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Using Abiotic and Biotic Factors to Predict the Range Expansion of White Perch in Lake Champlain

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ABSTRACT. *White perch (*Morone americana*) invaded Lake Champlain, New York-Vermont, in the mid-1980s, yet abundance of white perch and those factors controlling their abundance are unknown. To predict the expansion of white perch, we differentiated between the most likely factors affecting white perch abundance; habitat characteristics or an invasion gradient (i.e., abundance is greater near the point of entry). Therefore, we addressed three questions: 1) where are white perch currently established; 2) what is the relation of white perch abundance to environmental variables and to an invasion gradient; and 3) based on the most likely factors affecting abundance, where will white perch become abundant in Lake Champlain? Fish communities were sampled and ten environmental variables were measured at sites along the eastern shore of Lake Champlain. Among sites and across seasons, two abiotic factors (turbidity and conductivity) had the greatest effect on white perch abundance. Biotic factors, yellow perch* (Perca flavescens) *abundance and chlorophyll a, however had lesser effects. We predict white perch will not become abundant in habitats with low water conductivity, turbidity and chlorophyll a, and a high abundance of potential competitors. Our predictions are consistent with data from other systems, which indicate environmental characteristics are likely more important than an invasion gradient in contributing to white perch colonization.*

INDEX WORDS: *White perch,* Morone americana*, abundance, habitat factors, Lake Champlain.*

INTRODUCTION

Biological invasions have caused changes in the structure and function of aquatic ecosystems (Lodge 1993), as well as economic disasters (Mills *et al*. 1994). Because of the potential to invade new systems, considerable attention has been given to the invasibility of non-native species. Successful invaders are characterized as being plastic in their resource requirements (Lodge 1993), however, success may depend on habitat matching (Moyle and Light 1996) i.e., similarity in the environments between native and non-native (target) habitats (Elton 1958, Lodge 1993). Evidence also suggests that failed invasions outnumber successful invasions because exotic species typically have a limited ability to adapt to environmental conditions in the recipient community (Simberloff 1981).

Therefore, predicting invasion success depends on a detailed understanding of the characteristics of the invading species and the system being invaded (Pimm 1989, Moyle and Light 1996). Furthermore, the combined effects of environmental factors impeding invasion and the response of non-native species to biotic and abiotic factors in the new system should also be known (Lodge 1993, Moyle and Light 1996). In the few studies where sufficient quantitative data were available on the biology of the invader and the environmental conditions of the recipient system, researchers were able to predict range expansions and impacts of non-native species (Grosholz and Ruiz 1996).

In the past 50 years, white perch (*Morone americana)*, which are native to the east coast of North America (Scott and Crossman 1973), have invaded many freshwater systems (Boileau 1985, Prout *et*

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al. 1990, Danzmann *et al.* 1993), including the Great Lakes (Larsen 1954, Hurley and Christie 1977, Schaeffer and Margraf 1986a, Mills *et al.* 1994). White perch often exhibit exponential population growth after gaining access to new systems (Boileau 1985, Schaeffer and Margraf 1986b) generating potentially harmful interactions with resident species, e.g., competition with native fishes for food resources (Hurley and Christie 1977; Parrish and Margraf 1990, 1994). Although white perch experience a wide range of environmental conditions in their native range (Stanley and Danie 1983), evidence exists that environmental factors can affect survival (Johnson and Evans 1991, 1996) and abundance when they expand outside that range (Minns and Hurley 1986, Johnson and Evans 1990, Danzmann *et al.* 1993).

White perch were first reported in southern Lake Champlain in 1984 (Plosila and Nashett 1990). Based on sampling throughout the lake at that time, the most probable invasion route was through the Hudson River and the Champlain Canal (L. Nashett, NYDEC, pers. comm.). After more than 15 years in the lake, distribution and the environmental factors that affect white perch abundance remain unknown. The two most likely factors that affect white perch abundance in Lake Champlain are: 1) habitat characteristics; or 2) an invasion gradient (i.e., white perch abundance is greater near the point of entry). To differentiate between the importance of these two factors and to predict the future expansion of white perch, we asked three questions: 1) where are white perch currently established in Lake Champlain; 2) what is the relation of white perch abundance to environmental variables and to an invasion gradient; and 3) based on these factors, where do we expect white perch to eventually become abundant?

To answer the first question, we determined the abundance of white perch in shallow-water fish communities. To answer the second question, we determined selected abiotic and biotic variables of the shallow-water fish communities and compared the relation of white perch abundance to these environmental variables. Habitat variables were chosen that have been shown to be important factors to white perch abundance in their native habitat (Stanley and Danie 1983, Killgore *et al.* 1989). To predict the expansion of white perch, we attempted to differentiate between the effects of habitat and an invasion gradient on white perch abundance. To provide additional support for our predicted invasion pattern, we compared abundance patterns and habitat use of white perch in Lake Champlain to those in other systems, particularly the Great Lakes.

STUDY AREA

Lake Champlain lies in a north-south valley between Vermont and New York that extends a short distance into Quebec (Fig. 1). Lake Champlain has a surface area of 1,127 km^2, a mean width of 6.2 km, and a mean depth of 19.4 m (Myer and Gruendling 1979). The lake is approximately 200 km long, extending from the outlet of the Richelieu River in the north to where it connects with the Hudson-Champlain Canal at Lock 12 in the south. The canal flows via several locks into the Hudson River. Lake Champlain is comprised of five physically and ecologically distinct basins separated by numerous islands, peninsulas, and causeways (Myer and Gruendling 1979). Environmental conditions in

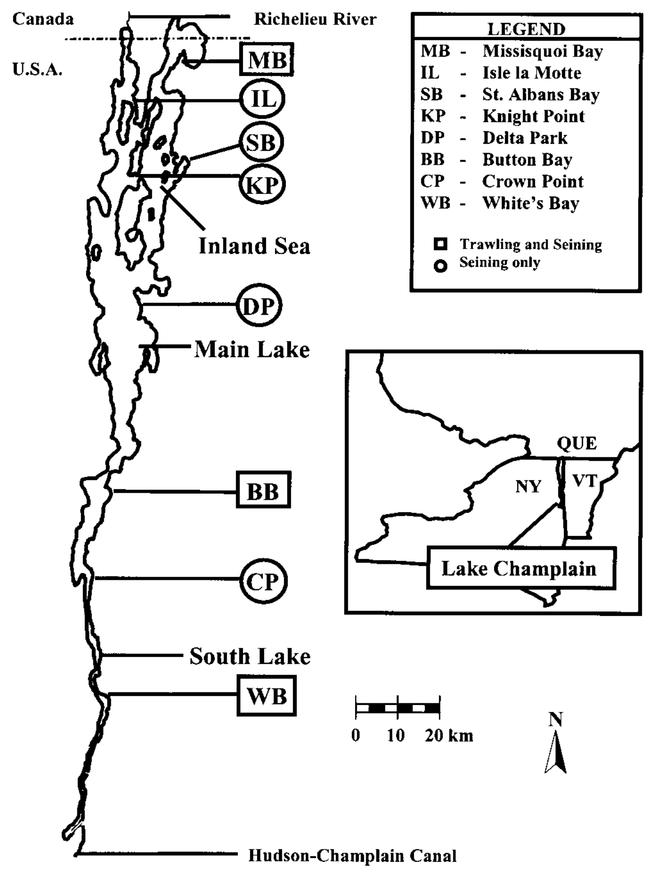

FIG. 1. Lake Champlain, its two major outlets, and the location of the eight sampling sites on a south-north gradient. Primary sampling sites (seining and trawling) are labeled squares and seining only sites are labeled circles.

the lake range from the riverine and eutrophic South Lake to the deep oligotrophic Main Lake. More than 300 tributaries empty into Lake Champlain and more than 80 species of warm, cool, and cold-water fish from over 20 families are present (Myer and Gruendling 1979).

Many areas of Lake Champlain, such as the Main Lake and Inland Sea, experience deep mixing in summer because of their size (Myer and Gruendling 1979). In winter, most bays and the shallow south end of the lake are covered by ice for about 4 months, but areas with deeper water, e. g., the large Main Lake, generally freeze for only 1 to 2 months.

METHODS

Fish Sampling

Sampling was conducted at eight locations (Table 1, Fig. 1). Three sites (White's Bay, Button Bay, and Missisquoi Bay) were sampled by shoreline seine and bottom trawl, and the other five sites were sampled by shoreline seine only (Fig. 1). Seining sites were sampled monthly from June to August in 1994 and 1995. Trawling sites were sampled monthly from June through August and October in 1994 and 1995. Button Bay trawling and White's Bay seining sites were not sampled in 1994.

Trawling sites were sampled with a 4-m bottom trawl (4-cm stretch mesh in net body) with a 2.6-m foot rope, 2.3-m head rope, and a 2-m cod end constructed of 5-mm mesh. Trawls were fished for 5 min along a constant depth (3- to 4-m deep) and boat speed (approximately 1 m $\cdot$ sec^{-1}) in a general direction from south to north. Boat speed and distance trawled were verified with a Trimble Navigation GPS Pathfinder unit, and depth was determined by a Lowrance depth finder. Four trawls were taken at each site between 0900–1200 h. Nearshore fish communities were sampled with a 21-m $\times$ 2-m seine of 1-cm mesh and a 3-m^3 bag pulled into shore by two individuals, enclosing an area that ranged from 1,200 m^2 to 1,600 m^2, depending upon the steepness of the littoral zone. Water depth at the deepest point of the enclosed area never exceeded 2 m. Three seine hauls were taken (when possible) between 0900-1400 h. To avoid resampling habitat disturbed by trawls and seines, parallel trawls and seines were at least 10 m apart from each other.

White perch and other dominant species (pumpkinseed *Lepomis gibbosus*, white crappie *Pomoxis annularis*, and yellow perch *Perca flavescens*) collected in trawls and seines were sorted into two age groups: age-0 and ≥ age-1. To determine individual growth rates, age-0 white perch were collected in October 1995, and ≥ age-1 white perch were collected in July 1995. A maximum of 25 age-0 white perch were retained on each date. All ≥ age-1 and older white perch collected were saved for analysis. In the laboratory, total length was measured to the nearest millimeter and fish were aged by scale analysis.

Environmental Sampling

Five abiotic (temperature, dissolved oxygen, conductivity, turbidity, and pH) and five biotic (vegetation biomass, chlorophyll *a*, and the abundance of the three dominant fish species; pumpkinseed, white crappie, and yellow perch) variables were collected in 1995. Data on abiotic factors were measured the same day as fish sampling. Chlorophyll *a* concentrations and vegetation biomass were taken within 5 days of fish sampling. Vertical profiles of conductivity (µmhos) were recorded at 1-m intervals with a YSI Model 33 S-C-T meter. Temperature (°C) and dissolved oxygen (mg/mL) profiles were taken at 1-m intervals with a YSI Model 58 temperature/oxygen meter. Mean temperature, conductivity, and dissolved oxygen were calculated by averaging all 1-m readings from each 2-m vertical profile at a site. Three 1-L water samples, taken 1 m from the water surface where the depth was 2 m, were collected to determine turbidity and pH. Turbidity was determined to the nearest NTU (Nephelometric Turbidity Unit) with a Hach Ratio Turbidimeter and pH was determined with an Orion Research Model 701 A digital analyzer with pH electrode. Vegetation biomass was estimated from ten petite ponar grabs (0.55-m^2 sampling area) taken along a 60- to 70-m long transect that was within 30 m, but not overlapping, each fish sampling transect. Sediment samples were removed from the ponar grab and vegetation was cut at the stem where it emerged from the sediment. In the laboratory, vegetation was rinsed with distilled water to remove sediment, dried at 105°C for 48 h (Greenburg *et al*. 1985), and weighed to the nearest 0.1 mg. Chlorophyll *a* concentrations were determined from integrated water samples taken from three depths (surface, 1 m, and 2 m) obtained using a Van Dorn sampler; triplicate samples ranging from 1 to 2 L were placed in a dark cooler in the field. In the laboratory, samples were vacuum-filtered using 65 µm filters and chlorophyll a was de-

TABLE 1. Mean (± SD) of each abiotic and biotic variable combined from June, July, and August 1995 sampling periods at eight sites in Lake Champlain.

Site	Latitude (N)	Turbidity (NTU)	Conductivity (μmhos)	Temperature (°C)	pH	Dissolved Oxygen (mg/mL)	Chlorophyll *a* (mg/mL)	Vegetation Biomass (g)	Pumpkinseed (#/100 m^2)	White Crappie (#/100 m^2)	Yellow Perch (#/100 m^2)
White's Bay	43°47′30″	104.55 (14.70)	260 (14.05)	24.08 (2.59)	8.02 (0.11)	8.04 (0.62)	7.11 (3.05)	0.35 (0.6)	0.02 (0.01)	4.09 (1.20)	0.05 (0.06)
Crown Point	44°02′00″	5.13 (4.02)	200 (7.06)	22.31 (0.71)	7.45 (0.19)	10.36 (1.22)	4.15 (1.01)	2.33 (1.88)	4.03 (0.90)	0.91 (0.92)	3.41 (1.10)
Button Bay	44°10′35″	0.95 (0.21)	160 (8.04)	20.0 (3.32)	7.08 (0.23)	10.27 (1.08)	1.03 (0.43)	1.14 (0.80)	1.02 (0.59)	0	1.08 (0.42)
Delta Park	44°44′32″	5.30 (0.73)	205 (10.05)	23.07 (0.82)	7.24 (0.09)	10.43 (1.02)	4.50 (2.44)	1.00 (0.29)	0.25 (0.12)	2.03 (1.0)	1.02 (0.51)
Knight Point	44°46′00″	0.82 (0.69)	140 (6.28)	20.55 (0.87)	7.18 (0.10)	8.03 (2.05)	1.00 (0.59)	0.82 (0.81)	0.30 (0.14)	0	1.33 (0.59)
St. Albans Bay	44°48′00″	5.19 (3.12)	152 (8.42)	22.64 (0.52)	7.77 (0.18)	9.70 (1.10)	4.43 (2.52)	1.20 (0.65)	3.88 (1.45)	0	4.10 (1.65)
Isle La Motte	44°54′00″	0.61 (0.10)	130 (5.54)	20.66 (1.38)	7.83 (0.27)	9.28 (0.91)	1.15 (0.83)	0.93 (0.75)	1.02 (1.01)	0	3.50 (0.93)
Missisquoi Bay	44°59′10″	3.14 (2.02)	125 (13.57)	20.58 (2.45)	6.91 (0.11)	9.39 (1.13)	4.38 (1.02)	3.78 (1.07)	5.07 (1.13)	0	8.05 (2.44)

termined with a Schimadzu 300 spectrophotometer via boiling ethanol extraction (Nusch 1980).

Calculations and Data Analysis

The abundance of white perch, pumpkinseed, white crappie, and yellow perch were standardized for each trawl and seine by: number of fish sampled / sampling area (m^2) · 100. White perch abundances were compared across seining and trawling sites separately by year with an ANOVA. Multiple time points at each site were regarded as replicates. To stabilize variances, abundance data were transformed to $\log_e(x + 1)$ prior to analysis. Percent occurrence of white perch was calculated in comparison to pumpkinseed, white crappie, and yellow perch because these four species usually comprised > 75% of the fishes in seine and trawl collections at all sites.

Data used in the tests below were means of each variable at each site from the August sampling period. Prior to univariate and multivariate tests, pH was converted to H+ concentration and all variables were $\log_e(x + 1)$ transformed to allow for appropriate tests of the relationships. Transformed variables met the assumption of normality if the normal probability plots of the residuals were normally distributed. Linear regressions were generated to describe the relation of white perch abundance to the environmental variables and to the distance from the proposed point of entry into Lake Champlain. White perch abundance was plotted against each individual variable separately and against the distance (m) of each site from the proposed point of entry (southern Lake Champlain). Multiple regression models were generated to differentiate between the effects of habitat characteristics versus an invasion gradient on white perch abundance. To increase multiple regression model accuracy, two variable reduction procedures were performed prior to analysis. If two variables were highly correlated ($|r| \geq 0.8$; Spearman's rank), the variable that exhibited the lower correlation to white perch abundance was excluded from the final model, using the assumption that the effects of one variable were described by the other. Individual plots of white perch abundance against remaining variables were used to further reduce model components that did not show any relation to white perch abundance. Stepwise multiple linear regression, r-square values, and significance tests ($\alpha = 0.05$) were used to select the best fitting models. Cluster analysis (UPGMA method based on squared semipartial correlations SPRSQ) was used based on original variables in combination, to group the eight seining sites into related groups. Variables selected to group sites were based on the components that explained the greatest variation in white perch abundance from linear regressions.

Repeated measures ANOVA was used to further examine the relation between the abundance of white perch and environmental variables. Data used were organized as a matrix of white perch abundance and environmental variables by date (June, July, and August). The abundance of ≥ age-1 white perch (dependent variable) was examined against each abiotic and biotic variable separately at two significance levels ($\alpha = 0.05$ and $\alpha = 0.1$) with a site · month interaction term in the model. Age-0 white perch were excluded from repeated measures tests because they were not susceptible to capture by the sampling gear employed during all time periods. All analyses were performed using SAS software (SAS Institute 1985).

RESULTS

White Perch Abundance and Individual Growth

White perch were more abundant in southern areas of Lake Champlain than in northern areas (1994: one-way ANOVA, $P = 0.01$, 1995: one-way ANOVA, $P = 0.02$, Fig. 2a). In 1995, white perch were seven to eight times more abundant at White's Bay, the southern-most site, than at other seining

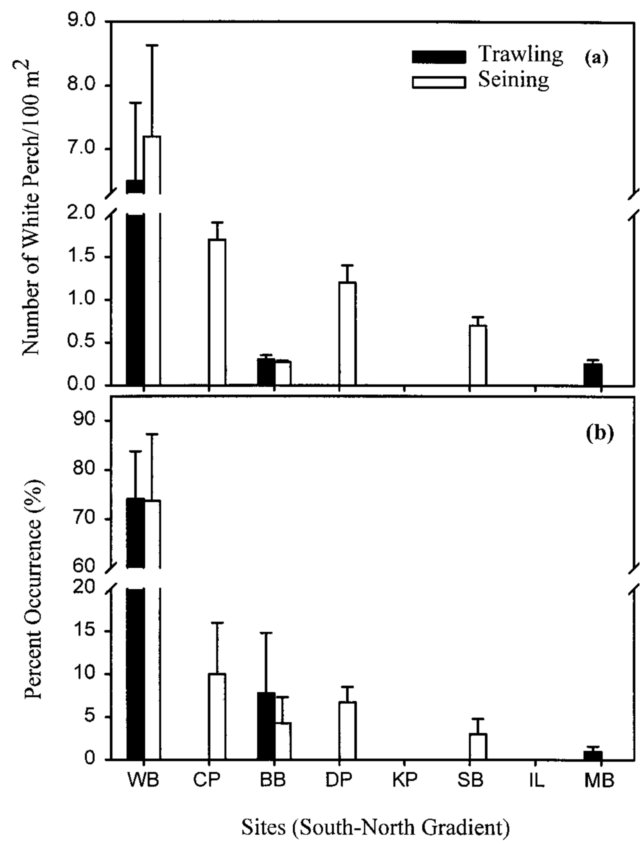

FIG. 2. Mean (+ SD) number (a) and percent occurrence (b) of white perch collected in seine hauls and trawls from June-August 1994-5 at eight seining sites. Site codes as listed in Figure 1.

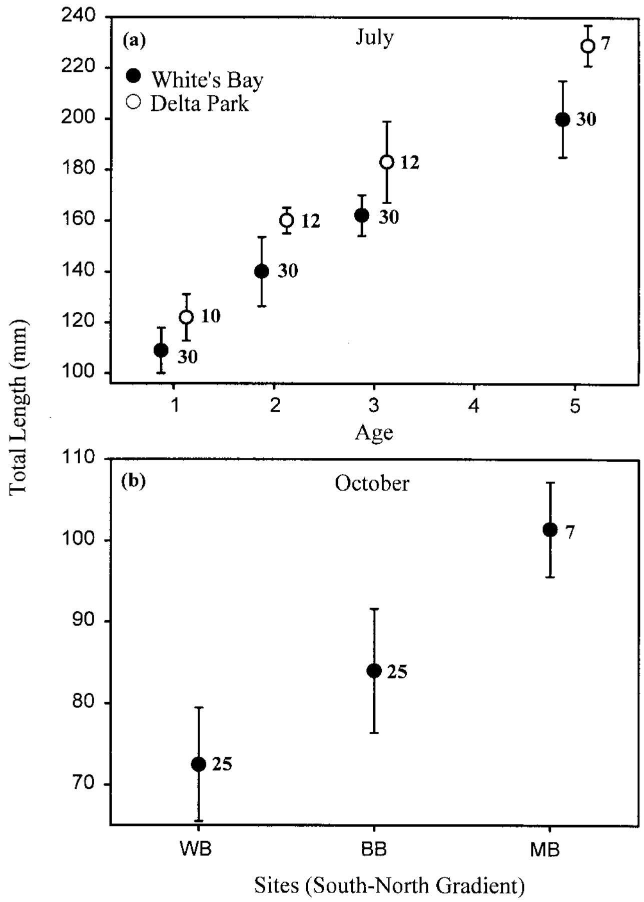

FIG. 3. Mean (± SD) total length of (a) age 1 and older white perch at Delta Park (open circles) and White's Bay (dark circles) from July 1995 and (b) age 0 white perch from White's Bay (WB), Button Bay (BB), and Missisquoi Bay (MB) from October 1995. Numbers next to means are sample sizes.

(two-way ANOVA, P = 0.003) and trawling (two-way ANOVA, P = 0.001) sites. There were no significant site · season interactions for seining sites (P = 0.21) or trawling sites (P = 0.31). At White's Bay, white perch were > 70% of the total fish abundance (Fig. 2b). In contrast, white perch comprised a small portion of the total fish abundance at sites in northern areas of Lake Champlain.

Length at age of white perch ≥ age 1 from Delta Park was greater (one-way ANOVA, P = 0.04) than white perch from White's Bay for all age-classes compared (Fig. 3a). There was also an increase in mean total length of age 0 white perch across sites on the south-north gradient (one-way ANOVA, P = 0.01). The largest differences in mean size were observed between white perch collected at White's Bay and Missisquoi Bay (Fig. 3b). Small sample sizes for particular age-classes and at various sites and times prevented comparisons among all sites.

Environmental Characteristics

All environmental variables varied significantly among sites, whereas the abundance of pumpkinseed and yellow perch, temperature, and chlorophyll *a* varied among seasons (Tables 1 and 2). Conductivity, turbidity, temperature, and chlorophyll a concentrations were greatest at White's Bay, and were significantly less at all other sites. In contrast, the abundance of pumpkinseed, yellow perch, and vegetation biomass were greatest at Missisquoi Bay, Crown Point, and St. Albans Bay.

TABLE 2. Summary of Analysis of Variance testing the effects of site and season on the five biotic and the five abiotic $log_e(x + 1)$ transformed variables. Asterisks indicate significant effects: $P \leq 0.05$

	Source of Variation	P-value
Biotic Variables		
Yellow Perch	Site	0.0205*
	Season	0.0381*
Pumpkinseed	Site	0.0350*
	Season	0.0443*
White Crappie	Site	0.0011*
	Season	0.0996
Chlorophyll *a*	Site	0.0223*
	Season	0.0357*
Vegetation Biomass	Site	0.0124*
	Season	0.1183
Abiotic Variables		
Dissolved Oxygen	Site	0.0431*
	Season	0.0902
Temperature	Site	0.0405*
	Season	0.0310*
Turbidity	Site	0.0050*
	Season	0.0688
Conductivity	Site	0.0023*
`	Season	0.0792
pH	Site	0.0483*
	Season	0.1007

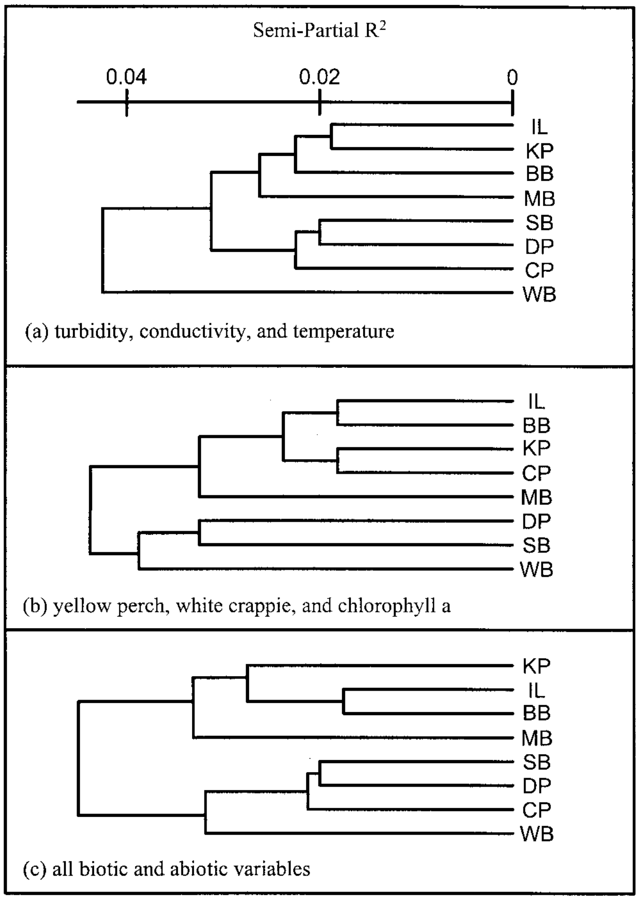

FIG. 4. Clustering of the eight sites based on (a) turbidity, conductivity and temperature, (b) abundance of yellow perch, white crappie, and chlorophyll* a*, and (c) all biotic and abiotic variables from Lake Champlain in 1995. All data used in this analysis were $log_e(x+1)$ transformed. Site codes as listed in Figure 1.

Cluster analysis of the sites based on the abiotic variables that displayed the greatest relation to white perch abundance from linear regressions (turbidity, conductivity, and temperature) revealed three major groups (Fig. 4a). One cluster included Delta Park, Crown Point, and St. Albans Bay. The second major cluster included Missisquoi Bay, Knight Point, Isle La Motte, and Button Bay. White's Bay comprised the third cluster and was widely separated from the other sites. Cluster analysis of the sites based on the combination of biotic variables (abundance of white crappie and yellow perch, and chlorophyll *a*) revealed two major groups (Fig. 4b). One cluster included Knight Point, Isle La Motte, Missisquoi Bay, Crown Point, and Button Bay. The second major cluster included St. Albans Bay, White's Bay, and Delta Park. Clustering of the sites based on all biotic and abiotic variables revealed a similar grouping pattern as the clustering based on turbidity and conductivity (Figs. 4a and c). However, White's Bay was clustered with Delta Park, Crown Point, and St. Albans Bay.

Relation of White Perch Abundance to Habitat Variables and an Invasion Gradient

From the linear regression analysis, the strongest abiotic predictors of white perch abundance were turbidity, conductivity, and temperature (Table 3). The strongest relation of biotic variables was between white perch and chlorophyll *a* and the abundance of yellow perch and white crappie (Table 3). The invasion gradient (i.e., distance to each site from the point of entry) explained less variation in white perch abundance than most of the abiotic and biotic variables (Fig. 5).

The multiple regression model with the best fit ($r^2 = 0.94$, $P = 0.07$) was white perch abundance against the selected abiotic variables (Table 4). Turbidity was the first variable to enter the model and explained 88% of the variation in white perch abundance alone (Table 4). Conductivity (correlated with turbidity, $r = 0.85$, $P = 0.03$) and temperature (correlated with turbidity, $r = 0.79$, $P = 0.03$) and pH (no relation to white perch abundance) were dropped from model building. For biotic variables, the model of yellow perch abundance and chlorophyll *a* explained 89% of the variation ($P = 0.04$) in white perch abundance. Chlorophyll *a* explained 74% of the variation ($P = 0.01$) in white perch abundance. The abundance of white crappie (highly correlated with chlorophyll *a*, $r = 0.88$, $P = 0.04$), pumpkinseed (highly correlated with yellow perch, $r = 0.75$, $P = 0.03$), and vegetation biomass (no relation to white perch abundance) were dropped from model building.

On a seasonal scale, conductivity and turbidity each had the greatest effect on white perch abundance (Table 5). Water temperature, yellow perch abundance, and chlorophyll a each had a lesser effect.

DISCUSSION

A general goal of studies on biological invasions is to predict potential outcomes (Moyle and Light 1996). A crucial step in such predictions is to determine what habitats are likely to be occupied in the

TABLE 3. Results of the relations of environmental variables to the abundance of white perch at eight sites in Lake Champlain using individual linear regressions. All data used in this analysis were $log_e(x+1)$ transformed.

	Model R-square	P-value	Slope-Intercept Equation
Abiotic Variables			
Turbidity	0.8774	0.0006	y = 0.8132x – 0.04384
Conductivity	0.8587	0.0009	y = –0.58x + 0.632113
Water Temperature	0.9483	0.0001	y = –0.3627x + 0.4984
Dissolved Oxygen	0.0031	0.5223	y = 0.6681x + 0.39012
pH	0.3169	0.1448	y = –0.2285x + 0.4193
Biotic Variables			
Yellow Perch	0.5538	0.0346	y = 1.7813x + 0.1932
Pumpkinseed	0.1386	0.3628	y = 0.3149x + 2.1399
Vegetation	0.1719	0.3133	y = 0.0889x + 1.3315
White Crappie	0.8108	0.0023	y = –3E–08x + 3E–08
Chlorophyll *a*	0.7381	0.0062	y = –0.0073x + 1.0189

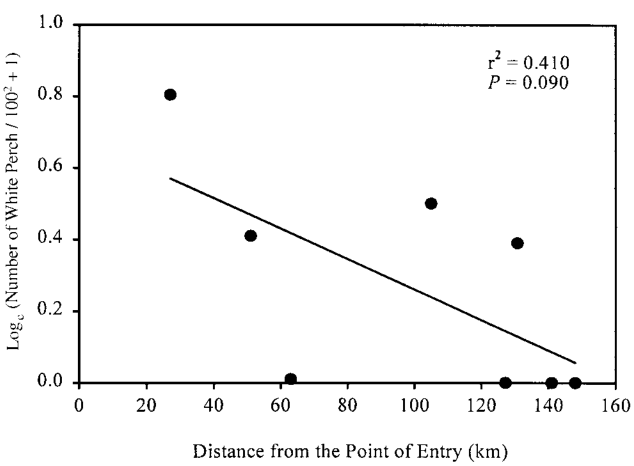

FIG. 5. Linear regression of white perch abundance against the distance of each site from the point of entry into Lake Champlain from data collected at eight seining sites in August 1995.

new system and what densities or abundances the invasive species will reach (Grosholz and Ruiz 1996). Because numerous environmental characteristics likely affect invasion success, predictive studies require a detailed understanding of abiotic and biotic components in the recipient system as well as the habitat preferences of the invader (Pimm 1989). Predictive studies lacking quantitative data for either the recipient system or the invasive species have been largely ineffective in determining outcomes of species invasions and introductions (Moyle and Light 1996).

To predict the expansion of white perch in Lake Champlain, we compared white perch abundance to environmental variables, and to an invasion gradient from this study, with information on environmental variables of preferred white perch habitats from other systems. After more than 15 years in Lake Champlain, white perch were present at most

TABLE 4. Results of stepwise multiple regression testing the effects of each variable or the combination of variables on white perch abundance. Asterisks (*) indicate significant effects: P ≤ 0.05. All data used in this analysis were $log_e(x+1)$ transformed.

	Step Number	Model R-square	P-value	Mean Square Error
Abiotic Variables				
Turbidity	1	0.88	0.01*	0.581
Turbidity • Dissolved Oxygen	2	0.94	0.07	0.312
Biotic Variables				
Chlorophyll *a*	1	0.74	0.01*	0.489
Yellow Perch • Chlorophyll *a*	2	0.89	0.04*	0.296

TABLE 5. Summary of repeated measures ANOVA testing for the effects of each variable on the abundance of white perch within sites. Asterisks indicate significant effects: * = 0.1 > P ≥ 0.05, ** = 0.05 > P ≥ 0.01. All data used in this analysis were loge(x+1) transformed.

	F-value	P-value
Abiotic Variables		
Turbidity	12.10	0.01**
Conductivity	9.59	0.02**
Water Temperature	8.73	0.09*
Dissolved Oxygen	1.72	0.90
pH	1.01	0.95
Biotic Variables		
Chlorophyll *a*	14.57	0.05*
Yellow Perch	13.22	0.09*
White Crappie	10.18	0.51
Vegetation	5.45	0.72
Pumpkinseed	4.70	0.83

sites in this study. However, white perch have established abundant populations only in southern areas of Lake Champlain. Furthermore, white perch dominated the fish community at White's Bay (the southernmost site), and of the sites in this study, white perch were most abundant at the two southernmost sites, but were only a small portion of the fish communities at northern sites.

Differences in the abundance of white perch among sites in Lake Champlain may have reflected differences in habitat characteristics or the recentness of invasion. Sites in this study exhibited a large range in biotic and abiotic variables. In particular, the two southernmost sites, White's Bay and Crown Point, along with Delta Park and St. Albans Bay (a northern site), had higher levels of turbidity, conductivity, and chlorophyll *a* than did Button Bay and most northern sites. Abiotic variables (turbidity, conductivity, and temperature) were consistently the best predictors of white perch abundance although white perch abundance was also significantly correlated with biotic variables (yellow perch and chlorophyll *a*). White perch were more abundant at locations with eutrophic and turbid conditions with high conductivity, but were generally less abundant at sites with high abundance of yellow perch. Further, results from the cluster analyses support this conclusion. Sites that were grouped together based on similar biotic and abiotic characteristics also had similar abundances of white perch.

In 1984, the first reported white perch was collected in southern Lake Champlain, nearest the predicted point of entry at the Hudson River-Champlain Canal (Plosila and Nashett 1990). It is likely that white perch had more time to establish reproducing populations in southern areas compared to sites in the north. Therefore, the greater abundance of white perch in the south compared to northern sites could potentially be the result of an invasion gradient. However, southern sites had the highest levels of turbidity and conductivity and results from regression analyses indicate that geographic distance from the presumed point of entry did not have as strong an effect on the abundance of white perch in Lake Champlain. Thus, the environmental variables of the sites near the point of entry likely had a greater effect on abundance and are likely the best predictors of future abundance of white perch.

Therefore, using environmental variables where white perch are currently abundant in Lake Champlain, we predict white perch will be more abundant in areas exhibiting turbidity > 5 NTU, conductivity > 200 µmhos, and chlorophyll a > 5 mg/mL. The values of these variables are consistent with those published for other habitats where white perch are abundant (Appendix). The abundance of white perch was lower at sites where turbidity, conductivity, and chlorophyll *a* values were generally less than those predicted for preferred white perch habitats. Although white perch may have only recently invaded northern areas, as indicated by greater individual growth rates at northern sites, the abundance of white perch will likely remain lower at these sites, compared to the more eutrophic sites in this study. Since the time of our study, white perch have expanded into additional shallow water habitats in the northern part of the lake (e.g., the area known as the Gut: M. Eisenhower and D. Parrish, VTCFWRU, unpub. data, and Keeler Bay: E. Marsden, UVM, unpub. data). These habitats more typically resemble the shallow habitats of the south lake than those of nearby deepwater habitats in the north lake.

Sites in Lake Champlain with lower turbidity, conductivity, and temperature were also associated with higher numbers of pumpkinseed and yellow perch. The negative relationship between the abundance of white perch and yellow perch may have been caused by interspecific competition for food (Prout *et al*. 1990) rather than the influence of abiotic factors. Also, it is not clear to what extent the abundance of white perch was determined directly from variables selected in this study or indirectly as a result of their effect on productivity or food abundance. However, there is good evidence to suggest that the major differences in white perch abundance among sites were related to the factors selected, and that white perch will not likely become a dominant part of fish communities in Lake Champlain with lower turbidity and conductivity and a high occurrence of potential competitors.

Our results show that environmental variables are more important than an invasion gradient to the expansion of white perch in Lake Champlain. To determine if white perch exhibit similar patterns of expansion and individual growth rates during invasion in other systems, we compared independent invasions in the Laurentian Great Lakes. These lakes are biologically and morphologically distinct and white perch invaded each lake at different times during a 30-year period between 1950 and 1980 (Boileau 1985, Johnson and Evans 1990).

A comparison of habitat usage in many of the Great Lakes shows white perch became a major component of many shallow, eutrophic habitats, but not deep, oligotrophic habitats (Lake Erie: Boileau 1985, Schaeffer and Margraf 1986b; Lake Ontario: Hurley and Christie 1977; Lake Superior: Sierszen *et al*. 1996; Lake Michigan: Savitz *et al*. 1996). Because few shallow water areas were located near the points of entry in many lakes, white perch had the opportunity to first establish reproducing populations in deepwater oligotrophic habitats (Boileau 1985). However, shallow water, eutrophic protected embayments were the first habitats successfully colonized by white perch although oligotrophic habitats were closer to the point of entry. In particular, white perch were first sampled in a habitat adjacent to the oligotrophic eastern basin of Lake Erie in 1953 (Larsen 1954), but it was not until the 1970s when white perch were sampled again in the more shallow and eutrophic western basin (Schaeffer and Margraf 1986b). Therefore, white perch established abundant populations approximately 260 km from the point of entry in Lake Erie. Individual growth rates of white perch across independent invasions also showed similar patterns, i.e., rates decreased as population numbers increased (Hergenrader and Bliss 1971, Hurley and Christie 1977, Schaeffer and Margraf 1986b).

Characteristics of white perch invasions appear to be consistent across systems, so it is reasonable to suspect white perch will exhibit similar patterns in Lake Champlain. To date, the invasion of white perch into Lake Champlain has many similarities to previous invasions; white perch were more abundant in shallow, productive, eutrophic habitats in other novel systems and in Lake Champlain, and were less abundant at sites having high water clarity and oligotrophic conditions. Also, white perch do not usually establish an abundance gradient when entering a new system, and habitat appears to determine expansion patterns of white perch regardless of the point of entry. Moreover, environmental characteristics and fish community attributes of recipient sites were effective indicators of which sites were successfully colonized by white perch and those in which densities were low.

White perch may exhibit wide tolerances to existing conditions, but success of white perch in Lake Champlain is likely dependent on the availability of suitable habitat. White perch are likely to become more abundant in areas similar to native habitats (e.g., habitats with high water conductivity, turbidity, and chlorophyll *a*). Likewise, white perch may not be at equilibrium densities in the northern parts of Lake Champlian. But white perch may successfully invade northern areas that exhibit habitat characteristics similar to their native habitats. This study underscores the importance of environmental factors as determinants of white perch abundance, and we predict that white perch will not become as dominant in fish communities with abiotic and biotic conditions that do not match its preferred environmental conditions.

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APPENDIX

Turbidity, conductivity, and chlorophyll* a *levels in native and non-native habitats where white perch are typically most abundant.

	Location	Reference
Turbidity (NTU)		
> 50	Nebraska reservoirs (non-native)	Hergenrader and Bliss 1971
> 6	Potomac River, Virginia (native)	Killgore *et al.*, 1989
10–50	Chesapeake Bay (native)	Monteleone and Houde 1992
Condictivity (μmhos)		
> 320	Chesapeake Bay (native)	Mansueti 1961
300–2,475	Potomac River, Virginia (native)	Killgore *et al.* 1989
250–1,500	Chesapeake Bay (native)	Monteleone and Houde 1992
Chlorophyll a (mg/ml)		
5–40	Potomac River, Virginia (native)	Killgore *et al.* 1989
> 5.5	Bay of Quinte, Lake Ontario (non-native)	Nicholls and Hurley 1989