of Chinook salmon reveal that this introduced species is not as well adapted as the native lake trout to this oligotrophic lake. Burbot exhibit a high degree of cannibalism and a high diversity of fish in their diet, which may indicate resource limitation (Schram et al. 2006). Lean lake trout utilize both nonnative rainbow smelt and native ciscoes, even as these prey populations fluctuate in abundance, so consequences of reduced forage may not be as evident

in this native predator until prey populations are quite low. Reduced lean lake trout growth reported in ecoregion 2 and density-dependent survival in all management zones except MN-2 (Corradin 2004) may already indicate that competition for prey is intense. Reduced survival of all stocked salmonids is an obvious and direct indicator that there is little capacity left in the western arm to support additional predators.

The superficial boundaries applied to this study, inclusive of Minnesota and Wisconsin waters only, are obviously irrelevant to fish that may range widely, and our conclusions apply beyond these borders. The type of ecosystem-based approach used here is applicable to other parts of Lake Superior and to other Great Lakes. The poor performance of introduced species relative to that of native cohorts and competitors has implications for natural resource managers with limited budgets and staff. This ecosystem-based evaluation has immediate practical applications as well. For example, bioenergetics modeling can assist in determining the allocation of prey fish to different fisheries. The low levels of rainbow smelt available in the western arm, and the relatively small impact of commercial fishing on coregonine and rainbow smelt populations compared with the high consumption levels by predator fish, have already been factored into determinations of allowable commercial harvest in Minnesota waters. Commercial harvest of rainbow smelt is limited, and quotas for the coregonine fishery will be based on hydroacoustic biomass estimates and total allowable catch calculations to maintain a productive fishery while adequately protecting the spawning stock (Schreiner et al. 2006).

Data that directly affect predator numbers and food quality (i.e., population estimates, mortality rates, growth, and prey caloric densities) have the greatest impact on bioenergetics model output, according to sensitivity analyses (Negus 1992). Focusing on these areas will therefore have the most impact on future refinement of bioenergetics analyses. Continual updates to the statistical catch-at-age models used to estimate lean lake trout populations are warranted. Siscowet population estimates are rudimentary at present, but if a fishery develops for this strain, statistical catch-at-age models could be very informative. Diet information from all seasons and life stages (especially for lean lake trout and siscowets) is still a critical need for accurate consumption estimates. Refined estimates of mortality (especially natural mortality), natural reproduction, and growth for both stocked and naturally reproduced fish will increase the accuracy of future bioenergetics evaluations and help in development of demographic models incorporating density-dependent processes and species interactions. Although less critical to model output (Negus 1992),

further acquisition of temperatures and depths occupied by siscowets and potamodromous species would increase our understanding of their habitat and migrations. The development of bioenergetics models for different life stages, and analysis of the sizes of prey fish utilized by different life stages, may assist in determining where bottlenecks exist in both predator and prey populations. Hydroacoustic sampling of the prey base in different seasons will provide needed perspective on these populations and assist in the calculation of realistic *P:B* ratios. Finally, periodic examinations of the relationship between predator demand and prey supply employing bioenergetics and hydroacoustics is helpful in the management of fisheries in large lakes, allocation of resources to various interest groups, and understanding of lake production and community dynamics.

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References

- Becker, G. C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison.
- Bence, J. R., and M. P. Ebener, editors. 2002. Summary status of lake trout and lake whitefish populations in the 1836 treaty-ceded waters of Lakes Superior, Huron, and Michigan in 2000, with recommended yield and effort levels for 2001. Technical Fisheries Committee, 1836 Treaty-Ceded Waters of Lakes Superior, Huron, and Michigan, Charlevoix, Michigan.
- Bronte, C. R., M. P. Ebener, D. R. Schreiner, D. S. DeVault, M. M. Petzold, D. A. Jensen, C. Richards, and S. J. Lozano. 2003. Fish community change in Lake Superior, 1970–2000. *Canadian Journal of Fisheries and Aquatic Sciences* 60:1552–1574.
- Bronte, C. R., J. H. Selgeby, J. H. Saylor, G. S. Miller, and N. R. Foster. 1995. Hatching, dispersal, and bathymetric distribution of age-0 lake trout at the Gull Island Shoal complex, Lake Superior. *Journal of Great Lakes Research* 21(Supplement 1):233–245.
- Corradin, L. M. 2004. Recruitment and growth dynamics of

- lake trout in western Lake Superior. Master's thesis. University of Wisconsin–Stevens Point, Stevens Point.
- Cox, S. P., and J. F. Kitchell. 2004. Lake Superior ecosystem, 1929–1998: simulating alternative hypotheses for recruitment failure of lake herring (*Coregonus artedii*). *Bulletin of Marine Science* 74:671–683.
- Devine, J. A., S. T. Schram, and M. J. Hansen. 2005. A food web analysis of the fishery in Chequamegon Bay, Lake Superior. Wisconsin Department of Natural Resources, Fisheries Management Report 150, Madison.
- Dieterman, D. J., W. C. Thorn, and C. S. Anderson. 2004. Application of a bioenergetics model for brown trout to evaluate growth in southeast Minnesota streams. Minnesota Department of Natural Resources Section of Fisheries Investigational Report 513.
- Ebener, M. P. 1995. Bioenergetics of predatory fish in western U.S. waters of Lake Superior. Completion Report to the Red Cliff Band of Lake Superior Chippewas, Red Cliff Fisheries Department, Bayfield, Wisconsin.
- Ebener, M. P., editor. 2005. The state of Lake Huron in 1999. Great Lakes Fishery Commission, Special Publication 05-02, Ann Arbor, Michigan.
- Ebener, M. P., editor. 2007. The state of Lake Superior in 2000. Great Lakes Fishery Commission, Special Publication 07-02, Ann Arbor, Michigan.
- Eby, L. A., L. G. Rudstam, and J. F. Kitchell. 1995. Predator responses to prey population dynamics: an empirical analysis based on lake trout growth rates. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1564–1571.
- ESRI (Environmental Systems Research Institute, Inc.). 1996. ArcView GIS. ESRI, Redlands, California.
- Foltz, J. W. 1974. Food consumption and energetics of the rainbow smelt (*Osmerus mordax* Mitchell) in Lake Michigan. Master's thesis. University of Wisconsin–Milwaukee, Milwaukee.
- Gardner, W. S., T. F. Nalepa, W. A. Frez, E. A. Cichocki, and P. F. Landrum. 1985. Seasonal patterns in lipid content of Lake Michigan macroinvertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* 42:1827–1832.
- Geving, S. 2007. Commercial fishing summary, Minnesota waters of Lake Superior, 2006. Minnesota Department of Natural Resources, St. Paul.
- Gorman, O. T. 2007. Changes in a population of exotic rainbow smelt in Lake Superior: boom to bust 1974–2005. *Journal of Great Lakes Research* 33(Supplement 1):75–90.
- Halpern, T. N. 2002. Lake Superior summer creel survey, 2002. Minnesota Department of Natural Resources, Project F-29-R(P)-22, Study 4, Completion Report, St. Paul.
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Fish bioenergetics 3.0. University of Wisconsin–Madison Center for Limnology and University of Wisconsin Sea Grant Institute, Madison.
- Hartman, K. J., and F. J. Margraf. 1992. Effects of prey and predator abundances on prey consumption and growth of walleyes in western Lake Erie. *Transactions of the American Fisheries Society* 121:245–260.
- Harvey, C. J., and J. F. Kitchell. 2000. A stable isotope evaluation of the structure and spatial heterogeneity of a Lake Superior food web. *Canadian Journal of Fisheries and Aquatic Sciences* 57:1395–1403.
- Harvey, C. J., S. T. Schram, and J. F. Kitchell. 2003. Trophic relationships among lean and siscowet lake trout in Lake Superior. *Transactions of the American Fisheries Society* 132:219–228.
- Hayes, J. W., J. D. Stark, and K. A. Shearer. 2000. Development and test of a whole-lifetime foraging and bioenergetics growth model for drift-feeding brown trout. *Transactions of the American Fisheries Society* 129:315–332.
- Heist, B. G., and W. A. Swenson. 1983. Distribution and abundance of rainbow smelt in western Lake Superior as determined from acoustic sampling. *Journal of Great Lakes Research* 9:343–353.
- Holey, M. E., and T. N. Trudeau, editors. 2005. The state of Lake Michigan in 2000. Great Lakes Fishery Commission, Special Publication 05-01, Ann Arbor, Michigan.
- Hrabik, T. R., O. P. Jensen, S. J. D. Martell, C. J. Walters, and J. F. Kitchell. 2006a. Diel vertical migration in the Lake Superior pelagic community, I. Changes in vertical migration of coregonids in response to varying predation risk. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2286–2295.
- Hrabik, T., D. Schreiner, M. Balge, and S. Geving. 2006b. Development of a hydroacoustic survey design to quantify prey fish abundance in the Minnesota waters of Lake Superior. Minnesota Department of Natural Resources Section of Fisheries Investigational Report 530.
- Hudson, P. L., J. F. Savino, and C. R. Bronte. 1995. Predator–prey relations and competition for food between age-0 lake trout and slimy sculpins in the Apostle Island region of Lake Superior. *Journal of Great Lakes Research* 21(Supplement 1):445–457.
- Johnson, T. B., M. H. Hoff, A. S. Trebitz, C. R. Bronte, T. D. Cory, J. F. Kitchell, S. T. Lozano, D. M. Mason, J. V. Scharold, S. T. Schram, and D. R. Schreiner. 2004. Spatial patterns in assemblage structures of pelagic forage fish and zooplankton in western Lake Superior. *Journal of Great Lakes Research* 30(Supplement 1):395–406.
- Johnson, T. B., D. M. Mason, S. T. Schram, and J. F. Kitchell. 1999. Ontogenetic and seasonal patterns in the energy content of piscivorous fishes in Lake Superior. *Journal of Great Lakes Research* 25:275–281.
- Jones, T. S., and D. R. Schreiner. 1997. Contribution of 1988–1990 year-classes of stocked and wild Chinook salmon to sportfishing and spawning in Minnesota waters of Lake Superior. Minnesota Department of Natural Resources, Fish Management Report 33, Duluth.
- Kitchell, J. F., S. P. Cox, C. J. Harvey, T. B. Johnson, D. M. Mason, K. K. Schoen, K. Aydin, C. Bronte, M. Ebener, M. Hansen, M. Hoff, S. Schram, D. Schreiner, and C. J. Walters. 2000. Sustainability of the Lake Superior fish community: interactions in a food web context. *Ecosystems* 3:545–560.
- Kitchell, J. F., J. F. Koonce, R. B. O'Neill, H. H. Shugart, Jr., J. J. Magnuson, and R. S. Booth. 1974. Model of fish biomass dynamics. *Transactions of the American Fisheries Society* 103:786–798.
- Lantry, B. F., and D. J. Stewart. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: an interlake

- comparison. Transactions of the American Fisheries Society 122:951–976.
- Linton, B. C., M. J. Hansen, S. T. Schram, and S. P. Sitar. 2007. Dynamics of a recovering lake trout population in eastern Wisconsin waters of Lake Superior, 1980–2001. North American Journal of Fisheries Management 27:940–954.
- Mason, D. M., T. B. Johnson, C. J. Harvey, J. F. Kitchell, S. T. Schram, C. R. Bronte, M. H. Hoff, S. T. Lozano, A. S. Trebitz, D. R. Schreiner, E. C. Lamon, and T. Hrabik. 2005. Hydroacoustic estimates of abundance and spatial distribution of pelagic prey fishes in western Lake Superior. Journal of Great Lakes Research 31:426–438.
- Mason, D. M., T. B. Johnson, and J. F. Kitchell. 1998. Consequences of prey fish community dynamics on lake trout (*Salvelinus namaycush*) foraging efficiency in Lake Superior. Canadian Journal of Fisheries and Aquatic Sciences 55:1273–1284.
- Mattes, W. P. 2004. Thermal and depth distribution of *namaycush* (lake trout) in MI-4 and MI-5. Great Lakes Indian Fish and Wildlife Commission, Odanah, Wisconsin.
- Mayo, K. R., J. H. Selgeby, and M. E. McDonald. 1998. A bioenergetics modeling evaluation of top-down control of ruffe in the St. Louis River, western Lake Superior. Journal of Great Lakes Research 24:329–342.
- Negus, M. T. 1992. Evaluation of bioenergetics modeling in the study of predator–prey dynamics in Minnesota waters of Lake Superior. Minnesota Department of Natural Resources Section of Fisheries Investigational Report 414. Available: files.dnr.state.mn.us/publications/fisheries/investigational_reports/414.pdf. (October 2007).
- Negus, M. T. 1995. Bioenergetics modeling as a salmonine management tool applied to Minnesota waters of Lake Superior. North American Journal of Fisheries Management 15:60–78.
- Negus, M. T. 2003. Determination of smoltification status in juvenile migratory rainbow trout and Chinook salmon in Minnesota. North American Journal of Fisheries Management 23:913–927.
- Negus, M. T., D. R. Schreiner, T. N. Halpern, S. T. Schram, M. J. Seider, and D. M. Pratt. 2007. Bioenergetics evaluation of the fish community in the western arm of Lake Superior in 2000 and 2004. Minnesota Department of Natural Resources Section of Fisheries Investigational Report 542. Available: files.dnr.state.mn.us/publications/fisheries/investigational_reports/542.pdf. (June 2008).
- Pangle, K. L., T. M. Sutton, R. E. Kinnunen, and M. H. Hoff. 2004. Overwinter survival of juvenile lake herring in relation to body size, physiological condition, energy stores, and food ration. Transactions of the American Fisheries Society 133:1235–1246.
- Peck, J. W., T. S. Jones, W. R. MacCallum, and S. T. Schram. 1999. Contribution of hatchery-reared fish to Chinook salmon populations and sport fisheries in Lake Superior. North American Journal of Fisheries Management 19:155–164.
- Post, J. R. 1990. Metabolic allometry of larval and juvenile yellow perch (*Perca flavescens*): in situ estimates and bioenergetic models. Canadian Journal of Fisheries and Aquatic Sciences 47:554–560.
- Rand, P. S., B. F. Lantry, R. O’Gorman, R. W. Owens, and D. J. Stewart. 1994. Energy density and size of pelagic prey fishes in Lake Ontario: implications for salmonine energetics. Transactions of the American Fisheries Society 123:519–534.
- Rand, P. S., and D. J. Stewart. 1998. Dynamics of salmonine diets and foraging in Lake Ontario, 1983–1993: a test of a bioenergetic model prediction. Canadian Journal of Fisheries and Aquatic Sciences 55:307–317.
- Ray, B. A. 2004. Spatial and temporal variability in prey fish composition and predator diet characteristics in Lake Superior from 1986–2001. Master’s thesis. University of Minnesota–Duluth, Duluth.
- Rottiers, D. V., and R. M. Tucker. 1982. Proximate composition and caloric content of eight Lake Michigan fishes. U.S. Fish and Wildlife Service Technical Paper 108.
- Rudstam, L. G., P. E. Peppard, T. W. Fratt, R. E. Bruesewitz, D. W. Coble, F. A. Copes, and J. F. Kitchell. 1995. Prey consumption by the burbot (*Lota lota*) population in Green Bay, Lake Michigan, based on a bioenergetics model. Canadian Journal of Fisheries and Aquatic Sciences 52:1074–1082.
- Scholl, D. K., P. J. Peeters, and S. T. Schram. 1984. Migratory brown and rainbow trout populations of the Bois Brule River, Wisconsin. Wisconsin Department of Natural Resources, Fish Management Report 123, Madison.
- Schram, S. 1983. Seasonal movements and mortality estimates of burbot in western Lake Superior. Wisconsin Department of Natural Resources, Fish Management Report 119, Madison.
- Schram, S. T., T. B. Johnson, and M. J. Seider. 2006. Burbot consumption and relative abundance in the Apostle Islands region of Lake Superior. Journal of Great Lakes Research 32:798–805.
- Schreiner, D. R., J. J. Ostazeski, T. N. Halpern, and S. A. Geving. 2006. Fisheries management plan for the Minnesota waters of Lake Superior. Minnesota Department of Natural Resources, Special Publication 163, Duluth.
- Schreiner, D. R., and S. T. Schram. 1997. Lake trout rehabilitation in Lake Superior. Fisheries 22(7):12–14.
- Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–88. Canadian Journal of Fisheries and Aquatic Sciences 48:909–922.
- Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout, *Salvelinus namaycush*: application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40:681–698.
- Stockwell, J. D., D. L. Yule, O. T. Gorman, E. J. Isaac, and S. A. Moore. 2006. Evaluation of bottom trawls as compared to acoustics to assess adult lake herring (*Coregonus artedii*) abundance in Lake Superior. Journal of Great Lakes Research 32:280–292.
- Yule, D. L., J. V. Adams, J. D. Stockwell, and O. T. Gorman. 2007. Using multiple gears to assess acoustic detectability and biomass of fish species in Lake Superior. North American Journal of Fisheries Management 27:106–126.
- Yule, D. L., J. D. Stockwell, D. R. Schreiner, L. M. Evrard, M. Balge, and T. R. Hrabik. 2008. Can pelagic forage fish and spawning cisco (*Coregonus artedii*) biomass in the western arm of Lake Superior be assessed with a single summer survey? Fisheries Research. DOI: 10.1016/j.fishres.2008.09.012.