The Role of Pollution and External Refugia in Structuring the Onondaga Lake Fish Community

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ABSTRACT

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Historical accounts of Onondaga Lake dating to the 1600's indicate that the lake once supported a coldwater fishery. By the late 1800's, severe degradation of the lake and adjacent tributary environments was accompanied by declines in the American eel (*Anguilla rostrata*), and extirpation of Atlantic salmon (*Salmo salar*) and whitefish (*Coregonus* sp.). Nine faunal surveys were conducted from 1927 to 1994. We used rarefaction analyses to standardize survey results by computing expected species richness values ($E(S_m)$) relative to the 1946 gill net catch (7 species, m=164 individuals). Linear regression applied to the expected richness values ($E(S_{164})$) over time showed a significant increase in richness from 1946 (YEAR=0) to 1994 (YEAR=47) for fish caught in gill nets [$E(S_{164}) = 0.153*YEAR + 6.785$, $r^2=0.79$, $P<0.005$] and trap nets [$E(S_{164}) = 0.226*YEAR + 3.723$, $r^2=0.89$, $P<0.01$]. Although species richness has increased, almost half of the species captured since 1989 show no evidence of juvenile recruitment from within the lake. This result points to the role of immigration in maintaining lakewide diversity. The present community structure has developed from 1) species specific declines and extirpations, 2) invasion and establishment of pollution tolerant species, and 3) fishes interacting with refugia.

Key Words: rarefaction, species richness, community structure, refugia, water pollution.

Fish communities are structured by the summation of regional and local abiotic and biotic influences through time (Tonn and Magnuson 1982). Odum (1985) suggested that, in stressed ecosystems, species diversity tends to decrease while dominance, as related to abundance or biomass distribution, will increase; if the original diversity is low, the reverse may occur. With the loss of salmon and whitefish in the 1800s, the surveys of 1927 and 1946 showed a low fish diversity (i.e., richness) in Onondaga Lake. We hypothesize that improvements in water quality due to phosphorus and ionic waste loading reductions (Effler and Hennigan 1996) would decrease stress on the Onondaga Lake ecosystem (Fig. 1) and lead to a subsequent decline in numerical dominance by a few species toward a more even (i.e. J', Pielou 1966) abundance distribution in trap and gill net surveys.

Industrial and cultural pollution for more than 100 years have severely altered the biotic and abiotic conditions of Onondaga Lake (Effler and Hennigan 1996). Paleolimnological analyses of the lake sediments indicate that the trophic state has shifted from mesotrophy to eutrophy during the past two centuries; hypereutrophy was evident by the mid 1900s (Rowell 1996). Anthropogenic effects on Onondaga Lake have been manifested by changes in turbidity, reduced oxygen resources, and physical habitat changes (Table 1), which have subsequently affected the fish community structure. There are numerous accounts of shifts in the dominance of fish communities from cold water species, such as coregonids and salmonids, to warmwater fishes (e.g., percids and cyprinids) associated with eutrophication (Larkin and Northcote 1971, Mason 1991). The Onondaga Lake fish community appears to have followed a similar pattern, with eutrophication and additional, regional anthropogenic effects (e.g. dam building on connected river systems; Clinton 1849, Herbert 1849, Mills et al. 1978) influencing the lake by the early 1900s.

Browne (1981) developed a species-area relationship for fishes in central New York lakes based on surveys of 12 lakes where: $S=10.12*A^{0.24}$, r=0.85, (P<0.01) and S=number of species, A=area (km^2). Based on this relationship and a lake area of 12 km^2 (Effler and Hennigan 1996) Onondaga Lake should yield about 18 species. Annual surveys during the 1990s have found 1.7-2.5 times this number (Table 2). However, nearly half of these species show no evidence of successful reproduction in the lake. We hypothesize that increases in fish species richness may be related to the availability of refugia and the effects of recent improvements in pollution control. Tonn and

Table 1. Historical events affecting the fish community of Onondaga Lake, NY.

Factor	Description	References
Lake lowering and dam construction	Lake level reduced 0.6 m with a resultant 20% reduction in lake area; vertical difference between the lake and outflowing river nearly eliminated (1822) Dam construction on the watershed (1800s); Erie Canal completed(1825).	Effler and Hennigan 1996 Murphy 1978
Influx of domestic wastes	Increased European settlement (circa 1783). Discharge of treated wastewater directly into the lake at 2.95 x 10^8 liters/day (1990s).	Effler et al. 1996a
	Free ammonia toxicity levels for fish frequently exceeded (1990')	Effler and Hennigan 1996 Effler et al. 1990
	Various upgrades in the waste water treatment facility (1979, 1981).	Effler and Hennigan 1996
	Manifestations of hypereutrophy continue in the 1990s.	
Influx of industrial wastes	Soda ash manufacturing (1884-1986).	Effler and Hennigan 1996
	Decreases in lake salinity from an annual average of 3ppt to 1ppt (1987-1995).	
	High rate of $CaCO_3$ precip-itation and formation of oncolites (1880s-1990s).	Effler et al. 1996b
	Chlor-alkali production and fish flesh contamination; fish remain contaminated (1990s).	Effler and Hennigan 1996
	Steel manufacturing; heavy metals (Hg 1946-1976); Treatment reduced loads in late 1970s.	Rowell 1996
	Deterioration of littoral zone habitat (1880s-1990s).	Madsen et al. 1996 Dean and Eggleston 1984
	Deterioration of lower reaches of major tributaries. (1896-1990s)	Effler and Hennigan 1996 Nemerow 1964

Magnuson (1982) suggest that a severe environment is expected to produce a depauperate community but may instead produce a diverse community if refuges are present. Environmental monitoring suggests that species richness in the Onondaga Lake fish community is increasing through time in parallel with increases in richness of phytoplankton (Makarewicz et al. 1995, Auer et al. 1996) and zooplankton (Makarewicz et al. 1995, Siegfried et al. 1996). Increased richness among the phytoplankton and zooplankton appears linked to the effects of pollution control measures in the lake since 1970 (Auer et al. 1996, Siegfried 1996).

In this paper we assess changes within the fish community structure of Onondaga Lake, NY, using historical fishery accounts from 1654 to 1900 and recent fish surveys from 1927 to 1994. Changes in the fish community are considered in the context of Onondaga Lake's perturbation and subsequent pollution control history. We hypothesize that the Seneca River is an important refuge to many fishes during the severe environments of summer and autumn found in Onondaga Lake. Increased richness in the fish community is considered in the context of the lake's connectivity with the Seneca River and the Oswego River drainage as available refugia from stressful conditions, fish movement patterns, and a history of fish species invasions to the region.

History

The early historical writings of Onondaga County suggest that coldwater species such as Atlantic salmon (*Salmo salar*), American eel (*Anguilla rostrata*), and whitefish (*Coregonus* sp.) were once abundant in Onondaga Lake (Beauchamp 1908, Nemerow 1964, Webster 1982). The first documented report of the fishery comes from Father Simon LeMoyne who observed Atlantic salmon in the lake in 1654 (Clark 1849, Beauchamp 1908). In 1655, Father Chaumont wrote "the eel is so abundant in autumn that some (fishermen) . . . take a thousand in a single night" (Beauchamp 1908). There are general accounts for few other species in the lake before 1900. In 1825, yellow perch (*Perca flavescens*) were recorded by DeKay (Beauchamp 1908). Nemerow (1964) draws on an account from 1866 where "large numbers of pike, perch, bass, and bullheads" were caught by fishermen. And in 1872, "salmon, trout, and bass" were stocked in the lake (Nemerow 1964). The Atlantic salmon were extirpated from Onondaga Lake by the late 1800's, most likely because of mill dam construction and deforestation (Webster 1982).

The Onondaga Lake "whitefish" (probably the short-jawed cisco, *Coregonus zenithicus*, Arrigo 1996) was in high demand throughout the east coast restaurant industry in the 1800s (Nemerow 1964). From 1894 to 1895, however, the commercial catch of the whitefish dropped suddenly from 9090 kg to only 455 kg. By 1893 large amounts of ionic wastes were being discharged into the lake by a local soda ash manufacturer (Effler and Hennigan 1996). In 1896 sewers were completed in Syracuse and raw sewage flowed directly into the lake and its tributaries. The cisco had completely disappeared from the lake by 1897 (Nemerow 1964).

The present rarity of some species in Onondaga Lake is linked with regional impacts dating back over 100 years. Mills et al. (1987) indicate that pickerel (*Esox niger*) and pike (*Esox lucius*) were common predators in the region in the late 1800's and early 1900's. However, draining of area wetlands and the construction of the Barge Canal system reduced the availability of spawning habitats, and their abundances declined (Mills et al. 1987). The eel fishery of the Oneida River, into which Onondaga Lake waters flow (Effler and Hennigan 1995; Fig. 1), was abandoned shortly after 1913 as eels also declined in the region (Mills et al. 1978).

From 1927 to 1994, nine surveys were conducted on the fish community of Onondaga Lake (Greeley 1928, Stone and Pasko 1946, Noble and Forney 1971, Chiotti 1981, Ringler et al. 1995). Seines, gill nets, trap nets, and set lines were used for the first faunal survey of Onondaga Lake conducted by the New York State Biological Survey in 1927 (Greeley 1928). Since 1946, trap nets continued to be used to fish the littoral zone during each survey except for 1969. From 1946 to 1994, six surveys were conducted with experimental gill nets fished on the bottom of the littoral and limnetic zones; in 1991 and 1993, suspended gill nets were used to survey the limnetic epilimnion. Seining results from 1946 and 1969 were largely unquantified compared with recent seining efforts.

Eight fish surveys were conducted from 1946 to 1994 which collected a wide range of species and numbers of individuals. Although trap and gill nets have been used consistently, effort (number of net-nights) has not been standardized among years. Therefore, community level comparisons based on the surveys were not readily comparable using common diversity indices. Instead, we used rarefaction (Sanders 1968, but see Hurlbert 1971, Tipper 1979), which permits species richness to be standardized for comparison among communities (James and Rathbun 1981). Regression analyses of the standardized richness values versus time was used to evaluate trends in community richness. This approach permitted an examination of community changes relative to the timing of pollution control measures.

Table 2.–Fish species collected from lake surveys, 1927-1994. (P=Present, but gear type unknown;G=Gill net; T=Trap net;S=Seine).

Species	1927	1946	1969	1980	1989	1990	1991	1993	1994
1. *Petromyzon marinus*							T		
2. *Lepisosteus osseus*				T	T	G	T	T	T,S
3. *Amia calva*				T	T	G,T	T	T	T
4. *Anguilla rostrata*							T	T	
5. *Alosa pseudoharengus*		G		T	T		G,T	G	G,T,S
6. *Dorosoma cepedianum*				G,T	T	G,T,S	G,T,S	G,T,S	G,T,S
7. *Ictalurus punctatus*		T	G	G,T	T	G,T	G,T	G,T	G,T
8. *Ameiurus nebulosus*			G,S	G,T	T	G,T	G,T	G,T	T,S
9. *Ameiurus natalis*						T	T	T	T
10. *Catastomus commersoni*	P		G,S	G,T	T	G,T	G,T,S	G,T	G,T,S
11. *Moxostoma macrolepidotum*	P	G,T	G	G,T	T	G,T	G,T	G,T	G,T
12. *Hypentelium nigricans*									T
13. *Cyprinus carpio*	P	G,T,S	G,S	G,T,S	T	G,T,S	G,T,S	G,T,S	G,T,S
14. *Semotilus atromaculatus*							S		T,S
15. *Semotilus corporalis*									T
16. *Notropis hudsonius*								T	S
17. *Cyprinella spiloptera*							T,S	S	
18. *Notemigonus crysoleucas*	P	G		T	T	T	G,T,S	T,S	G,T,S
19. *Notropis atherinoides*		S	S		T		T,S	T,S	T,S
20. *Pimephales notatus*	P						T,S	S	S
21. *Pimephales promelas*							T	T,S	T,S
22. *Scardinia erythrothalmus*							T	G,T	T
23. *Salmo trutta*					T	T	G,T	T	G
24. *Salmo salar*								T	T
25. *Oncorhyncus mykiss*							T	G	G
26. *Salvelinus fontinalis*							G		
27. *Salvelinus namaycush*				G					
28. *Salvelinus fontinalis x Salmo trutta*						T			
29. *Osmerus mordax*							T		T,S
30. *Umbra limi*							T	S	T
31. *Esox americanus vermiculatus*	P								
32. *Esox niger*							T		T
33. *Esox lucius*		G		G,T	T	T	G,T	G,T	G,T
34. *Esox musquinongy x Esox lucius*					T	T	T	G	T
35. *Lota lota*						T			
36. *Fundulus diaphanus*	P	S			T	T	T,S	T,S	S
37. *Culaea inconstans*			S			T	S		
38. *Labidesthes sicculus*					T	T,S	T,S		S
39. *Morone americana*			G,S	G,T,S	T	G,T,S	G,T,S	G,T,S	G,T,S
40. *Morone chrysops*		S			T	T	T	G	
41. *Micropterus dolomieu*			G	G,T,S	T	G,T	G,T,S	G,T,S	G,T,S
42. *Micropterus salmoides*	P			S	T	G,T,S	G,T,S	G,T,S	G,T,S
43. *Pomoxis annularis*				T	T	T	T		T
44. *Pomoxis nigromaculatus*				G,T	T	G	T,S	G,T,S	T
45. *Ambloplites rupestris*					T	T	T	T	T,S
46. *Lepomis macrochirus*			G,S	T,S	T	G,T,S	G,T,S	T,S	G,T,S
47. *Lepomis gibbosus*	P		G,S	G,T,S	T	G,T,S	G,T,S	T,S	G,T,S
48. *Lepomis cyanellus*							T		
49. *Percina caprodes*		S				T	T	S	T,S
50. *Etheostoma olmstedi*							S	S	S
51. *Perca flavescens*	P	G	G	T,S	T	G,T,S	G,T,S	T,S	G,T,S
52. *Stizostedion vitreum*		G,T	G	G,T	T	G,T	G,T	G,T	G,T
53. *Aplodinotus grunniens*			G	G,T,S	T	T	G,T	G,T	T
54. *Percopsis omiscomaycus*									T
TOTALS	10	12	14	22	28	31	45	38	4

1927=Greeley 1928.
1946=Stone and Pasko.
1969=Noble and Forney 1971.
1980=Chiotti 1981.
1989-1994=Ringler et al.

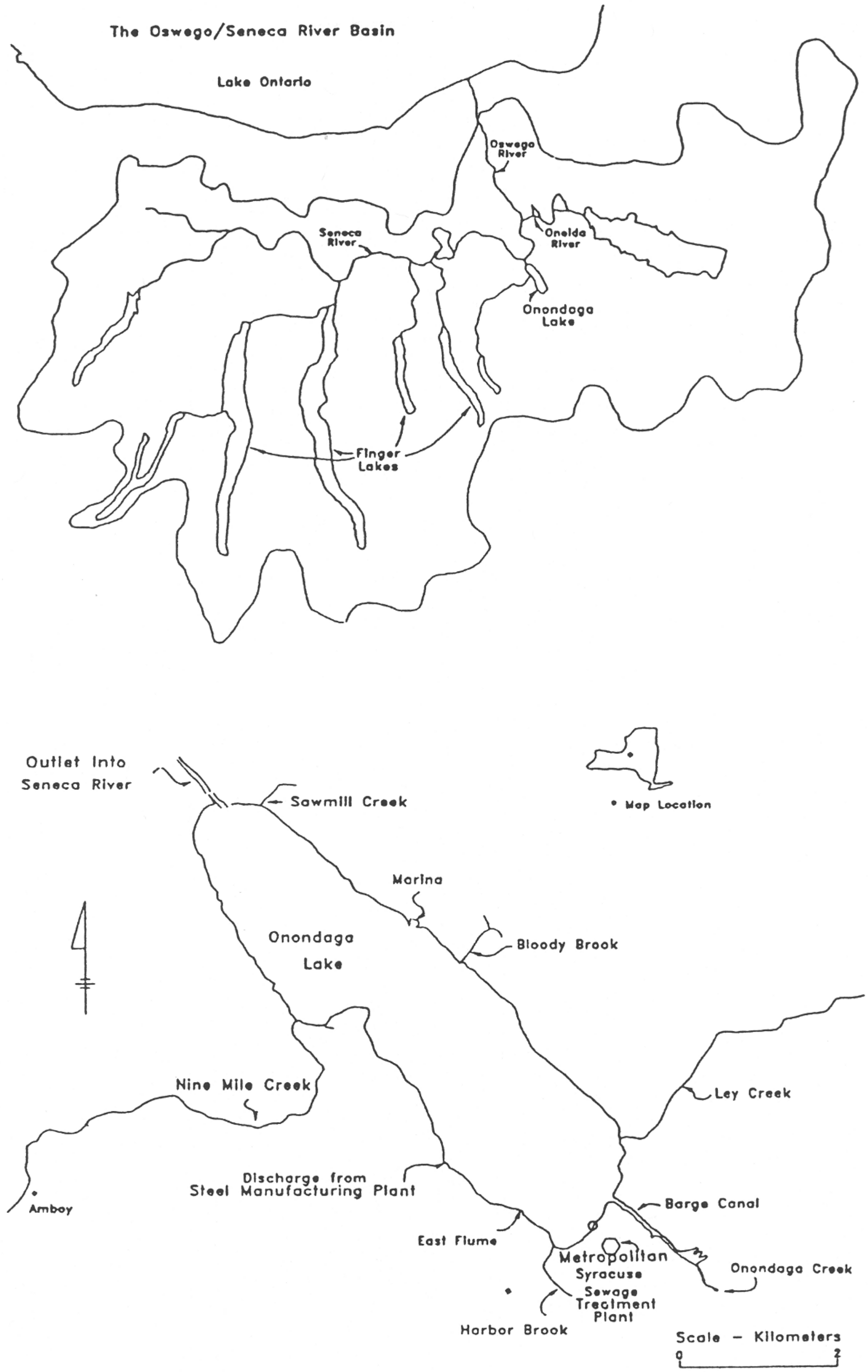

Figure 1.–Location of Onondaga Lake, NY, in the Oswego River drainage and the distribution of tributaries to the lake.

Methods

Field sampling

Sampling was conducted during the ice free months of April through November, 1990-1994, with the exception of 1992. However, sampling intensity has varied among the years. Indiana, Oneida, and South Dakota trap nets were fished in the littoral zone at eight sites along the lake margin (Ringler et al. 1996, Gandino 1996). Trap nets were set perpendicular to the shore with wings set at 45° angles to the leader and fished three to five days most weeks.

The limnetic epilimnion covers approximately 80% of the lake and had not been sampled prior to the 1991 and 1993 surveys. The gill net surveys were designed to evaluate the effect of low dissolved oxygen associated with fall turnover on the fish community. The lake was divided in half along its northeast- southwest axis, and this axis was perpendicularly bisected at five equidistant points resulting in twelve lake regions. During 1991 and 1993, we conducted summer and autumn surveys with experimental gill nets (stretched mesh 3.8, 5.1, 6.4, 7.6, 8.9, 10.2 cm, 50 m long, and 2 m wide) suspended at 1-3 m and 4-6 m depths in the limnetic zone across the twelve regions. Net nights were assigned randomly to a region (1-12) and a depth (1-3m or 4-6m) each week. Six nets were fished each of four consecutive nights during a week in July and October, 1991 and 1993. Experimental gill nets were also fished for 35 net nights in the littoral and limnetic zones from May to November 1994. Trap and bottom-fished gill net collections were used for comparison with the historical (1946-1980) surveys conducted in a similar manner.

Seining was conducted with a 20-m bag seine at four sites from 1989-91 using a single pass for 30 m. Eight sites were seined every three weeks throughout the summer in 1993 and 1994 using a triple pass reduction within a temporary, 20 m X 30 m enclosure (Ringler et al. 1996, Gandino 1996, Arrigo 1996).

We determined community structure from species identification and their abundances in the various gear hauls. Juvenile recruitment was identified from the presence of young-of-the-year fishes in the catch as judged on fish size and previous work with age-length relationships based on scale analysis (Gandino 1996).

Fish movements were evaluated based on seasonal patterns in net catches, tag returns, and radio telemetry. In 1991, we radio tagged three smallmouth bass (*Micropterus dolomieu*), two tiger muskellunge (*Esox lucius X Esox musquinongy*), one walleye (*Stizostedion vitreum*) and one channel catfish (*Ictalurus punctatus*). Twenty-one species of fish were tagged in the lake during 1990 and 1991 using floy tags inserted below the dorsal fin (Ringler et al. 1996, Gandino 1996). Distribution patterns among species in the net catches, tagged fish recaptures and telemetered fish movement patterns were related to declines in dissolved oxygen at fall turnover.

Temperature and dissolved oxygen levels (DO) were monitored with a YSI Model 54 temperature-DO meter during the 1990, 1991, 1993, and 1994 sampling periods. Vertical profiles were collected at 1-m intervals periodically in the summer and weekly in the fall through turnover in the deepest areas of the north and south basins of the lake.

Analytical methods

Rarefaction is a method for estimating the number of species expected [$E(S_m)$] in a random sample of standardized size taken from a census or collection (Sanders 1968, Hurlbert 1971, Heck et al. 1975, Tipper 1979, James and Rathbun 1981, Magurran 1988). Surveys were standardized to the catch levels of 1946, and the expected species richness values ($E(S_m)$) were compared over time. We applied the hypergeometric function (Hurlbert 1971) for rarefaction of the gill net data:

$$E(S_m)=\sum_{i=1}^{s}\left(1-\frac{\binom{N-N_i}{m}}{\binom{N}{m}}\right)$$

where $E(S_m)$ = the expected number of species in the collection to be rarefied, m= the standardized number of individuals (164 caught in 1946 in this paper), N=total number of individuals in the collection to be rarefied, N_i=the number of individuals in the ith species in the collection to be rarefied, and S = total number of species in that collection (Magurran 1988). For computational purposes, binomial coefficients in the form $\binom{n}{k}$ are meaningful when n and k are non-negative integers such that $0 \leq k \leq n$. However, n may be any real number, and if k>n, the coefficient $\binom{n}{k}$ = 0 (Meyer 1970).

The multinomial distributional form of the rarefaction measure (Heck et al. 1975, Tipper 1979) has been applied to the trap net data:

$$E(S_m)=S-\sum_{i=1}^{s}\left(1-\frac{N_i}{N}\right)^m$$

The variable definitions follow those described for the hypergeometric function. Because our trap net data met the condition m/N<0.10, we used the multinomial distribution as an approximation to the hypergeometric distribution (Heck et al. 1975, Tipper 1979).

We hypothesized that fish species richness and evenness (J'; Pielou 1966) would increase in response to improvements in water quality over the years 1946-1994. We used a least-squares regression of the expected species richness [E(S)] for the trap net and gill net results to assess trends in the community structure over time. Slopes were tested for significant positive trends in richness using a t-test at $\alpha = 0.05$ (Dowdy and Weardon 1983). We also conducted a test of homogeneity between the slopes (Steel and Torrie 1960) of the gill net and trap net data to evaluate alternative fish survey methods in detecting similar trends in the lake fish community.

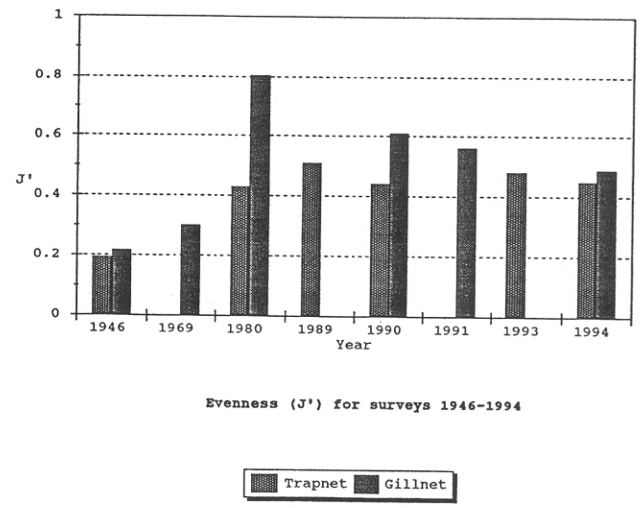

Figure 3.–Species evenness (J') through time for gill net and trap net surveys of the Onondaga Lake fish community, 1946-1994.

Results and Discussion

Community structure in the 1900s

Species richness has increased following the initial loss of Atlantic salmon and whitefish at the turn of the century. Fifty-four species were recorded during nine scientific surveys (Table 2) since 1927. Species richness increased among the surveys, but netting efforts in the surveys have also increased, especially in the 1990s. Standardization of the survey results through rarefaction (Hurlbert 1971, Tipper 1979) was used due to a wide variation in sampling effort and sample sizes. A significant trend for increasing species richness among the surveys standardized to the catch of 1946 (164 individuals) was found for the gill net [$E(S_{164}) = 0.153*YEAR + 6.785$, $r^2=0.79$, $P<0.005$] and trap net surveys [$E(S_{164}) = 0.226*YEAR + 3.723$, $r^2=0.89$, $P<0.01$]

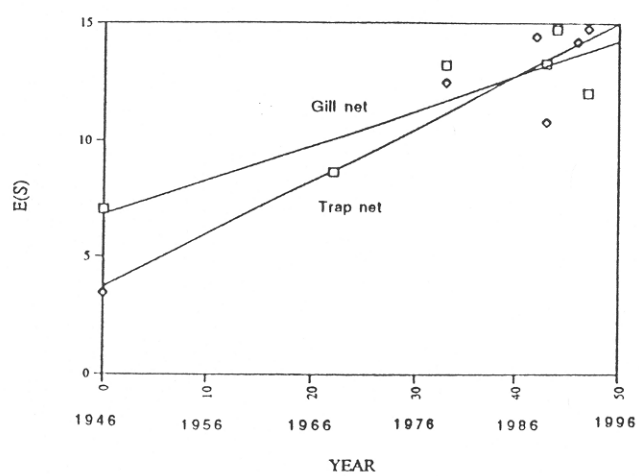

Figure 2.–Linear regressions of Expected Species Richness standardized to 164 individuals ($E(S_{164})$) vs. Year for gill net (squares) and trap net (diamonds) surveys of the Onondaga Lake fish community, 1946 (Year = 0) to 1994 (Year = 47).

(Fig. 2). Gill net surveys suggest that richness has increased for this rarefied level at a rate of .15 ± .11 species per year ($CI_{95\%}=(0.04 \leq b \leq 0.26)$) while trap net surveys suggest a species increase rate of .23 ± .11 species per year $CI_{95\%}=(0.12 \leq b \leq 0.34)$. Comparison of the two slopes suggests the rates of increase are not significantly different (P>0.5). Therefore, gill net and trap net results both appear to reflect the same rate of increase in richness between 1946 and 1994.

Evenness was low for the 1946 survey (Fig. 3). Following this low diversity period, dominated by a single species (common carp, *Cyprinus carpio*), evenness and richness have increased. Although the lake remains eutrophic, trophic state indicators have tended to improve during the last twenty-five years (Auer et al. 1996). Increased richness and evenness of the fish community structure may reflect the decrease in stress on the ecosystem as conditions improve in water quality. However, the species lists over time (Table 2) need to be interpreted carefully to understand the diversity in the community.

Richness initially increased in the mid-1900s despite severe pollution effects (i.e., low oxygen resources, high turbidity, low transparency, and high salinity; Effler 1987, Auer et al. 1996, Effler and Hennigan 1996). This increase is partially attributable to invasions by pollution tolerant species. White perch (*Morone americana*), gizzard shad (*Dorosoma cepedianum*), and freshwater drum (*Aplodinotus grunniens*) invaded the region via range expansions during the 1940s and 1950s (Dence 1952, Dence 1956, Mills et al. 1978, Mills et al. 1987). White perch were first recorded in neighboring Cross Lake in 1948 and the Seneca River in 1951 (Dence 1952). Mills et al. (1987) suggested that the species arrived in Oneida Lake in the late 1940s. Subsequently, white perch were the dominant species of the 1969 Onondaga Lake survey (Noble and Forney 1971). In 1916, gizzard shad were only recorded in small numbers from one lake in the Oswego River watershed, Cayuga Lake (Greeley 1928). Dence (1956) found several carcasses and concretions of shad on the Onondaga Lake shore in 1953 and 1954. However, the first survey to record live shad was completed in 1980 (Chiotti 1981). Freshwater drum were first recorded in Oneida Lake in the 1950s (Mills et al. 1978). This species has become a consistent element of the Onondaga Lake community since the 1969 survey. White perch, gizzard shad, and freshwater drum are tolerant of high turbidity and oligohaline to estuarine level salinities (Smith 1985). Despite the severe environmental conditions present before pollution controls were implemented, the arrival of species with broad ecological tolerances provides evidence for increased species richness before pollution controls were in place. These controls include phosphorus reductions through upgraded wastewater treatment and the closing of a soda ash manufacturing plant (Canale and Effler 1989, Effler and Hennigan 1996).

Stocking programs and immigration from within the Oswego River watershed have further enhanced species richness in the lake. Many species stocked elsewhere in the drainage basin rather than the lake itself have subsequently been recorded in lake surveys. For example, a single lake trout (*Salvelinus namaycush*) was collected in 1980, presumably reaching the lake from the Finger Lakes (Chiotti 1981). Rainbow trout (*Oncorhyncus mykiss*) fin clipped upon release in the Finger Lakes (Les Wedge, NYSDEC, Pers. Comm.) have been recovered during two Lake surveys in the 1990's. We collected Atlantic salmon smolts in the lake during 1993 and 1994. The smolts were almost certainly from an experimental Atlantic salmon stocking program that placed over 85,000 juveniles in Onondaga Lake tributaries (Murphy 1992, Millard and Ringler 1995).

The 1946 and 1980 seining surveys showed little young-of- the-year recruitment in the lake (Stone and Pasko 1946, Chiotti 1981), however, mesh sizes of the seines were not reported. Chiotti (1981) suggested that recruitment was sporadic for most species. Between 1989 and 1994, young-of-the-year fishes were collected for only twenty-eight of fifty-two species (54%); twenty-four species (46%) have shown no recruitment despite increased sampling efforts in the 1990's (Ringler et al. 1996, Gandino 1996, Arrigo 1996).

Additionally, the Oswego River drainage encompassing Onondaga Lake supports approximately 100 fish species (Werner 1980). Species such as green sunfish (*Lepomis cyanellus*), burbot (*Lota lota*), troutperch (*Percopsis omiscomaycus*) and brook trout (*Salvelinus fontinalis*) are among those fishes that range throughout the drainage and have only been recorded once in nine lake surveys (Table 2). Therefore, we consider native and stocked species, many of which appear to not be reproducing in the lake or capable of maintaining year-round populations, to interact with adjacent refugia (i.e. lake tributaries and the Seneca River system). This interaction allows for recent increases in species richness for the lake despite its continued polluted condition.

Refugia Effects on Fish Community Structure

The seasonality of fishes in our net catches relative to low DO events, coupled with movements of telemetered and tagged fishes out of the lake (Ringler et al. 1996, Gandino 1996), support the importance of the Seneca River to lake community dynamics. The large, anoxic hypolimnion of summer and lakewide hypoxia in fall (Fig. 4) are conditions considered highly stressful to many fishes (Petit 1973, Effler 1987). These conditions, for example, presumably limit year-round habitation by coldwater species (Ringler et al. 1996).

Evidence for fishes using the Seneca River during extreme low DO in the fall includes, for example, the movements of two smallmouth bass, a tiger muskie and a walleye radio tagged in the lake in early fall, 1991. Each fish moved into the refuge of the Seneca River as lakewide dissolved oxygen levels declined (Ringler et al. 1996). One tiger muskie returned to the lake the same season as reaeration of the water column occurred. Additionally, in 1991 and 1993, comparison of the gill

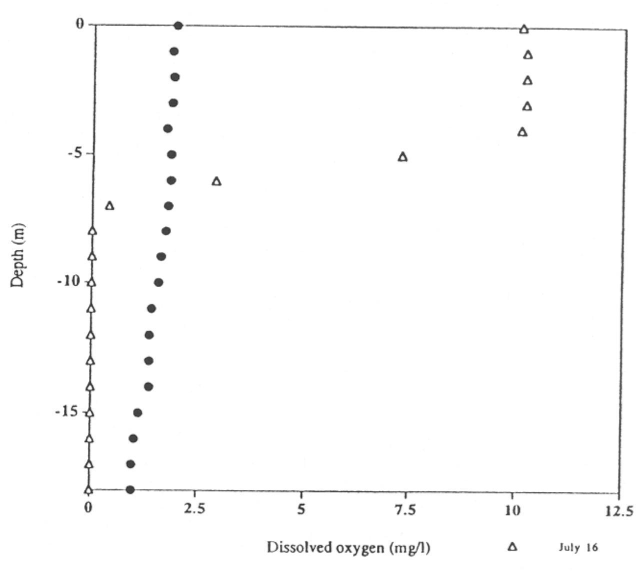

Figure 4.–Dissolved oxygen (mg/l) profiles for July 16, 1991 (triangles) and at fall turnover, October 20, 1991 (circles).

Table 3.–Limnetic gill net catch using suspended gill nets in the epilimnion of Onondaga Lake. (N = 24 nets per month, July and October, 1991 and 1993).

Species	Summer		Fall	
	1991	1993	1991	1993
1. *Alosa pseudoharengus*	79	0	287	11
2. *Aplodinotus grunniens*	1	0	1	0
3. *Cyprinus carpio*	2	2	0	0
4. *Dorosoma cepedianum*	448	39	624	144
5. *Ictalurus punctatus*	39	7	0	0
6. *Lepomis macrochirus*	0	1	0	0
7. *Micropterus dolomieu*	69	12	0	0
8. *Morone americana*	774	855	37	88
9. *Morone chrysops*	0	0	0	1
10. *Moxostoma macrolepidotum*	1	4	0	0
11. *Notemigonus crysoluecas*	0	0	1	0
12. *Oncorhyncus mykiss*	0	1	0	0
13. *Perca flavescens*	0	0	5	0
14. *Stizostedion vitreum*	12	6	0	10
Totals	**1425**	**927**	**955**	**254**

net catches between summer and the fall turnover show that gizzard shad and alewife (*Alosa pseudoharengus*) remained in the lake in the fall despite lakewide hypoxic conditions, while white perch numbers drastically declined (Table 3). The large predators (e.g., smallmouth bass) and benthivorous species (e.g., redhorse sucker *Moxostoma macrolepidotum,* and channel catfish) were absent from the net catches at autumn turnover, presumably having moved into the Seneca River. However, most species absent in autumn gill net efforts in 1991 returned as common catches in 1993 summer collections (Table 3). Presumably many species recolonize Onondaga Lake from the Seneca River.

The diversity in Onondaga Lake is associated with seasonally favorable habitat conditions. Annual fluctuations in habitat quality (vertical oxygen distribution and fall lakewide hypoxia) still limit many fishes from year-round residency. The surrounding refugia including the Seneca River provides a source pool of species that can recolonize the lake when conditions are favorable for growth, survivorship, and, in some species, reproduction. Water quality and physical habitat (e.g., submersed vegetation) are among the factors that have been positively correlated with ecosystem health as reflected in the fish community (Minns et al. 1994). The seasonal reliance of the Onondaga Lake fish community on refuges beyond the lake boundary suggests that much work remains to improve the health and habitat of this ecosystem.

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