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Survey of Siscowet Lake Trout at Their Maximum Depth in Lake Superior

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ABSTRACT. *The siscowet Salvelinus namaycush is a deepwater morphotype of lake trout in Lake Superior. As part of a standardized lake-wide survey in 2006 to assess siscowet populations, bottom-set, multi-mesh gill nets were fished at 36.6 m depth intervals from near shore areas to the deepest waters in south-central Lake Superior. Siscowet length distributions, diet compositions, and sea lamprey wounding rates were compared for three depth zones: shallow (< 200 m), deep (200–394 m), and deepest (395–399 m). There were 39 siscowets collected in proximity to Lake Superior's greatest recorded depth of 405 m. To our knowledge, this is the greatest depth that fish have been collected in the Great Lakes. Higher proportions of siscowets ≤ 500 mm were caught in the shallow zone compared to deeper zones. Deepwater sculpins were the dominant prey for small siscowets (< 600 mm) across all depth zones. The diet of large siscowets (≥ 600 mm) among all depth zones comprised mostly of coregonines and burbot Lota lota. Terrestrial insects were observed in the diet of siscowets in all depth zones, indicating migration to the surface. Type A sea lamprey wounding rates were higher for large (≥ 600 mm) than small siscowets among all depth zones. The highest wounding rate was observed on large siscowets in the deep zone. Recent work indicates that siscowets are the most abundant lake trout form and this research indicates that siscowets use the maximum depths of Lake Superior.*

INDEX WORDS: *Siscowet, lake trout, diet, sea lamprey, deep water, Lake Superior, depth distribution.*

INTRODUCTION

Lake Superior is the coldest (mean annual surface temperature = 3.6°C) and the deepest of the Great Lakes with the maximum depth at 405 m and an overall average depth of 147 m (Fuller *et al.* 1995, Horns *et al.* 2003). These attributes have shaped the fish fauna of Lake Superior, particularly the top predator lake trout *Salvelinus namaycush*. There are three recognized morphotypes of lake trout in Lake Superior: the lean form, the siscowet form, and the humper form (Eschmeyer and Phillips 1965, Lawrie and Rahrar 1973, Burnham-Curtis and Smith 1994). Leans occupy all of the Great Lakes and are the shallowest form found generally in waters less than 100 m. Siscowets are most abundant at depths greater than 100 m, though they are frequently observed in more shallow waters (Bronte *et al.* 2003). The humper is the least known and least common form of lake trout and derives its common name from its habitat, which are offshore sea mount-like structures (humps) (Burnham-Curtis and Bronte 1996). Outside of Lake Superior,

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FIG. 1. Lean (top) and siscowet (bottom) lake trout of Lake Superior.

humpers (also called klondikes) have been stocked recently in Lake Erie (GLFC 2007) and there were historic accounts of siscowet-like lake trout in Lakes Michigan and Huron (Brown *et al.* 1981). Furthermore, deepwater forms of lake trout similar to siscowets and humpers have been reported in other North American large, deep lakes (Zimmerman *et al.* 2006, 2007).

Most research and management has been focused on lean lake trout because of its long established socio-economic value and the tragic collapse of stocks in all of the Great Lakes in the middle part of the 20th century (Hansen 1999). Subsequent lean lake trout recovery programs have re-established self-sustaining populations in Lake Superior and maintained large standing stocks of hatchery-produced lake trout in all of the other Great Lakes (Elrod *et al.* 1995, Eshenroder *et al.* 1995, Hansen *et al.* 1995, Holey *et al.* 1995). Outside of Lake Superior, no significant amount of natural recruitment of lean lake trout has occurred in the Great Lakes since the 1940s, though low levels of natural reproduction has been observed in Lake Huron more recently (e.g., Reid *et al.* 2001, Riley *et al.* 2007). Research priorities for lake trout recovery programs in the lower four Great Lakes highlight the need to evaluate reintroductions of lake trout in deep water (Eshenroder *et al.* 1999, Janssen *et al.* 2007). There is little historical information documenting the population trajectories of siscowets before, during, and after the collapse of lean lake trout populations in Lake Superior. However, recent papers indicate that siscowet abundance has increased in the last 40 years (Bronte *et al.* 2003, Bronte and Sitar 2008).

The bathymetric distribution of lean and siscowet lake trout is associated with key anatomical differences. Leans have a fusiform body, long, pointed snout, small eyes, small fins, and relatively low lipid levels (hence the name lean). In contrast, siscowets, whose vernacular name is fat trout, have a stouter body, a shorter, convex snout, larger eyes, larger fins, and significantly higher lipid content (Fig. 1) (Khan and Qadri 1970, Burnham-Curtis 1993, Moore and Bronte 2001). The high lipid content in siscowets is thought to be an adaptation for vertical migration in deep water (Eshenroder and Burnham-Curtis 1999, Henderson and Anderson 2002, Hrabik *et al.* 2006). Similar depth-related morphological differences in lake trout forms have been reported from large, northern Canadian lakes (Zimmerman *et al.* 2006, 2007) which have both a shallow and deepwater lake trout morphotype. As in the lake trout forms in those large Canadian lakes, there are important ecological differences between leans and siscowets such as diet, bathymetric distribution, and time of reproduction.

Little has been reported on siscowets sampled in their principal habitat because few surveys have been conducted in deep water areas of Lake Superior until more recently. Recent papers indicate that siscowets are likely the most abundant predator in Lake Superior (Ebener 1995, Bronte *et al.* 2003) and given that Lake Superior is predominantly deep water, it is important to know how much of the abyss is occupied by siscowets and associated fish species.

As an effort to expand understanding of siscowet biology and distribution in Lake Superior, a coordinated inter-agency siscowet survey was initiated in 1997. The siscowet survey has been conducted every three years and attempts to sample all depths in selected areas across the lake using bottom-set gill nets. Prior to 2006, the maximum depth sampled in the siscowet survey was less than 300 m. In the 2006 siscowet survey, the sampling was expanded to include the greatest depth (405 m) in Lake Superior. The deepest recorded collection of fish in Lake Superior that was found was a 333 m deep bottom trawl survey in 2006, north of Grand Marais, Michigan (Lori M. Evrard, Lake Superior Biological Station, Great Lakes Science Center, U.S. Geological Survey, personal communication). This trawl tow collected siscowet lake trout, burbot *Lota lota*, and deepwater sculpin *Myoxocephalus thompsoni*. Based on this information and data from previous siscowet surveys, siscowets, burbot, and kiyi *Coregonus kiyi* were expected to be found at the deepest area in Lake Superior using bottom-set gill nets. Although deepwater sculpin may also inhabit the greatest depths of Lake Superior, they would not likely be detected because they would not be vulnerable to the gill nets.

The objectives of this paper were to: 1) document the first fish collected near the maximum depth of Lake Superior, and 2) provide brief comparisons of siscowets collected at the maximum depth with those sampled in shallower areas in south-central Michigan waters of Lake Superior. Overall, this paper explores whether there were indications that siscowet population structure and ecology differs with depth. The first hypothesis was that siscowet population structure in the deepest area of Lake Superior was similar to those in shallower waters. Thus, siscowet length compositions were compared among three depth zones: shallow (< 219 m), deep (between 200 and 394 m), and deepest (395–399 m). The second hypothesis was that siscowets in the deepest area of Lake Superior would differ in diet and sea lamprey wounding rates than in shallower areas. Therefore, diet compositions and sea lamprey wounding rates of small (< 600 mm) and large (≥ 600 mm) siscowets were compared among the three depth zones.

METHODS

In June 2006, as part of the inter-agency, lakewide, coordinated siscowet lake trout survey in Lake Superior, an 823 m long by 1.8 m high multimesh, bottom-set gill net gang was fished overnight at nearly every 36.6 m (20 fathoms) depth interval from the shallowest to the greatest depth in two regions near Marquette and Munising, Michigan (Table 1, Fig. 2). Each gill net gang (hereafter called net) comprised nine nylon, multifilament panels that were 91.4 m long by 1.8 m high with the following stretched mesh sizes: 5.1, 6.4, 7.6, 8.9, 10.2, 11.4, 12.7, 14.0, and 15.2 cm. There were 6 nets fished in the Marquette region with the deepest net at 194 m, and 11 nets in the Munising region with the deepest net at 399 m (W86°35.953′, N46°54.790′) which was in close spatial proximity to Lake Superior's deepest sounding. (The deepest sounding, 405.4 m, was obtained at W86°35.906′, N46° 54.480′, Nigel Wattrus, U. Minnesota-Duluth, personal communication.) All net positions were geo-referenced using a Northstar 951X differential Global Positioning System aboard the Michigan Department of Natural Resources' Lake Superior Research Vessel *Judy*. Depth recordings were measured using a Raytheon L365 Fishfinder and a Ratheon V900 color Echosounder.

Total length, weight, sea lamprey wounding, gender, and stage of maturity were recorded from each fish collected. Stomachs were extracted from most lake trout and frozen for subsequent laboratory analyses. Wet weight was measured for each prey category in each stomach and expressed as proportions by dividing the prey weight by total ration. Prey fishes were identified to the lowest possible

TABLE 1. Fish catch composition from the June, 2006 siscowet survey in Marquette and Munising areas of Lake Superior. Species codes are: Sis = siscowet lake trout, LLT = lean lake trout, Bur = burbot; Cis = cisco, Blo = bloater, Kiy = kiyi, SJC = shortjaw cisco, LWF = lake whitefish, RWF = round whitefish, and LNS = longnose sucker. The catch at each station was from a standardized 823 × 1.8 m multimesh, bottom gill net that was fished overnight. The net stretched mesh sizes were: 5.1, 6.4, 7.6, 8.9, 10.2, 11.4, 12.7, 14.0, and 15.2 cm.

Station number	Depth zone	Actual depth range (m)	Species									
			Sis	LLT	Bur	Cis	Blo	Kiy	SJC	LWF	RWF	LNS
Marquette												
566	shallow	29–33		11						1		
567	shallow	46–53	3	9	1							
570	shallow	102–107	19	1			2		1			
571	shallow	119–122	14			2	1					
573	shallow	148–159	38	3			1					
575	shallow	191–194	78	3	2	1		4				
Munising												
650	shallow	28–37		2		4				1	1	9
652	shallow	41–69	33	10		1				3		2
639	shallow	74–107	29	3			13		1	1		
640	shallow	110–134	34	3	1	4	1	3	6			
638	shallow	146–167	28	3		1		7	4			
642	shallow	186–195	29	4		1		5				
643	deep	214–241	32					3				
644	deep	258–280	13									
645	deep	290–312	17									
646	deep	330–346	23		3							
648	deepest	395–399	39									

taxon depending on the degree of digestion. Prey insects were identified to the order level when possible, and were categorized as terrestrial or aquatic insects for this paper. Key aquatic macro-invertebrates identified in the diet were opossum shrimp *Mysis* and the amphipod *Diporeia.* Prey item categories were established for prey that made up at least 2% of the diet. These included burbot, coregonines, kiyi, deepwater sculpin, unidentifiable fish remains, opossum shrimp, *Diporeia*, terrestrial insects, and unidentifiable salmonine. The coregonines category was for prey fish identified as a member of the *Coregonus* genus, but not distinguishable at the species level. This included cisco *C. artedi*, bloater *C. hoyi*, shortjaw cisco *C. zenithicus*, kiyi, lake whitefish *C. clupeaformis*, and round whitefish *Prosopium cylindraceum*. Kiyi warranted a separate category because significant numbers of this species were able to be identified in siscowet stomachs. Unidentified salmonines category was for prey fish identifiable to the following genera: *Salvelinus*, *Oncorhynchus*, and *Salmo*. Other prey items that each made up less than 2% of the diet were pooled into the *other* category, and in some instances included the prey species listed above.

Siscowet length distributions were compared among the three depth zones using the two-tailed Kolmogorov-Smirnov test (Siegel and Castellan 1988). Comparisons were made using 100 mm length bins with the null hypothesis that length distributions differed between depth zones. Statistical significance was established at $\alpha = 0.05$.

Siscowet diet compositions were compared by length group (small, large) and depth zone (shallow, deep, deepest). Siscowet length distributions from survey catches were compared among depth zones. The small and large siscowet length groups for comparing sea lamprey wounding rates and diet compositions were established because sea lampreys are size-selective parasites on lake trout (e.g., Swink 1991) and 600 mm is close to the length at which survival from sea lamprey attacks starts to asymptote in lake trout (Swink 2003). Moreover, ontogenetic changes in maturation and diet have been reported for lake trout near 600 mm (e.g., Madenjian *et al.* 1998, Ray 2004, Sitar and He

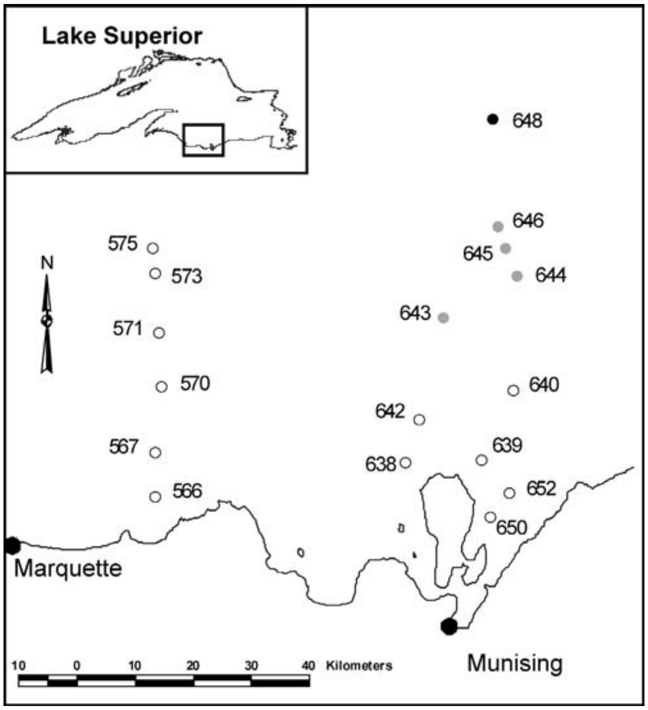

FIG. 2. Siscowet survey sampling stations in the Marquette and Munising areas of Lake Superior during June 2006. White circles are shallow depth zone (< 200 m) stations, gray circles represent deep zone stations (200–394 m), and black circle is the deepest zone station (395–399 m). Specific depth ranges for each station number are in Table 1.

2006). The shallow zone was delineated as the maximum depth range that lean lake trout have been sampled in this survey. The deep zone represented a depth range that siscowets and deepwater fishes have been sampled and lean lake trout have rarely been found. The deepest zone represented an area of Lake Superior that had not been previously sampled for fish.

Sea lamprey wounding rates and percentage of fish with wounds were estimated for small and large siscowets in each depth zone. Sea lamprey wounds on siscowet were categorized as type A, those penetrating the musculature, or type B, those not penetrating the musculature based on the classification by King (1980). Type A wounds can be lethal and are commonly used to index sea lamprey-induced mortality on lake trout (Bence *et al.* 2003). Type B wounds have low lethality (Swink 2003), but may be informative for indexing overall lamprey attack rates. Sea lamprey wounding rate was reported as wounds per 100 fish which was the total number of type A or B wounds divided by the number of fish sampled then multiplied by 100. Summarizing wounding rates this way infers that the rates can vary according to siscowet or sea lamprey abundance and can index the relative effects of sea lamprey predation (Ebener *et al.* 2003). The percentage of fish with wounds represented a measure of the overall incidence of wounds or the fraction of siscowets successfully attacked by sea lampreys. For sea lamprey wounding rates for each wound type (A or B), least square means were generated by ANOVA on square root transformed wounds per fish (see Sitar *et al.* 1997) to compare wounding rates by length group and depth zone (PROC GLM, SAS Institute 2003). Significant tests ($P < 0.05$) were conducted using the Tukey-Kramer procedure for multiple comparisons of least square means (Kutner *et al.* 2005).

RESULTS

Across all sampling stations, nine species of fish were collected: lake trout (lean and siscowet), burbot, cisco, kiyi, bloater, shortjaw cisco, lake whitefish, round whitefish, and longnose sucker *Catostomus catostmus*. Lean lake trout were caught only at depths less than 200 m, in comparison siscowets were caught only in waters > 40 m (Table 1). Siscowets were the only fish collected at the maximum depth sampled. The only other species caught in the nets beyond 280 m was burbot.

The length distribution of siscowets differed between the shallow and deep zones with higher proportions of small fish caught in the shallow zone ($P < 0.0003$) (Fig. 3). There were no statistical differences for all other comparisons of length distributions. However, in the deep and deepest zones, more than 60% of siscowets were larger than 500 mm. There were no siscowets less than or equal to 400 mm in the deepest zone and only 3.5% of siscowets of this size range were found in the deep zone. In the shallow zone, 16% of the siscowet caught were ≤ 400 mm and more than half were less than or equal to 500 mm.

Fish dominated the diet of siscowets in all depth zones and comprised principally of burbot and coregonines in large siscowets and deepwater sculpins in small siscowets (Fig. 4). In the shallow zone, the diet of small siscowets was diverse and comprised 30% invertebrates (mostly *Diporeia*) and 66% fishes (primarily coregonines and deepwater sculpin) (Fig. 4). The diet of large siscowets in the shallow zone comprised mostly of coregonines and

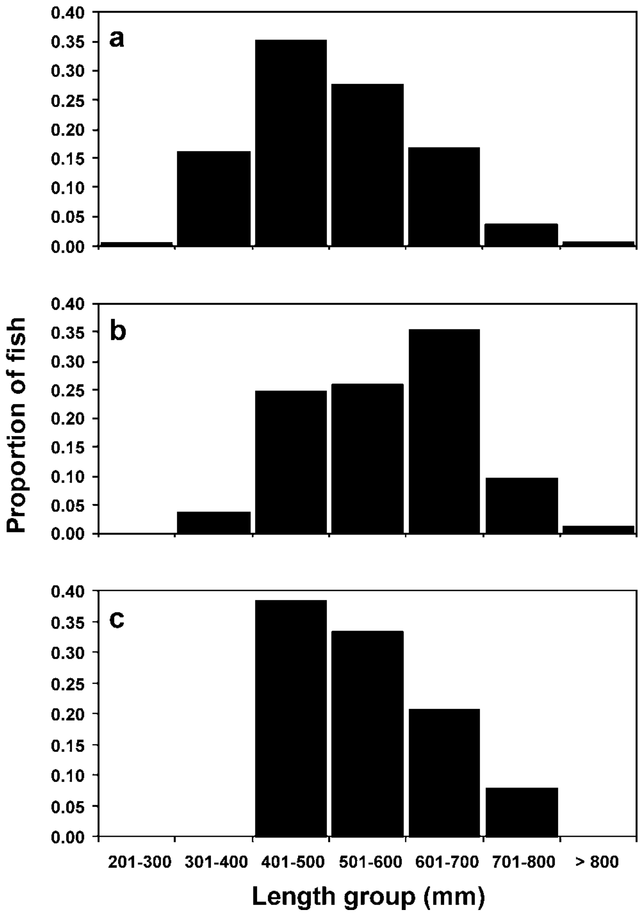

FIG. 3. Length distribution of siscowets sampled in the a) shallow (< 200 m), b) deep (200–394 m), and c) deepest (395–399 m) zones in the Marquette and Munising areas of Lake Superior during June 2006. Data presented as proportion of siscowets per 100 mm length group per depth zone.

burbot. In the deep zone, small siscowet diet comprised 62% deepwater sculpins and 27% kiyi and large siscowet stomachs contained mostly coregonines and burbot. In the deepest zone, deepwater sculpin made up more than 80% of small siscowet diet, and burbot dominated the diet of large siscowets. Overall, the dietary proportion of deepwater sculpin increased with depth in both small and large siscowets.

Notable prey items found in small amounts (< 2%) in siscowet diets among depth zones included fishes, terrestrial insects, *Mysis*, and *Diporeia*. Other fishes identified in small amounts in the shallow zone included ninespine stickleback *Pungitius pungitius*, rainbow smelt *Osmerus mordax*, and slimy sculpin *Cottus cognatus*. In addition, the stomach of a large siscowet in the deep zone contained a lake trout of unknown morphotype, which made up 5.6% of prey biomass. Terrestrial insects (e.g., ants *Hymenoptera* and beetles *Coleoptera*) were observed in the diet of siscowets in all depth zones. In all depth zones, *Mysis* were found in the diet of small and large siscowets. There were *Diporeia* found in diet of small siscowets in the shallow and deep zones, and in large siscowets in the shallow zone.

Sea lamprey wounds were observed on small and large siscowets in all depth zones and the incidence of fish with wounds ranged from 6.7% to 68.3% (Table 2). The percentage of siscowets with wounds was higher for large siscowets than for small siscowets. Type A wounding rates were significantly higher on large siscowets than on small siscowets. Small siscowet type A wounding rates ranged from 5.4 wounds per 100 fish in the shallow zone to 17.9 wounds per 100 fish in the deepest zone, but were not statistically different among depth zones. Large siscowet type A wounding rates were significantly higher in the deep zone than in the shallow zone. Large siscowet type A wounding rates did not differ significantly between the deepest zone and the other depth zones. The only statistical differences in type B wounding were between large and small siscowets in the shallow zone and between shallow zone large siscowets and deep zone small siscowets.

DISCUSSION

Siscowet lake trout have now been confirmed to inhabit the greatest depths in Lake Superior and the Great Lakes. In this survey across all depths of Lake Superior, siscowets were relatively abundant at all bottom depths starting at 40 m, whereas lean lake trout had a much narrower depth distribution, and were most abundant at depths shallower than 50 m. Despite their bottom depth distributional differences, both leans and siscowets can be found throughout the water column. Mattes (2004) reported that lean lake trout occupied all depths in the water column throughout all seasons based on data recovered from fish implanted with temperature and depth recorders during the fall. Siscowets and leans are harvested by sport anglers and commercial fisheries throughout the warm water season at various depths. Moreover, the presence of terrestrial insects in the stomachs of siscowets from Lake Superior also indicates both vertical movement to the surface and horizontal movement to near shore areas. The

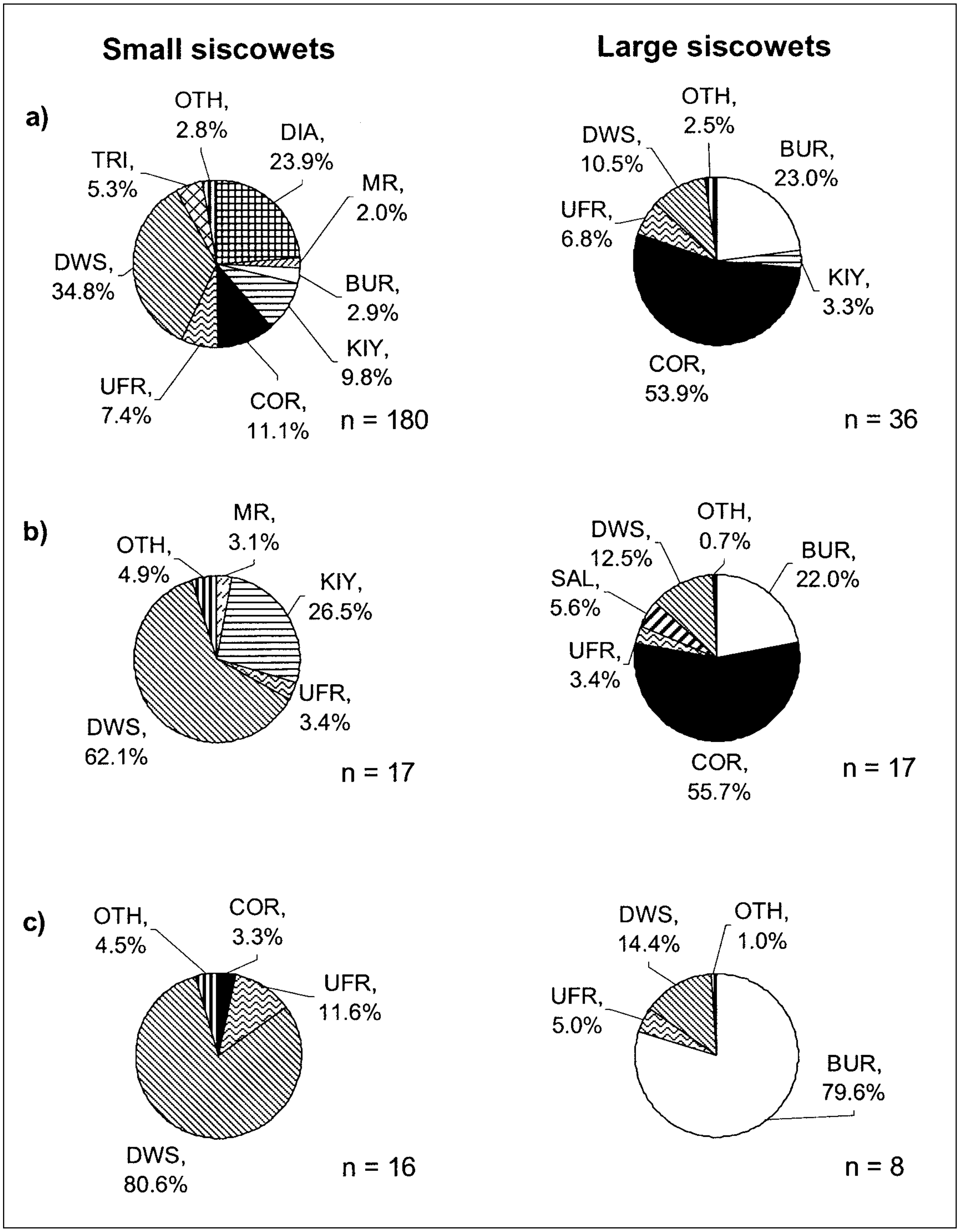

FIG. 4. Diet composition of small (< 600 mm) and large (≥ 600 mm) siscowet lake trout collected in the Marquette and Munising areas of Lake Superior during June 2006. Data are presented as percent wet biomass for three depth zones: a) shallow (< 200 m), b) deep (200 to 394 m), and c) deepest (395–399 m). Species codes are: BUR = burbot, COR = coregonines, DIA = Diporeia, DWS = deepwater sculpin, KIY = kiyi, MR = opossum shrimp, SAL = unidentifiable salmonine, TRI = terrestrial insects, and UFR = unidentifiable fish remains. Prey items composing less than 2% of the diet were pooled in the "other" (OTH) category.

TABLE 2. Sea lamprey wounding rate and percentage of small (< 600 mm) and large (≥ 600 mm) siscowet lake trout with sea lamprey wounds sampled in the Marquette and Munising areas of Lake Superior, June 2006. Depth zones were < 200 m for shallow, between 200 and 394 m for deep, and 395–399 m for deepest. Wounding rate was the total number of type A or type B wounds per 100 fish (King 1980). Values containing the same superscripts within each wound type are not significantly different from one another at α = 0.05. The Tukey-Kramer procedure was used to compare least square means from ANOVA of square root transformed wounding rate.

Depth zone	n	% of fish with any wounds	Wounding rate (wounds per 100 fish)	
			type A	type B
Small siscowets				
shallow	240	6.7	5.4^{A}	2.1^{X}
deep	46	15.2	4.7^{A}	4.3^{X}
deepest	28	17.9	17.9^{A}	$7.1^{X,Y}$
Large siscowets				
shallow	41	58.5	83.1^{B}	20.0^{Y}
deep	63	68.3	138.5^{C}	$10.3^{X,Y}$
deepest	11	63.6	$100.0^{B,C}$	$0^{X,Y}$

occasional occurrence of terrestrial insects in siscowet stomachs could be due to feeding on insects settled on the bottom or feeding at the surface, however, the presence of large numbers, as was observed in some stomachs in this study, implies surface feeding on a concentration of insects, e.g., through a "swarm" flying just above the water or due to Langmuir cells (Matthews 1998).

Although siscowets were the only fish found beyond 350 m, it is likely that there were other fishes inhabiting the deepest zone of Lake Superior. Coregonines, sculpins, and burbot were observed in the stomachs of siscowets from the deepest zone and may inhabit the greatest depths of Lake Superior. Pelagic coregonines (cisco, bloater, kiyi, and shortjaw cisco) were not caught beyond 280 m probably because the bottom-set gill nets extended only 1.8 m off the bottom and these species tend to be more abundant further up in the water column. Smaller fishes such as deepwater sculpin were not vulnerable to the gill nets because the meshes were too large.

There has been concern by some fisheries managers and the public that siscowets may compete with lean lake trout for prey. The diet data from this study support previous conclusions that there is nominal dietary competition between leans and siscowets (Harvey *et al.* 2003, Ray *et al.* 2007). The diet of siscowets sampled in this survey comprised nearly exclusively of native prey items. In Lake Superior, lean lake trout diet comprises mostly of non-native, rainbow smelt (Conner *et al.* 1993, Ray *et al.* 2007). In this study, a very small amount of rainbow smelt was observed only in the diet of small siscowets in the shallow zone.

The presence of sea lamprey wounds on siscowets in the deep water areas of Lake Superior indicates that great depth and distance from shore do not provide protection from sea lampreys. The level of sea lamprey wounding on siscowets rivals and even exceeds the wounding rates observed on lean lake trout from other surveys that are near shore (Sitar *et al.* 2007). However, the observed wounding on siscowets requires a different interpretation of sea lamprey-induced mortality than with leans. The only relationship between observed sea lamprey wounding and mortality for lake trout has been for the lean form (Swink and Hanson 1986, Swink 1990). Survival from sea lamprey attacks likely differs for siscowets because they occupy greater depths and lower temperatures than leans, which would lower the metabolism of both sea lampreys and siscowets, likely increasing healing time of lamprey wounds, and decreasing the probability of death from the attacks (Bence *et al.* 2003). This is consistent with previous studies reporting that lower host mortality from sea lamprey attacks was associated with lower temperatures (Farmer *et al.* 1977, Swink and Hanson 1986, Swink 2003).

Lean lake trout in Michigan waters of Lake Superior are near historic high levels (Wilberg *et al.* 2003), but they only occupy a narrow margin of the lake. In contrast, most of Lake Superior is suitable as siscowet habitat, and they have now been found at all depths. For that reason, it is logical that siscowet would be more abundant than lean lake trout (Ebener 1995, Bronte *et al.* 2003). There is plentiful information on lean lake trout biology (e.g., Martin and Olver 1980) and quantitative time series data to support stock assessments (e.g., Woldt *et al.* 2006). However, little information exists on siscowets. Furthermore, the basic descriptive biology of siscowets and quantitative abundance data are limited (e.g., Sitar *et al.* 2007). For example, no one has documented a specific siscowet spawning site, the spawning substrate of siscowets, or the depths at which they spawn. Furthermore, siscowet spawning time is not well documented though there have been some anecdotal field observations of ripe females during the months of April and September (Janssen *et al.* 2007).

Siscowets have a broad depth distribution in Lake Superior, but are more common and adapted to live in deep water. Light attenuation, constant low temperature, and high pressure are important factors that affect siscowets (and other fishes) living 400 m below the surface of Lake Superior. Siscowets in the deepest parts of Lake Superior experience about 41 atmospheres of pressure, a constant temperature of 4°C, and are subjected only to narrow portions of the light spectrum. Therefore, the selective pressures associated with deep water living are notably different than those encountered by leans in the shallow waters of Lake Superior, and provide a basis for comparative studies to improve understanding of lake trout ecology and deepwater fishes in Lake Superior. Future research should focus on expanding the basic descriptive biology of siscowets and continue to build time series of relative abundance data to better quantify population size. This will complement the extensive lean lake trout knowledge base. Furthermore, expanding the understanding of deepwater lake trout ecology in Lake Superior will be informative for lake trout recovery programs in the lower Great Lakes by providing a better insight into the role of deepwater habitat for lake trout, especially since those recovery programs have mostly focused on shallow water areas.

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