



Habitat use and recruitment: a comparison of long-term recruitment patterns among fish species in a shallow eutrophic lake, Oneida Lake, NY, U.S.A.

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Abstract

We analyzed inter-annual patterns in first-year abundance of 11 fish species in Oneida Lake, New York, USA, using trawl data collected from 1961 to 1997. We found two major recruitment patterns among the 11 species. One group (yellow perch, walleye, logperch and tessellated darter) decreased in abundance after the mid-1980s. These species are spring or early summer spawners with benthic juveniles. In the second group, most species increased during the early to mid 1980s (smallmouth bass, trout-perch, white bass, gizzard shad and freshwater drum), while two recruited episodically (white perch and pumpkinseed). These species spawned later than the first group and juvenile habitat use was variable. We investigated three specific mechanisms which could explain these patterns (1) competition with young-of-year (YOY) yellow perch, the dominant fish species in the lake, (2) buffering of predation by walleye by YOY yellow perch, and (3) correlation with water temperature and productivity (indexed through total phosphorus levels, TP). Buffering from predation by walleye was likely important for the species in the first group, as indicated by positive correlations between inter-annual abundance patterns of the four species. Even though species in the second group tended to increase as YOY yellow perch declined, we found little support for the competition hypothesis. Growth and abundance of these species were not significantly correlated with abundance of YOY yellow perch. Temperature was positively correlated with growth of 10 of the 11 species. Decreasing TP levels and associated changes in the lake could be causing a shift in the fish community, but the mechanism is not decreased food production. Pelagic zooplankton abundance, a direct link from nutrients to YOY fish production, has not declined since 1975.

Introduction

Recruitment of fishes is highly variable and strongly affected by mortality during their first year of life (Sissenwine, 1984). Habitat use likely affect recruitment. Mortality rates vary with season and habitat as young-of-year (YOY) fish grow through a gauntlet of different sized predators in different habitats (Werner & Gilliam, 1984; Luecke et al., 1990; Olson, 1996). In temperate lakes, larvae of many species move into pelagic habitats before returning to benthic

or littoral habitats (Werner, 1967; Werner & Gilliam, 1984; Keast, 1985; Post et al., 1995). For instance, yellow perch (*Perca flavescens*) hatch in the littoral zone, migrate to the offshore, pelagic zone to feed on zooplankton and then return to the littoral and/or benthic zone in late summer when they can also feed on benthic invertebrates (Noble, 1975; Post & McQueen, 1988). Growth rates are also affected by the use of habitat and faster growing fish are less susceptible to starvation and often less susceptible to predation than are slower growing fish (Werner & Gil-

Table 1. General life history characteristics during the first year of life of 11 species common in trawl data from Oneida Lake, NY, 1961–1997. Life history characteristics include larval habitat, juvenile habitat, and spawning season. (Life history data based on Rudstam, unpublished data from Oneida Lake and supported by Scott & Crossman, 1973; Smith, 1986; Post et al., 1995)

Family	Species	Larval habitat	Juvenile habitat	Spawning season
Clupeidae	Gizzard Shad (<i>Dorosoma cepedianum</i>)	Pelagic	Pelagic	Summer
Percopsidae	Trout-perch (<i>Percopsis omiscomaycus</i>)	Benthic	Benthic	Spring
Centrarchidae	Pumpkinseed (<i>Lepomis gibbosus</i>)	Pelagic	Littoral	Summer
	Smallmouth Bass (<i>Micropterus dolomieu</i>)	Littoral	Littoral	Summer
Percidae	Tessellated Darter (<i>Etheostoma olmstedii</i>)	Pelagic	Benthic	Spring
	Yellow Perch (<i>Perca flavescens</i>)	Pelagic	Benthic, littoral, and pelagic	Spring
	Logperch (<i>Percina caprodes</i>)	Pelagic	Benthic and littoral	Early Summer
	Walleye (<i>Stizostedion vitreum</i>)	Pelagic	Benthic and pelagic	Spring
Sciaenidae	Freshwater Drum (<i>Aplodinotus grunniens</i>)	Pelagic	Benthic	Summer
Moronidae	White Perch (<i>Morone americana</i>)	Pelagic	Benthic and pelagic	Early Summer
	White Bass (<i>Morone chrysops</i>)	Pelagic	Benthic and pelagic	Early Summer

liam, 1984; Post & Evans, 1989; Olson, 1996; Post et al., 1997). Since habitat use is coupled to growth and survival, we expect recruitment to be more similar among species that have similar patterns of habitat use in space and time during their first year of life.

We tested this hypothesis by examining recruitment patterns of 11 species in Oneida Lake, NY, U.S.A., from 1961–1997 (scientific names in Table 1). Oneida Lake is a shallow, naturally eutrophic, warm-water, percid-dominated lake occupying 20 700 ha on the Ontario plain of central New York State (Mills et al., 1978). Due to its large fetch and relatively shallow depth (mean depth of 6.5 m, maximum depth 15 m), the lake remains well mixed and isothermal throughout the summer and can therefore be classified as shallow. YOY yellow perch is considered a keystone species and a primary link in energy transfer between zooplankton and piscivores (primarily walleye, *Stizostedion vitreum*) (Mills & Forney, 1988). In Oneida Lake (Clady, 1976) and elsewhere (Eshenroder, 1977; Koonce et al., 1977), early mortality and therefore abundance of perch larvae are influenced by temperature and high winds. Large year-classes of YOY yellow perch in Oneida Lake can decrease populations of large-bodied daphnids (*Daphnia pulicaria* and *D. galeata mendotae*), thereby reducing their own growth rates (Mills & Forney, 1988).

Because of the dominance of YOY yellow perch in Oneida Lake, we explored two mechanisms associated with yellow perch abundance that could explain observed recruitment patterns. Forney (1974) hypo-

thesized that large year classes of YOY yellow perch will buffer predation by walleye on other fish species resulting in strong year classes of other species associated with strong year classes of yellow perch (*Buffering Hypothesis*, see also Lyons & Magnuson, 1987). Alternatively, competition for zooplankton and other resources with a strong yellow perch year class could negatively affect growth and therefore recruitment of other juvenile fish (*Competition Hypothesis*). Many species rely heavily on zooplankton during their first year of life (Schael et al., 1991; Gopalan et al., 1998) and larval and juvenile fish have often been found to compete with same-age or adult fish (Werner & Gilliam, 1984; Persson & Greenberg, 1990; Prout et al., 1990; DeVries & Stein, 1992; Helminen & Sarvala, 1994; Staggs & Otis, 1996). High abundance of yellow perch should then be correlated with low growth rates and low abundance of other species competing with yellow perch. Additionally, high daphnid biomass and zooplankton size should be correlated with high growth and abundance of other species. Both predation buffering and competition should be stronger for fish species sharing similar spatial and/or temporal habitat use patterns with yellow perch.

Other limnological factors also affect fish recruitment (*Limnology Hypothesis*). In general, warmer water temperature improves growth and therefore survival of YOY fishes (Clady, 1976; Koonce et al., 1977; Shuter et al., 1980; Staggs & Otis, 1996). In addition, other limnological variables such as nutrient concentrations, chlorophyll *a* levels and primary production

can be particularly important for age-0 fish recruitment if they impact overall productivity of a lake (Oglesby, 1977; Miller et al., 1988). We correlated annual growth and abundance of each species with water temperature and total phosphorus (as an index of lake productivity) measured in Oneida Lake since 1975 (E. L. Mills, Cornell Biological Field Station, unpublished data). These two factors should affect all species regardless of differences in habitat use.

Materials and methods

YOY fish abundance and growth

Relative abundance of YOY of 11 species of fish from 1961 to 1997 was determined using catch in an otter trawl with a 5.5 m foot rope and 6.4 mm mesh cod end. Samples were collected at 10 stations (Figure 1) at weekly intervals from mid-July or early August (when YOY yellow perch becomes vulnerable to the bottom trawl at a size of 1 g) to mid-October (10–16 sampling dates). Each trawl was towed for five min and swept an area of approximately 0.1 ha. YOY fish were identified, counted, and weighed to the nearest gram by measuring all individuals per sample by species and averaging the resulting weight per fish. We averaged all trawl hauls (100–160 hauls per year) to determine a yearly index of abundance for each species. While we recognize that species are not equally vulnerable to trawling and that catchability will change seasonally, our analysis of relative changes between years only requires the assumption that catchability for a given species did not change between years. Thus, we assumed that trawling provided us with a reliable index of abundance from 1961 to 1997 for each species. We used average September weight as an index of annual growth of each species (Keast & Eadie, 1984).

Limnological variables

Weekly sampling of water temperature, total phosphorus, daphnid biomass and average zooplankton size at five sites in Oneida Lake (Figure 1) from 1975 to 1996 were available for our analysis (E.L. Mills, CBFS, unpublished data). A YSI meter (before 1992) and a Hydrolab H20 multiprobe (during and after 1992) were used to measure water temperature at 1 m intervals from surface to bottom (which were used to calculate mean water column temperature for each site). Total phosphorus was measured from integrated water samples using persulfate digestion (Menzel &

Corwin, 1965). Zooplankton were collected using a 0.5 m diameter, 153 μm mesh, 2 m long nylon net (assuming 100% capture and filtering efficiency) and later counted using a micro projector at 20 \times magnification to species, excluding immature copepods, which were classified as nauplii or copepodites. The database includes density, average size, and biomass (using length-dry weight regression equations) for each species.

Data analysis

To describe and characterize annual recruitment patterns, we used correlation (Pearson) and principle components analysis (PCA) (Wilkinson, 1990). We first $\ln(x+1)$ transformed data to homogenize variance and normalize residuals. We plotted unrotated factor loadings for each species on factors 1, 2 and 3 of the PCA to categorize species recruitment patterns. Percent variance explained by the each factors is the sum of the squared loadings on that factor. We tested for relationships between life history characteristics and groups of species with similar inter-annual recruitment patterns (as determined by PCA) using two-tailed Fisher's Exact Tests. We used the following life history characteristics (Table 1): larval habitat (pelagic vs. non-pelagic), spawning season (spring vs. early summer and summer) and use of benthic, pelagic, and littoral habitat as juveniles. The 11 species we used for these comparisons use habitat differently during their first year of life (based on CBFS, unpublished data; supported by Scott and Crossman, 1973; Smith 1986; Post et al., 1995; summarized in Table 1). Yellow perch, walleye, tessellated darter, and logperch are pelagic as larvae and use benthic and littoral habitats as juveniles (yellow perch can also use pelagic habitats). Freshwater drum, white perch and white bass have pelagic larvae and use benthic habitats and for white perch and white bass also pelagic habitats, as juveniles. Pumpkinseed are pelagic as larvae and littoral as juveniles. Finally, trout-perch (benthic), smallmouth bass (littoral), and gizzard shad (pelagic) do not typically shift habitat during first year of life. The appearance of YOY of these 11 species also differs temporally: yellow perch, walleye, tessellated darter, and trout-perch hatch in spring (late May, early June), freshwater drum, logperch, smallmouth bass, white bass and white perch hatch in early summer (June) and gizzard shad and pumpkinseed hatch in summer (late June–July).

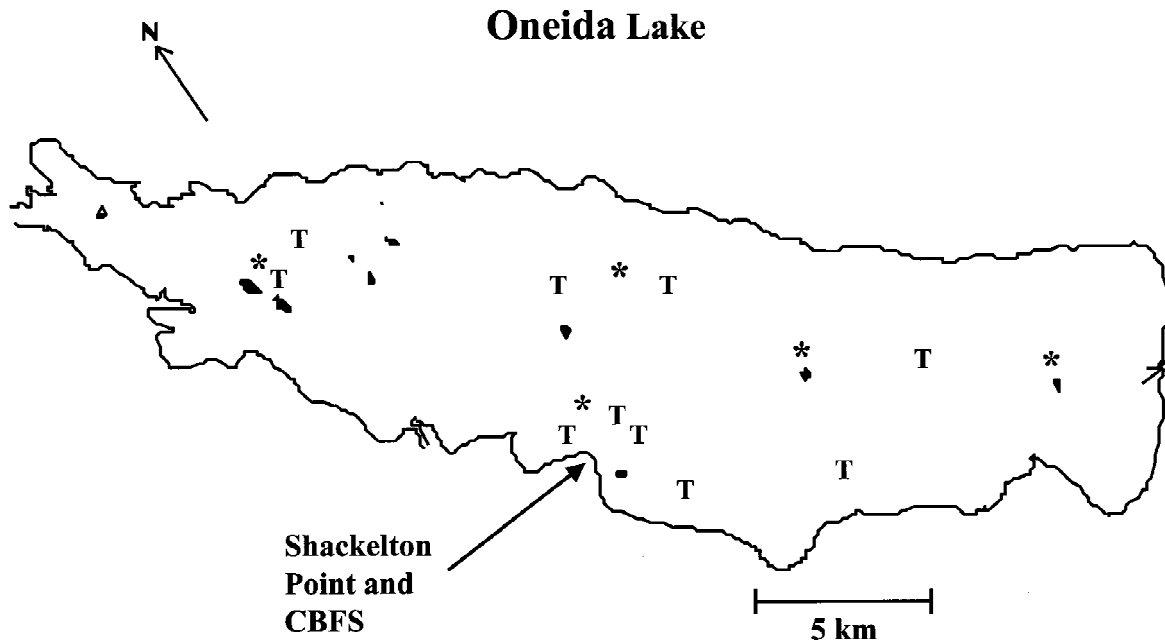


Figure 1. Map of Oneida Lake, NY, showing trawling sites (T) and limnology sampling sites (*).

We used correlation analysis (Pearson correlation coefficient) to test for relationships between variables. We correlated abundance and growth (indexed as mean September weight) of each species with abundance of yellow perch, and with average size of zooplankton, daphnid biomass, water temperature and TP, averaged for the months of June through August of each year from 1975 to 1996. For each correlation analysis we kept an overall $\alpha = 0.05$ (or $\alpha = 0.10$ for slightly significant correlations) using a Bonferroni correction of α .

We used a simple intervention analysis to investigate if patterns of species abundance in time reflect changes of abundance of yellow perch (Proc ARIMA; SAS Institute, 1989). After visual inspection of dynamics of abundance of YOY yellow perch (Figure 2), we chose 1986 as the year of the 'intervention', dividing the time series into 1961–1985 (i.e. years of higher abundance of yellow perch) and 1986–1997 (years of reduced abundance of yellow perch). To remove serial dependencies in recruitment patterns of each species, we used an autoregressive time series model of the form:

$$(1 - \phi_1 B_1)(Z(t) - \mu) = a(t) + \alpha S,$$

where $Z(t)$ is the time series of the response variable, μ is the series mean, ϕ is the autoregressive (AR)

parameter, B_i is the backshift operator ($B_i Z(t) = Z(t-i)$), $a(t)$ is the time series of residuals, α is the intervention effect, and S is a variable that represents the yellow perch 'intervention'. This tests for concomitant changes in two time series. Any causal interpretation hinges on ecological evidence (Rudstam et al., 1993). We fit a model with one – three autoregressive terms, depending upon inspection of the auto-correlations and partial auto-correlations.

Results

Dominant recruitment patterns and correlation with habitat use

Abundance of age-0 fishes in Oneida Lake changed dramatically between 1961 and 1997. Temporal trends of age-0 abundance of 11 species showed two major patterns. Four species (yellow perch, walleye, logperch, and tessellated darter) were abundant and highly variable before the early 1980s but declined after the mid-1980s (Figure 2A–D). Abundance of these four species were positively and significantly correlated (Table 2) and they formed a distinct group in the PCA, separating from the other species on factor 1 (Figure 3). Correlations were stronger between walleye and yellow perch and between tessellated darter

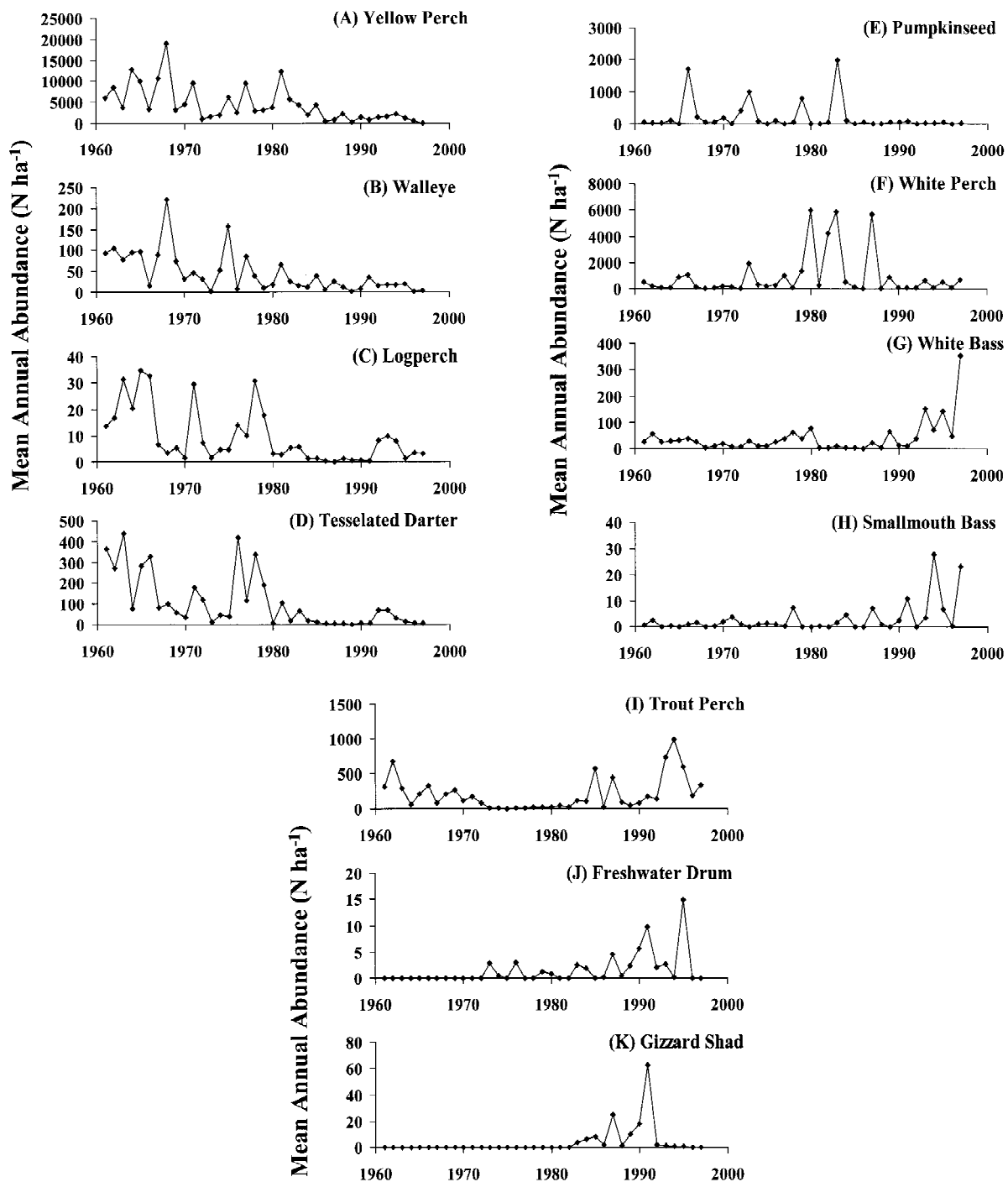


Figure 2. Mean abundance of age-0 fish of 11 species in Oneida Lake, NY, 1961–1997, averaged July–October captured in weekly sampling in bottom trawls.

Table 2. Correlation matrix (Pearson correlation coefficient) of $\ln(X+1)$ transformed abundance of 11 most common species of fish in bottom trawl samples from Oneida Lake, NY, 1961–1997. Species codes: yellow perch (YP), walleye (WE), logperch (LP), tessellated darter (TD), pumpkinseed (PS), white perch (WP), white bass (WB), smallmouth bass (SB), trout-perch (TP), gizzard shad (GS) and freshwater drum (FD). Data used are yearly averages. * indicates significance at Bonferroni corrected $\alpha = 0.0018$ (0.10/55), ** at $\alpha = 0.0009$ (0.05/55), and *** at $\alpha = 0.0001$ (0.01/55).

	YP	WE	LP	TD	PS	WP	WB	SB	TP	FD
WE	0.76***									
LP	0.50*	0.40								
TD	0.64***	0.56**	0.88***							
PS	-0.07	-0.25	0.05	0.13						
WP	-0.03	-0.18	-0.01	-0.05	0.18					
WB	-0.31	-0.23	0.28	0.09	0.01	0.35				
SB	-0.38	-0.11	-0.13	-0.14	0.00	0.00	0.37			
TP	-0.09	0.10	0.04	0.02	-0.06	-0.14	0.25	0.41		
FD	-0.40	-0.42	-0.47	-0.37	0.21	0.26	0.20	0.31	0.31	
GS	-0.42	-0.28	-0.62*	-0.56**	-0.01	0.03	-0.23	0.29	0.20	0.65***

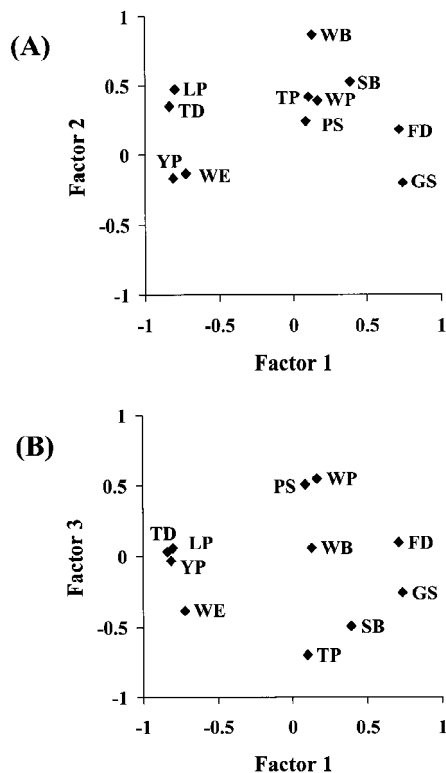


Figure 3. Loadings of factors 1 with factors 2 and 3, resulting from PCA of mean $\ln(X+1)$ transformed abundance of age-0 fishes in Oneida Lake, NY, 1961–1997. The first factor explained 35%, the second 17% and the third 14% of the variance. Species codes: YP = yellow perch, TD = tessellated darter, WE = walleye, LP = logperch, TP = trout-perch, WB = white bass, SB = smallmouth bass, PS = pumpkinseed, WP = white perch, GS = gizzard shad and FD = freshwater drum.

and logperch than among other combinations within this group (Table 2). The first three factors explained 69%–86% of the variance for these species.

A second group of species generally had relatively low abundance before the mid-1980s and increased in abundance after the mid-1980s (smallmouth bass, white bass, trout-perch, freshwater drum, gizzard shad) or showed episodic recruitment patterns (white perch and pumpkinseed) (Figures 2E–K and 3). In this grouping of species, only abundance of gizzard shad and freshwater drum were significantly correlated (Table 2). Factors 1–3 explained 32%–77% of the variance of this group. Within this group, freshwater drum and gizzard shad separated from the other species along factor 1 (Figure 3). Additionally, factor 3 separated pumpkinseed and white perch from trout perch and smallmouth bass (Figure 3). These sub-groups reflect similarities in recruitment patterns (Figure 2); pumpkinseed and white perch both showed episodic recruitment, freshwater drum and gizzard shad had very low abundance in the 1960s and 1970s, and trout-perch and smallmouth bass increased in the 1990s but were present throughout the time series.

The two major groupings of the 11 species were related to two habitat (temporal and spatial) variables. Habitat attributes that separated the two groups were spring hatch coupled with the use of benthic habitat as juveniles (Fisher’s Exact test, two-tailed: $P=0.015$). Non-significant habitat variables included species using pelagic habitat as larvae ($P=0.49$), using benthic habitat as juveniles in general ($P=0.24$), using pelagic

habitat as juveniles ($P=1.00$) and using littoral habitat as juveniles ($P=0.58$). Thus, the group of species, which declined after the early to mid-1980s, spawned in spring and used benthic habitats as juveniles. The group which generally increased in the 1980s and 1990s was more heterogeneous and tended to spawn later in the summer and occupied a variety of habitats.

Influence of yellow perch – buffering and competition hypotheses

We used time-series analysis to determine if patterns of abundance of the other 10 species reflected changes in abundance of YOY yellow perch, using 1986 as the intervention year. For walleye, tessellated darter, and logperch, 1986 significantly or marginally significantly divided periods of higher abundance (before 1986) and lower abundance (after 1986) (Table 3). In the second major recruitment group, 1986 is a marginally significant intervention year only for pumpkinseed (Table 3). All other species began increasing before or after 1986 (Table 3, Figure 2). Pumpkinseed recruited episodically, but each of the four major recruitment years (1966, 1973, 1979, 1983) occurred before 1986 (Figure 2H), yielding a negative intervention result (Table 3). Several species showed cyclical patterns of recruitment: smallmouth bass showed positively correlated three year cycles and negatively correlated two year cycles, tessellated darters and white bass showed positively correlated two year cycles, and year classes of trout-perch and logperch correlated positively with that of the previous year (Table 3).

We also examined relationships between abundance of yellow perch, average size of zooplankton, and biomass of daphnids, on abundance of each species. Average size of zooplankton was positively and significantly correlated with abundance of logperch only (Table 4). Abundance of yellow perch was not correlated with zooplankton size (Table 4). Abundance of both walleye and yellow perch was negatively correlated with daphnid biomass, although only the correlation with walleye was significant using Bonferroni correction of α (Table 4).

Finally, we examined relationships between growth of each species and abundance of yellow perch, zooplankton size, and daphnid biomass (Table 5). Only growth of yellow perch was correlated with abundance of yellow perch (Table 5). Daphnid biomass and average zooplankton size was positively correlated with walleye growth and negatively correlated with yellow perch growth, although only yellow

perch growth and daphnid biomass was significant using the Bonferroni corrected α (Table 5). No other correlations of yellow perch abundance, zooplankton size and daphnid biomass with average September size were significant (Table 5).

Limnology hypothesis

Water temperature (averaged June–August) was positively correlated with growth rates for 10 of the 11 species. This represents a significant positive across species effect of temperature (one-tailed Z-test, $P<0.01$), although these correlations were not significant with Bonferroni correction of α levels for individual species except for white perch (Table 5). Temperature was also negatively correlated with abundance of logperch and tessellated darter and positively correlated with abundance of smallmouth bass, trout-perch, and freshwater drum (all $P<0.10$, but none statistically significant using Bonferroni corrections of α) (Table 4). A post-hoc evaluation of water temperatures in both May and June revealed no significant correlations with abundance of spring spawners (yellow perch, walleye, tessellated darter, trout-perch), a somewhat surprising result. Total phosphorus was correlated positively with abundance of yellow perch, possibly indicating an impact of reduced nutrient loading to the system (Table 5). In contrast, freshwater drum and white bass were both negatively and significantly correlated with total phosphorus.

Discussion

Our analysis showed two general inter-annual patterns of abundance of YOY fish over 37 years in Oneida Lake. Species with similar temporal and spatial habitat use tended to group together. Early spawners with pelagic larvae and utilizing benthos as juveniles (yellow perch, log perch, tessellated darter and walleye) have decreased since the middle of the 1980s. Species spawning in summer (most of the other species) have increased since the 1980s. The only spring spawner that has increased in abundance since the 1980s is trout-perch.

We investigated three hypotheses to explain these recruitment patterns. YOY yellow perch are the most abundant YOY fish species in this data set (Figure 2). This species is considered a keystone species in Oneida Lake and is the primary link between zooplankton production and piscivores (Mills & Forney,

Table 3. Results of time series intervention analysis (autoregressive model) of annual untransformed abundance of 11 species of fishes (yellow perch, walleye, logperch, tessellated darter, smallmouth bass, white bass, trout-perch, white perch, pumpkin-seed, gizzard shad and freshwater drum, respectively) of Oneida Lake, 1961–1997 (1973–1997 for gizzard shad and freshwater drum). Intervention year was 1986. For each species, degrees of freedom, AIC, estimate, approximate standard error and *T*-ratio for mean, intervention, and autoregressive terms are presented. (***) significant at $\alpha = 0.001$, ** at $\alpha = 0.05$, * at $\alpha = 0.10$). Species codes as in Table 2

Species	DF	AIC	Parameter	Estimate	Approx. SE	<i>T</i> -ratio
YP	34	716.45	Mean	6062	771	7.85***
			Intervention	−5047	1352	−3.73***
			AR1	0.04	0.17	0.20
WE	34	386.17	Mean	60.3	10.2	5.90**
			Intervention	−46.3	17.7	−2.61**
			AR1	0.17	0.17	0.99
LP	34	269.10	Mean	11.9	2.93	4.07***
			Intervention	−8.17	4.89	−1.67*
			AR1	0.42	0.16	2.68**
TD	33	457.70	Mean	148.9	40.9	3.64***
			Intervention	−110.9	66.2	−1.67*
			AR1	0.18	0.16	1.14
			AR2	0.30	0.17	1.77*
PS	34	559.15	Mean	279.9	79.9	3.50***
			Intervention	−253.3	141.1	−1.79*
			AR1	−0.12	0.17	−0.70
WP	34	657.86	Mean	999.3	371.0	2.69**
			Intervention	−281.5	647.7	0.55
			AR1	0.09	0.17	−0.43
WB	33	402.56	Mean	47.03	38.21	1.23
			Intervention	33.40	35.62	0.94
			AR1	−0.01	0.26	−0.07
			AR2	0.77	0.26	2.97**
SB	32	218.41	Mean	2.31	1.74	1.33
			Intervention	3.49	2.15	1.62
			AR1	0.12	0.16	0.75
			AR2	−0.25	0.15	−1.70*
			AR3	0.72	0.16	2.97**
TP	34	505.08	Mean	182.2	69.6	2.62**
			Intervention	84.3	119.8	0.7
			AR1	0.40	0.16	2.42**
FD	23	137.16	Mean	0.91	0.69	1.32
			Intervention	2.74	1.02	2.69**
			AR1	−0.26	0.20	−1.30
GS	23	209.55	Mean	1.35	3.61	0.38
			Intervention	8.82	5.30	1.66
			AR1	0.05	0.21	0.82

Table 4. Pearson correlation coefficients (R) and P -values resulting from correlations of abundance of the 11 most common fishes ($\ln(X+1)$ transformed) in bottom trawl data from Oneida Lake, 1961–1997 (1975–1996 for limnological variables). ** and * indicate significant at a Bonferroni corrected $\alpha=0.00455$ (0.05/11) and $\alpha=0.0091$ (0.10/11) for each limnological variable, respectively. Limnology data represented averages of weekly samples taken June through August. Limnology variables included mean water temperature ($^{\circ}\text{C}$) total phosphorus ($\mu\text{g l}^{-1}$) ($\ln(X+1)$ transformed to increase normality), average size of zooplankton (mm), and biomass of daphnids (*D. pulicaria* and *D. galeata*, dry weight in $\mu\text{g l}^{-1}$)

Species	Average Size		Daphnid Biomass		Water Temperature		Total Phosphorus	
	R	P	R	P	R	P	R	P
Yellow Perch	-0.13	>0.50	-0.43	0.05	-0.17	0.45	0.52	0.01
Walleye	-0.42	0.06	-0.66	0.001**	0.28	0.21	0.41	0.06
Logperch	0.62	0.003**	-0.23	0.30	-0.53	0.01	0.09	>0.50
Tessellated Darter	0.38	0.09	-0.32	0.14	-0.45	0.03	0.18	0.43
Pumpkinseed	0.07	>0.50	0.30	0.18	-0.15	0.49	-0.07	>0.50
White Perch	-0.09	>0.50	-0.07	>0.50	0.05	>0.50	0.11	>0.50
White Bass	0.53	0.01	-0.01	>0.50	0.03	>0.50	-0.56	0.007*
Smallmouth Bass	-0.15	>0.50	-0.23	0.15	0.47	0.03	-0.34	0.13
Trout-Perch	0.06	>0.50	0.23	0.31	0.38	0.08	-0.53	0.01
Freshwater Drum	0.00	>0.50	0.25	0.26	0.23	0.30	-0.55	0.008
Gizzard Shad	-0.48	0.03	0.00	>0.50	0.19	0.40	-0.40	0.07

1988). A dominant species such as yellow perch can affect recruitment of other species through at least two mechanisms: by competing for shared prey and by acting as a buffer from predators in the lake. Both of these mechanisms should be stronger for species using similar habitats, but they result in different predictions of recruitment patterns. If competition is important, growth and abundance should be negatively correlated with abundance of yellow perch and potentially with average size of zooplankton and biomass of daphnids. If predation buffering is important, abundance should be positively correlated with abundance of YOY yellow perch.

Yellow perch – buffering hypothesis

Two lines of evidence are consistent with the buffering hypothesis. Abundance of yellow perch, walleye, logperch, and tessellated darter are all correlated positively and significantly (Table 2), and 1986 was a significant year dividing higher and lower abundance for each of these species (Table 3). Predation by walleye is the major source of mortality for juvenile age-0 yellow perch and age-0 walleye in Oneida Lake (Chevalier, 1973; Forney 1974, 1977; Mills et al., 1987). By providing a predation buffer, large year classes of yellow perch have been hypothesized to increase survival of walleye and white perch in Oneida Lake (Forney, 1974; Clady and Nielsen, 1978). In Sparkling

Lake, WI, yellow perch provided a predation buffer for darters but not for cyprinids (Lyons & Magnuson, 1987). Thus, our conclusion that yellow perch act as a predation buffer for species occupying the same spatio-temporal habitat but not others is supported by observations elsewhere.

Predation buffering by YOY yellow perch is not important for the second major recruitment group as these species are not positively correlated with abundance of yellow perch. We suggest that yellow perch do not buffer these species because most of them do not overlap in time and space with YOY yellow perch. Even at the current lower abundance of yellow perch in Oneida Lake, walleye still feed primarily on yellow perch (VanDeValk & Rudstam, 1997), thus restricting predation on these species even when yellow perch abundance is low. One exception is the spring-spawning, benthic trout-perch which does overlap with yellow perch. Walleye do eat trout-perch in the laboratory (A. VanDeValk, CBFS, unpublished data), but trout-perch are seldom eaten by walleye in the field (Forney, 1974; VanDeValk & Rudstam, 1997). Many species (white bass, white perch, gizzard shad, pumpkinseed and drum) are deeper-bodied than yellow perch (Smith, 1986), which may also reduce their vulnerability to predation (Hambright, 1994), although walleye do consume all the species analyzed here (VanDeValk & Rudstam, 1997).

Table 5. Pearson correlation coefficients (R) and P -values resulting from correlations of abundance of the 11 most common fishes in bottom trawl data from Oneida Lake, 1961–1997 (1975–1996 for limnological variables). ** and * indicate significant at a Bonferroni corrected $\alpha=0.00455$ (0.05/11) and $\alpha=0.0091$ (0.10/11) for each limnological variable, respectively. Limnology data represented averages of weekly samples taken June through August. Limnology variables included mean abundance of YOY yellow perch (number ha^{-1} , $\ln(X+1)$ transformed), average size of zooplankton (mm), and biomass of daphnids (*D. pulicaria* and *D. galeata*, dry weight in $\mu\text{g l}^{-1}$), mean water temperature ($^{\circ}\text{C}$), and total phosphorus ($\mu\text{g l}^{-1}$). (Number of observations in parentheses: with yellow perch, with limnology variables, respectively)

Species	Yellow Perch		Average Size		Daphnid Biomass		Water Temp		Total Phosphorus	
	R	P	R	P	R	P	R	P	R	P
Yellow Perch (37,21)	-0.53	0.001**	0.46	0.04	0.54	0.009*	0.28	0.33	-0.47	0.03
Walleye (37,21)	-0.04	<0.50	-0.44	0.04	-0.40	0.0	0.33	0.14	0.04	<0.50
Logperch (27,18)	0.01	<0.50	-0.48	0.04	-0.19	0.45	0.39	0.14	0.09	<0.50
Tessellated Darter (31,20)	-0.18	0.33	-0.26	0.27	0.05	<0.50	0.34	0.14	0.08	<0.50
Pumpkinseed (35,21)	-0.25	0.14	0.16	<0.50	0.20	0.41	0.25	0.31	-0.59	0.008*
White Perch (37,21)	0.03	<0.50	-0.15	<0.50	0.04	<0.50	0.58	0.006*	-0.02	<0.50
White Bass (37,21)	0.03	<0.50	-0.35	0.13	0.07	<0.50	0.37	0.10	-0.29	0.21
Smallmouth Bass (17,14)	-0.27	0.30	-0.12	<0.50	0.10	<0.50	0.64	0.01	-0.28	0.34
Trout-perch TP (27,19)	-0.21	0.29	-0.19	0.42	-0.28	0.24	-0.10	<0.50	-0.27	0.28
Freshwater Drum (15,13)	-0.32	0.24	-0.49	0.09	-0.49	0.09	0.65	0.02	-0.31	0.30
Gizzard Shad (14,13)	0.12	<0.50	-0.03	<0.50	0.59	0.03	0.35	0.24	0.22	0.48

Yellow perch – competition hypothesis

Abundance of several species increased during and after abundance of yellow perch declined, as predicted by the competition hypothesis. However, our analysis does not indicate that release of competition with yellow perch was the primary cause for these increases. First, decrease of yellow perch did not coincide significantly with increase of other species (excluding pumpkinseed, Table 3). Second, growth of these species were not related to abundance of yellow perch (Table 5). In fact, yellow perch abundance only affected intra-specific growth, evidence of density-dependent growth in their first year of life (Staggs & Otis, 1986; Mills & Forney, 1988; Post & McQueen, 1994). Finally, correlations involving the two zooplankton variables did not indicate that zooplankton biomass or size was limiting growth of species in the second recruitment group except possibly for gizzard shad. Not surprisingly, the main correlations with daphnid biomass were consistent with past work on Oneida Lake. During years of high abundance of yellow perch, *Daphnia* populations crashed, yellow perch growth rate decreased, and growth and survival of piscivorous YOY walleye increased because small YOY perch were then available to YOY walleye (Mills & Forney, 1988).

These findings are interesting, particularly considering the importance given to competition in the liter-

ature (Serns, 1982; Hanson & Leggett, 1986; Persson & Greenberg, 1990). Prout et al. (1990) evaluated potential competitive interactions of YOY white perch and YOY yellow perch in Oneida Lake. Both species feed on *Daphnia*, although competitive interactions were asymmetric: yellow perch populations affected growth of white perch but not vice-versa. Asymmetry existed both because they can crash *Daphnia* populations and because they have a growth advantage, due to earlier spawning time (Prout et al., 1990). However, our analysis of the longer time series did not support these observations, perhaps due to a decoupling of this interaction in recent years. Roseman et al. (1996) found little evidence that gizzard shad and yellow perch compete in Oneida Lake which is similar to the results presented here. Although both species can depress daphnid populations and are important planktivores (Shepherd & Mills, 1986; DeVries & Stein, 1992), yellow perch can eat benthos and gizzard shad switch to phytoplankton and/or detritus (Roseman et al., 1996). Although all species analyzed in this paper have been documented to rely on zooplankton during part of their first year of life (Schael et al. 1991; Gopalan et al. 1998), such prey switching may alleviate competitive pressure from yellow perch even when zooplankton biomass decline from perch predation. But since we did not observe a negative correlation between growth rates of other species and abundance

of yellow perch, competition with yellow perch should not be important regardless of which food item the fish compete for.

Limnology hypothesis

Our analysis indicates that temperature may play a role for recruitment dynamics of fishes in both groups. Temperature affect all habitats equally in Oneida Lake (because the lake is polymictic) and should affect growth and abundance of all species. Although only one correlation was significant (white perch), we found positive correlations of water temperature with growth for 10 of the 11 species. Water temperature has been shown to impact abundance, growth and recruitment of several species of fish (Forney, 1971, 1972; Koonce et al., 1977; Serns, 1982; Henderson & Nepszy, 1988; Staggs & Otis, 1996). Although the signal was not strong, year-to-year fluctuations in water temperature likely contribute to recruitment dynamics of YOY fish in Oneida Lake.

Over the past 20+ years, total phosphorus in Oneida Lake has declined by 50% to an average of 15–20 $\mu\text{g l}^{-1}$ (Mayer, 1998). Decreasing abundance of YOY yellow perch and the other three species in recruitment group 1 are correlated with declining phosphorus concentrations, while four species in the second recruitment group increased with decreasing phosphorus concentrations. Changes in fish communities have been related to changes in productivity (Leach et al., 1977; Persson et al., 1992) and changes in YOY fish abundance in Oneida Lake may reflect shifts in the overall fish community caused by decreased nutrient loading rates. Interestingly, the decrease in phosphorus content has not been accompanied by a decrease in zooplankton or biomass of benthic invertebrates (Idrisi, 1997; Mayer, 1998), suggesting that other correlates of lake productivity, such as increased light penetration and increased extent of macrophyte beds (also the result of zebra mussels, Mayer, 1998) may be driving fish community changes. This would be consistent with our findings of low competition between YOY fish in Oneida Lake.

Additional considerations and implications for Oneida Lake

We have discussed the results given the assumption that our abundance index reflect differences in survival among years. However, our index could also reflect differences over time in spawning populations of these fish species. For two species, freshwater drum

and gizzard shad, it is likely that the increasing trend in YOY abundance over time is due to an increase in the adult population. Few adults of these species were caught in our index gill nets before 1975, and for gizzard shad, few adults have been caught after 1994 (VanDeValk & Rudstam, 1997). However, even for these two species, year-to-year variability between the mid 1980s and mid 1990s is not due to differences in spawning stock as both species are long lived and the adult populations have been relatively stable during these years (VanDeValk & Rudstam, 1997). For all other species, our index trawling and gill nets indicate that an adult population has been present throughout the time period. Unfortunately, adult spawning stock and recruitment will be correlated if there is a time trend in recruitment success, even if there is no stock–recruitment relationship (Gilbert, 1997). A more detailed analysis of this problem is beyond the scope of this paper.

The YOY fish community of Oneida Lake changed significantly during the 37 years while this data set was collected. Our analysis indicate that yellow perch, by far the numerically dominant species, affect recruitment of other species using similar habitat by providing a buffer from predation by walleye. In contrast, except for intra-specific competition within YOY yellow perch, we did not find evidence for effects of competition with YOY yellow perch, even though several species have increased in abundance as yellow perch declined. Instead, we suggest that the increase in abundance of these other species is the result of a combination of factors, including temperature, changes in the lake associated with lower productivity and possibly changes in spawning stocks of these species.

Although inter-specific competitive interactions are believed to be important in many lakes, they do not appear to be important in Oneida Lake. Predation by walleye may reduce importance of inter-specific competition with yellow perch. Compared with other percid-dominated lakes in New York State, walleye growth rate is low and yellow perch growth rates high (Rudstam et al., 1996). The biomass of age four and older walleye in Oneida Lake is similar to the biomass of age three and older yellow perch (long term average biomass of adult walleye is 18.7 kg/ha and of adult yellow perch is 23.7 kg/ha, Rudstam, unpubl. data). This large walleye biomass rely almost entirely on the production of YOY fish, particularly yellow perch. This indicates that Oneida Lake is dominated by predators and we suggest that in such systems,

predator-prey interactions are more important than competitive interactions for young fish recruitment.

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