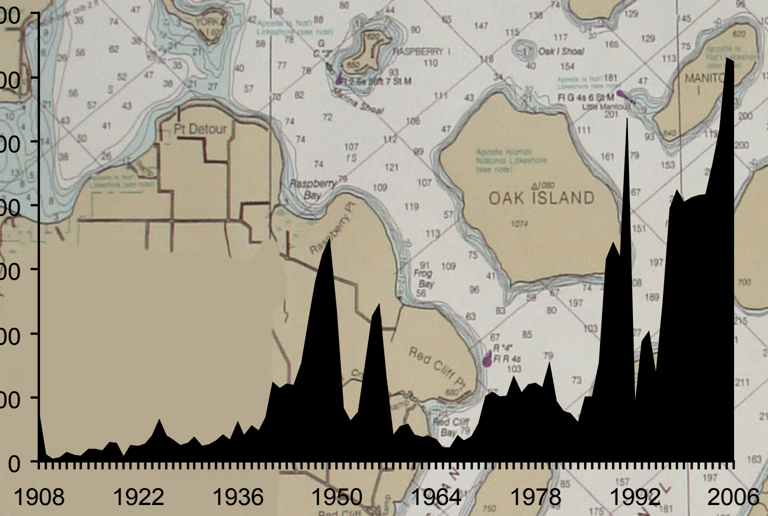
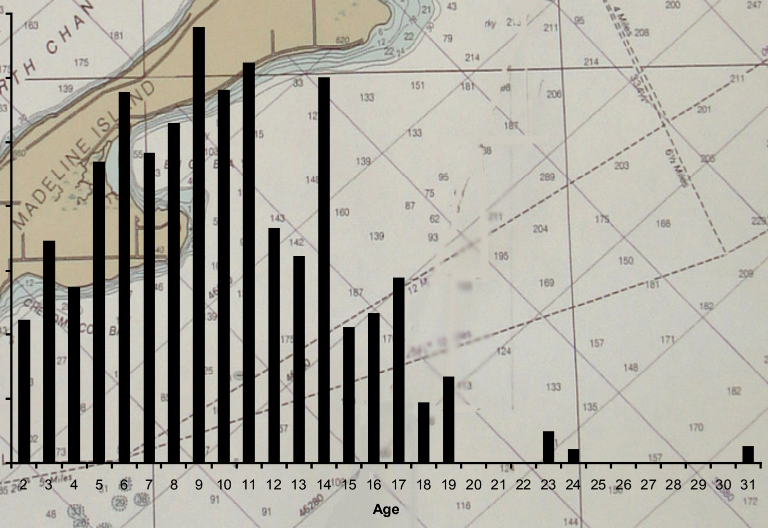
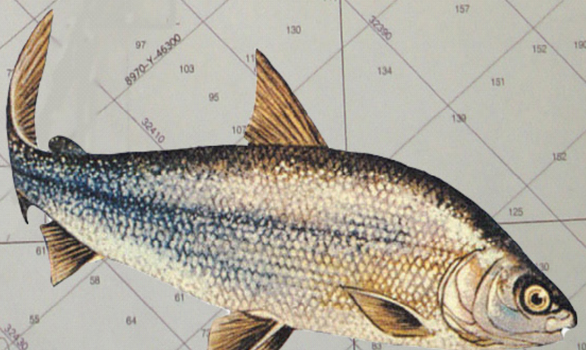
Population Dynamics of Lake Whitefish in the Apostle Islands Region of Lake Superior







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Population Dynamics of Lake Whitefish in the Apostle Islands Region of Lake Superior

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Abstract. - Lake whitefish (*Coregonus clupeaformis*) is one of the most valuable commercial species throughout the Great Lakes and currently the dominant commercial species in the Apostle Islands region of Lake Superior. Although whitefish are widely considered resilient to commercial exploitation, the sustainability of the current harvest of whitefish is still a management concern. The objective of this report was to consolidate available data to better understand the population characteristics of whitefish in the Apostle Islands region. Commercial and sport harvest and fishery independent surveys indicated whitefish abundance has increased since the 1970s. Since 1999, growth and condition fluctuated but appeared to decline slightly after 2002. Annual mortality rates were relatively low compared to other commercially exploited whitefish populations in Lake Superior. Amphipods were an important prey item throughout the year although whitefish diet changed seasonally. Since amphipod densities have not changed recently a slight decrease in growth and condition is probably due to density dependence as seen in other populations in Lake Superior. Conservative regulation of the whitefish fishery through measures such as commercial gill net effort control, fish refuges, and closed seasons is likely providing biological sustainability in the face of historically high commercial harvest.

Lake whitefish, *Coregonus clupeaformis*, is widely distributed in North American fresh waters from the Atlantic coast westward across Canada and the northern United States, to British Columbia, the Yukon Territory and Alaska (Scott and Crossman 1973). Whitefish inhabit large rivers and coldwater lakes within their geographic range. In Wisconsin, they occur in the Mississippi River, Lake Michigan and Lake Superior drainage basins (Becker 1983). Whitefish in Lake Superior generally inhabit waters 18-64 m deep (Dryer 1966; Lawrie 1978) but have been found as deep as 145 m (Selgeby and Hoff 1996; M. J. Seider, Wisconsin Department of Natural Resources (WDNR), unpublished data). Almost 60% of the water in the Apostle Islands region is less than 80 m deep. The complex bathymetric features around the islands such as bays and reefs likely provide habitat suitable for all life stages of whitefish. Whitefish move into relatively shallow water in the fall and generally spawn over rocky substrates (Scott and Crossman 1973; Becker 1983). Coberly and Horrall (1980) indentified thirty-nine whitefish spawning reefs in the Apostle Islands region.

Past tagging studies indicated whitefish in the Apostle Islands region reside within a relatively small home area. All whitefish recaptured after being tagged during 1955-1959 by Wisconsin Conservation Department biologists were recovered in the Apostle Islands. Dryer (1964) recorded tagged whitefish traveling as far as 40 km; however most were recaptured within 8 km of the tagging site. The WDNR tagged spawning whitefish from 1969 to 1974 and recaptured fish in subsequent years at their original location, suggesting some degree of homing. Another WDNR study in 1974 again showed tagged whitefish remaining within the Apostle Islands region.

History of Fishery

Historically the whitefish was one of the most valuable commercial species throughout the Great Lakes and is currently the dominant commercial species in the Apostle Islands region of Lake Superior. Production of whitefish in Wisconsin waters contributed about 35% of the total U.S. output in Lake Superior during the first half of the 20th century (Dryer 1964) and still contributed 40% as of 1999 (Baldwin et al. 2008). Total commercial harvest in Wisconsin waters (majority from Apostle Islands region) gradually increased from 1903 to 1939 and then rapidly increased in the 1940s (Baldwin et al. 1979). Except for another brief increase in the late 1950s, harvest rapidly decreased through the 1960s.

The commercial fishery in the Apostle Islands has changed dramatically due to many technological innovations. Organized commercial fishing in the region began during the early 1800s. La Pointe, on Madeline Island, was one of the first Lake Superior fishing stations of the American Fur Company. Initially, fishing was done off small sailing vessels relatively close to the mainland. Whitefish and both the lean and siscowet forms of lake trout, *Salvelinus namaycush*, were harvested, packed in barrels, and shipped via schooner to Sault Ste. Marie, Michigan. By 1880, over 250 people were employed in the fishing business at Bayfield. Gradually the small sailing vessels were replaced

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Mackinaw boats similar to this one were used for commercial fishing in the Apostle Islands in the late 1800s. Photo provided by Michigan Maritime Museum.

with wooden steamers allowing commercial fishers access to fishing grounds farther offshore. Commercial fish camps became common on many of the Apostle Islands. The camps served as remote drop off sites where the fish were eventually picked up from the islands and brought to Bayfield. A major advancement for the commercial fishery was the use of mechanical gill net lifters, which made fishing much less physically demanding and allowed fishers to lift more net. Brown et al. (1999) thoroughly discussed many of the technological innovations in gear development, transportation, processing, and preservation that resulted in improved efficiency of the Great Lakes commercial fishery. The present fishery operates from ports along the main shoreline with typical commercial fishing tug boats and open deck trap net boats.

Prior to the sea lamprey invasion, many commercial fishers only operated intermittently, some fishing only under the ice and others fishing only when catches and prices were high. In 1938, two years after mandatory monthly commercial reporting began, there were 165 licenses. In 1970 a limited entry fishery was established with 21 licenses. In 1972, a Wisconsin Supreme Court decision (called the Gurnoe decision) reaffirmed the treaty rights of the Lake Superior Chippewas to fish commercially (Blust et al. 1988). Since the Gurnoe decision state and tribal commercial fishers have been managed separately. The number of tribal commercial licenses has varied depending on the band (Red Cliff and Bad River) and whether or not the license is classified as a big boat (meaning it has a mechanical gill net lifter) or small boat (no lifter). Lastly, the state fishery was reduced to 10 licenses after retirement of 11 licenses in 1997.

Whitefish have traditionally been captured in the Apostle Islands region with seines, gill nets, pound nets and more recently, trap nets. Seines were used in areas where fish congregated near shore during migrations or spawning (Brown et al. 1999). Their use was limited if the bottom was rough or rocky (Dryer 1963) and as near shore stocks of fish were depleted (Brown et al. 1999). Gill nets can be set over a variety of habitats and have always been an important gear. Linen gill nets were initially used but were replaced with cotton twine in the late 1920s. Beginning in the early 1950s, nylon gill nets were used and finally monofilament nets have been used since the early 1970s. In addition to net material, mesh size has also changed. In 1838 the typical gill net mesh size for whitefish was 152 mm (stretch-measured; Nute 1944). Today the standard monofilament gill net stretched mesh size used is 114 mm. Larger mesh size used historically may suggest lightly exploited populations with a greater size structure than found today. A decrease in mesh size over time is also a reflection of more conservative fisheries management.

The pound net was first fished in the Apostle Islands area in the early 1870s, and by 1885 about 125 were in use (Dryer 1963). Pound nets consist of vertical walls of netting maintained in position by a series of stakes driven into the lake bottom (Brown et al. 1999). Fish captured by pound nets were alive and allowed fishers to release non-target species. Pound nets were limited by the time needed to set and remove them. Fishers were restricted from setting pound nets in water deeper than 23.7 m; however most were set in water less than 18.2 m because of the length of stakes required. The depth limitation was imposed to prevent bloating of sublegal whitefish and sport fish which were released alive. Because they were at the surface of the water, pound nets were subject to damage from storms and boats. As the double-crested cormorant, *Phalacrocorax auritus*, population increased during the 1970-

Table 1. Average dockside value of commercially caught lake whitefish from the Apostle Islands region, 1904-2006.

Year	Average Value ($)
1904 – 1920	0.05 – 0.10
1920 – 1930	0.10 – 0.15
1930 – 1936	0.04 – 0.08
1937 – 1940	0.08 – 0.12
1941 – 1945	0.45 – 0.65
1946 – 1955	0.5
1956 – 1960	0.50 – 0.65
1961 – 1969	0.65
1970 – 1976	0.64
1989 – 1993	0.45 – 0.50
2002 – 2006	0.72

1980s commercial fishers had to deal with predation on whitefish in pound nets. The birds would perch on top of the net stakes and dive into the open net. As a result many whitefish would be gilled in the net mesh when trying to avoid predation and/or scarred from cormorant attacks making them less marketable. To better avoid cormorant predation, fishers switched to submerged trap nets. The last pound net fished in the Apostle Islands was in 2001. Trap nets were first used in 1970; however they were not used extensively until the early 1990s. In addition to reducing cormorant predation, trap nets are preferred over pound nets because they are easier to deploy and move between locations. Currently 6 of the 10 state commercial fishers use trap nets during portions of the year.

Commercial harvest has at times fluctuated dramatically (Baldwin et al. 1979), yet the dockside value of whitefish has changed relatively little in the last 100 years (Table 1). During the 1930s depression era much of the commercial catch was bartered rather than sold and prices remained similar to earlier in the century. Whitefish value changed greatly during and after World War II and has remained

Commercial fishers netting lake whitefish from a pound net in the 1930s.

near an average of $0.50 per pound. Within an average year, prices usually fluctuate seasonally due to reduced availability during transitional periods when fishers cannot set gear (generally early winter). Even with seasonal fluctuations in value, the average price did not change for almost 60 years. Recently the average price has increased, due in part to reduced availability of whitefish in the lower Great Lakes.

Since European settlement whitefish populations in Lake Superior have followed similar trends as the other Great Lakes. Whitefish harvest was high during the 19th century, declined in the early to mid 20th century and increased during the World War II era (Baldwin et al. 1979). Abundance declined throughout Lake Superior in the 1950s due to sea lamprey predation (Lawrie 1978; Smith and Tibbles 1980). Subsequent sea lamprey control benefited the entire fish community of Lake Superior. Widespread salmonid stockings were generally believed to provide a sea lamprey buffer for whitefish although it could not be quantified (Lawrie 1978).

Current Management. - Whitefish management in Wisconsin is primarily guided by two documents. The 1972 Gurnoe Decision of the Wisconsin Supreme Court reaffirmed Lake Superior treaty rights under the 1854 Treaty that created the Red Cliff and Bad River reservations. Numerous, time consuming court cases regarding the permissible scope of state regulation led the parties to seek a negotiated approach to the exercise of off-reservation treaty rights. The Lake Superior State-Tribal Agreements – signed in 1981, 1986, 1995, and 2005 – have been the result of those negotiations and form the basis of the current fisheries management program on Wisconsin waters of Lake Superior. The Fish Community Objectives for Lake Superior (Horns et al. 2003) provide further guidance. The objective for whitefish is to maintain self-sustaining populations of lake whitefish within the range of abundance observed during 1990-99." This objective is intended to have whitefish remain a significant component of the fish community.

Lake trout rehabilitation has been a major objective of the WDNR since overexploitation and sea lamprey, *Petromyzon marinus*, predation caused the population to nearly collapse during the late 1940s and 1950s (Pycha and King 1975; Swanson and Swedberg 1980; Schram et al. 1995). As lake trout rehabilitation has progressed in the Apostle Islands region, commercial fishers have been allowed to fish more large mesh gill net effort. Lake trout and whitefish are sympatric species and the effect of increasing commercial gill net effort on the whitefish population is unknown. Whitefish are widely considered resilient to commercial exploitation; still the sustainability of the current harvest of whitefish is a management concern. Although they are the primary commercial species, population characteristics of whitefish in the Apostle Islands have not been recently examined. Furthermore, consolidation of all whitefish data would be desirable for potential development of a statistical catch at age (SCAA) model for the Apostle Islands region.

Study Objectives. - The objectives of this study were to consolidate all available data on whitefish in the Apostle Islands region to 1) better understand the population dynamics of whitefish, 2) establish baseline data that may help document potential food web changes occurring due to invasive species and 3) determine the diet of whitefish in an attempt to correlate diet to relative abundance of a known prey item, the benthic amphipod *Diporeia* spp.

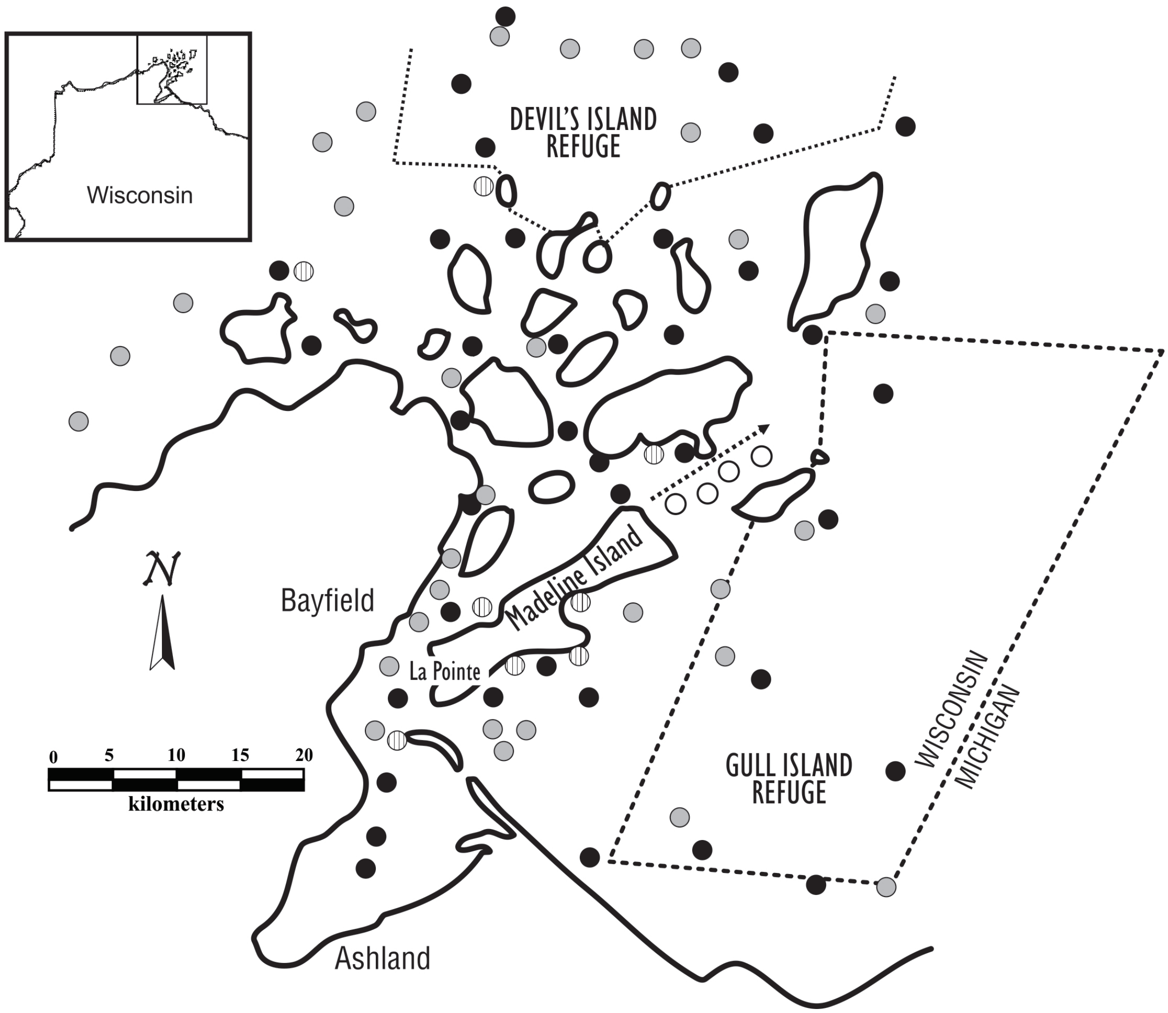


Figure 1. The Apostle Islands region of Lake Superior. Grey circles indicate spring survey net locations, black circles indicate summer survey net locations, open circles indicate siscowet survey net locations, hatched circles indicate monitored commercial nets, and dashed arrow indicates benthic sampling station locations. The Devils Island refuge boundary extends north beyond map coverage following the 64m depth contour.

STUDY AREA

Whitefish were collected in the Apostle Islands region of Lake Superior (including Chequamegon Bay) (Figure 1). The Apostle Islands region is more productive than most of Lake Superior, largely due to relatively shallow bathymetry. Water depths rarely exceed 65 m, with the exception of a trench near the eastern edge of the islands, where the bottom depth reaches 140 m. The region (4473 km^2) is characterized by 22 islands and the adjacent mainland, with a shoreline of red clay, sand, sandstone and boulders. Bottom substrate is a mix of sand, clay, detritus, and glacial debris (Nuhfer and Dalles 1987). Abundant rocky shoals provide spawning habitat for whitefish (Coberly and Horrall 1980). The Apostle Islands region contains two fish refuges that are closed to commercial and recreational fishing (Figure 1). The Gull Island Shoal refuge has a surface area of 336 km^2 and the Devils Island Shoal refuge has a surface area of 283 km^2.

METHODS

State and tribal commercial harvest data from 1970 to 2006 were compiled from mandatory catch reports and on-board monitoring by WDNR staff. Commercial effort from state fishers only was separated by entrapment nets (nights out) and 114 mm stretch mesh gill nets (meters of net) to look for temporal changes in preferred gear type. Recreational angler harvest in the Apostle Islands region was estimated from creel surveys conducted at all major ports during 1980-2006.

Whitefish were collected during several annual fishery independent surveys conducted off the *R/V Hack Noyes*. Whitefish were sampled as part of a spring large-mesh gill net survey (hereafter spring survey) conducted annually by WDNR during 1981-2006, except not in 1996 and 2001. The spring survey was established to monitor lake trout relative abundance and sea lamprey wounding

State and tribal fishers set and lift gill nets from a typical Great Lakes gill net tug.

rates. Eighteen to 31 stations were sampled annually throughout the Apostle Islands (Figure 1). This survey was conducted using standardized bottom-set gill nets of 114-mm stretched-mesh, 210/2 multifilament nylon twine, 18 meshes deep, hung on the 1/2 basis, soaked for 24-120 hours, and fished from late April through early June.

Whitefish were collected during a lake-wide coordinated siscowet survey (hereafter siscowet survey) in the Apostle Islands in 2006. Four locations within designated depth strata were sampled with graded mesh monofilament gill nets (Figure 1). All bottom set nets contained nine (91 m) panels of different stretch meshes from 51 to 152 mm in 12.7 mm increments (total length = 819 m).

Whitefish were also sampled during an annual graded-mesh fish community survey (hereafter summer survey) conducted in July and August. Standard locations were sampled in the Apostle Islands every year from 1970 to 1979, and every even numbered year from 1980 to 2006, except for 1996 (Figure 1). Eleven locations were sampled throughout the time series and used to examine annual catch trends. Biological data from whitefish caught at additional sites sampled in 2006 were used in other analyses. Nylon nets were used from 1970 through 1990, and monofilament nets were used from 1991 through 2006. Monofilament nets may have a higher catchability than nylon nets although no attempt was made to compare catchability using different net materials. All bottom set nets contained twelve (91 m) panels of different stretch meshes from 38 to 178 mm in 12.7 mm increments (total length = 1092 m).

Annual geometric mean catch-per-unit-effort (CPUE) was calculated for the spring and summer surveys. Soak time varied during the spring survey; thus all CPUEs were converted to one night with a gill net saturation equation developed for lake trout (Hansen et al 1998):

$$\text{Adjusted CPUE} = \alpha(1 - \exp(-\beta \bullet \text{time}))$$

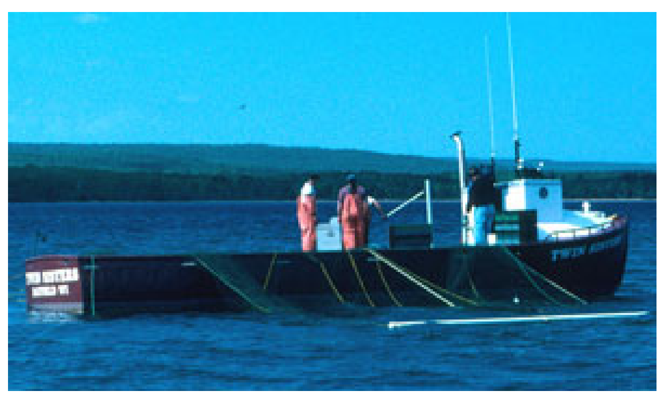
where α = 211.443 and β = -ln(1 (CPUE/211.443))/time, CPUE was number of whitefish per 1000 m of net, and time was nights the nets were set. The net saturation equation for lake trout was applied because one has not been developed specifically for whitefish. However, whitefish behavior may differ from lake trout. Soak time during summer survey did not exceed one night, hence CPUEs were not converted using the above equation. For both surveys geometric mean CPUE was calculated by averaging, across lifts, the $\log_e$ (x+1) number of whitefish caught per 1000 m and then back-transformed. The CPUE was defined as the number of whitefish caught per 1000 m net night.

Subsamples of whitefish captured during spring surveys in 1999-2006 were measured (total length) and weighed. Least square means for weight were calculated for each year by analysis of variance (ANOVA; SYSTAT 2007) to measure potential changes in whitefish condition. Only 114-mm stretched mesh gill net was used during the spring survey therefore whitefish within a similar length range were captured each year. Thus potential changes in annual mean weight may reflect changes in whitefish condition. Differences in least square means were tested for significance at the 0.05 level with Tukey's post hoc comparisons. Changes in condition from 1999 to 2006 were also examined by estimating annual length-weight parameters from the following equation:

$$\log_{10}(W) = a + b(\log_{10}L)$$

where W = weight (g), a = y-intercept, b = slope, and L = length (mm).

Scales and otoliths were collected from subsamples of whitefish from the spring and summer surveys. Both



Trap nets used to catch lake whitefish are lifted from special open deck boats.

structures were collected from individual fish during spring survey in 2002-2006 to compare age estimates from scales and otoliths. Only ages estimated from otoliths were used for the following analyses. Mean length at age was calculated for all ages captured during spring survey

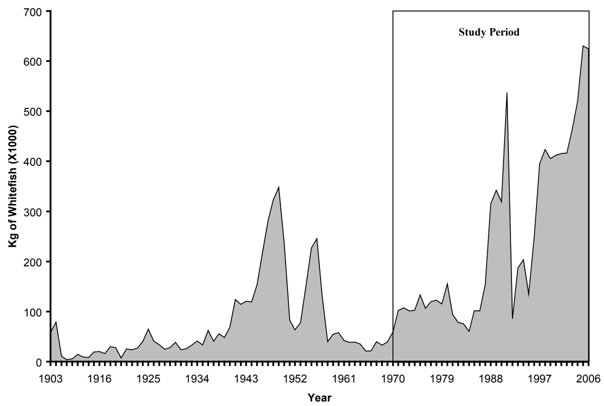


Figure 2. Commercial harvest of lake whitefish in Wisconsin waters of Lake Superior, 1903-2006. Harvest in 1903-1970 from Baldwin et al. (1979).

2002-2006. Least square means lengths were calculated for age 11 whitefish with ANOVA to analyze temporal trends in growth (SYSTAT 2007). Age 11 was chosen because fish at this age were likely fully vulnerable to 114 mm

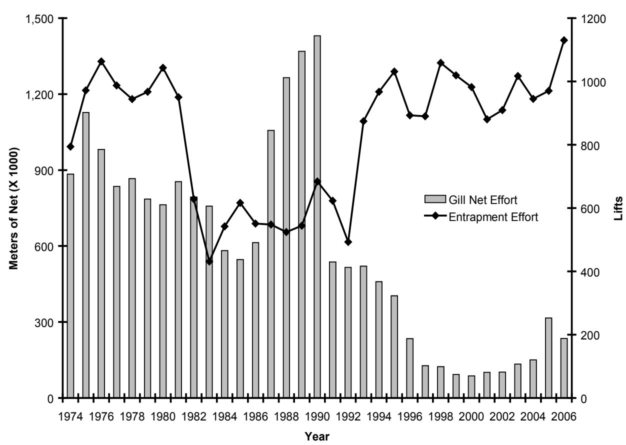


Figure 3. Gill net effort (meters of net) and entrapment net effort (lifts) for state commercial fishers, 1974-2006.

stretched mesh gill nets based on the age distributions of spring survey catches.

Growth was further examined by estimating the parameters of the von Bertalanffy growth equation:

$$L_t = L_\infty \, (1\text{-}e^{-k*(t-to)})$$

where L_t = total length (mm) at age t, L_∞ = asymptotic length, k = Brody growth coefficient, t_0 = theoretical age at length 0. The von Bertelanffy growth parameters and mean lengths at age were calculated using data from fish collected during summer survey in 2006. Mean length at age was estimated from the raw data (sample means). Residuals were then calculated from the difference between sample mean lengths at age and those predicted by the von Bertalanffy growth equation and weighted by sample size. Iterative changes were made to the von Bertalanffy

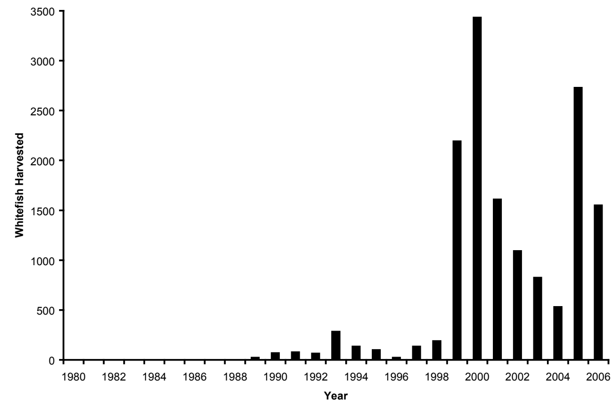


Figure 4. Estimated sport harvest of lake whitefish in the Apostle Islands region, 1980-2006.

growth parameters until the residual sum of squares was minimized.

Age-length keys were constructed for each year from spring survey 2003-2006 and summer survey 2006 to examine age distribution and to estimate annual mortality rates. Total annual mortality rates were calculated by linear regression of the descending limb of the annual age distributions. For each year the natural logarithm of catch at the modal age and the following age classes containing at least 5 fish were used in linear regressions. The negative slope of the descending limb estimates the annual instantaneous mortality rate (Z). Annual mortality could not be calculated for 2002 because

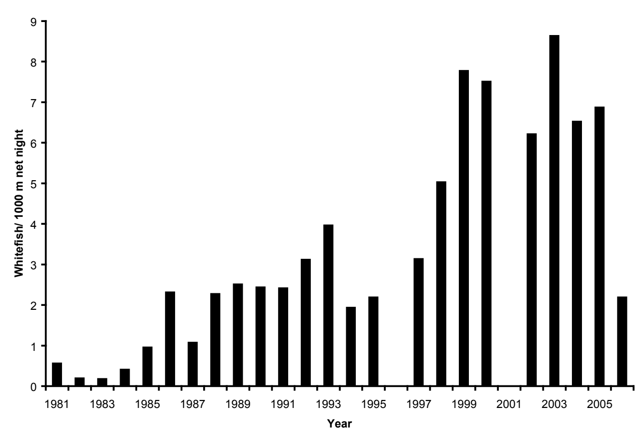


Figure 5. Geometric mean catch-per-unit-effort of lake whitefish from the spring survey in the Apostle Islands region, 1981-2006. Spring survey not conducted in 1996 and 2001.

data were not sufficient. Ages 10-16 were used for mortality estimates from the spring survey while ages 9-19 were used from the summer survey. Instantaneous natural mortality (M) was calculated using Pauly's equation (Pauly 1980; Quin and Deriso 1999). The von Bertalanffy growth parameters from summer survey and an average water temperature of 4.6° C were used to calculate instantaneous natural mortality. We assumed a constant natural mortality across years for calculation of instantaneous fishing mortality (F) and annual mortality rates (Kohler and Hubert 1999).

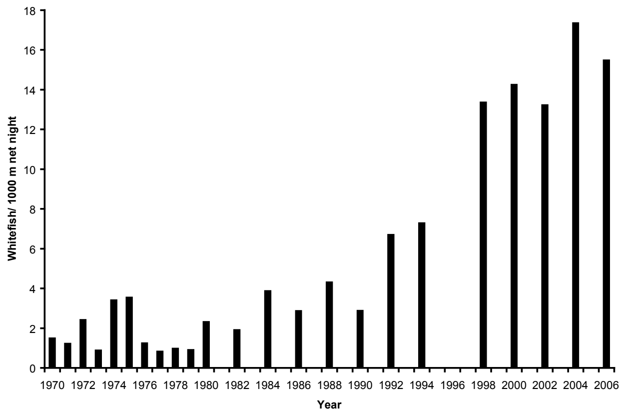


Figure 6. Geometric mean catch-per-unit-effort of lake whitefish from the summer survey in the Apostle Islands region, 1970-2006. Summer survey conducted annually from 1970 to 1979 and in even numbered years from 1980 to 2006. Summer survey not conducted in 1996.

Whitefish stomach samples were collected during annual surveys and commercial monitoring during 2006 and January 2007. Stomachs were collected throughout 2006 except during autumn. Whitefish spawn during October/November and reduced feeding during spawning has been observed in other Lake Superior fishes (M. J. Seider, WDNR, unpublished data). For each fish the stomach was removed and frozen. In the laboratory, stomachs were dissected and food items were separated, identified (to lowest taxonomic level), enumerated, and weighed by prey group (wet weight). Of the 506 stomachs collected 20% were empty and not used in subsequent analyses. Stomach contents were segregated by seasons, winter (December, January), spring (April, May, June), and summer (July, August). Frequency of occurrence and percent composition by weight of food items were

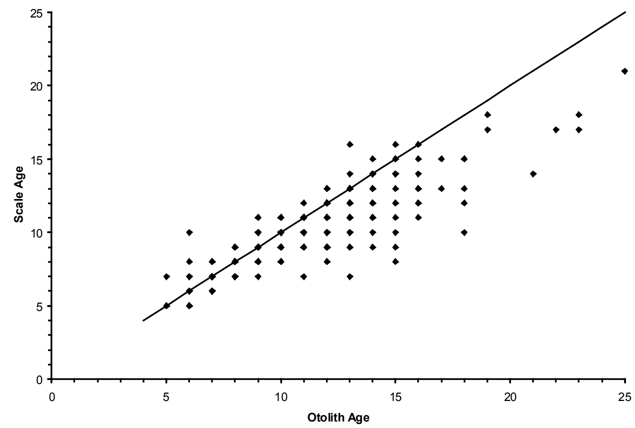


Figure 7. Paired otolith and scale ages from lake whitefish collected during spring survey, 2002-2006. Line represents 100% agreement between aging structures.

calculated by season and age of fish. Percent composition by weight in diet also was assessed by depth strata (<50 m, 50-90 m, >90 m). Percent composition by weight was calculated as the proportion each diet item comprised of the total weight of prey consumed by all fish for a particular season or depth stratum. Benthic debris was included in all calculations of frequency of occurrence and percent composition by weight but not considered a prey group.

Benthic samples were obtained from 5-6 locations between Madeline and Stockton Islands during late September/early October from 2003 to 2006 (Figure 1). At this location, the bathymetry slopes in such a way to include all of the depth categories recommended for *Diporeia* spp. monitoring (T. F. Nalepa, Great Lakes Environmental Research Laboratory, personal communication). Samples were collected in triplicate at five depth intervals (<30 m, 31-50 m, 51-70 m, 71-90 m, >90 m) during 2003-2006 and at an additional

Table 2. Mean weight, length range, and length-weight equation parameters for lake whitefish in the Apostle Islands region, 1999-2006. Mean weights with same superscripts were not significantly different from one another at alpha = 0.05. Standard errors in parentheses.

	Year						
Parameter	1999	2000	2002	2003	2004	2005	2006
Sample	175	191	99	114	37	143	91
Length range (mm)	414-721	406-683	419-622	427-676	447-571	361-645	386-589
Mean weight (g)	1473 (446)a	1080 (290)b	1044 (277)b	1215 (434)c	1168 (282)b,c	1100 (299)b,c	980 (235)b
L-W Intercept	-12.3	-12.0	-13.1	-12.6	-13.1	-9.9	-10.2
L-W Slope	3.11	3.06	3.23	3.16	3.24	2.71	2.77

Table 3. Mean length at age (mm) of lake whitefish from spring survey in the Apostle Islands region, 2002-2006 (sample size).

	Age									
Year	7	8	9	10	11	12	13	14	15	16
2002	457 (1)	480 (2)	490 (10)	499 (10)	501 (13)	525 (24)	518 (7)	533 (1)	519 (3)	573 (2)
2003	460 (1)	469 (5)	469 (7)	484 (12)	503 (8)	504 (22)	520 (12)	536 (14)	524 (5)	510 (4)
2004	467 (6)	465 (11)	482 (12)	471 (20)	489 (10)	478 (14)	517 (14)	509 (22)	481 (8)	487 (6)
2005	446 (4)	471 (16)	475 (7)	488 (5)	500 (10)	495 (18)	518 (11)	536 (7)	545 (6)	555 (2)
2006	-	414 (3)	462 (17)	473 (13)	478 (15)	465 (7)	483 (6)	505 (7)	509 (6)	532 (3)

103-m site in 2005 and 2006. Samples were collected with a Ponar dredge that had a screen mesh of 500 microns and a sampling area of 522 cm^2. Samples were filtered in the field using a 500 micron mesh screen and preserved with 10% formalin solution containing rose bengal stain. In the laboratory, organisms were identified to lowest possible taxonomic level, counted, and archived in ethyl alcohol. Although our sampling was intended to monitor *Diporeia* spp. other amphipod species may have been present (and not properly identified) in the shallower depth strata, so densities were calculated for total amphipods. Amphipod density (number / m^2) was calculated by dividing the average amphipod count for each depth interval by the sampling area (0.0522 m^2).

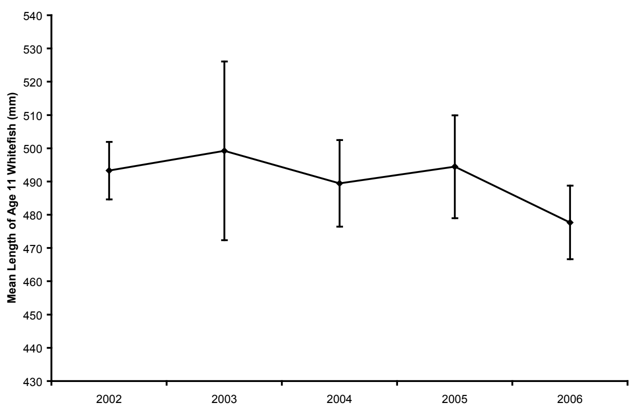


Figure 8. Mean length (95% confidence intervals) of age 11 lake whitefish from spring survey in the Apostle Islands region, 2002-2006.

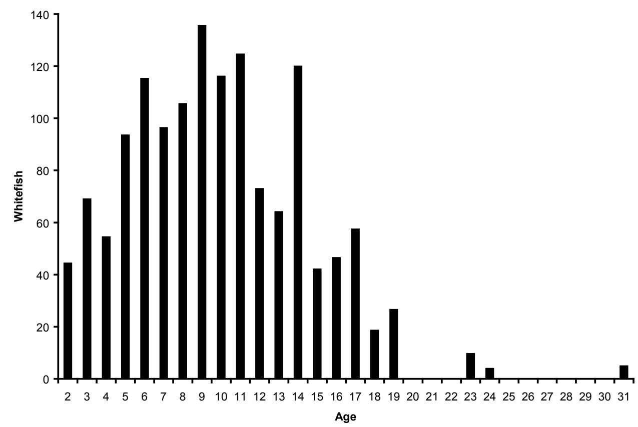


Figure 9. Age distribution of lake whitefish captured during summer survey in the Apostle Islands region, 2006.

RESULTS

Commercial harvest of whitefish was variable but generally increased from 1970 to 2006 (Figure 2). Harvest ranged from 59,422 kg in 1970 to 630,388 kg in 2005 (Appendix I). During the late 1980s and after 1997, commercial harvest exceeded the highest values recorded since 1903 (Figure 2; Baldwin et

Table 4. Lake whitefish mortality rates estimated from spring survey and summer survey, 2003-2006.

	Spring survey				Average	Summer survey
Mortality rate	2003	2004	2005	2006	2003-06	2006
Instantaneous						
Total (Z)	0.47	0.14	0.57	0.22	0.35	0.17
Fishing (F)	0.36	0.03	0.46	0.11	0.24	0.06
Natural (M)	0.11	0.11	0.11	0.11	0.11	0.11
Annual						
Total (A)	0.37	0.13	0.44	0.20	0.29	0.16
Fishing (u)	0.29	0.03	0.35	0.10	0.19	0.06
Natural (v)	0.09	0.10	0.08	0.10	0.09	0.10
N	323	404	169	283	-	825
Age range	12-16	10-16	12-15	9-17	-	9-18

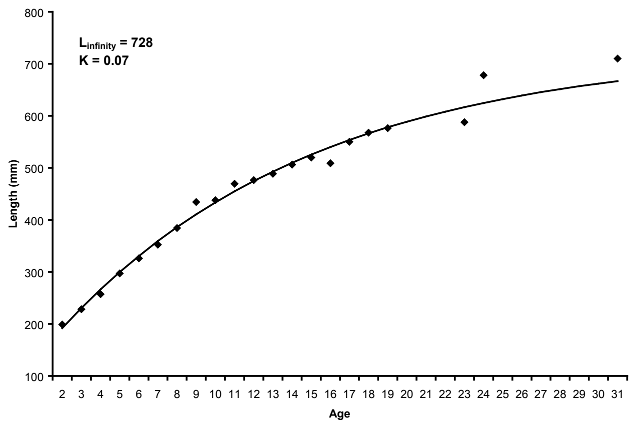


Figure 10. Estimated mean length at age from von Bertalanffy growth equation developed from lake whitefish captured during summer survey in the Apostle Islands region (line). Dots represent empirical mean length-at-ages from sample.

al. 1979). Beginning in 1970, commercial harvest increased until 1991 and then decreased substantially following the initiation of a commercial gill net effort control program. The effort control program decreased the total annual gill net effort by limiting each fisher's gill net effort seasonally based on their lake trout catch rates in previous years. After 1992 commercial harvest increased dramatically and exceeded the previous historical record highs every year after 1997. The preferred gear of state commercial fishers has gradually changed since 1974. Gill net effort was relatively stable in the 1970s but then increased dramatically in the late 1980s (Figure 3). After peaking in 1990, gill net effort generally declined and remained stable until 2005. Entrapment effort has fluctuated since 1974 but has generally increased since the early 1980s.

A recreational fishery for whitefish has emerged since the late 1990s. Estimated sport harvest was initially low, ranging from 0 to 287 fish from 1980 to 1998 (Figure 4; Appendix I). Since 1999 harvest has annually exceeded 500 whitefish with a high of 3,436 in 2000. The majority of sport harvest was reported during the ice fishery.

Spring and summer survey CPUE both indicated an increase in whitefish abundance since 1970. Spring survey CPUE ranged from 0.2 fish/ 1000 m net night in 1982 and 1983 to 8.6 fish/ 1000 m net night in 2003 (Figure 5; Appendix I). Summer survey CPUE exhibited similar trends as those from spring survey but the extended times series recorded low relative abundance in the 1970s. Summer survey CPUE ranged from 0.8 fish/ 1000 m net night in 1977 to 17.4 fish/ 1000 m net night in 2004 (Figure 6; Appendix I).

During the spring survey in 1999-2006, 4,265 whitefish were measured and of those 850 were weighed. Measured

Table 5. Frequency of occurrence (%) of stomach contents from lake whitefish collected during winter season in the Apostle Islands region, 2006-2007.

Diet Item	Age N	5 1	6 10	7 12	8 11	9 9	10 7	11 12	12 14	13 5	14 5	15 7	16 3	17 1	20 1	21 1	27 1	Weighted average
Sphaeriidae		100	80	100	90	75	83	80	64	75	80	100	100	0	0	0	100	81
Amphipoda		0	0	17	50	38	50	70	36	25	60	17	50	100	0	100	100	38
Smelt/ unidentified fish		0	0	0	0	13	17	0	7	0	0	0	0	0	0	0	0	3
Mysis relicta		0	0	0	10	25	0	30	7	25	40	0	0	0	0	0	0	11
Fish eggs		100	100	100	90	63	50	60	50	50	40	50	50	0	0	0	0	66
Chironimidae		0	40	25	80	50	67	60	43	50	80	33	50	0	0	100	0	50
Other invertebrates		0	0	8	30	50	50	50	36	0	20	17	0	0	0	0	0	25
Benthic debris		0	10	17	90	100	100	100	100	75	100	100	0	0	100	0	100	73

Table 6. Frequency of occurrence (%) of stomach contents from lake whitefish collected during spring season in the Apostle Islands region, 2006.

Diet Item	Age N	7 2	8 5	9 17	10 17	11 10	12 11	13 11	14 8	15 12	16 7	17 4	18 4	19 2	20 2	21 1	22 1	23 3	Weighted average
Sphaeriidae		100	25	80	64	78	100	89	25	67	75	100	50	100	100	100	100	100	76
Amphipoda		0	75	67	45	78	100	33	50	33	50	100	50	100	0	0	0	33	57
Smelt/ unidentified fish		0	0	13	9	0	0	11	25	50	25	0	0	0	0	100	0	0	12
Mysis relicta		0	25	7	9	11	13	11	75	0	0	50	0	0	0	0	0	0	12
Fish eggs		0	0	27	18	22	38	11	25	0	25	50	50	0	100	0	0	0	20
Chironimidae		100	50	60	18	44	75	33	25	50	50	50	100	100	0	0	0	100	49
Gastropoda		0	75	7	0	0	0	11	0	0	0	0	0	0	0	0	0	33	7
Other invertebrates		100	25	27	18	33	13	0	0	50	0	0	0	0	0	0	0	100	2
Benthic debris		100	150	80	18	67	100	100	25	33	100	50	50	100	100	100	200	100	75

Table 7. Frequency of occurrence (%) of stomach contents from lake whitefish collected during summer season in the Apostle Islands region, 2006.

Diet Item	Age	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	23	24	31	Weighted average
	N	2	4	3	13	15	12	14	12	10	13	5	7	12	7	6	9	3	3	1	1	2	
Sphaeriidae		50	100	67	85	67	83	79	67	40	54	60	86	33	86	83	44	67	33	100	0	50	66
Amphipoda		0	0	0	23	60	58	43	67	50	77	40	86	33	57	67	56	67	33	100	0	50	51
Smelt/ unidentified fish		0	0	0	8	0	8	0	8	20	23	40	14	25	14	0	11	0	67	0	0	50	12
Mysis relicta		0	0	0	0	13	0	7	0	0	8	0	0	17	29	0	11	0	0	0	0	0	6
Fish eggs		0	0	0	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Chironimidae		0	0	33	62	60	58	57	50	60	38	40	57	25	86	67	44	67	33	100	100	0	51
Gastropoda		0	0	33	0	0	0	7	17	20	0	0	0	8	0	0	0	0	0	100	0	0	5
Bythotrephes cederstroemi		0	25	33	8	13	0	21	8	20	23	0	0	25	14	17	22	33	0	0	0	0	14
Other invertebrates		0	25	0	0	0	17	0	17	0	8	0	0	25	0	0	11	0	0	100	0	0	7
Benthic debris		0	0	0	46	47	67	57	67	50	62	100	86	58	71	83	67	67	0	100	100	50	58

Table 8. Composition by weight (%) of stomach contents from lake whitefish collected during winter season in the Apostle Islands region, 2006-2007.

Diet Item	Age	5	6	7	8	0	10	11	12	13	14	15	16	20	Weighted average
	N	2	5	17	15	10	10	11	8	11	4	4	2	2	
Sphaeriidae		0	0	0	65	1	21	6	12	0	8	26	28	0	14.6
Amphipoda		0	0	0	2	0	0	1	6	0	48	0	71	0	6.0
Smelt/ unidentified fish		0	0	0	0	81	74	0	42	0	0	0	0	0	19.0
Mysis relicta		0	0	0	0	0	0	9	0	0	0	0	0	0	1.1
Fish eggs		100	100	100	33	18	5	83	39	100	0	63	0	0	55.1
Chironimidae		0	0	0	0	0	0	0	0	0	44	0	1	0	2.3
Benthic debris		0	0	0	0	0	0	1	0	0	0	11	0	100	2.0

Table 9. Composition by weight (%) of stomach contents from lake whitefish collected during spring season in the Apostle Islands region, 2006.

Diet Item	Age	7	8	9	10	11	12	13	14	15	16	17	18	19	20	23	Weighted average
	N	2	5	17	15	10	10	11	8	11	4	4	2	2	1	3	
Sphaeriidae		0	0	42	50	9	60	24	0	0	0	0	100	3	0	5	23.8
Amphipoda		0	0	9	50	91	36	56	0	3	0	38	0	97	0	0	31.2
Smelt/ unidentified fish		0	0	44	0	0	0	15	100	93	100	0	0	0	100	0	30.9
Gastropoda		0	100	0	0	0	0	0	0	0	0	0	0	0	0	0	5.9
Other invertebrates		0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0.3
Benthic debris		100	0	5	0	0	4	5	0	0	0	63	0	0	0	96	7.9

Table 10. Composition by weight (%) of stomach contents from lake whitefish collected during summer season in the Apostle Islands region, 2006.

Diet Item	Age	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	23	31	Weighted average
	N	3	3	13	15	11	13	12	10	13	5	7	12	7	6	9	3	3	1	2	
Sphaeriidae		0	0	90	61	46	33	21	0	3	0	29	1	7	10	13	4	0	25	3	25.6
Amphipoda		0	0	0	4	4	8	3	2	10	2	52	1	10	54	30	0	0	50	87	11.1
Smelt/ unidentified fish		0	0	0	0	32	0	17	53	46	96	9	81	60	0	47	0	100	0	10	29.5
Mysis relicta		0	0	0	28	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	3.0
Chironimidae		0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2
Gastropoda		0	100	0	0	0	0	38	1	0	0	0	1	0	0	0	0	0	0	0	5.2
Bythotrephes cederstroemi		0	0	0	0	0	52	0	44	39	0	0	3	0	26	4	67	0	0	0	14
Other invertebrates		100	0	0	0	12	0	0	0	0	1	1	1	0	0	0	0	0	0	0	3.1
Benthic debris		0	0	10	4	6	8	21	0	2	2	9	12	23	10	7	29	0	25	0	8.5

Table 11. Percent composition, by weight, separated by depth strata, of stomach contents from lake whitefish collected in the Apostle Islands region, 2006-2007.

		Depth strata (m)		
		< 50	50-90	> 90
Diet item	N	345	39	23
Sphaeriidae		10.8	36.8	32.5
Amphipoda		11.2	45.6	23.
Smelt/ unidentified fish		38.7	0.0	0.0
Mysis relicta		0.6	0.7	1.3
Fish eggs		20.8	0.0	0.0
Chironimidae		0.4	0.7	0.0
Gastropoda		2.1	0.0	0.0
Bythotrephes cederstroemi		8.9	0.0	0.0
Other invertebrates		0.7	0.0	0.0
Benthic debris		5.8	16.2	42.4

fish ranged from 343 mm to 726 mm. Fish weights ranged from 431 g to 3482 g. Mean weight ranged from 980 g in 2006 to 1473 g in 1999 (Table 2). Mean weight varied significantly among some years but generally declined after 2003 (F = 32.9, df = 6, P = 0.00). Annual length-weight equation parameters also declined slightly in 2005 and 2006 (Table 2).

Ages were estimated from both the scales and otoliths for 313 whitefish collected during spring survey. Scale and otolith agreement ranged from 0% for ages 17-25 to 75% for age 5 (Figure 7). Variability in the scale age estimates at a given otolith age increased with fish age. Assuming otoliths provide a more accurate age estimate, scales generally underestimated the true age of whitefish after age five. Although age estimates from both scales and otoliths were not determined for younger fish, the available data indicated a likely high agreement of scale and otolith ages for fish less than age five.

The ages of 473 whitefish were estimated with otoliths from spring survey in 2002 through 2006. Mean lengths for most ages appeared to decrease initially, increase in 2005 and then decrease again in 2006 (Table 3). Mean length of age 11 whitefish did not change significantly from 2002 to 2006 (Figure 8; F = 1.18, df = 4, 75, P = 0.32).

Ages were estimated with otoliths from 246 of the 1,423 whitefish measured during the summer survey in 2006. The remaining measured fish were assigned ages using a length-age key to examine age distribution of summer survey catch. The age of whitefish ranged from 2 to 31 and the mean age was 9 (Figure 9). The whitefish with estimated ages (246) were used to estimate von Bertalanffy growth parameters. Mean length at age from summer survey ranged from 199 mm at age 2 to 710 mm at age 31 (Figure 10). The von Bertalanffy growth parameters L_∞ and K were 728 mm and 0.07, respectively.

Whitefish mortality rates were calculated from the age distributions developed from age-length keys for spring and summer surveys. Age groups used to estimate spring mortality rates ranged from 9 to 17 (Table 4). Annual total mortality (A) varied from 0.13 in 2004 to 0.44 in 2005 with a mean of 0.29 from 2003 to 2006. Age groups used to calculate mortality rates from summer survey were 9-18. Total annual mortality estimated from the summer survey was 0.16 in 2006.

Three hundred and seventy-one whitefish stomachs were examined to calculate frequency of occurrence (winter = 100, spring = 117, summer = 154). Although the diversity of prey groups changed with season, the most commonly consumed groups were similar throughout the year. During winter, the three most prevalent prey groups found in whitefish stomachs across age classes were Sphaeriidae (81%), fish eggs (66%), and Chironimidae (50%) (Table 5). During the spring season, the three most common prey groups across all ages were Sphaeriidae (76%), Amphipoda (57%), and Chironimidae (49%) (Table 6). During summer, the top three prey groups were Sphaeriidae (66%), Amphipoda (51%), and Chironimidae (51%) (Table 7). Age specific trends in prey occurrence were not apparent within any season but the number of different prey groups present increased from winter to summer. Benthic debris was commonly found in whitefish stomachs across seasons, however it likely was not purposely ingested but rather reflects a general benthic-siphon feeding strategy.

Table 12. Mean density (total number / m2) of amphipods by depth in Apostle Islands, 2003-2006. Standard deviation in parentheses. Samples not taken in 117 m stratum in 2003 and 2004.

	Depth strata (m)					
Year	< 27	27-46	46-64	64-82	> 82	117
2003	313 (392)	958 (743)	1315 (349)	2018 (508)	2631 (139)	
2004	64 (40)	1558 (655)	1730 (475)	1711 (537)	1481 (1189)	
2005	217 (161)	1098 (406)	1028 (295)	2465 (537)	2120 (346)	683 (250)
2006	223 (174)	773 (277)	1194 (310)	1501 (293)	2292 (710)	415 (165)

Three hundred and fifty whitefish stomachs were used to estimate percent composition by weight (winter = 97, spring = 105, summer = 148). Total stomach contents of 20 whitefish used to calculate frequency of occurrence were not used to calculate percent by weight. The prey items in these stomachs were too small to be weighed given our scale's precision. Neither the individual prey items nor the total stomach contents exceeded 0.0 so they were not used in analyses. During winter, fish eggs, rainbow smelt, *Osmerus mordax*, unidentified fish, and Sphaeriidae constituted 55.1%, 19.0%, and 14.6% of whitefish stomach contents, respectively (Table 8). During spring, fish eggs were too few to represent even 0.5% of the diet by weight, but amphipods became a more prominent component of diet (31.2%), along with smelt/ unidentified fish and Sphaeriidae (Table 9). Summer diet was still composed of primarily smelt/ unidentified fish, Sphaeriidae, and amphipods but also included *Mysis relicta* and spiny water flea (*Bythotrephes cederstromoemi*) (Table 10). Diet composition became more diverse from winter to summer, but within each season no age specific trends in whitefish diet were apparent. Depth specific changes in whitefish diet were found, with the most prey diversity found in waters less than 50 m deep (Table 11).

Lead author (MJS) collecting biological data from lake whitefish caught during annual surveys conducted off the *R/V Hack Noyes*.

Sixty-six benthic samples were collected from six depth strata during 2003-2006. Mean amphipod densities ranged from 64 individuals/ m^2 in <27 m depth strata (2004) to 2,631 individuals/ m^2 in >82 m depth strata (2003) (Table 12). High variability between station replicates resulted in the mean densities often having high standard deviations. Mean amphipod density generally increased with depth until the 117 m depth stratum (Table 12). Temporal trends in amphipod density were not apparent for any depth stratum from 2003 to 2006.

DISCUSSION

Management strategies aimed at lean lake trout rehabilitation have likely aided the recovery of the whitefish fishery since the 1970s. Many commercial regulations developed to protect lake trout may have been just as effective at rehabilitating whitefish (Ebener 1997). Commercial effort control was initiated to protect the lake trout from over harvest but also restricts whitefish harvest. Closure of the fishery during the spawning period in October and November also benefits both species. The creation of the Gull Island Refuge in 1976 (Schram et al.1995) and the Devils Island Refuge in 1981 (Bronte et al. 2002) established large areas closed to commercial and sport fishing. We feel these refuges in conjunction with other restricted use areas protect portions of the whitefish fishery and may serve as source populations. Given the apparent resiliency of the whitefish population to high commercial harvest, an important component of whitefish recovery may have been reestablishing lake trout as a buffer from sea lamprey predation. Even though other species contribute to sea lamprey production, lake trout are the preferred sea lamprey host in Lake Superior (Harvey et al. 2008). A disproportionate amount of scarring on lake trout given high abundance of both whitefish and lake trout in the Apostle Islands region further confirms sea lamprey preference for higher trophic predators (M. J. Seider, WDNR, unpublished data). The absence of top level predators during the period of lake trout population collapse and low abundance likely resulted in significant sea lamprey predation on whitefish.

The significant decline of smelt due to rehabilitation of many native species including lake trout may have also allowed whitefish populations to recover. Smelt are planktivorous and able to feed on the eggs and young of other species (Evans and Loftus 1987) and may compete with young whitefish for zooplankton. Direct evidence of a negative interaction in the Apostle Islands region is lacking however the decline of coregonines and other native species has been correlated with increased smelt abundance in the Great Lakes and inland lakes. Loftus and Hulsman (1986) determined smelt predation was the primary cause of whitefish recruitment failure in an inland lake in Ontario. Extensive stocking of lean lake trout and non-native salmonids coupled with an increase in the siscowet form of lake trout caused a significant decline in smelt abundance in the Apostle Islands region during the late 1970s (Gorman 2007; M. J. Seider, WDNR, unpublished data). Although commercial harvest was relatively low throughout the 1960-1970s whitefish abundance did not begin to rapidly increase until the substantial reduction of smelt. Further rehabilitation of lake trout and other native species continue to suppress smelt abundance which may greatly benefit whitefish reproduction.

The commercial fishery in the Apostle Islands region has changed dramatically since the 1970s. Commercial harvest remained relatively stable during the 1970s when whitefish abundance was low. Reallocation of the commercial fishery in the late 1970s due to the Gurnoe decision resulted in more fishers and therefore more effort deployed annually. During the 1980s, gill net effort and also catch rates increased due to greater whitefish abundance. Managers were concerned with the amount of gill net effort in the late 1980s and its effects on sustainability of the lake trout and whitefish fisheries. Commercial effort control was instituted to better regulate the fishery by limiting each fisher seasonally based on previous lake trout catch rates, which resulted in a rapid decline in gill net effort. Increased commercial harvest during the 1990s reflected the changes in whitefish abundance and the proliferation of trap net use in the state fishery. Trap net effort is not restricted by gill net effort control because the catch may be sorted. Thus trap net fishers can harvest whitefish and not be limited by gill net effort control. The commercial retirement program in 1997 reduced the number of licensed state fishers and further reduced the annual gill net effort. The recent increase in gill net effort has been due to mild winters allowing for more nets to be fished from a boat rather than through the ice. Deployment of gill nets from a boat is less labor intensive allowing for more nets set in the same amount of time.

The preferred gear of state fishers has shifted from gill nets to entrapment nets since the 1970s. Overall entrapment effort dropped during the 1980s but is currently similar to the 1970s. During the 1970-1980s pond nets were the primary entrapment gear but were gradually replaced by trap nets. Unlike gill nets, trap nets allow for live release of non-target species and sub-legal sized whitefish. State fishers continue to use gill nets during the winter and spring but most use trap nets the remainder of the year. In contrast to state fishers, the preferred gear of tribal fishers has been and continues to be gill nets. Currently only one tribal commercial fisher deploys trap nets in Wisconsin waters.

A recreational fishery has emerged with increased whitefish abundance. Although annually variable, the overall increase in estimated sport harvest follows observed population trends. Currently sport harvest is almost exclusively during the ice fishery and dependent on safe ice conditions (which vary annually). Increased catchability due to higher abundance and better technologies has enabled sport fishers to more consistently catch whitefish. Sport harvest is underestimated because the creel survey was designed to sample the lake trout fishery which does not always overlap spatially and temporally with the whitefish fishery.

The spring and summer surveys were not initiated to target whitefish but CPUEs from both surveys reflected an increase in whitefish abundance. Spring survey stations were chosen to pursue lake trout and whitefish are not consistently captured at all stations which may contribute to annual CPUE fluctuations. For example, 74% of the total catch since 1980 was recorded in only 11 of the 31

Sport anglers generally catch lake whitefish during the ice fishery.

current stations. Given the disparity of station catches, the spring survey may still provide a long term indicator of whitefish abundance since the general increasing trend was supported by the summer survey. The summer survey is a graded mesh survey and samples a wider size range of fish and should be a better indicator of whitefish abundance. However, not all summer survey sampling locations are in known whitefish habitats. Thus to ideally monitor population characteristics, a targeted whitefish survey could be established.

Growth and condition did not change dramatically as has been observed in the other Great Lakes. Whitefish growth and condition has declined since the early 1990s in Lake Michigan (Pothoven et al. 2001; Madenjian et al. 2002; Debruyne et al. 2008), Lake Huron (Mohr and Ebener 2005), and Lake Ontario (Lumb et al. 2007). Although several potential causes have been suggested, a major factor in some regions has been the establishment of the exotic zebra mussel (*Dreissena polymorpha*). Reduced availability of *Diporeia* spp. following zebra mussel invasion has caused whitefish to switch to less energetically valuable prey items (Pothoven et al. 2001; Pothoven and Madenjian 2008). Consumption of less energetically valuable prey items has reduced dietary lipid which has reduced growth and condition (Wright and Ebener 2005). Unlike the other Great Lakes, Lake Superior has thus far not seen drastic ecosystem changes related to the invasion of dreissenid mussels. Zebra mussels are present in low densities in Lake Superior but our benthic surveys have not shown a reduction of amphipods that would possibly cause a similar decline in whitefish growth and condition. Both the length-weight parameters and mean length at ages indicated slight decreases in growth and condition after 2002. Slight decrease in whitefish growth and condition in the Apostle Islands region is probably due to density dependence as seen in other populations in Lake Superior (Kratzer et al. 2005).

Relatively low total mortality rates estimated from spring and summer surveys (0.29 and 0.16) were unexpected given the current level of commercial harvest. A similar total annual mortality rate (0.24) was reported in Chequamegon Bay where commercial harvest is not allowed (Devine et al. 2005). Estimated annual mortality rates from other commercially exploited waters in Lake Superior ranged from 0.30 to 0.75 during 1998-2000 (Petzold 2007). Schneeberger (2006) reported a total instantaneous mortality rate of 0.52 (total annual mortality = 0.40) for Michigan waters of Lake Superior adjacent to the Apostle Islands in 2000-2004. The Gull Island and Devils Island fish refuges could influence mortality rates but their exact effect could not be quantified. Low sample size prevented separate calculation of mortality rates both inside and outside the refuges. Commercial harvest is at historic highs yet annual mortality estimates were below those of adjacent Michigan waters and those reported in Healey (1975) for exploited populations. We feel the combination of existing commercial fishing regulations and the effect of the refuges is currently buffering the population against over-exploitation.

Historical growth and mortality reported for whitefish were likely influenced greatly by the use of scales instead of otoliths for aging. To our knowledge, the accuracy of otoliths for aging whitefish has not been validated. Muir et al. (2008) warned the scale method of age estimation for whitefish from Lake Huron may be unreliable under certain growth conditions. Validation of aging methods for other Lake Superior fishes has consistently suggested the need to use otoliths especially for larger (older) fish (Schreiner and Schram 2000). Whitefish tag returns have further validated the longevity of whitefish and the need to use otoliths (M. J. Seider, WDNR, unpublished data). For example, a whitefish (703 mm) tagged during a spawning survey in 1979 was recaptured in commercial nets in 1998. Age at maturity may have been younger when abundance was lower but given the fish's size we still feel the fish was at least 10 years old when initially tagged and was a minimum of 29 years old when recaptured. The summer survey age distribution additionally showed the longevity of whitefish even during the current period of high commercial harvest. Age distributions and mean length at ages reported by Dryer (1963) indicated whitefish populations were dominated by young fish that grew relatively fast when compared to our data. While these population characteristics could be expected, given many of the stocks studied by Dryer (1963) were likely being over-exploited, we believe these conditions were an artifact of under aging caused by the use of scales. Historical analyses of growth and mortality may not truly reflect past conditions and may not aid evaluations of current conditions. Continued monitoring and development of long term data sets may better aid in the evaluation of current population status.

Similar to elsewhere in the Great Lakes, amphipods constituted a large portion of whitefish diets in the Apostle Islands region. Anderson and Smith (1971) reported amphipods were the main prey item of young whitefish (< 260 mm) throughout the year in western Lake Superior. When available *Diporeia* spp. was an important diet item in Lake Michigan whitefish during 1999-2001 (Pothoven 2005). Owens and Dittman (2003) found whitefish were highly reliant on *Diporeia* spp. for food in Lake Ontario. Lumb et al. (2007) discovered amphipods were seasonally important in Lake Ontario but did not specifically find *Diporeia* spp. present in any whitefish stomachs. Examinations of whitefish diet in Lake Huron during 2002-2004 found *Diporeia* spp. were not a significant prey item (Pothoven and Nalepa 2006). However, *Diporeia* spp. abundance was much lower than historically reported and may not have been abundant enough to be a profitable food source (Pothoven and Nalepa 2006).

Whitefish commonly fed on amphipods, sphaerid clams, and chironomids throughout the year but they were also opportunistic predators. Prey items such as fish eggs, rainbow smelt/unknown fish, and spiny water fleas were seasonally more notable likely due to increased availability. Similar to previous studies, fish eggs were found in stomachs especially during the fall and winter months (Anderson and Smith 1971; Lumb et al. 2007). In 2006, a sample of fish eggs collected from whitefish stomachs during winter were determined to be from cisco (*Coregonus artedi*) (W. Stott, United States Geologic Service Great Lakes Science Center, unpublished data). Ciscos spawn in fall/early winter, broadcasting their eggs over large areas, providing a readily available and abundant prey item for whitefish. During the summer season diet items were especially diverse; possibly a reflection of greater prey availability throughout the warmer months. Regardless of season, prey diversity was almost always higher in waters less than 50 m. In addition to amphipods, whitefish consumed rainbow smelt, spottail shiners (*Notropis hudsonius*), trout perch (*Percopsis omiscomaycus*), and spiny water fleas in Chequamegon Bay, an area less than 25 m in depth (Devine et al. 2005). Diets of Lake Michigan whitefish collected from nearshore (<30 m) and offshore (31-46 m) areas differed but the offshore diet was still more diverse than found in this study (Pothoven 2005). Whitefish diet in Lake Huron varied with fish size, season, and geographic location (Pothoven and Nalepa 2006). Seasonal and bathymetric diversity in prey items found in this study further supports the reported dietary flexibility of whitefish in the Great Lakes (Anderson and Smith 1971; Devine et al. 2005; Pothoven 2005; Pothoven and Nalepa 2006; Lumb et al. 2007).

Bathymetric trends in amphipod density from this study were similar to those observed in other regions of Lake Superior. Similar to this study, Auer and Kahn (2004) found low abundance of *Diporeia* spp. in shallow water, peak abundance in depths 50-100 m and lower abundance in water greater than 200 m. They attributed peak abundance to the sediment transition from pure sand in the near shore to silt, clay sediment found in intermediate depths. A similar bathymetric trend in the proportion of amphipods in whitefish stomachs also supports reported abundance trends (Table 11). Low abundance of amphipods and greater potential prey variety in shallower water probably explains the increased whitefish diet diversity in waters less than 50 m.

Amphipod densities have not declined in the Apostle Islands as they have in portions of the Great Lakes. Scharold et al. (2004) reported *Diporeia* spp. populations in the western half of Lake Superior did not decline from 1994 to 2000 and we did not find consistent changes in amphipod densities from 2003 to 2006 (Table 12). *Diporeia* spp. abundance is actually relatively higher in the Apostle Islands region than adjacent waters (Scharold et al. 2004). We feel higher amphipod densities are probably due to the amount of area with the optimal depth and sediments that contribute to peak amphipod density (Auer and Kahn 2004).

SUMMARY AND MANAGEMENT RECOMMENDATIONS

Commercial harvest and fishery independent surveys both indicated whitefish abundance has increased dramatically since 1970. Commercial harvest is at an all time high yet relative abundance of whitefish from spring and summer surveys continues to increase. Available data indicated growth and condition of whitefish may be beginning to decline. Although diverse, whitefish diets indicated the importance of benthic organisms, especially amphipods. Benthic surveys have not shown a consistent decline in amphipods within the Apostle Islands region, thus no major shifts in forage appear to be causing a decline in whitefish growth and condition. More likely increased abundance has caused a density dependent reduction in growth and condition as seen in other Great Lakes populations (Kratzer et al 2005; Debruyne et al. 2008). Density dependent decrease in growth in the face of high commercial harvest is counterintuitive considering Healy (1975) showed that growth of previously unexploited whitefish populations increased when populations became exploited. Conservative regulation of the whitefish fishery through measures such as commercial gill net effort control, fish refuges, and closed seasons is likely providing biological sustainability in the face of high commercial harvest.

We recommend the following:

1) Expand the collection of otoliths from whitefish throughout the Apostle Islands region. Collection of aging structures across all year classes is essential for improved growth analyses and the development of catch-at-age models.

2) Continue to monitor whitefish diet. Diet information will be a critical component of measuring the potential effects of future invasive species on native species.

3) Benthic sampling should be done annually. Highly variable sampling densities cause annual variability that may not reflect actual population changes. Monitoring long term trends may be more appropriate than reacting to annual variability.

4) Develop further whitefish surveys that target infrequently captured life stages. Summer survey captures relatively few young whitefish and may not accurately reflect year class strength at early ages. Although current surveys capture spawning sized fish, fall surveys may better monitor population trends. A targeted survey could help further supplement data required for the development of a whitefish catch-at-age model.

5) Conduct another tagging study to compare movement during past periods of low abundance and the current period of higher abundance.

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Appendix I. Commercial harvest (kg), estimated sport harvest (number), summer and spring survey geometric catch-per-unit-effort (CPUE) with 95% confidence intervals in parentheses.

Year	Commercial harvest (kg)	Sport harvest (#)	Summer survey CPUE (95% CI)	Spring survey CPUE (95% CI)
1970	59,422	-	1.5 (0.0-10.1)	-
1971	102,060	-	1.2 (0.0-5.6)	-
1972	107,503	-	2.4 (0.2-8.5)	-
1973	101,153	-	0.9 (0.1-2.3)	-
1974	102,514	-	3.4 (1.0-8.7)	-
1975	133,358	-	3.6 (0.6-11.7)	-
1976	106,596	-	3 (0.1-3.5)	-
1977	119,750	-	0.8 (0.0-2.4)	-
1978	122,926	-	1.0 (0.1-2.5)	-
1979	115,214	-	0.9 (0.0-2.6)	-
1980	155,131	0	2.3 (0.3-7.6)	-
1981	94,349	0	-	0.6 (0.0-1.6)
1982	78,473	0	1.9 (0.4-4.9)	0.2 (0.1-0.3)
1983	75,298	0	-	0.2 (0.0-0.4)
1984	60,329	0	3.9 (0.8-12.4)	0.4 (0.0-0.9)
1985	101,606	0	-	1.0 (0.5-1.6)
1986	101,153	0	2.9 (0.4-9.9)	2.3 (1.4-3.7)
1987	154,224	0	-	1.1 (0.6-1.8)
1988	315,252	0	4.3 (1.0-12.9)	2.3 (1.3-3.7)
1989	342,468	26	-	2.5 (1.5-3.9)
1990	318,881	73	2.9 (0.6-8.8)	2.4 (1.4-4.0)
1991	537,062	80	-	2.4 (1.3-4.0)
1992	85,730	69	6.7 (2.5-15.9)	3.1 (1.8-5.2)
1993	187,337	287	-	4.0 (2.3-6.6)
1994	203,213	138	7.3 (1.6-26.0)	1.9 (1.1-3.1)
1995	135,173	104	-	2.2 (1.1-3.8)
1996	247,666	27	-	-
1997	395,086	137	-	3.1 (1.6-5.6)
1998	423,209	192	13.4 (3.7-43.0)	5.0 (2.9-8.4)
1999	405,518	2,197	-	7.8 (4.3-13.5)
2000	411,869	3,436	14.3 (3.5-50.3)	7.5 (4.2-12.9)
2001	415,498	1,612	-	-
2002	416,405	1,095	13.2 (4.3-37.4)	6.2 (3.0-12.2)
2003	464,620	828	-	8.6 (4.4-16.4)
2004	519,290	534	17.4 (7.2-40.1)	6.5 (3.1-12.9)
2005	630,388	2,733	-	6.9 (3.3-13.6)
2006	624,479	1,554	15.5 (3.6-57.9)	2.2 (0.8-4.6)