FISH COMMUNITY ECOLOGY OF A HYPEREUTROPHIC URBAN LAKE

By

Peter J. Tango

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State University of New York
College of Environmental Science and Forestry
Syracuse, New York

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Peter J. Tango
Environmental Research Statistician

Office: (410) 260-8649
Fax: (410) 260-8640
E-Mail:
ptango@dnr.state.md.us

Maryland Department of Natural Resources
Resource Assessment Service
580 Taylor Avenue, D-2 Annapolis, Maryland 21401

Approved
Faculty of Environmental and Forest Biology

Major Professor
Dr. Neil H. Ringler

Chair, Examining Committee
Dr. Robert H. Frey

Faculty Chair
Dr. Neil H. Ringler

Dean, Instruction and Graduate Studies
Dr. Robert H. Frey

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ABSTRACT

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, as well as dam building throughout the Oswego River drainage were accompanied by declines in the American eel (Anguilla rostrata), and extirpation of Atlantic salmon (Salmo salar) and whitefish (Coregonus sp.). I conducted fishery surveys in Onondaga Lake during 1991, 1993 and 1994 that complimented the existing data on the fish community from surveys conducted between 1927 and 1990. Rarefaction analyses were used to standardize survey results and develop an expected species richness ($E(S_m)$) relative to gill and trap net catches in 1946. Linear regression applied to $E(S_{164})$ 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.

Analysis of the spatiotemporal dynamics of dissolved oxygen demonstrated seasonal and annual differences in the availability of oxygen refugia during severe conditions. While fall turnover conditions varied in severity of dissolved oxygen depression lakewide, there was a persistent absence of species known to be tolerant of hypoxic habitats. Such seasonal community dynamics suggested that more than dissolved oxygen controlled the community

composition through time. Sequence in the invasion history was an important determinant in annual community dynamics. Life history patterns, however, particularly those tied to breeding behaviors and juvenile recruitment, also helped explain dynamics of the adult fish community.

The present fish community structure has developed from 1) species specific declines and extirpations, 2) invasion history and establishment of pollution tolerant species, 3) life history patterns for breeding and 4) fishes interacting with refugia.

KEY WORDS: Fish communities, eutrophication, refugia, pollution tolerance, rarefaction, Onondaga Lake, lake restoration, exotics, breeding guilds, gradient analysis, dissolved oxygen, hypereutrophic.

Author's name in full: Peter John Tango

Candidate for the degree of: Doctor of Philosophy Date: May 1999

Major Professor: Dr. Neil H. Ringler

Faculty: Department of Environmental and Forest Biology

State University of New York College of Environmental Science and Forestry,

Syracuse, New York.

Signature of Major Professor: _____

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Chapter 1. The Role of Pollution History and External Refugia in Structuring the Onondaga Lake Fish Community.

INTRODUCTION

Fish communities are structured by the summation of regional and local abiotic and biotic influences through time (Tonn and Magnuson 1982). The stresses of over 100 years of industrial and cultural pollution have severely altered the 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 included lake lowering, domestic waste loading and industrial waste disposal which have been manifested in turbidity effects, reduced oxygen resources, and physical habitat changes (Table 1.1), subsequently affecting 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 history of 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) by the early 1900's.

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=lake area (km^2). Based on a lake area of 12 km^2 (Effler and Hennigan 1996) I

Table 1.1 Historical events affecting the fish community of Onondaga Lake, NY.

Factor	Description	References
Lake lowering	0.6m and 20% of the lake area; Elimination of gradient from the lake to the river; dam building on the watershed; formation of the Barge Canal.	Effler and Hennigan 1996 Murphy 1978
Domestic wastes	From the lake watershed since the development of the region; presently treated wastewater is Discharged directly into the lake at 80 MGD.	Effler et al. 1996a
	Free ammonia toxicity levels for salmonid and nonsalmonid fishes is frequently exceeded.	Effler and Hennigan 1996 Effler et al. 1990
	Various upgrades in the waste water treatment facility. Manifestations of the resultant hypereutrophy: 1. High primary productivity and phytoplankton blooms 2. Hypolimnetic anoxia 3. Lakewide hypoxia in autumn	Effler and Hennigan 1996
Industrial waste	Soda ash manufacturing starting in 1884, ceasing 1986; decreases in lake salinity from annual average of 3ppt to 1 ppt.	Effler and Hennigan 1996
	High rate of $CaCO_3$ precipitation and formation of oncolites.	Effler et al. 1996b
	Chlor-alkali production and fish flesh contamination.	Effler and Hennigan 1996
	Steel manufacturing; heavy metals; treatment reducing loads in the late 1970's.	Rowell 1996
	Deterioration of littoral zone habitat.	Madsen et al. 1996
	Deterioration of lower reaches of major tributaries.	Effler and Hennigan 1996

would predict Onondaga Lake to yield about 18 species. Annual surveys during the 1990's have found 1.7-2.5 times this value (Table 1.2). Consideration should be given for the fact that different gear types were used among the studies and a refinement of a regional species-area relationship should better account for trophic condition of the lakes as a strata in such an analysis.

Tonn and 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. The results of environmental monitoring suggest that species richness has increased in the Onondaga Lake fish community since the mid 1900's, in parallel with increases in richness of phytoplankton (Auer et al. 1996, Makarewicz et al. 1995) 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). I hypothesized that increases in fish species richness may be related to refugia and pollution control effects.

OBJECTIVES

In chapter 1, I 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. The objective is to evaluate the relationship of fish community diversity with respect to Onondaga Lake's perturbation and subsequent pollution control history.

In chapter 2, I use analyses of spatial and temporal patterns in dissolved oxygen along with fish movement patterns to assess how a diverse fish community relates to habitat

Table 1.2. Fish species collected from lake surveys 1927-1994. (P=Present but gear type for collection 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	T, G	T	T	T
4. Anguilla rostrata							T	T	
5. Alosa pseudoharengus		G		T	T		T, G	G	T,G,S
6. Dorosoma cepedianum				T,G	T	T,G,S	T,G,S	T,G,S	T,G,S
7. Ictalurus punctatus		T	G	T,G	T	T,G	T,G	T,G	T,G
8. Ameiurus nebulosus			G,S	T,G	T	T,G	T,G	T,G	T,S
9. Amieurus natalis						T	T	T	T
10. Catastomus commersoni	P		G,S	T,G	T	T,G	T,G,S	T,G	T,G,S
11. Moxostoma macrolepidotum	P	T,G	G	T,G	T	T,G	T,G	T,G	T,G
12. Hypentelium nigricans									T
13. Cyprinus carpio	P	T,G,S	G,S	T,G,S	T	T,G,S	T,G,S	T,G,S	T,G,S
14. Semotilus atromaculatus							S		T,S
15. Semotilus corporalis									T
16. Notropus hudsonius								T	S
17. Cyprinella spiloptera							T,S	S	
18. Notemogonus chrysoleucus	P	G		T	T	T	T,G,S	T,S	T,G,S
19. Notropis aetherinoides	P	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	T,G	T
23. Salmo trutta					T	T	T,G	T	G
24. Salmo salar								T	T
25. Oncorhynchus mykiss							T	G	G
26. Salvelinus fontinalis							G		
27. Salvelinus namaycush				G					
28. S. fontinalis X S. 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		T,G	T	T	T,G	T,G	T,G
34. E. musquinongy X E. lucius					T	T	T	G	T
35. Lota lota						T			
36. Fundulus diaphanus	P	S			T	T	T,S	T,S	S
37. Culea inconstans			S			T	S		
38. Labidesthes sicculus					T	T,S	T,S		S
39. Morone americana			G,S	T,G,S	T	T,G,S	T,G,S	T,G,S	T,G,S
40. Morone chrysops		S			T	T	T	G	
41. Micropterus dolomieu			G	T,G,S	T	T,G	T,G,S	T,G,S,	T,G,S
42. Micropterus salmoides	P			S	T	T,G,S	T,G,S	T,G,S	T,G,S
43. Pomoxis annularis				T	T	T	T		T
44. Pomoxis nigromaculatus				G,T	T	G	T,S	T,G,S	T
45. Ambloplites rupestris					T	T	T	T	T,S
46. Lepomis macrochirus			G,S	T,S	T	T,G,S	T,G,S	T,S	T,G,S
47. Lepomis gibbosus	P		G,S	T,G,S	T	T,G,S	T,G,S	T,S	T,G,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	T,G,S	T,G,S	T,S	T,G,S
52. Stizostedion vitreum		T,G	G	T,G	T	T,G	T,G	T,G	T,G
53. Aplodinotus grunniens			G	T,G,S	T	T	T,G	T,G	T
54. Percopsis omiscomaycus									T
Total species	11	12	14	22	28	31	45	38	43

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

conditions. Objectives of work covered in Chapter 2 are to 1) determine whether or not dissolved oxygen refugia might exist within Onondaga Lake during the period surrounding fall turnover and 2) determine fish distribution patterns relative to lake refugia versus external refugia.

Chapter 3 covers the history of fish species invasions to Onondaga Lake. The sequence of invasions and life history characteristics of the species common to net catches is used to evaluate how species integrate themselves into an existing community. Objectives of this work are 1) to evaluate the hypothesis that how well integrated the species is within the community is directly related to the timing of a species invasion. A measure of community integration is developed through correlation analysis from catch per unit effort data; the unit of effort in this case is a net-night. I further use the measure of community integration in a gradient analysis towards objective 2), which is to evaluate the hypothesis that life history patterns among species play a role in structuring the patterns of community integration.

HISTORY

The early historical writings of Onondaga County suggest that coldwater species such as Atlantic salmon (Salmo salar) and whitefish (Coregonus sp.) were 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,

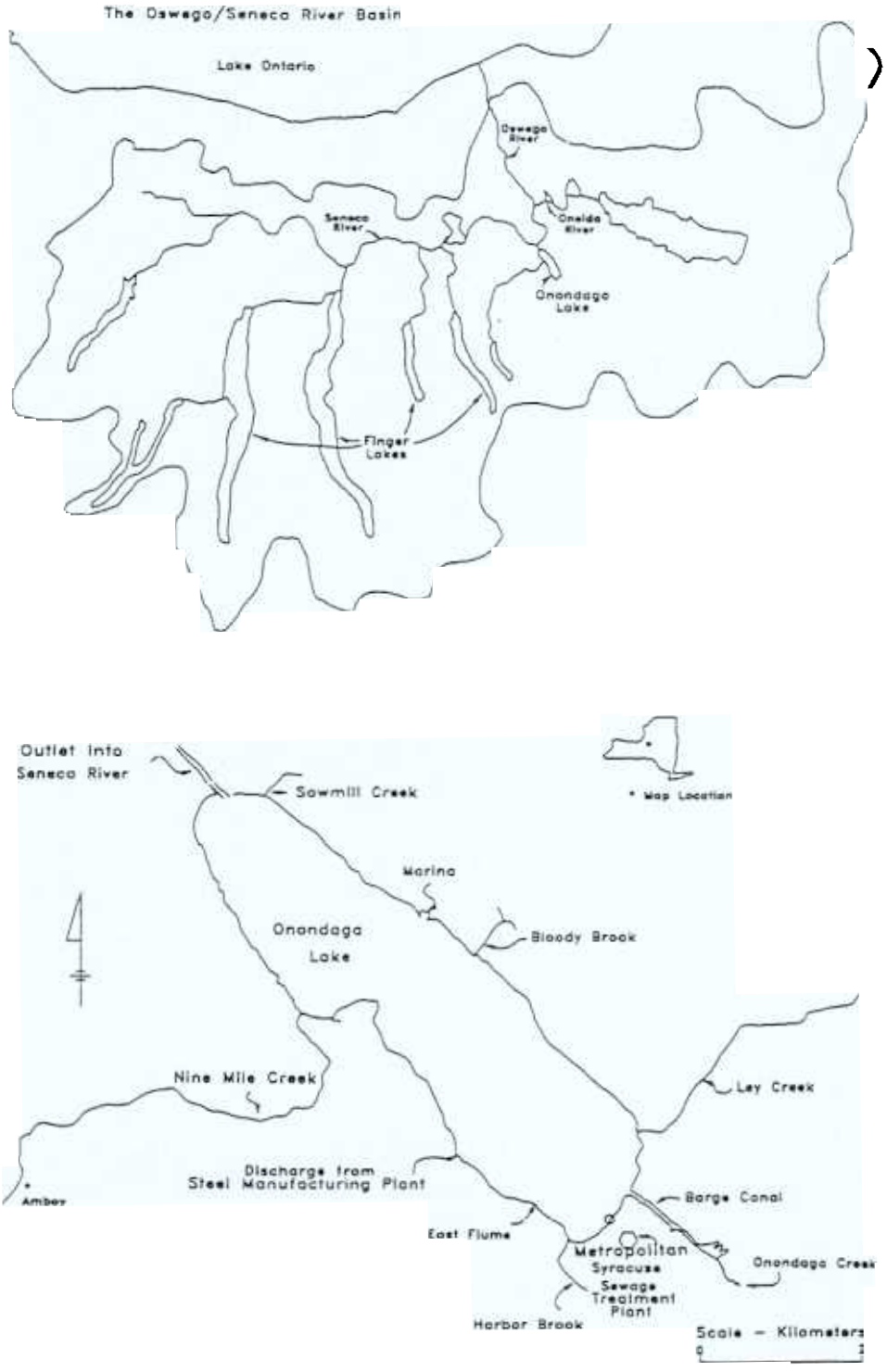


Figure 1.1. Location of Onondaga Lake, NY, in the Oswego River drainage and the local tributary system to the lake.

1928, Stone and Pasko 1946, Noble and Forney 1971, Chiotti 1981, Gandino 1996, Arrigo 1998, this study). 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 worked with C. Gandino and M. Arrigo in 1991,1993 and 1994 on trap net surveys used for analyses in this dissertation. From 1946 to 1994, six surveys were conducted with experimental gill nets fished on the bottom of the littoral and limnetic zones. Once again, I worked with C. Gandino and M. Arrigo on gill netting in 1993 and 1994. In 1991 and 1993, used a technique of suspending gill nets from the surface with buoys to survey the limnetic epilimnion. Seining results from 1946 and 1969 were largely unquantified compared with recent efforts conducted largely by Arrigo (1998) and therefore were not used in these comparative analyses

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, I used rarefaction (Sanders 1968, but see Hurlbert 1971, Tipper 1979), which permits standardizing the species richness for comparison among communities (James and Rathbun 1981). I then used regression analyses of the standardized richness values versus time to evaluate trends in community richness. This approach permitted an examination of community changes relative to the timing of pollution control measures.

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 1800's, the surveys of 1927 and 1946 showed a low fish diversity (i.e., richness) in the lake. I suggest that improvements in water quality due to reductions in phosphorus and ionic waste loadings since the early 1970's (Effler and Hennigan 1996) would represent a decrease in stress on the Onondaga Lake ecosystem. I also expected a community response to the decreased stress resulting from remediation would be expressed as improved evenness in the abundance distribution of species in the community (i.e., reduced numerical dominance).

METHODS

Field sampling.

Sampling was conducted during the ice free months of April through November. Sampling intensity has varied among the programs. Trap nets of three types (i.e., 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, Arrigo 1998, this study). Trap nets were set perpendicular to the shore with wings angled at 45° to the leader. The nets were fished from three to five days most weeks from May to September 1990-1994, with the exception of 1992.

During 1991 and 1993, I 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 at twelve sites. The limnetic epilimnion covers approximately 80% of the lake and had not been sampled prior to the 1991 and 1993

surveys. Surveys were designed to evaluate the effect of low dissolved oxygen associated with fall turnover. Six nets were fished on four consecutive nights during a week in July and October, 1991 and 1993. Net nights were assigned randomly to one of twelve regions in the lake. Experimental gill nets were also fished for 35 net nights throughout the lake 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 surveys between 1946 and 1980 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 1998).

Community structure was determined from species identification and abundances in the various gear hauls. Juvenile recruitment was identified from the presence of young-of-the-year fishes in the catch judged on the basis of 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 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 correlated with

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 of 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 Rathburn 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. I applied the hypergeometric function (Hurlbert 1971) for rarefaction of the gill net data:

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

where $E(S_m)$ = the expected number of species in the rarefied sample, m = the number of individuals to which a sample is standardized (gill net and trap net data for year=1946 in this chapter), 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

the 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:

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

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

I hypothesized that fish species richness and evenness (J'; Pielou 1966) would increase in response to improvements in water quality over the years 1946-1994. I 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 α=0.05 (Dowdy and Weardon 1983). I 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. Evenness (J'; Pielou 1966) was computed for trap and gill net surveys and graphical analysis was used to evaluate this secondary hypothesis of increased evenness as a fish community response to reduced stress from pollution control effects.

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 1.2) since 1927. Species richness increased among the surveys, but netting efforts in the surveys have also increased, especially in the 1990's. 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 1.2). Gill net surveys suggest that richness has increased for this rarefied level at a rate of 0.15 ± 0.11 species per year ($CI_{95\%}=(0.04 \leq b \leq 0.26)$) while trap net surveys suggest a species increase rate of 0.23 ± 0.11 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 (Figure 1.3). Following this low diversity period, dominated by a single species (common carp, Cyprinus carpio), evenness and richness have increased. Although the trophic state of the lake remains eutrophic, trophic state indicators have tended to improve during the last twenty-five years (Auer et al. 1995). Increased richness and evenness of the fish community structure may reflect the decrease in stress on the ecosystem as conditions improve in water quality. The species lists over time

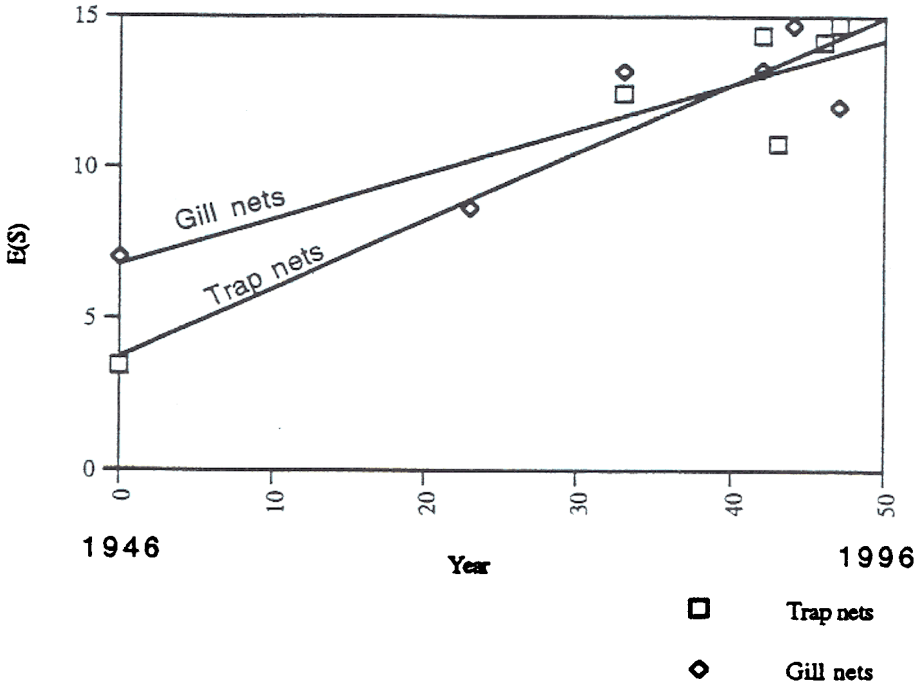
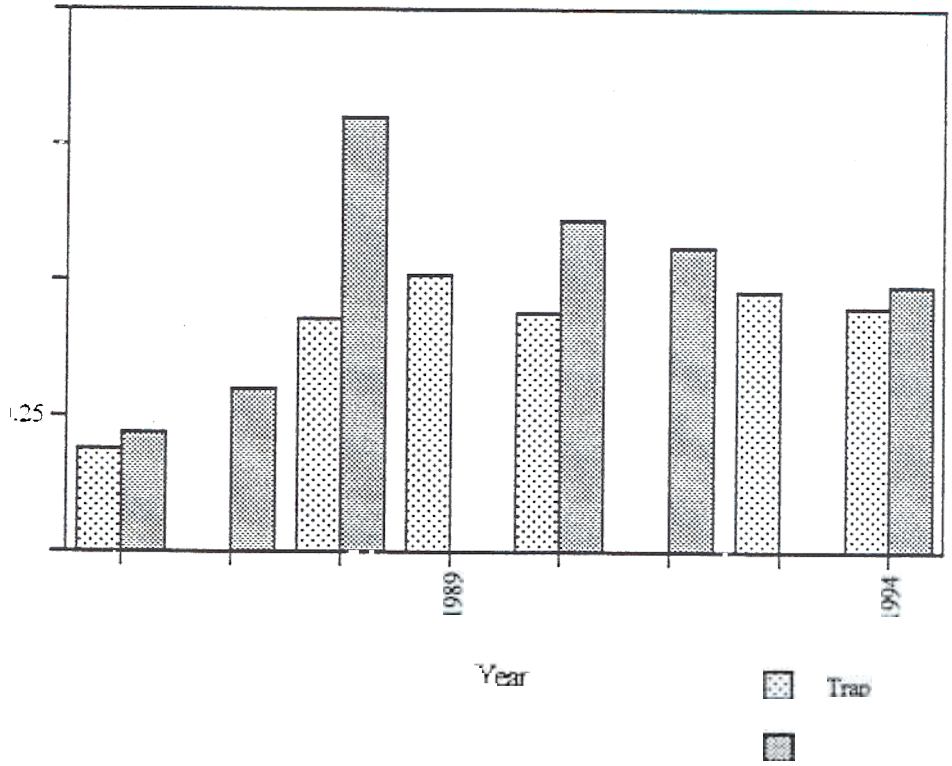


Figure .2. Linear regressions of Expected species richness ($E(S_{164})$) vs. Year for gill net and trap net fish surveys on Onondaga Lake, 1946 (Year=0) to 1994 (Year=47).



gure pec evenne (J for trap and gill fish ey. 946 to 994

(Table 1.2), however, need to be interpreted carefully to understand the diversity in the community.

Richness has initially increased this century 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 1940's and 1950's (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 1940's. 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. The first survey to record live shad was completed in 1980 (Chiotti 1981). Freshwater drum were first recorded in Oneida Lake in the 1950's (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 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). Mesh sizes of the seines, however, 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 1998).

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 1.2). Therefore, we consider immigration of 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

I hypothesized that the Seneca River is an important refuge to many fishes. The refuge is particularly important during the severe environments of summer and autumn found in Onondaga Lake (Figure 1.4) such as the degraded condition of the water column in summer (i.e., anoxic hypolimnion) and hypoxia throughout the lake in fall which are considered highly stressful to many fishes (Petit 1973, Effler 1987). These conditions presumably limit year-round populations of coldwater species (Ringler et al. 1996).

Evidence for fishes using the Seneca River during extreme low DO in the fall (Figure 1.4a) includes, for example, the movements of two smallmouth bass, a tiger muskie and a walleye radio tagged in the lake in early fall. 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 as reaeration of the water column occurred. Additionally, in 1991 and 1993, comparison of the gill net catches between summer and the fall turnover show that gizzard shad and alewife (Alosa pseudoharengus) remained in the lake despite hypoxic conditions, while white perch numbers drastically declined (Table 1.3). The large predators (e.g., smallmouth bass) and benthivorous species (e.g., redhorse sucker Moxostoma

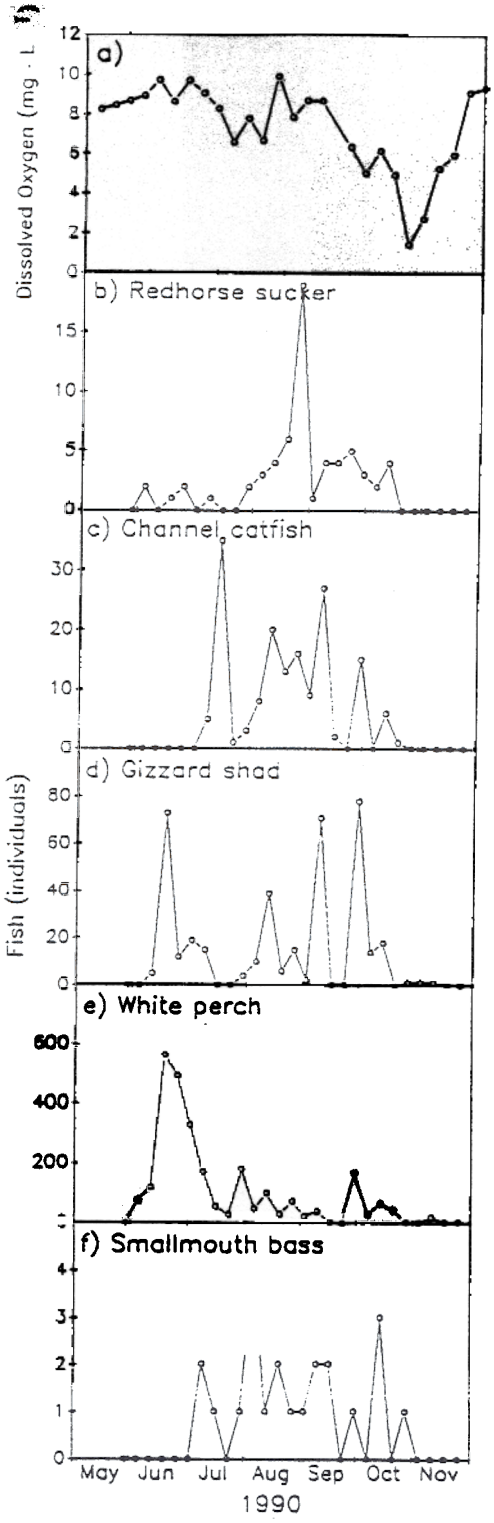


Figure 1.4. Temporal distributions in Onondaga Lake, 1990 for: a) dissolved oxygen in the surface waters, and trap net catches of b) redhorse sucker, c) channel catfish, d) gizzard shad, e) white perch and f) smallmouth bass.

Table 1.3. Limnetic gill net results from suspended nets in the epilimnion, n=24 nets per month, July and October 1991, 1993.

Species	Summer		Fall	
	1991	1993	1991	1993
Alosa pseudoharengus	79	0	285	11
Lepomis macrochirus	0	1	0	0
Ictalurus punctatus	42	6	0	0
Cyprinus carpio	2	2	0	0
Aplodinotus grunniens	1	0	0	0
Dorosoma cepedianum	448	38	617	144
Notemigonus chrysoleucus	0	0	1	0
Oncorhynchus mykiss	0	1	0	0
Moxostoma macrolepidotum	1	4	0	0
Micropterus dolomieui	52	24	0	0
Stizostedion vitreum	9	11	0	10
Morone chrysops	0	0	0	1
Morone americana	765	855	37	88
Perca flavescens	0	0	0	5

macrolepidotum, and channel catfish) were absent from the net catches at the time of autumn turnover, presumably having moved into the Seneca River. Most species that were absent in autumn gill net efforts in 1991, however, returned as common catches in 1993 summer collections (Table 1.3). Presumably many fish returned from the Seneca River.

More than four thousand fish were tagged in the lake during 1990 and 1991 (Ringler et al. 1996, Gandino 1996). Tag returns from bluegill, channel catfish, largemouth bass and yellow perch have ranged from 10 km upstream to 25 km down river of the lake outlet (Ringler et al. 1996). 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 support the importance of the Seneca River to lake community dynamics.

The annual 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 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 a 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.

Chapter 2. Fish Movements and The Potential for Oxygen Refugia During Autumn Hypoxia in Onondaga Lake, New York.

INTRODUCTION

Availability of dissolved oxygen in Onondaga Lake, NY, is considered one important factor affecting the dynamics of the fish community (Tango and Ringler 1996). Avoidance of hypoxic conditions has been reported for many species (Doudoroff and Shumway 1970), but a literature review of this issue by Doudoroff and Shumway (1970) was inconclusive regarding the evidence to support avoidance behavior. Species distribution patterns in a polluted river system have been associated with variation in oxygen concentrations; subsequent shifts in the community have been observed during restoration efforts which improved oxygen resources in the river (e.g., Mason 1991). Gradients in lake fish community composition and abundances have also been associated with dissolved oxygen gradients (Rahel 1984, Tonn and Magnuson 1982).

Vertical oxygen gradients are severe in Onondaga Lake. Anoxia begins in the hypolimnion in mid-May and by late July the entire hypolimnion is devoid of oxygen (Gelda and Auer 1996). At turnover in October, dissolved oxygen concentrations declines over the entire water column; levels below 2.5 mg/L have been recorded (Tango and Ringler 1996). Dissolved oxygen profiles show the vertical distribution of oxygen with ~~the implicit assumption of~~ little horizontal variation in a lake.

Wetzel (1975) suggests that horizontal variations in the distribution of dissolved oxygen in the pelagic zone are often small during the period of fall circulation. Large horizontal variations in dissolved oxygen, however, have been found in lakes of complex

basin morphometry (Wetzel 1975). Significant spatial variation of dissolved oxygen concentrations has also been shown in studies of estuarine embayements receiving pollution from tributary systems (Rossi and Posa 1990, Posa and Rossi 1991). Based on the range of conditions considered stressful to fishes (6 mg/l: Petit (1973) to 1-3 mg/l : Knights et al. 1995), and the minimum of 4 mg/L for the existence of a healthy aquatic community in lakes under the Clean Water Act of 1972, I selected 4 mg/L as a value defining the boundary of an oxygen refuge. I hypothesized that oxygen refugia for fishes existed in the lake as horizontal variations in oxygen concentrations and allowed for fish survival during severe hypoxia in the fall.

The objectives of this work were 1) to evaluate the vertical and horizontal distribution of dissolved oxygen by mapping oxygen levels weekly from late summer to fall turnover, and 2) to examine the correlation of community changes and fish movement patterns with reductions in dissolved oxygen resources in the fall.

METHODS

Statistical Analysis

Various statistical techniques were used to describe the patterns of dissolved oxygen in Onondaga Lake. Geostatistical analyses were conducted using SURFER software (Golden Software, Golden, Colorado). The geostatistical gridding technique of kriging (Isaaks and Srivastava 1989) was used to interpolate for dissolved oxygen values in unsampled locations. Several factors are involved in kriging: the variogram model, drift type and nugget effect. The variogram model selected was the linear interpolation model as a basic, first

approximation for the dissolved oxygen patterns. Variogram models summarize how spatial continuity varies as a function of distance and direction from a point. The linear model used is:

$$\gamma(h) = Ch$$

where $\gamma(h)$ is the moment of inertia - the function defining the spatial relationship of the data. The scale parameter, C, is for the structured component of the variogram and h is the anisotropically rescaled relative separation distance. Default parameter values of C=5.78 and h=3920 suggested by the technique were used to produce the interpolations for 1991 data. Because I had no prior knowledge of underlying trends in the spatial oxygen data, no drift parameter was used. This produces an ordinary kriging model used in this analysis.

Nugget effect is a model parameter that can account for variation in sampling error and short scale variability of the measured parameters. Sampling error and short scale variability that results in high discontinuities over small distances can increase the nugget effect (Isaaks and Srivistava 1989). In this study, a nugget effect of zero was used since 1) I am assuming no significant measurement error for each data point and 2) the mixing dynamics of water in the epilimnion coupled with natural processes are not expected to produce large discontinuities at small distances in the x-y plane. Spatial dependence between the variables at different locations within the area of interest is inferred (Rossi and Posa 1990).

Anisotropy implies a preferred direction of continuity between data points requiring a weighting of data in one direction over another. Short distance variability of dissolved oxygen has been assumed to be similar in all directions around a location in other studies

(Posa and Rossi 1991). This condition is known as isotropy (equal weighting to surrounding points) and has thus been applied to this analysis.

Estimates of unsuitable habitat to support fish (<4mg/L O_2) were made based on the spatial models for each date and depth layer. I used linear regression to estimate correlations of the percentage of unsuitable habitat area among the surface and 1-meter layers. Estimates of the percent oxygen saturation at each sampling location were based on temperature and dissolved oxygen using the nomograph of Truesdale, Downing and Lowden (1965) as redrawn in Goldman and Horne (1983). Mean saturation over the lake was computed based on the spatially distributed sample sites.

Water Quality and Fish Collections

The methods for vertical profiles of water quality parameters were described in Tango and Ringler (1996). Briefly, I utilized a YSI Model 54 meter to measure dissolved oxygen in the water column during the times of fish collections. I also used a YSI 3000 Temperature-Level-Conductivity meter to obtain profiles of temperature and conductivity. Measurements were made at 1-meter intervals. I also collected spatial data on the distribution of dissolved oxygen (mg O_2/L) in the lake during 1991, 1993, and 1994. Temperature (°C) and conductivity (uS/cm) measures were made coincident with dissolved oxygen measurements. In 1991, four sites around the lake were sampled (Sites 2, 4, 9, and 11; Figure 2.1) in vertical profile during the hours 0700-0900 on five consecutive days during summer gill net efforts. During the period 26 September to 07 November 1991, sampling occurred at 3-4 day intervals. The number of sites was expanded in the fall to 15 stations stations across

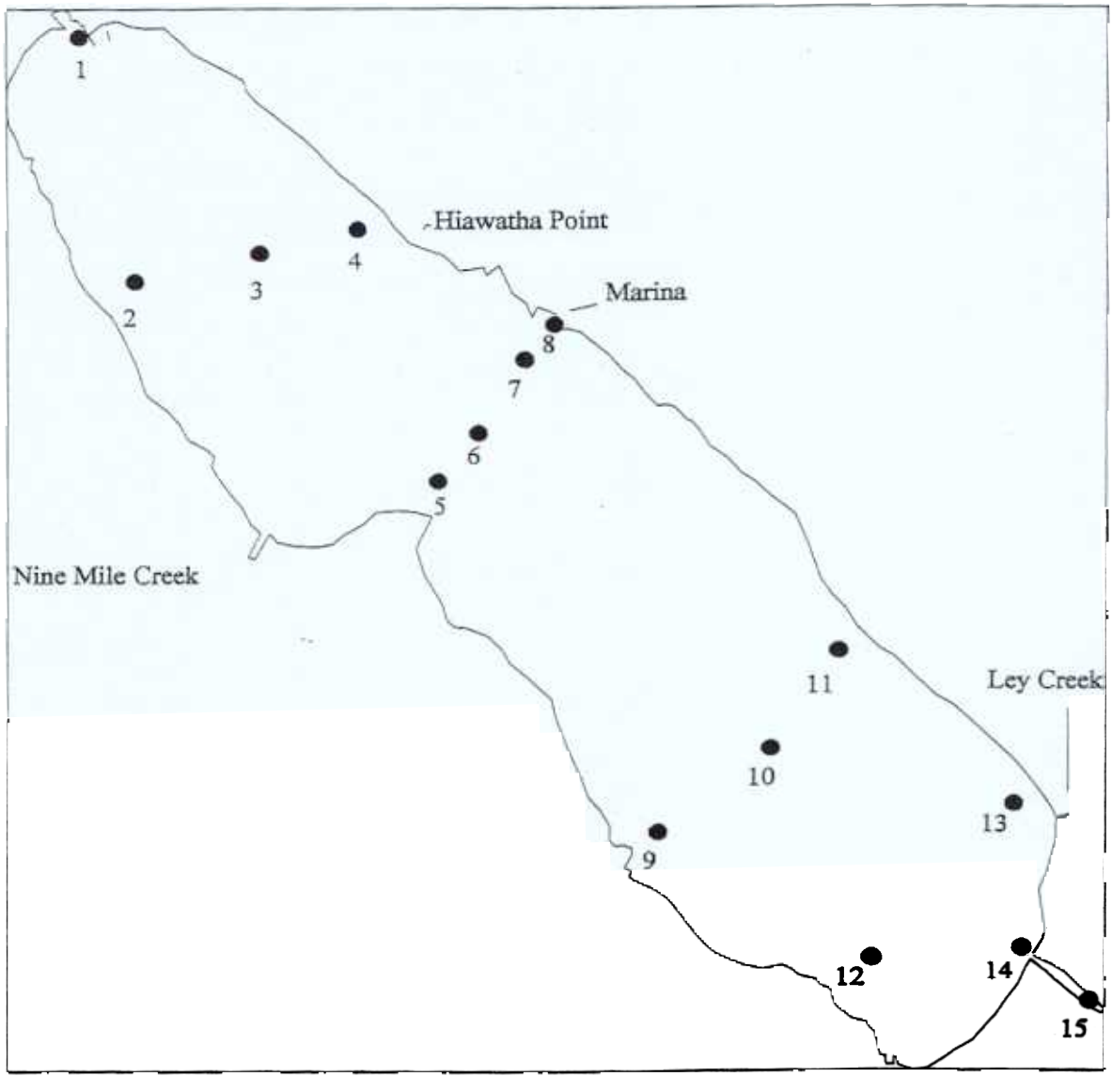


Figure 2.1. Water quality data collection locations in Onondaga Lake, NY, 1991.

Onondaga Lake, the inlet of Onondaga Creek, and the outlet to the Seneca River (Figure 2.1). Sampling was conducted between the hours 2000 and 2359 most days to minimize variation caused by community respiration on nocturnal oxygen levels. One profile of the lake was taken at Site 6, approximately the middle of the lake, each sampling day. At the remaining 14 stations, measurements were taken at the surface, 1-meter, and 3-4 meters, depending on the depth of the site. During 1993, I collected water quality data from September through the gill netting period in October. In 1994, I again collected profiles of the parameters at one site in the north basin during the period prior to and including fall turnover in October. A single site in the littoral zone located on the west shore of the north basin was monitored for comparisons of oxygen levels during the progression toward fall turnover. Dissolved oxygen profiles and trap net catches from 1990 (Ringler et al. 1996) for redhorse sucker (Moxostoma macrolepidotum), channel catfish (Ictalurus punctatus), gizzard shad (Dorosoma cepedianum), white perch (Morone americana) and smallmouth bass (Micropterus dolomieui) are included for comparison among years.

Radio telemetry

Radio signals are attenuated more rapidly in water than in air. In water the amount of radio signal strength is inversely proportional to conductivity (Tyus 1982). Onondaga Lake and the Seneca River presently have relatively high conductivities (1600-2300 uS/cm and 700-1900 uS/cm, respectively) and considerable loss of transmitter strength was expected. I tested the range of the 49 MHz radio-telemetry transmitters provided by Hi-Tech Services, Syracuse, NY, and our receiver (Advanced Telemetry Systems, Isanti, MN) from a

Cessna Skyhawk aircraft with a strut-mounted antenna, and by boat during the summer of

With this equipment, the tests indicated that fish could potentially be radio tracked while maintaining depths ≤ 2 meters in the lake and at least 3 meters in the Seneca River.

Seven individuals of four species were equipped with radio tags prior to fall turnover in 1991 (Table 2.1). Fish were located by boat and aircraft. Locations were plotted on United States Geologic Survey 1:24,000 topographic quadrangles based on the method of homing to the signal. The fish were monitored for 22-45 days between 10 October and 22 November

RESULTS

Lake Limnology

1991

A narrow, vertical aerobic stratum was evident in Onondaga Lake as illustrated by the dissolved oxygen profile from 16 July 1991 (Figure 2.2). Anoxia existed from 8 m to the lake bottom. The dissolved oxygen concentrations at the 6-8 m strata measured ≤ 3 mg O_2/L, concentrations considered stressful to lethal for many freshwater fishes (Petit 1973). Between 5 and 6 m depth a steep gradient existed from > 7 mg O_2/L to < 3 mg O_2/L. Well oxygenated waters were found from 5 m to the surface at this site.

Dissolved oxygen concentrations below levels designated stressful to fish were

Table 2.3. Comparison of physical parameters in the limnetic and littoral zones of Onondaga Lake, October 14 through November 16, 1994.

Date	Limnetic site			Littoral site		
	T(°C)	D.O.(mg/l)	Cond.(us/cm)	T(°C)	D.O.(mg/l)	Cond.(us/cm)
10/14	15.0	7.3	---	15.8	11.2	----
10/20	14.5	8.6	2310	15.7	10.2	2180
10/26	13.4	6.5	2350		----	----
10/27	----	---	----	13.1	7.9	2320
10/28	13.0	5.3	2370	----		----
11/7	12.2	5.1	2330	12.0	6.4	2280
11/10	11.7	5.4	2350	11.0	6.4	2340
11/16	11.0	6.3	2330	9.7	8.6	1997

Table 2.4. Spatial sampling results for the physical parameters of temperature and dissolved oxygen at 1-meter, November 3 and 17, 1994.

November 3, 1994

Littoral sites	T(°C)	D.O.(mg/l)	Limnetic sites	T(°C)	D.O.(mg/l)
Iron Bridge	11.0	7.5	South Deep	12.3	5.6
Marina	12.8	5.8	Midlake	12.5	5.2
Grandstand Pt	12.9	6.3	North Deep	12.1	4.4
Atlantis	12.3	3.3	Midlake-North	12.2	4.4
Dover Cliffs	12.2	4.8			
Crucible Bay	12.0	5.5			
Mean	12.2	5.5		12.3	4.9
Std Error	0.3	0.6		0.1	0.3

November 17, 1994

Littoral sites	T(°C)	D.O.(mg/l)	Limnetic sites	T(°C)	D.O.(mg/l)
South Pt	11.1	7.1	South Pt-Deep	10.8	6.9
Grandstand Pt	10.8	6.6	South Deep	10.7	6.8
Wetland site	10.2	8.3	Crucible Pt	10.8	6.9
			Grandstand Deep	10.7	6.4
			Midlake-North	10.6	6.5
Mean	10.7	7.3		10.7	6.7
Std Error	0.3	0.5		0.04	0.1

Table 2.5. 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).

	Summer		Fall	
Species	1991	1993	1991	1993
1. Alosa pseudoharengus	79	0	287	11
2. Aplodinotus grunniens		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 dolomieui	69	12	0	0
8. Morone americana	774	855	37	88
9. Morone chrysops	0	0	0	1
10. Moxostoma macrolepidotum		4	0	0
11. Notemigonus chrysoluecus	0	0	1	0
12. Oncorhynchus mykiss	0	1	0	0
13. Perca flavescens	0	0	5	0
14. Stizostedion vitreum	12	6	0	10
Totals	1425	927	955	254

Species richness was equal each summer (9 species) and showed a similar pattern of decline between summer and fall. Common species of summer remained the most common during the fall. Rare species varied in representation among the two seasons. The total catch and biomass netted was dominated by planktivorous fishes each year (Table 2.6). Vertical distribution of fish in the catch during 1991 was more equitable in summer than the fall when severe hypoxia was evident. In 1993, hypoxia was less severe, and summer and autumn catches showed a more even distribution between the two depths sampled in the limnetic zone (Table 2.7).

White perch and gizzard shad were the most commonly captured species during summer. The total catch for white perch declined in the fall to 5% and 10% of summer levels in 1991 and 1993, respectively. Gizzard shad were the second most common species in the catch each summer. Although the white perch catch was consistent between the two years, the summer catch of shad declined by 92% from 1991 to 1993. The decline is attributed to two successive, cold winters impacting the survivorship of the adults. The autumn shad catch was greater than the summer catch each year due to recruitment of young-of-the-year to our net gear.

Alewife (Alosa pseudoharengus) were the third most abundant species captured during the summer of 1991 and ranked second in autumn of 1991. In 1993, however, the alewife was absent from the summer catch and only 1 individuals were collected that fall.

Smallmouth bass were the most common predaceous species captured in the summer of 1991 and 1993. Catch rates of channel catfish and walleye followed smallmouth bass each summer (Table 2.5). During the fall of 1991, all three species were absent from our gill nets.

Table 2.6. Biomass relationships between dominant piscivorous and planktivorous fishes in Onondaga Lake, NY, gill net catches,1991 and 1993.

Species	1991 Summer Planktivores kg	1991 Summer Piscivores kg	1991 Autumn Planktivores kg	1991 Autumn Piscivores kg
Dorosoma cepedianum	154.5		96.5	
Morone americana	97.7		11.9	
Alosa pseudoharengus	5.3		22.5	
Perca flavescens	0		1.4	
Micropterus dolomieui		23.9		0
Ictalurus punctatus		22.8		0
Stizostedion vitreum		9.0		0
Totals	257.5	55.7	132.3	0
% of season total	82.2	17.8	100	0

Species	1993 Summer Planktivores kg	1993 Summer Piscivores kg	1993 Autumn Planktivores kg	1993 Autumn Piscivores kg
Dorosoma cepedianum	19.6		11.1	
Morone americana	128.3		21.1	
Alosa pseudoharengus	0		1.5	
Micropterus dolomieui		3.9		0
Ictalurus punctatus		4.3		0
Stizostedion vitreum		4.4		0
Morone chrysops		0		0.5
Oncorhynchus mykiss		0.6		0
Totals	147.9	13.2	33.7	0.5
% of season total	91.8	8.2	98.5	.5

Table 2.7. Vertical distribution of the catch in gill nets at the surface (1-3m) and deep (4-6m) strata, summer and autumn, 1991 and 1993.

Species	1991			
	Summer		Autumn	
	Surface	Deep	Surface	Deep
Ictalurus punctatus	11	28	0	0
Micropterus dolomiuei	50	19	0	0
Stizostedion vitruem	7	5	0	0
Alosa pseudoharengus	76	3	213	74
Dorosoma cepedianum	214	234	526	98
Morone americana	408	366	19	18
Cryprinus carpio	0	2	0	0
Aplodinotus grunniens	1	0	0	1
Notemigonus chrysoleucus	0	0	0	1
Moxostoma macrolepidotum	0	1	0	0
Perca flavescens	0	0	0	5
Totals	767	658	758	197

	1993			
	Summer		Autumn	
	Surface	Deep	Surface	Deep
Ictalurus punctatus	4	3	0	0
Micropterus dolomiuei	12	0	0	0
Stizostedion vitruem	5	1	8	2
Alosa pseudoharengus	0	0	9	2
Dorosoma cepedianum	19	20	89	55
Morone americana	534	321	45	43
Cryprinus carpio	0	2	0	0
Aplodinotus grunniens	0	0	0	1
Oncorhynchus mykiss	0	1	0	0
Moxostoma macrolepidotum	0	4	0	0
Lepomis macrochirus	1	0	0	0
Totals	575	352	151	103

In 1993, smallmouth bass and channel catfish were absent while walleye were captured at the same rate as the summer season.

Rarities in net catches varied between 1991 and 1993. They included freshwater drum (Aplodinotus grunniens)(1), carp (Cyprinus carpio) (4), bluegill (Lepomis macrochirus)(1), white bass (Morone chrysops) (1), shorthead redhorse (5), golden shiner (Notemigonus chrysoleucus) (1), rainbow trout (Oncorhynchus mykiss)(1), and yellow perch (Perca flavescens)(5). This group of species includes fish that are most common in the littoral zone (bluegill, carp, golden shiner) and bottom feeding fishes (freshwater drum and shorthead redhorse). The white bass are truly rare in Onondaga Lake based on the low catches in all gear types during the 1989-1994 sampling seasons. They presumably enter the lake from the Seneca River system. Rainbow trout are considered unable to survive the midsummer conditions in lakes that lack a well oxygenated hypolimnion. It is another rare species in the lake that is supported by immigration from neighboring systems (Tango and Ringler 1996).

Bottom fished gill nets 1994.

A total of 851 fish representing seventeen species was recorded (Table 2.8). White perch (59.7%) and gizzard shad (20.6%) were the most abundant species in the catch. Seasonal effects of juvenile shad recruitment to the net catches in the fall were evident as had been observed in 1991 and 1993; 102 of the total 175 shad were young-of-the-year fish captured in one net during early November. Two species captured only in gill nets this year were brown trout (Salmo trutta) and rainbow trout. Fin clips on the rainbow trout indicated

Table 2.8. Gill net catch for 35 net nights, Onondaga Lake, NY, 1994

Species	Catch	CPUE
1. Morone americana	508	14.51
2. Dorosoma cepedianum	175	5.00
3. Perca flavescens	42	1.20
4. Catastomus commersoni	36	1.03
5. Stizostedion vitreum	19	0.54
6. Ictalurus punctatus	17	0.49
7. Moxostoma macrolepidotum	10	0.29
8. Esox lucius	9	0.26
9. Cyprinus carpio	8	0.23
10. Lepomis gibbosus	7	0.20
11. Micropterus dolomieui	5	0.14
12. Salmo trutta	4	0.11
13. Notemigonus chrysoleucus	4	0.11
14. Lepomis macrochirus	2	0.06
15. Oncorhynchus mykiss	2	0.06
16. Alosa pseudoharengus	2	0.06
17. Micropterus salmoides	1	0.03
Total	851	

that they were stocked in the Finger Lakes and had traveled to Onondaga Lake (Les Wedge-NYSDEC, pers. comm.)

Spatial distribution of the catch indicated that the littoral zone had the greatest richness (Table 2.9). The highest catch rates for sixteen of the seventeen species were recorded in the littoral zone. Species encountered uniquely in the littoral zone were northern pike (Esox lucius), largemouth bass (Micropterus salmoides), white sucker (Catostomus commersoni), and brown trout. Yellow perch were caught more frequently in the profundal zone than in the littoral or limnetic zone. Catches in the late summer and early fall occurred at water depths that had been anoxic in midsummer but were reoxygenated with the lake's progression toward turnover.

Fish Movements

Of the seven fish radio-tagged in 1991, a walleye (Stizostedion vitreum), smallmouth bass, and tiger muskellunge (E. musquinongy x E. lucius) were captured in the lake and moved to the Seneca River during the period of lowest dissolved oxygen (mid-late October). The tiger muskie (tm337) was relocated in the lake on 1 November 1991 during the period of reoxygenation of lake waters. The walleye (w262) and smallmouth bass (smb285) remained in the river into November (Table 2.10).

A second smallmouth bass (smb137) was captured in the river and released at the Onondaga Lake Marina. This bass was located 8 days later in the Seneca River approximately at its initial capture site. This bass remained in the river until the end of the study season. A second tiger muskellunge (tm810) was radio-tagged in the lake and located

Table 2.9. Spatial distribution of fish in the gill nets, May-November 1994, Onondaga Lake, NY.

Species	Littoral	Epilimnion	Profundal
1. Morone americana	423	21	64
2. Dorosoma cepedianum	127	48	0
3. Perca flavescens	17	0	25
4. Catastomus commersoni	33	0	3
5. Stizostedion vitreum	17	2	0
6. Ictalurus punctatus	16	0	1
7. Moxostoma macrolepidotum	9	1	0
8. Esox lucius	9	0	0
9. Cyprinus carpio	6	1	
10. Lepomis gibbosus	7	0	0
11. Micropterus dolomieui	3	1	1
12. Salmo trutta	3	0	1
13. Notemigonus chrysoleucus	4	0	0
14. Lepomis macrochirus	2	0	0
15. Oncorhynchus mykiss	1	1	0
16. Alosa pseudoharengus	0	2	0
17. Micropterus salmoides	1	0	0

Table 2.10. Movements of radio-tagged fish in Onondaga Lake/Seneca River system, Autumn 1991.

Species	Fish ID number	Locations (N)	Monitoring period (days)	Maximum Range from release site (km)
1. Micropterus dolomieui	smb137	6	42	7.09
2. Micropterus dolomieui	smb238	6	42	2.22
3. Micropterus dolomieui	smb285	3	30	7.96
4. Esox musquinongy x E. lucius	tm337	5	22	5.56
5. Esox musquinongy x E. lucius	tm810	2	40	2.82
6. Stizostedion vitreum	w262	7	45	2.33
7. Ictalurus punctatus	cc331		1	

again 40 days later in lake. No conclusions can be drawn about its locations during the intervening period. A channel catfish (cc337) was radio-tagged in October but never relocated.

Smallmouth bass exhibited the widest range of movements from the point of release (2.22-7.69 km; Table 2.10). The walleye showed the greatest movement out of the lake and then remained in a relatively small area near the Onondaga Lake outlet into the Seneca River. Tiger muskellunge movements were measured as the shortest distance across the lake from the capture site to the lake outlet; the actual range most likely followed the shoreline and range length may be slightly greater than was reported.

Radio-telemetry in 1991 suggested that at least the adults of some species of fish leave the Onondaga Lake system at the time that dissolved oxygen levels decline approaching fall turnover. Tiger muskellunge and probably other species return to the lake as reoxygenation of the water column is occurring after turnover. These results have illustrated the fishes combined use of the Seneca River and Onondaga Lake.

DISCUSSION

Effects of low dissolved oxygen on the Onondaga Lake Fish Community

Fish community dynamics are correlated with the severity of the hypoxia each year. Movements of telemetered fishes from Onondaga Lake into the Seneca River were correlated with the timing of lakewide hypoxia in the fall 1991. Additionally, the significantly lower dissolved oxygen levels in 1991 at fall turnover (<3 mg/L) correlate with lower catches among predator species than in 1993, when oxygen concentrations in the

Table 2.11. History of movements of radio tagged fish in Onondaga Lake, NY around the time of fall turnover, 1991.

Species	Capture location	History of movements
Micropterus dolomiuei	Lake 10/2	River 10/22-11/1 (n=2)
Micropterus dolomieui	Lake 10/11	River 10/19-11/22 (n=5)
Micropterus dolomieui	Lake 10/11	River 10/13-11/22 (n=5)
Stizostedion vitreum	Lake 10/8	River 10/11-11/22 (n=5)
Esox musquinongy x E. lucius	Lake 10/10	Lake 10/11, River 10/13-22 (n=2), Lake 11/1
Esox musquinongy x E. lucius	Lake 10/1	Lake 11/1

pelagic zone were >4 mg/L . Smallmouth bass and channel catfish were caught in the summer 1991 and 1993, during periods of high oxygen availability in the epilimnion, but were absent from the autumn net catches during these years. Walleye had followed the same pattern as the bass and catfish in 1991 but were as abundant in the fall of 1993 as they were in that years' summer catch. Although summer gill netting results recorded the same number of species for both years, the most severe conditions observed in autumn 1991 produced a catch of fewer species than 1993. During another episode of severe fall turnover conditions in 1990, Ringler et al. (1996) and Gandino (1996) reported the absence of many species usually taken in summer trap net catches during the fall. Such results would be expected if these predators leave the lake, as suggested by the telemetry results.

The absence of a salmonid population and seasonal abundance of certain coldwater (e.g., alewife) and warmwater species (e.g., gizzard shad) in the fall suggest that not all species are equally impacted by the lakewide hypoxia. Such differences in effects on species may be explained by annual variations in limnology of the lake and physiological differences among species. The actual oxygen content of the blood can be affected by many factors, including the partial pressure of oxygen in the water, partial pressure of carbon dioxide, and pH (Bond 1979). There is a decreased affinity of hemoglobin for oxygen molecules when pH is low (Bond 1979). The pH in Onondaga Lake is above neutral (Effler 1996), suggesting low pH should not be a factor in affecting the ability of lake fish to acquire oxygen during periods of hypoxia. The partial pressure of oxygen declines under conditions of hypoxia making it more difficult for fish to respire. For these reasons, New York State law has set standards for daily average oxygen at 5 mg/L and a minimum of 4 mg/L for the existence of a healthy

aquatic community in lakes under the Clean Water Act of 1972

The limnology of Onondaga Lake is such that as the hypolimnion becomes anoxic there is an accumulation of reduced chemical compounds such as hydrogen sulfide (Effler 1987). As the lake progresses towards turnover, incorporation of the hypolimnion results in mixing of the lower waters and oxidation of the reduced chemical compounds. A significant reduction in available oxygen in the upper waters of the lake was evident in our work and the work of Effler (1996). A particularly important chemical reaction at this time of the year involves the oxidation of accumulated methane which produces carbon dioxide and water (Addess and Effler 1996). While low dissolved oxygen content of waters has been shown to induce fish to increase ventilation rates, the increase in the partial pressure of carbon dioxide is known to reduce the capacity for blood to be saturated with oxygen (Bond 1979). Therefore, there would appear to be at least two significant chemical stimuli affecting the ability of fish to respire and remain in the lake preceding and including turnover. The partial pressure of carbon dioxide may pose an additional important factor during fall turnover for fish respiration.

Horizontal variations in oxygen concentrations may create oxygen refugia in the lake. In 1991, oxygen concentrations between 4-5 mg/L were measured at the Onondaga Creek inlet and near the Onondaga Lake marina during the most severe hypoxia. Spatial models suggested that less than 17% of the lake may be considered refugia given the boundary condition of 4 mg/L during the most severe period of hypoxia. In 1994, oxygen concentrations in the fall showed levels in the littoral zone above 6 mg/L, while offshore levels were below 6 mg/L. The area with high dissolved oxygen may not be sufficiently

extensive to support large populations of fishes found in Onondaga Lake in the summer. Variation in dissolved oxygen was most pronounced in the littoral zone, but this is not the preferred habitat for the highly abundant, pelagic species. Therefore, refugia external to the lake presumably provide the most reliable habitat for survival of these species during the periods of severe hypoxia within the lake.

The Potential Role of Varied Life History Patterns and Migration Behaviors

The absence of some fish species during a year without severe hypoxia (i.e., 1993) suggests that additional mechanisms are working to shape the community. Migratory behavior has been reported for at least 19 of the 54 fish species captured during our survey (Scott and Crossman 1973, Smith 1985). Anadromy, potamodromy, and catadromy are characteristic migration patterns among species collected from the lake. White perch have often been the most abundant species collected in surveys since they were first reported in the 1969. This pattern, however, primarily reflects the results of summer surveys. Catch rates of white perch declined significantly from summer to autumn each year in our study.

The origin of this white perch stock is considered to be the Hudson River (Mills et al. 1987), where this species makes long range movements downriver each fall (Smith 1985). Given that white perch populations are derived from the Hudson River stock, autumn downstream movements out of Onondaga Lake into the Seneca River system may be expected as a genetically driven behaviour and not a response to severe hypoxia.

Movements of smallmouth bass between Onondaga Lake and the Seneca River from summer to fall may be triggered by declining temperatures and the lack of overwinter habitat

attractive to bass rather than declining oxygen levels. Smallmouth bass have been shown to travel 69-87 km downriver in the fall to reach wintering ranges on the Embarrass-Wolf River, WI (Langhurst and Schoenicke 1990). Smallmouth bass in Cayuga Lake, NY (60 mi^2) migrate in large numbers during September, congregating on only a few acres of prime wintering habitat (Webster 1954). A limestone ledge system with its underwater caves, cracks, and recesses is considered the favored wintering habitat in Cayuga Lake. The bottom of Onondaga Lake is largely soft, calcareous sediment containing little visible structure attractive to overwintering bass populations. Without appropriate wintering habitat in the lake we may hypothesize that movements into the river in search of overwintering sites.

Additional work will be required to elucidate the effects of temperature, habitat, and D.O. relative to the fall movements of smallmouth bass in the lake. Autumn movements of smallmouth bass have been associated with declining water temperatures reaching 15.5-16.0 °C (Webster 1954, Langhurst and Schoenicke 1990). Bass movements out of the lake could have been driven by the temperature change. Dissolved oxygen in the upper 1 meter of the lake was still above 6 mg/L at this time. In 1994, the temperature threshold that triggers fall movements of bass in other systems (15.5-16.0 °C: Webster 1954, Langhurst and Schoenicke 1990) was reached coincident with the first D.O. records below 6 mg/L.

Channel catfish also show a degree of potamodromy. Their characteristic wintering habitat in river systems is a deep depression in the channel. As has been seen in trap net catches (Gandino 1996, Ringler et al. 1996), this species does not appear to arrive in the lake in substantial numbers until June. Channel catfish are often absent from trap net and gill net catches in the fall (Ringler et al. 1996). We suggest that this is another species that may leave

Onondaga Lake in the fall for its river wintering grounds due to a life history patten of potamodromy.

SUMMARY

Potential oxygen refugia can exist within Onondaga Lake during periods of severe hypoxia. Creek mouths (e.g., Onondaga Creek) and the area around the Onondaga Lake marina supported relatively oxygen rich waters when the lakewide average was low. The marina effect may extend locally into the limnetic zone. Additionally, the littoral zone may provide oxygen rich habitat, but physical habitat may not be attractive to the limnetic species (i.e., alewife, gizzard shad, white perch) which dominate the lake community. The variation in dissolved oxygen declines as the lakewide average oxygen concentrations decline in the fall. Therefore, large scale refugia appear unlikely to exist in the pelagic zone. The absence of species in the fall that are highly abundant during the summer (e.g., white perch and smallmouth bass) suggests that more than oxygen concentration controls community dynamics. The accumulation of reduced chemical compounds in the hypolimnion such as methane leads to chemical reactions during fall which produce carbon dioxide. This may compound the effect of low oxygen for fish due to physiological changes in hemoglobin affinity for the oxygen molecule due to increasing carbon dioxide in the environment. Life history patterns may also play an important role in fish movements for several abundant summer species that are often absent in the fall (e.g., smallmouth bass and white perch). A refined study of the late summer to early autumn movement patterns will help elucidate the factors most responsible for community dynamics.

CHAPTER 3. Utilization of invasion history, breeding behavior and trophic group to interpret population dynamics in Onondaga Lake, NY.

INTRODUCTION

Resident Versus Invading Species Dynamics.

In Chapter 1 I indicated that many species found in the lake are dependent upon adjacent refugia (lake tributaries and the Seneca River). This interaction has facilitated recent increases in species richness in the lake (Tango and Ringler 1996). The aquatic habitats of Onondaga Lake have, however, undergone severe anthropogenic impacts through the drainage of area wetlands in the 1800's and disposal of human and industrial wastes over the last century (Gandino 1996, Tango and Ringler 1996, Effler 1996). It is theorized that such highly disturbed habitats are characteristically more easily invaded than more stable environments (Herbold and Moyle 1988, Meffe and Carroll 1994). Drake (1990) concluded that the "sequence or order of invasions determines the set of rules under which a given ensemble of species assembles... To fully understand communities, one must not only have a knowledge of the extant community, but must also understand the historical processes which created that community". Due to the anthropogenic disturbances on the system it is apparent that the Onondaga Lake fish community has been transformed and is no longer on a natural trajectory for the region.

Pimm (1991) reviewed terrestrial and aquatic cases of introductions and subsequent community effects, which he defined as significant density changes for the species, including extinctions. Pimm suggests that few communities are resistant to the presence of a newly

established species. Coblentz (1990) indicates that while effects of habitat alterations and pollution may be corrected and reversed over years or decades, exotic species that are well established are virtually impossible to remove from the community. Given the likelihood that introduced species tend to cause additions to a community rather than losses, and exotic species that are well established are difficult to excise from a community (Pimm and Hyman 1987), we should consider how new species integrate themselves into the community of endemic species.

Under the assumption that dynamics in the CPUE index (i.e., catch per trap net night) tracks population dynamics, I hypothesized that population dynamics of species reaching to the lake ecosystem more recently in time (i.e., invaders) will have less correlation with the population fluctuations of species previously existing in the system (i.e, resident). The Onondaga Lake fish community continues to evolve due to species invasions and establishments as well as extirpations. Species extinctions were evident around the turn of the century with the losses of Atlantic salmon and whitefish (Tango and Ringler 1996). Evidence exists for the relatively recent invasion and establishment of four species: white perch, gizzard shad, freshwater drum and common carp. Common carp were transplanted to North America in 1831 (Page and Burr 1991) and are evident in the earliest formal lake survey conducted in 1927 (Greeley 1928). White perch, gizzard shad and freshwater drum subsequently invaded the region during the 1940's and 1950's (Dence 1952, Dence 1956, Mills et al. 1978, Mills et al. 1987). White perch and freshwater drum have been consistent elements of fish surveys in Onondaga Lake since 1969, whereas gizzard shad have been recorded consistently in surveys since 1980 (Tango and Ringler 1996). I hypothesize that the

population dynamics of the recently arriving species have not had time to be well integrated with the pattern of population density changes of the longer established and resident species.

Additional Patterns in Population Dynamics.

Invasion history of the fish community may be one link to understanding the relationships among populations. An alternative hypothesis regarding species relationships in the Onondaga Lake fish community is that the degree of relation in population dynamics, as indexed by CPUE, is dependent on species sharing life history patterns. Our telemetry and netting work suggests that many species may leave the lake in the fall and overwinter beyond the lake boundary. Due to differing habitat conditions in and out of the lake, species that annually migrate to and rely on habitats outside the lake boundaries (e.g., white perch, smallmouth bass, channel catfish, bowfin, brown bullhead, yellow bullhead, etc.) may have weaker correlations with population density changes of resident lake species. In this case, the two groups of species are exposed to separate conditions that can differentially affect survival of the migratory, transient and resident populations found using the lake.

Similarly, species sharing a dependency on the littoral zone for substrate spawning may be more highly linked in their annual changes in population density than with limnetic spawning fishes. A review of spawning seasons among the 18 species suggests that they are largely spring and summer spawners (Smith 1985). Species sharing a common spawning area resource (i.e, spring littoral zone) are exposed to more similar environmental conditions than species spawning in other regions or seasons. Such niche separation may again influence the degree of synchronicity in population fluctuations among species. The effects

on spawning behavior and success can be expected to translate into varied degrees of correlation among patterns in population changes.

A third hypothesis regarding correlations in patterns of population change among species in a community is that the trophic character of the adults of invading species will affect the pattern of relationships in a predictable manner. Zaret and Paine (1973) reported the disappearance of native fishes in Lake Gatun, Panama, with the introduction of the Peacock Bass (*Cichla* sp.). Similarly, in Lake Victoria, East Africa, Miller (1989) indicated that the introduction of the predatory Nile perch (*Lates niloticus*) has drastically altered the cichlid community. Once a diverse fishery of more than 300 species, the fish community in Lake Victoria has essentially been reduced to a three species complex of Nile perch, lake sardine (*Rastineobla argentea*) and tilapia (*Oreochromis niloticus*) (Stiassny 1996). In Pimm's review of herbivore, and omnivore/predator species introductions into new environments, herbivores had significant effects on the resident community. Pimm indicates that omnivore/predators had severe effects in 32% of the cases reviewed; predator effects dominated those cases. In the case of common carp, the establishment of the invasive species occurred well before major fishery surveys were conducted in Onondaga Lake. Predator loss or introduction has more typically shown drastic community effects. I hypothesize that the benthivorous trophic habit of carp could have been less disruptive to the existing fish community than a predator or omnivorous species.

Freshwater drum exhibit plankti-insectivorous preferences as juveniles and grow into a fish and crayfish diet as adults (Smith 1985). Plankti-insectivores are abundant in Onondaga Lake (e.g., bluegill and pumpkinseed) as indicated by their catch rates (Gandino

suggesting that juvenile drum might do well. Juvenile sunfish as a potential prey base for adult drum are often abundant between years but their abundances are patchily distributed around the lake within a year (Arrigo 1998). Crayfish have rarely been encountered in lake sampling (personal observation,1991-1994). The lack of crayfish evidently leaves the drum to compete with other piscivores in the lake for a fish diet.

Gizzard shad are largely omnivorous, feeding on zooplankton as larvae, then phytoplankton, zooplankton, insect larvae and exuvia, molluscs and detritus as adults (Pierce, Wissing and Megrey 1981, Drenner, deNoyelles, Jr. and Kettle 1982). As omnivores shad may have had little resistance invading the resident community. As adults they have few predators. In Oneida Lake the shad have been known to have explosive population swings in the 1950's and again in the 1980's (Mills et al. 1987). With such boom and bust populations I hypothesize that gizzard shad have population density dynamics not well correlated with other species in the system.

White perch are largely planktivorous, feeding heavily on zooplankton, chironomid larvae and *Gammarus;* individuals larger than 200 mm they are largely piscivorous (Smith

Zooplankton have increased significantly since the mid-1980's with the closing of Allied Chemical and subsequent shifts from a copepod to a cladoceran-dominated zooplankton community (Siegfried et al. 1996). Additionally, chironomids are one of the most abundant invertebrates in the sediment of Onondaga Lake (B. Wagner, unpubl. report, 1993) providing an addition to the potentially diverse prey base that white perch could feed on. Again, as a largely omnivorous species, white perch patterns in population density through time may be weakly correlated with dynamics of other species in the community.

I evaluated direct correlation strength among species population density changes in Onondaga Lake using trapnet CPUE as a population index for each species in the period 1989-1994. I considered the hypotheses that linkage strength, as identified by correlations among the species, has been governed by 1) the sequence in species arrival time, 2) linkages dependent on migration and spawning behaviors, and 3) the trophic category of the invaders. Linkages are evaluated using annual catch data for comparison throughout the study period to develop a Community Index of Integration among the species as a tool for evaluating community structure.

METHODS

Field methods

Trap net data were summarized as CPUE from Gandino (1996), Auer et al. (1996), and personal data where effort was defined as a net-night. Netting methods were previously described in Tango and Ringler (1996), Auer et al. (1996), and Gandino (1996). Briefly, trap nets were deployed in the littoral zone between April and November from 1989-1994 with the exception of 1992. Nets were fished 3-4 days per week; some nets were periodically removed to clean off fouling algal growths. Fish were removed each day, identified to species, counted, and selected specimens were processed further for lengths, weights and tags before release.

Statistical Methods

Eighteen species were common to the trap net catches during the five years of study

(exception of 1992; no data). For the period 1989-94, a nonparametric Mann-Kendall test (Mann 1945, Kendall 1975, Gilbert 1987) was used to test for significance of linear trends in CPUE through time among these species; significance level was set at ($P<0.10$). This method was selected as the best to explain monotonic trends over a parametric technique due to the small sample sizes. Least-squares linear and quadratic models, however, were also evaluated on the species CPUE through time. Significance was set at a p-value of 0.20 to compensate for the lower power of the parametric method than comparable nonparametric techniques at small sample sizes.

Pearson correlations were computed among the 18 species annual average CPUE's. The product moment correlations that were tested assuming no lag time and N=5 years. Initially, each of the correlations of a species with the other seventeen species were categorized as low (r^2=0-0.32), medium (r^2=0.33-0.66), or high (r^2=0.67-1.0). The distributions on the number of correlations in each category for each species were compared to a null hypothesis of an even distribution (ie., no tendency for any of the species to have a higher or lower set of correlations with the other species) through a contingency table analysis (18 species x 3 categories of correlation strength). A Chi-square test of homogeneity ($P \leq 0.10$) was conducted where a significant result in this test suggested that a gradient in responses may exist (i.e., some species highly correlated while others are highly disjunct).

A median correlation was then developed for each species based on correlations with the seventeen other species in the ensemble. The median correlations were further used to rank the species according to degree with which they were deemed integrated within the dynamics of the species pool. I hypothesized that low median scores represent a low

relationship of pattern in population fluctuation to the annual population dynamics of all other species in the analysis; conversely, high median scores were expected to represent high similarity with the population dynamics of the remaining species. The gradient of median correlations, which I will give the term the "gradient of community integration" is a new tool developed here for the first time to use in further gradient analyses. The community integration gradient was first used to examine whether the time line for invading species was related to their degree of interrelationship with community dynamics. Additional comparisons were made using the gradient and further contingency table analyses to assess other hypotheses about community structure related to life history characteristics, invader or resident status, juvenile index from 1991 (high, low and none), and migratory tendency. Spawning habitat preference (in-lake, lake tributaries and out of lake) was compared to the gradient. Species were also classified according to breeding guilds using the ecoethological guild structure introduced by Balon (1975). The characteristics of breeding behaviour used in the analyses allowed division of the species into two groups: Guarder, Nest Spawners (GNS) and Nonguarder, Open substrate spawners (NOS). Further division of species that could be provided by Balon's classification produced categories with sample sizes too small for analysis. This level of classification reflects the broad distinctions in habitats available in Onondaga Lake. Eight of the eighteen species were classified as GNS and the remaining species were NOS (Table 3.1). These analyses were considered as an assessment of the characteristics that produce highly integrated versus less integrated dynamics among the Onondaga Lake fish community.

Table 3.1. Ecoethological guilds of 50 species caught in Onondaga Lake, 1989-1994.

A11. Nonguarder, open substrate spawner, pelagophil

American eel	Emerald shiner	Freshwater drum

A12. Nonguarder, open substrate spawner, litho-pelagophil

Burbot	Gizzard shad

A13. Nonguarder, open substrate spawner, lithophil

Trout perch	White sucker	Walleye
Shorthead redhorse	Rainbow smelt	Northern hogsucker

A14. Nonguarder, open substrate spawner, phyto-lithophil

Alewife	White bass	Yellow perch
Brook silverside	White perch	

A15. Nonguarder, open substrate spawner, phytophil

Longnose gar	Central mudminnow	Common carp
Chain pickerel	Golden shiner	Northern pike
Rudd	Banded killifish	

A16. Nonguarder, open substrate spawner, psammophil

Logperch	Spottail shiner

A21. Nonguarder, brood hider, lithophil

Sea lamprey	Creek chub	Fallfish
Brown trout	Rainbow trout	Brook trout
Atlantic salmon		

B21. Guarder, nest spawner, lithophil

Rock bass	Bluegill	Smallmouth bass
Green sunfish		

B22. Guarder, nest spawner, phytophil

Bowfin	Largemouth bass	White crappie
Black crappie		

B25. Guarder, nest spawner, speleophil

Channel catfish	Brown bullhead	Yellow bullhead
Spotfin shiner	Bluntnose minnow	Fathead minnow
Tesselated darter		

B26. Guarder, nest spawner, polyphil

Pumpkinseed sunfish

B27. Guarder, nest spawner, ariadnophil

Brook stickleback

RESULTS

Catch per unit effort

Average annual CPUE (i.e., average catch per net night within a year) varied from a low 0.01 in 1994 for northern pike to a high of 21.35 for white perch, also in 1994 (Table 3.2). The greatest change in CPUE for the period occurred for gizzard shad. In 1989 and 1990, gizzard shad catch rates were recorded at 13.12 and 13.97 respectively, second only to white perch in those years. By 1993, however, gizzard shad showed evidence of a population crash with a catch rate of 0.24 (1993) and 0.33 (1994). Pumpkinseed and bluegill were consistently ranked third and fourth with the exception of 1991 when CPUE of adults was well above average.

Comparisons of the range of CPUE from 1989-94 with 1980 results shows seven species with stable populations over the 14 year period. Nine species were recorded with greater catch rates in 1980; all nine had a CPUE at least twice that of their maximum for the 1989-94 period. This may partly be a function of fewer net nights (21 net nights; NYSDEC Cortland Office, personal comm. 1994) between the two periods. White perch, however, were captured at a rate nearly seven times greater in 1980 than 1989-94. White perch remain the dominant species in the more recent surveys, but CPUE is more equitable with the remainder of the community than in the earlier period. Largemouth bass and bluegill were the only two species of the 18 to have been captured at lower levels in 1980 than at anytime between 1989-94. This may represent one of the most significant community shifts in the last 14 years in that bluegill have become one of the most abundant species in the lake in the mid 1990's.

Table 3.2 Catch per unit effort (catch per trap net night) for trap netting in Onondaga Lake, NY, 1980 and 1989-1994.

Species	1980[1]	1989	1990	1991	1993	1994
Bowfin	0.19	0.11	0.12	0.36	0.67	0.51
Gizzard Shad	4.19	13.12	13.97	11.63	0.24	0.33
Brown Bullhead	4.24	0.47	0.24	1.5	1.12	1.36
Channel Catfish	2.81	0.83	0.38	0.74	1.07	0.53
White Sucker	0.67	0.71	0.23	1.17	0.58	0.58
Shorthead Redhorse	0.19	0.34	0.08	0.09	0.10	0.11
Carp	2.24	0.56	0.31	0.84	0.77	0.41
Golden Shiner	0.24	0.06	0.11	1.62	0.07	0.33
Northern Pike	0.43	0.03	0.02	0.04	0.01	0.02
White Perch	138.52	19.56	14.44	19.94	21.16	21.35
Pumpkinseed	5.57	2.49	1.58	12.63	3.33	5.18
Bluegill	0.52	4.87	4.36	19.11	6.55	7.21
Smallmouth Bass	4.33	0.12	0.04	0.40	0.34	0.18
Yellow Perch	5.48	0.33	0.37	1.47	0.38	0.54
Walleye	0.81	0.16	0.03	0.02	0.08	0.10
Freshwater Drum	0.71	0.13	0.28	0.39	0.97	0.18
Largemouth Bass	0	0.23	0.09	0.36	0.24	0.20
Black Crappie	2.52	0.31	0.31	0.48	0.19	0.28

1. Chiotti, T. 1981

Temporal Patterns in trap net CPUE

Bowfin and white perch were the only two of the eighteen species to show a significant, positive monotonic change (P=0.084) during the period 1989-1994 based on the Mann-Kendall test of trend (Table 3.3). It is obvious from the data set, however, that gizzard shad populations crashed between 1991 and 1993; parametric linear and quadratic models better capture the significant decline for the shad (P=0.02 and P=0.09 respectively, Table 3.4).

Correlation Patterns in Catch-Per-Unit-Effort

Fourteen of 153 pairs of correlations had an $r^2 \geq 0.88$ ($P \leq 0.10$) which included twelve species of the eighteen; six species showed no significant correlations with other species patterns of population density change in the assemblage (Table 3.5, 3.6). These correlations were further analyzed as follows:

Trophic category. The gradient of community integration failed to show a distinct correlation pattern to trophic category. The lower, middle and upper third of the gradient each contain two species of piscivore. The upper and lower third of the species each contain one species of planktivore and one species of benthic insectivore (Table 3.7). Two species of omnivore were distributed between the lower and middle third of the gradient and plankti-insectivores were found in the upper and middle third of the gradient. Trophic category correlations then appear to transfer little information regarding patterns of community integration at the five year time scale used in this study.

Table 3.3. Mann-Kendall Nonparametric Test of Trend by species for trap net CPUE through time, 1989-1994. (n=5; no data for 1992).

Species	S	Two sided p-value	Trend
Bowfin	+8	0.084*	increasing
Gizzard Shad	+6	0.234	
Brown Bullhead	+4	0.484	
Channel Catfish	0	1.184	
White Sucker	- 1	.	
Shorthead Redhorse	+2	0.816	
Common Carp	0	1.184	
Golden Shiner	+4	0.484	
Northern Pike	- 3	.	
White Perch	+8	0.084*	increasing
Pumpkinseed	+4	0.484	
Bluegill	+4	0.484	
Smallmouth Bass	+2	0.816	
Yellow Perch	+6	0.234	
Walleye	0	1.184	
Freshwater Drum	+4	0.484	
Largemouth Bass	+0	1.184	
Black Crappie	+0	1.184	

* = Significant P<0.10.

Table 3.4. Parametric linear and quadratic regressions that model species CPUE through time. Significant models (P<0.20). Estimates of CPUE for 1992 were determined from significant regressions or the mean of the period when regressions were not significant.

	Linear		Quadratic		Model Estimate
Species x Time model tests	r^2	P	r^2	P	for 1992
Bowfin	.81	.04[1]	.85	.15	0.36
Gizzard Shad	.89	.02[2]	.91	.09	6.05
Brown Bullhead	.50	.18[3]	.58	.42	1.12
Channel Catfish	.01	.85	.03	.97	0.71
White Sucker	0	.97	.09	.91	0.65
Shorthead Redhorse	.32	.32	.79	.21	0.14
Common Carp	.01	.88	.29	.71	0.58
Golden Shiner	0	.99	.36	.64	0.44
Northern Pike	.26	.38	.28	.72	0.02
White Perch	.37	.28	.42	.58	19.29
Pumpkinseed	.02	.81	.31	.69	5.04
Bluegill	.01	.90	.40	.60	8.42
Smallmouth Bass	.17	.50	.51	.49	0.22
Yellow Perch	.001	.96	.38	.62	0.62
Walleye	.01	.88	.79	.21	0.08
Freshwater Drum	.17	.49	.47	.53	0.39
Largemouth Bass	.01	.87	.13	.87	0.22
Black Crappie	.15	.52	.31	.69	0.31

1.Bowfin Linear Model

CPUE = 0.1059*Year- 210.5955

2.Gizzard Shad Linear Model

CPUE =-3.1660*Year+6312.723

3.Brown Bullhead Linear Model

CPUE =0.1898*Year-376.9649

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	BF	GZ	BB	CC	WS	SR	C	GS	NP	WP	PS	BG	ne	YP	W	FD	LB	BC
BF	1.00																	
GZ	-.92	1.00																
BB	.75	-.59	1.00															
CC	.51	-.36	.30	1.00														
WS	.16	.08	.68	.41	1.00													
SR	-.49	.33	-.41	.28	.11	1.00												
C	.47	-.15	.61	.80	.80	-.03	1.00											
GS	.07	.22	.64	-.02	.84	-.33	.58	1.00										
NP	-.49	.64	.19	-.15	.75	.26	.30	.77	1.00									
WP	.72	-.71	.77	.65	.55	.14	.58	.18	-.02	1.00								
PS	.22	.05	.77	.09	.89	-.32	.65	.98	.71	.36	1.00							
BG	.19	.12	.71	.12	.88	-.33	.69	.99	.71	.29	.99	1.00						
SB	.67	-.37	.83	.64	.77	-.33	.93	.67	.22	.65	.76	.77	1.00					
YP	.10	.19	.66	0	.84	-.35	.60	1.00	.75	.20	.98	.99	.69	1.00				
W	-.09	-.17	-.22	.34	-.09	.86	-.14	-.57	-.14	.42	-.48	-.54	-.31	-.58	1.00			
FD	.72	-.52	.29	.69	.01	-.42	.59	-.06	-.54	.29	0	.07	.61	-.03	-.25	1.00		
LB	.34	-.08	.75	.67	.98	.06	.90	.77	.59	.66	.84	.84	.87	.78	-.07	.21	1.00	
BC	-.41	.61	.26	-.29	.69	-.06	.28	.88	.94	-.15	.80	.81	.28	.87	-.45	-.44	.54	1.00

Table 3.6. Significant correlations among species and those least correlated with others in the assemblage.

Pairs of correlations			r^2
White Sucker	x	Bluegill	.88
Black Crappie	x	Golden Shiner	.88
White Sucker	x	Pumpkinseed	.89
Common Carp	x	Largemouth Bass	.90
Bowfin	x	Gizzard Shad	- .92
Common Carp	x	Smallmouth Bass	.93
Black Crappie	x	Northern Pike	.94
White Sucker	x	Largemouth Bass	.98
Pumpkinseed	x	Golden Shiner	.98
Pumpkinseed	x	Yellow Perch	.98
Pumpkinseed	x	Bluegill	.99
Bluegill	x	Golden Shiner	.99
Bluegill	x	Yellow Perch	.99
Yellow Perch	x	Golden Shiner	1.00

Species without significant correlations in the assemblage

Shorthead Redhorse	Freshwater Drum
Brown Bullhead	Walleye
Channel Catfish	White Perch

Table 3.7. Species and median correlation with the remainder of the ensemble

Rank	Species	Median Correlation	Trophic Category[1]	Invader/ Resident[2]	91Juv Index[3]	Spawning location[4]	EE Guild[5]
1	Gizzard Shad	0.275	Om		H	L	NOS
2	Walleye	0.28	Pi	R	0	O	NOS
3	Freshwater Drum	0.285	Pi		0	O	NOS
4	Shorthead Redhorse	0.325	BeIn	R	0	O	NOS
5	Channel Catfish	0.350	Om	R	0	O	GNS
6	White Perch	0.390	Pl		H	L	NOS
7	Bowfin	0.440	Pi	R	0	O	GNS
8	Black Crappie	0.445	Pl-In	R	L	L	GNS
9	Northern Pike	0.515	Pi	R	0	O	NOS
10	Common Carp	0.585	Be-In		L	L	NOS
11	Golden Shiner	0.610	Pl-In	R	L	L	NOS
12	Brown Bullhead	0.625	Om	R	0	O	GNS
13	Yellow Perch	0.630	Pl	R	H	L	NOS
14	Largemouth Bass	0.665	Pi	R	H	L	GNS
15	Smallmouth Bass	0.670	Pi	R	L	L	GNS
16	Pumpkinseed	0.680	Pl-In	R	H	L	GNS
17	White Sucker	0.685	Be-In	R	L	O	NOS
18	Bluegill	0.700	Pl-In	R	H	L	GNS

1. Trophic Category based on "Food and Feeding" section of species accounts in Smith (1985): Om=Omnivore; Pi=Piscivore; BeIn=Benthic Insectivore; Pl=Planktivore; Pl-In=Plankti-insectivore
2. Invader/Resident: Invader=I; Resident=R.
3. 91 Juv Index: H=top 6 most abundant juvenile species; L=7-11th most abundant juvenile species; 0=no juveniles captured.
4. Spawning location: L=Within the lake; O=outside of the lake or beyond the lake proper.
5. EE= Ecoethological Guild classification. GNS=Gaurder, Nest Spawner; NOS=Nongaurder, Open Substrate.

Invasion History. The three most recent species to invade (white perch, gizzard shad and freshwater drum) were among the lower third of species in the community integration gradient, all with median correlations of $r^2 \leq 0.39$, suggesting their patterns of population dynamics are not well integrated with the remainder of the species ensemble. Common carp preceeded the invasion of the other three species by at least 25 years and was in the middle third of correlations along the gradient. This suggests better integration with the dynamics among species for longer established species. The upper third of the correlations gradient belonged to resident species believed endemic to the watershed before the invasion of the four species. This observed correlation lends support to the hypothesis that invasion history plays a significant role in the internal relationships of species in the community.

1991 Juvenile Index. A gradient in reproductive success is evident with respect to the correlation gradient of community integration. Among the species of the lower third of the correlation gradient were four species (67%) with no evidence of juveniles recorded in the lake. While the most abundant juveniles are species of recent invasion history, the population dynamics of these species are relatively uncorrelated among other species in the ensemble. The middle third of the gradient contains 50% of species with no evidence of recruitment. The species of the upper third of the correlation gradient show the most integrated dynamics and juveniles of each species were recorded. This pattern of presence or absence of juvenile recruitment generally supports a community pattern where species without evidence of reproduction within the lake system are less likely to be well integrated into the community.

Ecoethological Guild. In Onondaga Lake, species exhibiting greater parental care and providing nests (Guarder, Nest Spawners) are more likely to be correlated with population density dynamics of the species ensemble than are species without parental care (Nonguarding, Open Substrate Spawners). A contingency table analysis comparing the distribution of correlations in the Guarders, Nest spawners versus Nonguarders, Open Substrate Spawners indicates they were significantly different (X^2=8.9, 0.025<P<0.01, Table 3.8). Inspection of the results shows a tendency for higher correlations among species within the Guarder, Nest Spawners and lower correlations within the Nonguarder Open Substrate Spawners.

DISCUSSION

Invasion history of the Onondaga Lake fish community affects the degree to which species have become integrated into the population dynamics in the lake. Given that three of the eighteen species considered are recent invaders to Onondaga Lake, there is a very low probability that, by chance, these species would be grouped among the lowest overall intercorrelations in the community. Since they are not exclusively linked to the three lowest relationships among community members, however, other factors are linked to defining the distribution of interrelationships among the species that form the structure of the community integration gradient.

Life history characteristics, specifically breeding behavior and spawning success as measured in the juvenile index in the lake, also demonstrate an influence on the interrelationships among population density changes observed in the community. While three

Table 3.8. Contingency Table analysis between guilds.***Absolute values of the correlations were used.

OBSERVED	Low	Medium	High
Guarders/Nest Spawners	8	5	15
Non guarders, open substrate spawners	21	15	9

EXPECTED	Low	Medium
Guarders/Nest Spawners	11.1	7.7
Non guarders, open substrate spawners	17.9	12.3

Chi-square critical value (2df) = 5.991
Chi-square = 8.9, $P(0.025<P<0.01)$

of the six least intercorrelated species were recent invaders, the remaining three (walleye, shorthead redhorse and channel catfish) have not demonstrated successful reproduction as measured by seine surveys. The most highly interrelated dynamics of population dynamics were among species which are all successful spawners in the lake. Breeding success in the lake is also linked with breeding behaviors as defined through the ecoethological guilds. Linked with breeding success is the fact that guarding, nest spawning species are more highly interrelated in their dynamics than non-guarding, open substrate spawners occupying the lower end of the correlation gradient. This may suggest that a future invader into this community, with characteristically less parental care for their young than average among the present species, could experience little resistance from to population establishment from the existing community. A species poised for such an invasion includes the rudd (Scardinius erythrothalmus) which has been captured with increasing frequency during this study and with the potential for rapid population growth. Conversely, an introduction or invasion by a species providing more parental care may be less likely due to the high interrelationships among species already present.

There was no clear pattern concerning trophic level and the gradient of community integration. This suggests that trophic group of an indigenous or invading species is a poor predictor of how a species will correlate to the population dynamics within the existing community. While large predator species introductions have devastated ecologically diverse communities in such places as Lake Victoria, Africa (Miller 1989), the smaller bodied invaders to Onondaga Lake (e.g., white perch, gizzard shad) evidently have not had the same power of rapidly altering species composition. White perch and freshwater drum can be

piscivorous at larger adult sizes, but the size structure, at least for white perch and relatively low numbers of drum captured, suggest these populations in the lake would not produce such sustained, large scale piscivory. It is evident, however, that there have been important shifts in the dominance relationships while not yet producing any apparent extinctions due to their arrival. Because of the openness and connectivity of Onondaga Lake to the Seneca River system, extinction of another species would likely have to be a basin-wide phenomenon, as no species are soley endemic to Onondaga Lake at this time; regional extirpations may be detected in the future before such larger scale phenomena occurs. Trophic category can certainly be important as a factor shaping the community structure but remains a poor predictor of how well the changes in population densities among species were correlated through time in this study.

There was a lack of significant trend in population density as indexed by CPUE for most of the species considered in the 1989-94 study period. The lack of trends should not be surprising. Most, if not all, species involved in the analysis have life expectancies equal to or exceeding that of the 6 year study period. Species with low variation in CPUE (e.g. northern pike) tended to be longer lived species and shorter lived species had greater variation (e.g. gizzard shad), a pattern observed in other taxon by Pimm (1991). Due to the longevity of the species involved, significant patterns may not be detectable for two or more generations, giving us an indication of the response to larger scale environmental patterns. When we include the 1980 data compared with 1989-94 to get a possible two to three generation view of the population changes we observed a decline in catch rates for many species. As in Chapter 1 where we indicated that richness has increased over time, declining

catch rates among dominant species may again indicate equitability has improved among the species in response to water quality improvements on a scale of the last fifteen years. Together, the changes in richness and equitability may represent improved biotic integrity within the lake system but we cannot forget that this is largely augmented by the relationship of the lake to the Seneca River.

SUMMARY

A gradient of interrelationships among the community members was developed as gradient of community integration for the 18 species common to the 1989-94 fishery surveys in Onondaga Lake. Invasion history was an important factor related with the gradient of community integration. Breeding behavior and juvenile recruitment in the lake, however, also helped explain the distribution of species along the gradient relative as related to degree of parental care offered to the young. The structure of the community associated with trophic level was poorly related to the gradient. These findings suggest characteristics about the invasion and community evolution process. A future invasion and establishment of a species is not expected to be well integrated with the population density dynamics of the existing community initially but may increase in degree of integration through time. The probability of invasion is greater for species that provide low parental care to their offspring and may have little to do with its trophic character.

There were few species vs. time trends evident in the CPUE data set. This is likely related to the generation time of the species involved and the time it takes to assess such trends relative to larger scale changes in the environment. Including 1980 data (Chiotti

1981), where 17 of the 18 species being evaluated in the 1989-94 data set were also captured during trap net work on Onondaga Lake, comparisons indicate that many species, based on catch rates, were either stable or have declined in density over a period of 15 years. The more equitable distribution in present day catch numbers coupled with increasing richness may suggest greater biointegrity of the Onondaga Lake fish community than two decades ago. This apparent improvement, however, is highly mediated by and reliant on fish interactions between Onondaga Lake, the Seneca River system and other tributaries of this system. The arrival of pollution tolerant species, not a return of indigenous fauna to the lake, underlies the recent fish community structure.

CONCLUSIONS

Onondaga Lake has undergone significant physical, chemical and biological changes since its first recorded history of the 1600's. Within the 20th century, lake condition reached its nadir in the 1950's and 60's and has been recovering through restoration efforts ever since. Our results signify a fish community exhibiting signs of increasing richness, however, largely mediated by species interacting with connected waterways and a history of invasion by pollution tolerant species. In Chapter 1 we defined a fish survey history where rarefaction analysis aided our determination of increasing richness within the fish community. This trend is also apparent among elements of the algal and zooplankton communities in the recent decades (Effler 1996). In terms of algae and zooplankton, responses are dominated by salinity shifts historically related to an increase in lake salinity during the era of salt production and industrial salt and $CaCo_3$ discharge to the lake, then subsequent decreased salinity since the end of industrial salt and $CaCo_3$ discharge in the mid 1980's (Effler and Hennigan 1996, Rowell 1996, Siegfried et al. 1996). Fish species such as white perch, gizzard shad and freshwater drum have reached the system in recent decades and have broader range salinity tolerances than many species. Richness has been increased , but biointegrity remains compromised as the increase presently relies on pollution and salinity tolerant species rather than a return of indigenous community member species.

In Chapter 2 I provided evidence that the fish populations in the lake are still limited by low dissolved oxygen. While diversity has increased through time in the lake, this is largely augmented by the lake community interaction with the Seneca River system that acts as a refuge for species in the fall. Refuge areas of >4 mg/L may persist in the southern region

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VITA

Name: Peter J. Tango

Date and place of birth: October 13, 1963, Passaic, New Jersey

Education:

	Name and location	Dates	Degree
High School	Monticello High School Monticello, New York	1977-1981	Regents
College	Orange County Community College, Middletown, New York	1982-1984	
	SUNY College of Environmental Science and Forestry, Syracuse, New York	1984-1986	
	West Virginia University Morgantown, West Virginia	1986-1988	

Experience:

Employer	Dates	Type of Employment
Maryland Department of Natural Resources	2/99 - Present	Natural Resource Planner
Maryland Department of Natural Resources	4/97 - 2/99	Environmental Research Statistician
Maryland Department of Natural Resources	11/96-3/97	Biostatistician
Performance Technology Inc.	6/92-12/92	Associate Field Technician
U.S. Fish and Wildlife Service	12/90-3/91	Biotechnician (Wildlife)
Douglaston Salmon Run	8/90-10/90	Assistant Riverkeeper
Environmental Labs, Inc.	3/90-6/90	Avian Technician