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ARTICLE

Controls on Abundance and Distribution of Yellow Perch: Predator, Water Quality, and Density-Dependent Effects

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Abstract
Unraveling the diverse forces controlling the abundance and distribution of fish across a landscape has been challenging, in part because few techniques exist to address multiple factors simultaneously in a single analysis. We used spatially explicit, varying-coefficient generalized additive models to relate the summertime abundance and distribution of yellow perch *Perca flavescens* to a variety of predatory, water quality, landscape, and density-dependent factors. The model used 25 years of fishery-independent trawling data from southern Green Bay, Lake Michigan, an area that supported major fisheries for yellow perch until their decline in the 1990s. Local catch per unit effort (CPUE) of both age-0 and age-1 and older yellow perch was affected by the abundance of double-crested cormorants *Phalacrocorax auritus*, dissolved oxygen, water clarity, and bottom depth, but not water temperature. In addition, the local response of age-0 yellow perch CPUE to most predictor variables, including their own global density, had a unique spatial structure. For instance, increased cormorant abundance was related to declines in local yellow perch CPUE, especially near cormorant nesting islands, while increased dissolved oxygen levels were correlated with increased local yellow perch CPUE in shallow nearshore areas of southern Green Bay. In addition, local yellow perch CPUE increased near the mouth of the Fox River during years with higher water clarity, suggesting that water quality may be limiting to yellow perch in this region. Our results suggest that it is important to explicitly account for the different ways in which predictor variables influence fish abundance across the aquatic landscape.

Understanding the primary determinants of the abundance and distribution of fishes is a fundamental endeavor that bridges and unifies the fields of fish ecology and fisheries science. The abundance and distribution of fish is notoriously variable over space and time, resulting from complex mechanisms of habitat selection (Chesson 1998). Myriad factors are known to influence the abundance (i.e., number of individuals at a particular location) and distribution (i.e., spatial patterns of local density) of fishes, including abundance and distribution of predators (Gilliam and Fraser 1987; Ciannelli et al. 2007), competitors (Robertson 1996), water quality (Bacheler et al. 2009b), physical habitat (Lobb and Orth 1991), and density of conspecifics (Fretwell and Lucas 1969; Post et al. 1997). Disentangling these diverse and often competing forces has been a challenge because

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few techniques exist that can address these factors simultaneously in a single analysis.

One novel approach that has been used recently to address the numerous influences on the abundance and distribution of fish is varying-coefficient generalized additive models (GAMs; Hastie and Tibshirani 1993). A GAM is a nonlinear, nonparametric regression technique that does not require a priori specification of the functional relationship between the response and predictor variables (Hastie and Tibshirani 1990; Wood 2006). The addition of varying-coefficient terms in a GAM can be used to determine specific locations where fish are expected to increase or decrease in local abundance with changes in any of the predictor variables in the model (Bacheler et al. 2009a). For instance, Bacheler et al. (2009a) used varying-coefficient GAMs to demonstrate that spawning biomass, water temperature, and ocean current transport combined to affect the spawning distribution of walleye pollock *Theragra chalcogramma* in Shelikof Strait, Alaska. Using a similar varying-coefficient GAM, Bartolino et al. (2011) found ontogenetic and sex-specific differences in density-dependent habitat selection for yellowfin sole *Limanda aspera* in the eastern Bering Sea. Varying-coefficient GAMs have shown great promise to simultaneously evaluate the multitude of forces controlling the abundance and distribution of fish in a spatially explicit manner.

Varying-coefficient GAMs could be used to enhance our understanding of the various controls of the abundance and distribution of yellow perch *Perca flavescens*. In Lake Michigan, yellow perch is an economically and ecologically important species, supporting recreational and commercial fisheries since the late 1800s (Wells and McLain 1972). Age-1 and older yellow perch spawn in nearshore areas during the spring, and return to deeper, offshore waters after spawning (Glover et al. 2008). Yellow perch larvae migrate to limnetic areas for 30–40 d before returning to nearshore demersal environments (Noble 1975; Fisher et al. 1999). Tagging results indicate that most adult yellow perch are recaptured near their tagging locations, but a small proportion of the population may stray up to 100 km (Smith and Van Oosten 1940). During the 1980s and 1990s, yellow perch were the most popular sport fish in Lake Michigan (Bence and Smith 1999). Dramatic variation in yellow perch population abundance and distribution has been observed throughout their range (Koonce et al. 1977; Henderson and Nepszy 1988), complicating assessment and management (Francis et al. 1996). Since the late 1980s, however, yellow perch in Lake Michigan have declined, presumably because of poor recruitment (Francis et al. 1996; Marsden and Robillard 2004).

A multitude of factors are thought to influence yellow perch abundance and distribution. One of the most studied causes of fluctuations in yellow perch population abundance has been fish and avian predators. For instance, double-crested cormorants *Phalacrocorax auritus* have been implicated in declines of yellow perch in Lake Huron (Fielder 2008), Lake Ontario (Burnett et al. 2002), Oneida Lake (VanDeValk et al. 2002; Rudstam et al. 2004), and Green Bay (Meadows 2006), although some discount cormorant predation as a major cause of yellow perch declines (Diana et al. 2006). Walleyes *Sander vitreus* have also been shown to significantly reduce yellow perch populations in some areas (Nielsen 1980; Hartman and Margraf 1993) but not others (Fielder 2008).

Water quality and physical habitat have also been shown to affect yellow perch abundance and distribution in some aquatic systems. A number of water quality variables such as water temperature (Fisher et al. 1999; Fielder 2008), dissolved oxygen (Roberts et al. 2009), water clarity (Mayer et al. 2000), and pH (Carey and Mather 2009) have been related to catch or abundance of yellow perch in various places, as have physical habitat and landscape variables such as substrate and bottom depth (Fisher et al. 1999; Janssen and Luebke 2004). Some water quality variables may influence the distribution of yellow perch over relatively short time scales (e.g., individuals avoiding hypoxic waters), while others can influence abundance over longer time frames (e.g., the filtering of dreissenid mussels that increases water clarity and influences food web dynamics). Despite much research attention in diverse aquatic systems throughout their range, however, there has been a notable lack of consistent relationships between yellow perch and various habitat variables.

The objective of this study was to develop quantitative models to identify the factors controlling the abundance and distribution of age-0 and age-1+ (age 1 and older) yellow perch. We used 25 years of trawling data from Green Bay, Lake Michigan, to create varying-coefficient GAMs to assess the spatially explicit effects of a predator (double-crested cormorants) and various water quality and landscape variables on age-0 and age-1+ yellow perch abundance and distribution. Density-dependent habitat use has also been documented for age-0 yellow perch (Post et al. 1997), so we tested for its presence in our study by incorporating a varying-coefficient global index of abundance term in our GAM model.

METHODS

Study area.—The Bay of Green Bay (hereafter, Green Bay) is a shallow estuary-like bay in the northwest corner of Lake Michigan (Figure 1). Green Bay is approximately 190-km long, extending from the mouth of the Fox River northeast to Big Bay de Noc; it averages 37-km wide and 20-m deep. The western shoreline of Green Bay primarily consists of wetlands and soft sediments, but a higher proportion of rocky substrates exists along the eastern shoreline. The Green Bay watershed drains an area of approximately 40,000 km^2, about one-third of the total Lake Michigan basin, and consists of agricultural, urban, and forested land (Bertrand et al. 1976). Many rivers drain into Green Bay, the largest being the Fox River (Figure 1). The lower Fox River and Green Bay are designated an "Area of Concern" by the U.S. Environmental Protection Agency, based on poor water quality conditions stemming from runoff pollution from urban and rural areas, municipal and industrial wastewater discharges, and degraded habitats (Manchester-Neesvig et al. 1996). The

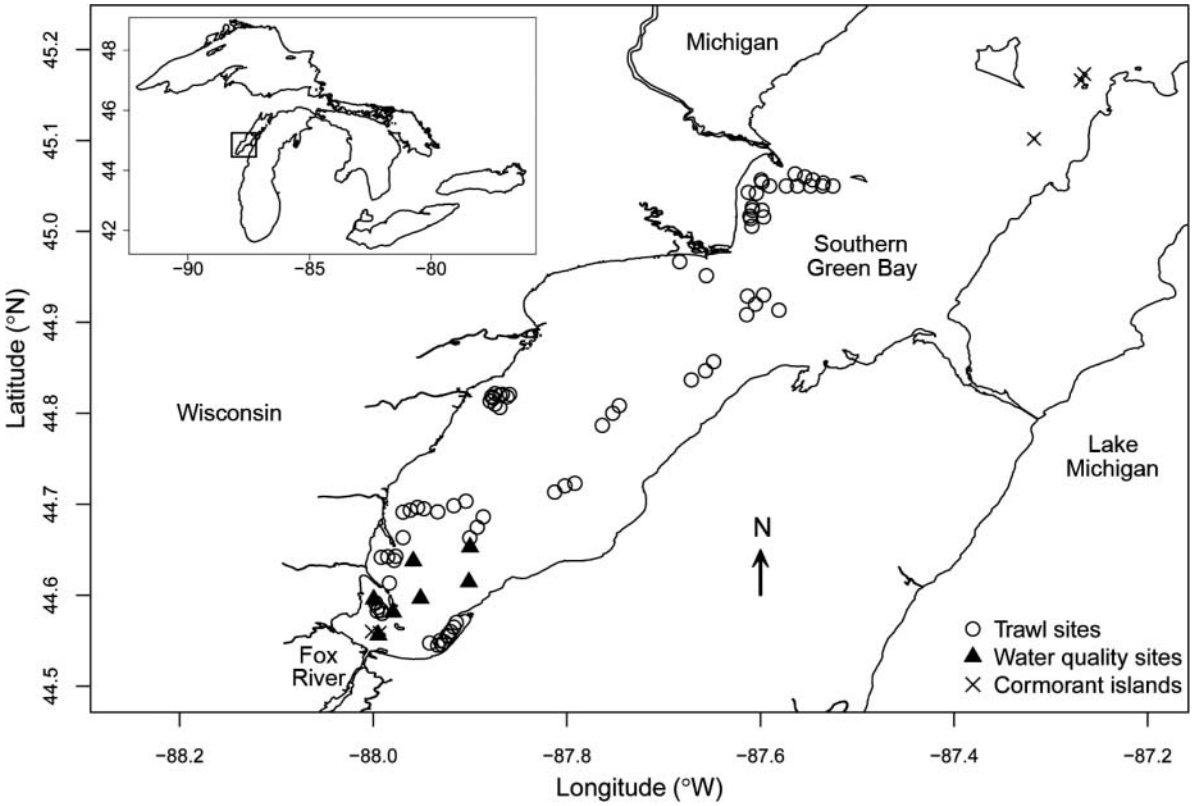

FIGURE 1. Study area in southern Green Bay showing the 78 trawling sites, seven water quality sampling sites, and five double-crested cormorant nesting islands. Trawling and water quality sampling was conducted from 1985 to 2009.

once significant commercial and recreational fishing activities in Green Bay, including those for yellow perch, are currently thought to be impaired by water quality conditions as well as negative interactions with exotic species (Reed et al. 2004).

Southern Green Bay trawl survey.—The Wisconsin Department of Natural Resources initiated a fishery-independent trawl survey in 1978 to index yellow perch in southern Green Bay. Seventy-eight permanent trawling sites were eventually chosen, based on feasibility of trawling (lack of rocks) or on historical commercial catches (Figure 1); trawling sites were assumed to be representative of all habitats in southern Green Bay. Sites were sampled a single time in August or September of each year (Table 1). Trawl sites were inconsistently sampled in space and time before 1985, so we only included data from 1985 to 2009 in our analyses.

Yellow perch catch per unit effort (CPUE; number/min) at each site was quantified via an otter trawl deployed from a research vessel. The otter trawl was 7.6-m wide, had a 7.9-m headrope, 38-mm mesh wings and body, and a 13-mm mesh tail bag. Trawls were deployed for 5 min (timed from the end of deployment to beginning of retrieval) at a speed of 4.6–5.6 km/h during daylight hours. All yellow perch caught were enumerated, and a subsample of 100 age-0 and 500 age-1+ yellow perch were measured for total length (TL) within each of the 12 clusters of sampling sites (Figure 1). Yellow perch less than 100 mm TL were considered to be age 0, and those 100 mm TL or more were classified as age 1+. For verification purposes, within each region, an aging structure was taken from a subsample of 20 yellow perch per 10-mm increment for age-1+ fish (>100 mm): scales for fish less than 150 mm, and anal spine cross sections for larger fish. Scales from a sample of the largest fish less than 100 mm were used to verify the assignment of age 0. Counts of age-0 and age-1+ yellow perch from each trawl were adjusted in the rare case that an age-0 or age-1+ was misclassified based its length.

Varying-coefficient GAMs.—A varying-coefficient GAM was used to test for the spatial and temporal effects of various predictor variables on age-0 or age-1+ yellow perch trawl CPUE in southern Green Bay. Generalized additive models extend traditional additive models by allowing for alternative distributions of the underlying random variation, just as generalized linear models allow for alternative distributions for linear models. A notable advantage of GAMs is their use of nonparametric smoothed curves to account for nonlinearities between predictor and response variables, common in ecological studies (Hastie and Tibshirani 1990). The GAMs use a nonparametric smoother instead of the traditional least-squares approach in multiple linear regression.

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TABLE 1. Yellow perch trawl survey data collected by the Wisconsin Department of Natural Resources in southern Green Bay (1985–2009), which were used to index yellow perch abundance.

Year	Number of hauls	Earliest date	Latest date	Number of yellow perch		Mean (SE) number/haul	
				Age 0	Age 1+	Age 0	Age 1+
1985	56	Aug 06	Sep 25	16,306	5,457	58.4 (16.6)	19.5 (4.6)
1986	52	Aug 12	Sep 22	18,202	6,933	70.0 (17.1)	26.7 (5.1)
1987	61	Aug 24	Sep 03	4,643	9,713	15.3 (4.1)	31.9 (5.1)
1988	75	Aug 09	Sep 13	9,408	16,748	25.1 (5.0)	44.7 (4.3)
1989	67	Aug 08	Aug 30	2,008	7,060	6.0 (1.5)	21.2 (2.7)
1990	78	Aug 22	Sep 11	3,544	4,803	9.1 (2.2)	12.3 (2.0)
1991	77	Aug 07	Aug 28	12,778	5,459	33.2 (4.4)	14.2 (1.7)
1992	75	Aug 11	Sep 01	1,948	10,440	5.2 (2.1)	27.8 (4.1)
1993	77	Aug 10	Aug 31	178	4,800	0.5 (0.1)	12.6 (1.6)
1994	64	Aug 08	Aug 23	1,264	3,637	4.0 (1.0)	11.4 (2.5)
1995	63	Aug 08	Aug 22	2,203	1,380	7.0 (2.2)	4.4 (0.8)
1996	64	Aug 06	Aug 29	1,048	1,260	3.3 (1.4)	3.9 (0.9)
1997	76	Aug 04	Aug 25	619	670	1.6 (0.5)	1.7 (0.3)
1998	75	Aug 04	Aug 27	6,554	528	18.3 (4.4)	1.4 (0.3)
1999	77	Aug 10	Sep 02	424	2,445	1.2 (0.4)	6.5 (1.2)
2000	78	Aug 09	Aug 28	837	719	2.2 (0.5)	1.9 (0.4)
2001	74	Aug 21	Sep 05	2,148	363	5.9 (1.4)	1.0 (0.2)
2002	74	Aug 13	Aug 28	3,077	691	9.0 (3.3)	1.9 (0.7)
2003	78	Aug 04	Aug 18	50,820	564	148.6 (42.6)	1.6 (0.3)
2004	78	Aug 02	Aug 19	4,680	4,343	12.0 (3.3)	11.2 (2.5)
2005	78	Aug 09	Aug 25	10,080	1,269	25.8 (7.2)	3.2 (0.5)
2006	78	Aug 09	Aug 23	7,514	685	19.2 (7.2)	1.8 (0.4)
2007	78	Aug 07	Aug 16	19,612	394	50.3 (12.7)	1.0 (0.2)
2008	78	Aug 04	Aug 20	5,551	746	14.2 (4.5)	1.9 (0.3)
2009	77	Aug 03	Aug 18	10,099	403	26.3 (10.7)	1.0 (0.2)
Total	1,808	Aug 02	Sep 25	195,545	91,510	4.5 (2.3)	2.1 (0.5)

We used a unique type of GAM called a varying-coefficient GAM (Hastie and Tibshirani 1993) to relate yellow perch to predictor variables. Varying-coefficient GAMs can relate the spatial and temporal dynamics of yellow perch to the potentially spatially heterogeneous effects of density-dependent and density-independent variables (e.g., Bacheler et al. 2009a). In our case, we used varying-coefficient GAMs to predict how local (i.e., at a given trawling site) yellow perch CPUE is expected to be more affected by overall global (i.e., the entire southern Green Bay) changes in yellow perch indices of abundance, water quality, and predation variables. These spatially explicit models have only very recently been used in ecological studies but have shown great promise in elucidating spawning dynamics and habitat use of marine fish (e.g., Bacheler et al. 2009a, 2010; Bartolino et al. 2011). Local age-0 and age-1+ yellow perch CPUE data, the response variables, were $\log_e$ transformed to achieve normality and reduce heteroscedasticity.

We examined the influence of seven predictor variables on local yellow perch CPUE: global yellow perch indices of abundance, cormorant abundance, water temperature, dissolved oxygen, water clarity, bottom depth, and position (Figure 2). These particular predictor variables were chosen based on the availability of reliable data from southern Green Bay and previous research on yellow perch elsewhere throughout their range (Post et al. 1997; Fisher et al. 1999; Mayer et al. 2000; Meadows 2006; Fielder 2008; Roberts et al. 2009). Some potentially important predictor variables (e.g., walleye and zebra mussel *Dreissena polymorpha* abundance) were not included in the GAM models because reliable population size or density data were unavailable for these species in Green Bay. We used Pearson's product-moment correlation analysis to test for significant collinearities among predictor variables that may influence model results.

Global age-0 and age-1+ yellow perch indices of abundance for southern Green Bay were included as predictor variables in the GAM analyses. Global age-1+ indices of abundance were estimated from a statistical catch-at-age model for southern Green Bay (referred to as Age1+index in the model) that was based upon commercial effort and harvest, recreational effort and harvest, and trawling survey data (T. Paoli, unpublished data). Commercial effort and harvest were weighted more

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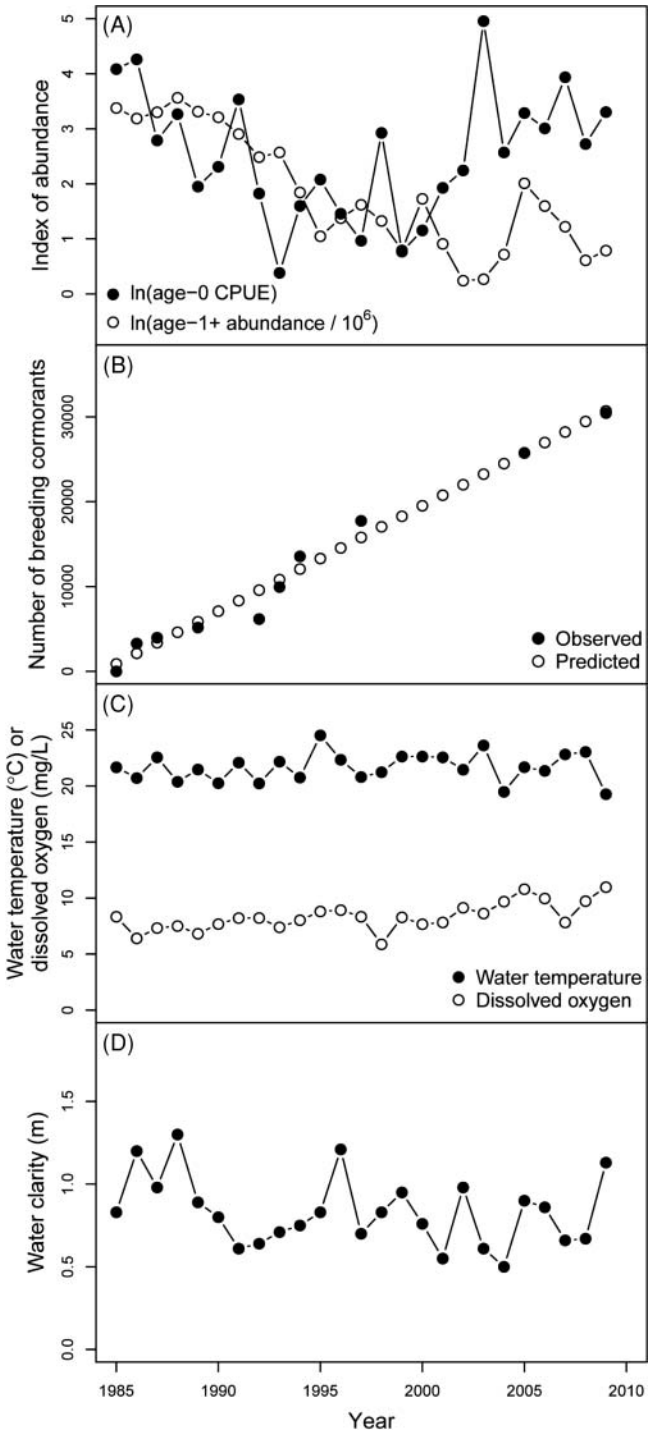

FIGURE 2. Predictor variables included in the generalized additive models for yellow perch abundance and distribution in southern Green Bay, 1985–2009: **(A)** mean annual (global) $\log_e$ transformed age-0 catch per unit effort (CPUE; number/min) from the trawling survey (i.e., Age0index) and annual $\log_e$ transformed age-1+ abundance, as estimated from a statistical catch-at-age model for southern Green Bay (i.e., Age1+index); **(B)** observed and predicted numbers of breeding double-crested cormorants; **(C)** mean August and September water temperature and dissolved oxygen at seven monitoring sites in southern Green Bay (see Figure 1); and **(D)** mean August and September water clarity.

heavily in the model than other inputs, based on the assumption that these are the most reliable and consistent indices. Annual model-based estimates of the total number of age-2 and older yellow perch composed the index; numbers of age-1 yellow perch were excluded from the index owing to highly variable estimates of this age-class in recent years, probably because of retrospective errors in the statistical catch-at-age model (Hilborn and Walters 1992). The total number of yellow perch was $\log_e$ transformed before inclusion in the model as the Age1+index (Figure 2A). The statistical catch-at-age model, however, did not provide estimates of age-0 abundance for Green Bay because commercial and recreational fisheries do not harvest this age-class. To create a global age-0 index (Age0index) of abundance for southern Green Bay, we instead used a log-transformed mean age-0 CPUE from the annual trawling survey as Age0index (Figure 2A).

Double-crested cormorant (hereafter, cormorant) abundance in southern Green Bay was estimated from nest counts by the U.S. Department of Agriculture, Wildlife Services (C. Lovell, USDA, personal communication). Cormorants nest on five islands in southern Green Bay: Cat and Lone Tree islands near the mouth of the Fox River and Hat, Jack, and Little Strawberry islands in the northern part of our study area (Figure 1). The Wildlife Services has conducted nine annual surveys of cormorant nest abundance between 1985 and 2009; each annual survey consisted of one to three counts by foot, boat, or airplane between late May and early July (Matteson et al. 1999). Because cormorants can forage at least 40 km away from nesting islands (Custer and Bunck 1992), cormorant nest counts from all islands within 40 km of southern Green Bay were used in this analysis. Annual adult cormorant abundance was assumed to be twice the mean number of nests counted during each survey (Figure 2B). Because our GAM required annual data on adult cormorant abundance, we predicted cormorant annual abundance (Cormorant) between 1985 and 2009 using a simple linear regression. This is a reasonable assumption because of the near linear increase of cormorants in southern Green Bay since 1985 ($R^2 = 0.97$; Figure 2B).

Water quality information for southern Green Bay has been recorded by the Green Bay Metropolitan Sewerage District (GBMSD) since 1985 (T. Valenta, GBMSD, unpublished data). Water temperature (Temp), dissolved oxygen (Oxygen), and water clarity (Clarity) were not regularly measured at each trawling site in the trawling survey. Instead, we used mean August and September water quality values from GBMSD from seven sites in southern Green Bay (Figure 1). At each site, vertical profiles of water temperature and dissolved oxygen and a single surface Secchi disk reading (i.e., water clarity) were taken four or five times throughout August and September. Water quality data were then averaged across depth and sampling period to provide a single mean value of water temperature, dissolved oxygen, and water clarity for each year (Figure 2). We assume that fluctuations in water quality conditions at the seven monitoring sites track with water quality conditions throughout southern

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Green Bay. Annual water quality data allowed us to examine the ways in which environmental conditions influenced the spatial distribution of age-0 or age-1+ yellow perch on a yearly time scale but not how local CPUE was influenced by local environmental conditions. That question would have required water quality information for each trawl site, which was unavailable.

We began by coding a full (most-complex) spatially explicit, varying-coefficient GAM for age-0 yellow perch, which included smoothed functions for depth and position and varying-coefficient terms for all other predictor variables. Depth was not included as a varying-coefficient term because its annual relationship to space was invariant, and position was either excluded or included as a smoothed nonlinear term. The full age-0 model was

$$\begin{aligned} x_{y,(\phi,\lambda)} = {} & a + s_1(\text{Depth}) + s_2(\phi,\lambda) + g_1(\phi,\lambda) \\ & \times \text{Cormorant}_y + g_2(\phi,\lambda) \times \text{Age0index}_y + g_3(\phi,\lambda) \\ & \times \text{Temp}_y + g_4(\phi,\lambda) \times \text{Oxygen}_y + g_5(\phi,\lambda) \\ & \times \text{Clarity}_y + e_{y(\phi,\lambda)}; \end{aligned} \tag{1}$$

$x_{y,(\phi,\lambda)}$ = the local log-transformed age-0 yellow perch CPUE in year y at latitude ϕ and longitude λ;
y = mean annual values (predictor variables lacking the y subscript were measured at each trawling site);
a = the intercept;
Depth = bottom depth measured at each trawl site;
ϕ = latitude of each trawl site;
λ = longitude of each trawl site;
Cormorant = cormorant abundance;
Age0index = the mean (global) age-0 yellow perch CPUE;
Temp = mean water temperature;
Oxygen = mean dissolved oxygen;
Clarity = mean water clarity;
$s_{1–2}$ = nonparametric smoothing functions;
$g_{1–5}$ = nonparametric varying-coefficient functions;
$e_{y,(\phi,\lambda)}$ = the random error assumed to be normally distributed (on a log scale) with a mean of zero and finite variance.

A separate (full) GAM was also developed for age-1+ yellow perch. The only difference between the age-1+ model and equation (1) is that Age1+index (global age-1+ index of abundance) was substituted for Age0index.

Model selection.—The full age-0 and age-1+ models were compared with a variety of reduced models using Akaike information criterion (AIC) and standard model diagnostics. The AIC balances the number of parameters of a model and its likelihood (Burnham and Anderson 2002), and models with lowest AIC scores were selected over models with higher scores. Reduced models consisted of different forms of each predictor variable, described here from most to least complex: (1) varying-coefficient terms, where local yellow perch CPUE is allowed to vary differently across space with changes in the predictor variable, (2) nonlinear smoothed terms, where local yellow perch CPUE is allowed to vary nonlinearly across the range of predictor variable values (but the same across space), (3) linear terms, where local yellow perch CPUE is a simple linear function of the predictor variable, and (4) the predictor variable is excluded from the model. The full model was compared with various reduced models by maintaining the most complex forms of all predictor variables, except for a single predictor variable that was included with different levels of reduced complexity.

The most parsimonious form of each predictor variable was chosen based on ΔAIC values. We computed simple differences (Δ_i) between the best model (AIC_{min}) and the ith model (AIC_i) as

$$\Delta_i = \text{AIC}_i - \text{AIC}_{\text{min.}} \tag{2}$$

In our analyses, we selected the form of each variable with the lowest AIC scores (i.e., $\Delta_i = 0$). In the case of varying-coefficient or smoothed terms, estimated degrees of freedom were chosen using automatic software selection.

All models were coded and analyzed via the mgcv library (version 1.6–2; Wood 2008) in R version 2.11.1 (R Development Core Team 2010) and the Gaussian family model and identity link function. Other distribution types were evaluated but compared unfavorably with the Gaussian distribution on log-transformed data. The gam.check function was used to verify that all models presented in this paper met assumptions of constant variance and normal residuals. There were also no consistent patterns in the relationship between the semivariance of the model residuals and distance between sampling points, indicating negligible spatial autocorrelation in the residuals.

RESULTS

A total of 1,808 trawl samples from 1985 to 2009 were used in our study, ranging from 52 to 78 annually (Table 1). Most of the trawling each year occurred in August, with the exception of a few years in the 1980s when some trawling was conducted into late September. Overall, 195,545 age-0 and 91,510 age-1+ yellow perch were caught in the trawling survey (Table 1). There was substantial variation in annual yellow perch CPUE. Age-0 CPUE was highest in 1985, 1986, and 2003 and lowest in 1993, 1997, and 1999, while age-1+ CPUE was highest in 1987, 1988, and 1992 and lowest in 2001, 2007, and 2009.

There were only two significant correlations between predictor variables in our study (Table 2). The Age1+index was negatively related to Cormorant ($r = -0.84$; $P < 0.05$), and Cormorant was positively related to Oxygen ($r = 0.46$; $P < 0.05$). All other correlations were insignificant at $P = 0.05$. Collinearities were not deemed numerous enough to drop any predictor variables from the GAM analyses.

Based on AIC scores, the best GAM model explaining local age-0 yellow perch CPUE included all predictor variables except

TABLE 2. Pearson's correlation matrix for predictor variables used in the age-0 and age-1+ yellow perch generalized additive models built on trawling data from 1985 to 2009 in southern Green Bay. Asterisks indicate significance ($P < 0.05$). Variable descriptions are provided with equation (1).

Predictor variable	Depth	Age0 index	Age1+ index	Cormorant	Temp	Oxygen	Clarity
Depth	1.0						
Age0index	−0.02	1.0					
Age1+index	−0.01	0.02	1.0				
Cormorant	0.02	0.05	−0.84*	1.0			
Temp	−0.02	−0.01	0.30	0.09	1.0		
Oxygen	−0.02	0.10	−0.40	0.46*	−0.09	1.0	
Clarity	−0.03	0.09	0.26	−0.27	−0.20	−0.03	1.0

Temp (Table 3). The age-0 model included Depth as a linear term; Position as a smoothed term; and Age0index, Cormorant, Oxygen, and Clarity as varying-coefficient terms. Overall, the age-0 model explained 63.1% of the deviance in local age-0 yellow perch CPUE (Table 4).

The best age-1+ yellow perch GAM model included the same predictor variables as the age-0 GAM model, but two of the predictor variables were included in different forms (Table 3). In the age-1+ model, Depth, Position, and Age1+index were included as smoothed terms, while Cormorant, Oxygen, and Clarity were included as varying-coefficient terms (Table 4). The age-1+ model explained 65.0% of the deviance in local age-1+ yellow perch CPUE (Table 4).

The effects of Position on local yellow perch CPUE from the GAM models corresponded very closely with mean trawling site-specific yellow perch CPUE (Figure 3). For instance, mean age-0 yellow perch CPUE was highest along the western and southern shorelines of the study area and lowest offshore and along the eastern shoreline, which matched the model-estimated effects of position very closely (Figure 3). Mean age-1+ yellow perch CPUE was more evenly distributed in southern Green Bay compared with age-0 CPUE, except for a lower CPUE in the eastern section of our study area. Similar to age-0 fish, the spatial effects from the age-1+ GAM model corresponded closely to mean site-specific age-1+ CPUE.

Bottom depth was also an important predictor of local yellow perch CPUE. Local age-0 yellow perch CPUE was negatively related to Depth (i.e., highest effect on CPUE in the shallowest water), while age-1+ yellow perch displayed a dome-shaped

TABLE 3. ΔAIC values for generalized additive models of age-0 and age-1 and older yellow perch constructed from 1985–2009 trawling data for southern Green Bay. The column headings refer to the four tested forms for each predictor variable: (1) varying coefficient, (2) smoothed nonlinear, (3) linear, or (4) excluded from the model. Variable descriptions are provided with equation (1). Bold italics indicate variables included in the final models; blank cells indicate terms that are not applicable to the models.

	Form			
Predictor variable	Varying coefficient	Smoothed nonlinear	Linear	Excluded
Age-0 model				
Depth		0.0	***0.0***	2.7
Position		***0.0***		3.4
Age0index	***0.0***	155.9	191.6	737.2
Cormorant	***0.0***	141.7	196.4	195.3
Temp	5.5	4.7	4.7	***0.0***
Oxygen	***0.0***	96.9	97.5	109.1
Clarity	***0.0***	9.9	39.1	62.6
Age-1+ model				
Depth		***0.0***	72.2	72.7
Position		***0.0***		1.5
Age1+index	14.9	***0.0***	8.0	586.9
Cormorant	***0.0***	14.6	46.1	53.3
Temp	11.6	5.6	5.6	***0.0***
Oxygen	***0.0***	1.3	3.5	2.6
Clarity	***0.0***	9.7	18.3	36.6

TABLE 4. Estimated degrees of freedom for the predictor variables in the final generalized additive models for age-0 and age-1 and older yellow perch based on 1985–2009 trawling data for southern Green Bay. The deviance explained by the final age-0 model was 63.1%, versus 65.0% for the age-1+ model. Variable descriptions are provided with equation (1); na = the predictor variable was not applicable to that particular model and ex = the predictor variable was excluded from the model based on Akaike information criterion score.

	Model	
Variable	Age-0	Age-1+
Depth	1.0[a]	7.5[b]
Position	17.8[b]	12.7[b]
Age0index	22.8[c]	na
Age1+index	na	6.5[b]
Cormorant	21.0[c]	18.6[c]
Temp	ex	ex
Oxygen	17.2[c]	16.3[c]
Clarity	11.6[c]	13.0[c]

[a]The predictor variable used in the final model was linear.
[b]The predictor variable used in the final model was smoothed nonlinear.
[c]The predictor variable used in the final model was varying coefficient.

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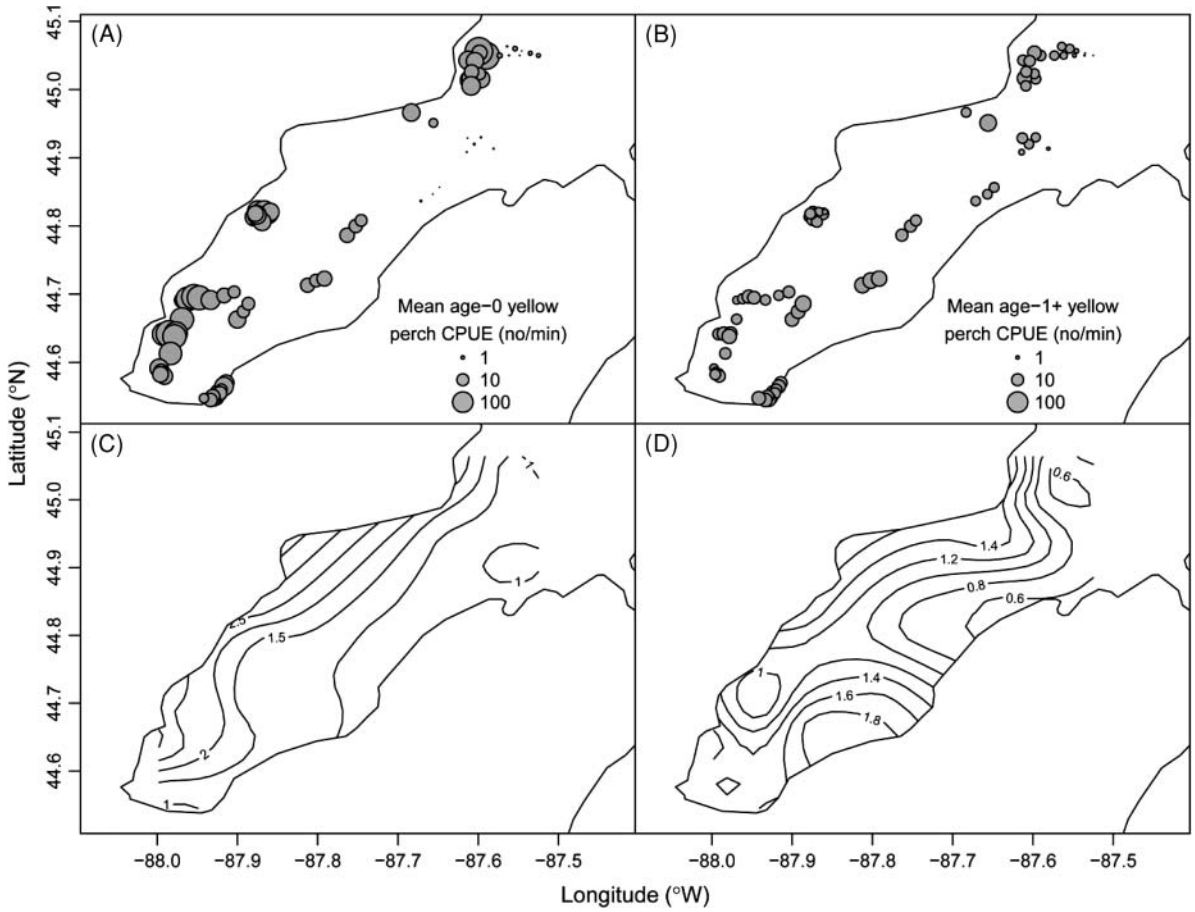

FIGURE 3. Observed and predicted local yellow perch trawl survey catch per unit effort (CPUE; number/min) in southern Green Bay, 1985–2009: **(A)** mean local age-0 and **(B)** age-1+ CPUE and **(C)** partial effects of position (latitude and longitude) on $\log_e$ transformed local age-0 and **(D)** age-1+ CPUE at average values of all other predictor variables.

response to Depth that reached its maximum at approximately 13 m (Figure 4).

Global indices of abundance (Age0index or Age1+index) affected local age-0 yellow perch CPUE differently than local age-1+ CPUE. We observed a spatially variable (varying-coefficient) response of local age-0 CPUE to a 1-unit increase in Age0index (Table 4); local age-0 CPUE increased throughout the study region but particularly in nearshore areas of the western shoreline of southern Green Bay, and much less so in deeper, offshore areas (Figure 5A). In contrast, local age-1+ CPUE was included in the age-1+ model as a smoothed (not varying-coefficient) term. Therefore, the increase observed in local age-1+ CPUE as Age1+index increased was found to increase the same amount throughout southern Green Bay (Figure 5B).

We observed spatially explicit effects of Cormorant, Oxygen, and Clarity on local yellow perch CPUE, as measured by the varying-coefficient terms of the GAMs (Table 3). Both local age-0 and age-1+ yellow perch CPUE decreased with increasing Cormorant, but declines were most obvious in regions nearest to cormorant nesting islands in the far northern and southern sections of our study area (Figure 6). Increased Oxygen was related to increases in local age-0 and age-1+ yellow perch CPUE, particularly in nearshore areas along the western shoreline. Last, increased Clarity was related to increased local age-0 and age-1+ yellow perch CPUE near the mouth of the Fox River.

DISCUSSION

Previous work has shown that water quality, landscape, density-dependent, and predator variables affect the abundance and distribution of fish species, but these factors have typically been studied in isolation from other important variables. Alternatively, we used a novel varying-coefficient GAM to show that cormorants, dissolved oxygen, water clarity, bottom depth, and global yellow perch indices of abundance combined to affect the abundance and distribution of age-0 and age-1+ yellow perch in Green Bay. The local response of yellow perch CPUE to four of these factors (i.e., global yellow perch indices of abundance, cormorants, dissolved oxygen, and water clarity) had a unique spatial structure, suggesting that local yellow perch CPUE was

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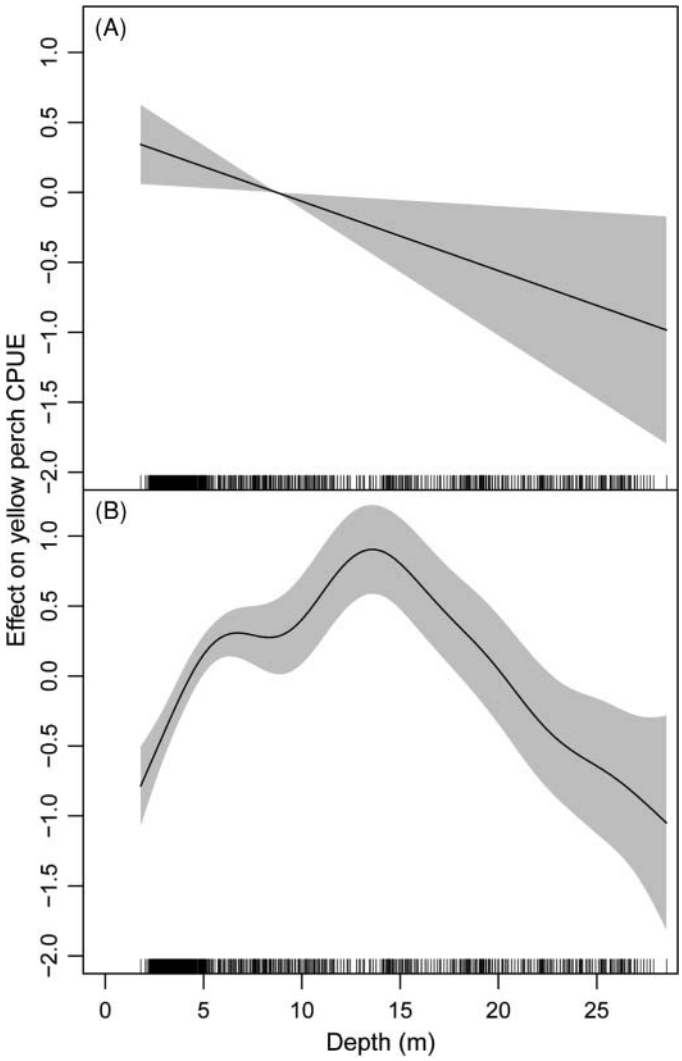

FIGURE 4. Partial effect of bottom depth on $\log_e$ transformed local **(A)** age-0 and **(B)** age-1+ yellow perch catch per unit effort (CPUE; number/min) in the southern Green Bay trawl survey, 1985–2009, at average values of all other predictor variables. The shaded areas are 95% confidence intervals, and the small bars on the *x*-axes indicate sampling intensity.

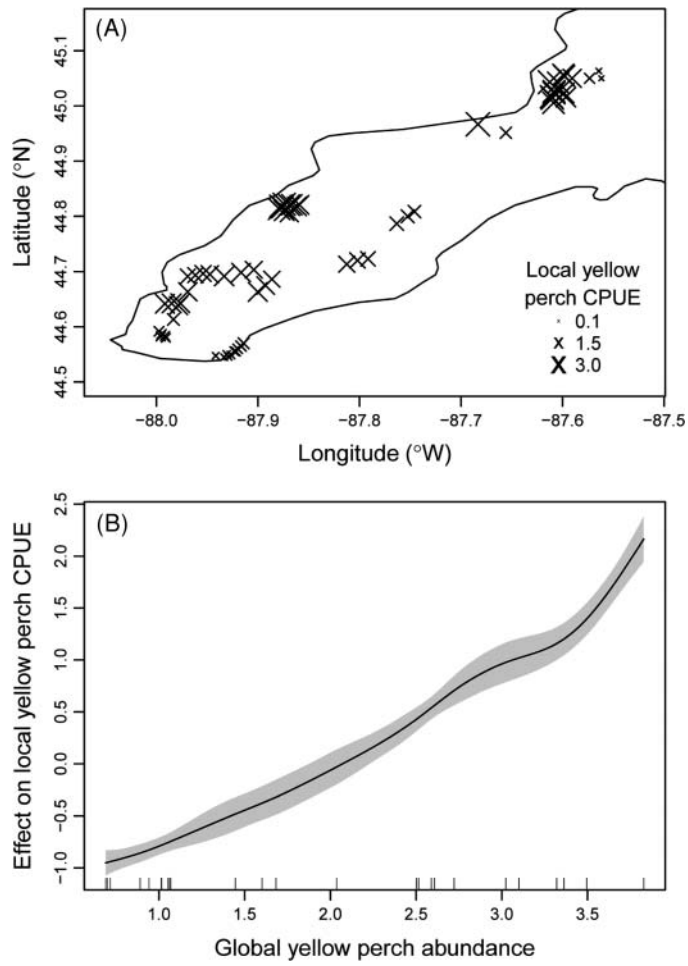

FIGURE 5. Panel **(A)** shows the spatially explicit effect of increased global age-0 yellow perch catch per unit effort (CPUE; number/min) on local age-0 CPUE from the southern Green Bay trawl survey, 1985–2009. The × symbols indicate expected increases (black) or decreases (gray) in local yellow perch CPUE with a 1-unit increase in global CPUE. The sizes of the symbols indicate the sizes of the positive or negative effects (effects not significantly different from zero were excluded). Panel **(B)** shows the effect of global age-1+ abundance on $\log_e$ transformed local age-1+ yellow perch CPUE at average values of all other predictor variables. The shaded areas are 95% confidence intervals, and the small bars on the *x*-axes indicate sampling intensity.

affected differently across space as these predictor variables increased or decreased.

Water quality in southern Green Bay has been historically degraded due to excessive nutrients and sediments entering the bay from the Fox River (Klump et al. 1997), which has resulted in decreased water clarity and dissolved oxygen levels (Kennedy 1982). Both age-0 and age-1+ yellow perch were found at higher local CPUE near the mouth of the Fox River during years of higher water clarity and in nearshore areas during years with higher dissolved oxygen levels, suggesting that reductions in water clarity or dissolved oxygen may limit local yellow perch CPUE in these areas. Given that the extreme southern portion of Green Bay has historically been a major center of abundance for yellow perch, the ecological and fishery consequences of reduced water clarity could be significant. Local age-0 and age-1+ yellow perch CPUE were not influenced by summertime water temperature in our study, probably because the range of summertime water temperatures experienced over the study was not limiting to yellow perch. We note that water quality information from individual trawl locations was not available, so we instead used average annual summertime water quality estimates. The disadvantage of this approach is not being able to elucidate yellow perch preferences of environmental conditions that may be varying over small temporal or spatial scales.

Age-0 yellow perch in Green Bay displayed density-dependent habitat use, expanding into deeper, offshore waters at

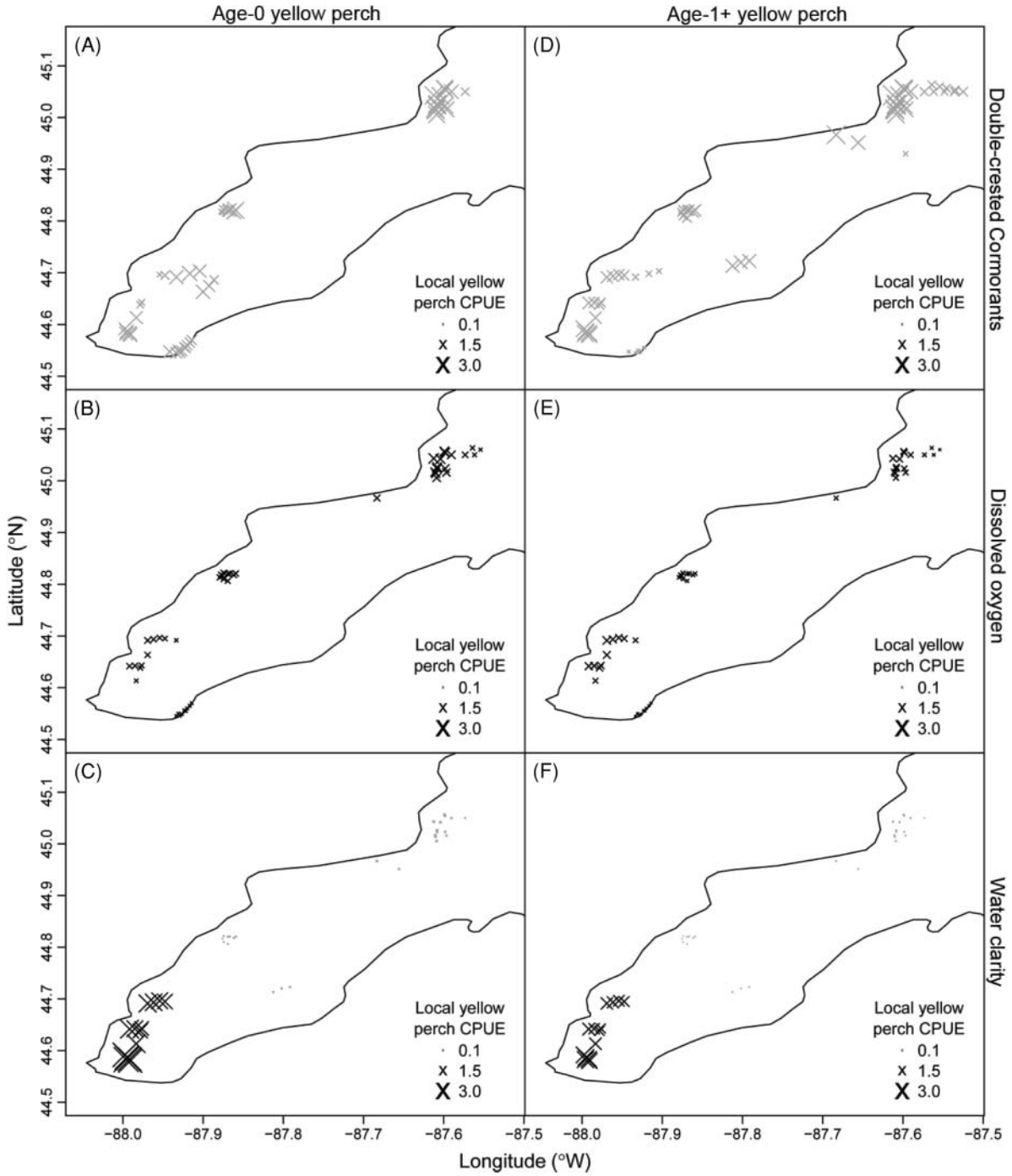

FIGURE 6. Spatially explicit effects of increased double-crested cormorant abundance **(A, D)**, dissolved oxygen **(B, E)**, and water clarity **(C, F)** on local age-0 (left column) and age-1+ (right column) yellow perch catch per unit effort (CPUE) from the southern Green Bay trawl survey, 1985–2009. See Figure 5 for additional details.

high global CPUEs and retracting into shallow areas of southwest Green Bay at low global CPUEs. Many marine (e.g., MacCall 1990; Swain and Sinclair 1994; Marshall and Frank 1995) and some freshwater fishes (e.g., Venne and Magnan 1995; Post et al. 1997) have been shown to exhibit density-dependent habitat use, and interference or exploitative competition are typically inferred as the primary mechanisms explaining patterns of distribution. At high CPUE, it is unknown whether age-0 yellow perch in Green Bay can locally deplete their primary food resources of zooplankton or benthic invertebrates.

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Age-1+ yellow perch did not exhibit density-dependent habitat use, however, suggesting competition for prey resources or space is not as important for older age-classes of yellow perch as it is for age-0 individuals. These results are broadly consistent with previous studies that suggest density-dependence is more likely in early life history stages (Houde 1987; Leggett and Deblois 1994). Further research into the causes and consequences of yellow perch density-dependent habitat use in Green Bay and elsewhere throughout their range is warranted.

Cormorants have been implicated in the decline of yellow perch in many places (Burnett et al. 2002; VanDeValk et al. 2002; Rudstam et al. 2004; Meadows 2006; Fielder 2008). Our GAM models suggested that cormorant abundance was negatively related to local age-0 and age-1+ yellow perch CPUE in southern Green Bay, and declines were especially obvious near cormorant nesting islands. Although not resident to southern Green Bay before the early 1900s, cormorants increased dramatically from 7 breeding birds in 1973 to over 30,000 breeding birds in 2009 (C. Lovell, personal communication), concurrent with the collapse of yellow perch over the same time frame (Paoli 2009). Using stomach content analysis, Meadows (2006) determined that yellow perch was the most numerically abundant prey item of southern Green Bay cormorants in 2004 (37.0% by number), and third most abundant in 2005 (9.9% by number). Based on a consumption model, she concluded that cormorants ate substantially more yellow perch in southern Green Bay than the combined commercial and recreational harvest from the same period (Meadows 2006). The weight of modeling and diet evidence suggests that cormorant predation negatively affects yellow perch abundance in southern Green Bay.

There are some limitations to a GAM regression approach. The flexibility of GAMs allows them to fit observed data very well, but when sample sizes are small the models can overfit data at the expense of generality (Wood 2006). The large number of samples taken and the high degree of consistency between age-0 and age-1+ yellow perch GAM models suggests that the patterns we observed were robust and not subject to overfitting. Our GAM models also explained 63–65% of the variation in yellow perch CPUE, which is quite high compared with similar habitat models but still suggests that a substantial amount of unexplained variation remains. Unfortunately, we lacked reliable data on some potential predators (walleyes, American white pelicans *Pelecanus erythrorhynchos*) and competitors (alewives *Alosa pseudoharengus*, round gobies *Neogobius melanostomus*) of yellow perch, so our models can be considered a baseline to which additional predator or competitor variables could be added in the future as more data become available.

We used 25 years of trawling data in a varying-coefficient GAM to document the various ways that local yellow perch CPUE and distribution was affected by predatory, water quality, landscape, and density-dependent factors. Our results suggest that future work on fish population dynamics should not only consider variables that directly influence CPUE, but also on how those variables influence the spatial distribution of fish species. Improved understanding of the controls of both the spatial and temporal dynamics of fish species will help us better explain the underlying causes of fluctuations of fish populations.

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REFERENCES

Bacheler, N. M., K. M. Bailey, L. Ciannelli, V. Bartolino, and K. S. Chan. 2009a. Density-dependent, landscape, and climate effects on spawning distribution of walleye pollock *Theragra chalcogramma*. Marine Ecology Progress Series 391:1–12.

Bacheler, N. M., L. Ciannelli, K. M. Bailey, and J. T. Duffy-Anderson. 2010. Spatial and temporal patterns of walleye pollock spawning in the eastern Bering Sea inferred from egg and larval distributions. Fisheries Oceanography 19:107–120.

Bacheler, N. M., L. M. Paramore, J. A. Buckel, and J. E. Hightower. 2009b. Abiotic and biotic factors influence the habitat use of an estuarine fish. Marine Ecology Progress Series 377:263–277.

Bartolino, V., L. Ciannelli, N. M. Bacheler, and K. S. Chan. 2011. Ontogenetic and sex-specific differences in density-dependent habitat selection of a marine fish population. Ecology 92:189–200.

Bence, J. R., and K. D. Smith. 1999. An overview of recreational fisheries of the Great Lakes. Pages 259–306 *in* W. W. Taylor and C. P. Ferreri, editors. Great Lakes fisheries and policy management: a binational perspective. Michigan State University Press, East Lansing.

Bertrand, G., L. Lang, and J. Ross. 1976. The Green Bay watershed: past/present/future. University of Wisconsin, Sea Grant College, Technical Report 229, WI-SG-76–229, Madison.

Burnett, J. A. D., N. H. Ringler, B. F. Lantry, and J. H. Johnson. 2002. Double-crested cormorant predation on yellow perch in the eastern Basin of Lake Ontario. Journal of Great Lakes Research 28:202–211.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.

Carey, M. P., and M. E. Mather. 2009. Identifying across-system sources of variation in a generalist freshwater fish: correlates of total and size-specific abundance of yellow perch. Ecology of Freshwater Fish 18:145–155.

Chesson, P. 1998. Making sense of spatial models in ecology. Pages 151–166 *in* J. Bascompte and R. V. Sole, editors. Modeling spatiotemporal dynamics in ecology. Springer-Verlag, New York.

Ciannelli, L., G. E. Dingsør, B. Bogstad, G. Ottersen, K. S. Chan, H. Gjøsæter, J. E. Stiansen, and N. C. Stenseth. 2007. Spatial anatomy of species survival: effects of predation and climate-driven environmental variability. Ecology 88:635–646.

Custer, T. W., and C. Bunck. 1992. Feeding flights of breeding double-crested cormorants at two Wisconsin colonies. Journal of Field Ornithology 63:203–211.

Diana, J. S., S. Maruca, and B. Lowe. 2006. Do increasing cormorant populations threaten sport fishes of the Great Lakes? A case study in Lake Huron. Journal of Great Lakes Research 32:306–320.

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Fielder, D. G. 2008. Examination of factors contributing to the decline of the yellow perch population and fishery in Les Cheneaux Islands, Lake Huron, with emphasis on the role of double-crested cormorants. Journal of Great Lakes Research 34:506–523.

Fisher, S. J., C. R. Pyle, and D. W. Willis. 1999. Habitat use by age-0 yellow perch in two South Dakota glacial lakes. Ecology of Freshwater Fish 8: 85–93.

Francis, J. T., S. R. Robillard, and J. E. Marsden. 1996. Yellow perch management in Lake Michigan: a multijurisdictional challenge. Fisheries 21(2): 18–20.

Fretwell, S. D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distributions in birds. Acta Biotheoretica 19:16–36.

Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with stream-dwelling minnows. Ecology 68:1856–1862.

Glover, D. C., J. M. Dettmers, D. H. Wahl, and D. F. Clapp. 2008. Yellow perch (*Perca flavescens*) stock structure in Lake Michigan: an analysis using mark-recapture data. Canadian Journal of Fisheries and Aquatic Sciences 65:1919–1930.

Hartman, K. J., and F. J. Margraf. 1993. Evidence of predatory control of yellow perch (*Perca flavescens*) recruitment in Lake Erie, U.S.A. Journal of Fish Biology 43:109–119.

Hastie, T. J., and R. J. Tibshirani. 1993. Varying-coefficient models. Journal of the Royal Statistical Society B 55:757–796.

Hastie, T. J., and R. J. Tibshirani. 1990. Generalized additive models. Chapman and Hall, London.

Henderson, B. A., and S. J. Nepszy. 1988. Recruitment of yellow perch (*Perca flavescens*) affected by stock size and water temperature in lakes Erie and St. Clair, 1965–85. Journal of Great Lakes Research 14:205–215.

Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Kluwer Academic Publishers, Boston.

Houde, E. D. 1987. Fish early life dynamics and recruitment variability. Pages 17–29 *in* R. D. Hoyt, editor. 10th Annual larval fish conference. American Fisheries Society, Symposium 2, Bethesda, Maryland.

Janssen, J., and M. A. Luebke. 2004. Preference for rocky habitats by age-0 yellow perch and alewives. Journal of Great Lakes Research 30:93–99.

Kennedy, J. A. 1982. Water-mass structure and exchanges in Green Bay, Lake Michigan. Master's thesis. University of Wisconsin, Milwaukee.

Klump, J. V., P. Sager, and D. N. Robertson. 1997. Sedimentary phosphorus cycling and a phosphorus mass balance for the Green Bay ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 54:10–26.

Koonce, J. F., T. B. Bagenal, R. F. Carline, K. E. F. Hokanson, and M. Nagiec. 1977. Factors influencing year-class strength of percids: a summary and model of temperature effects. Journal of the Fisheries Research Board of Canada 34:1900–1909.

Leggett, W. C., and E. Deblois. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Netherlands Journal of Sea Research 32:119–134.

Lobb, M. D., and D. J. Orth. 1991. Habitat use by an assemblage of fish in a large warmwater stream. Transactions of the American Fisheries Society 120:65–78.

MacCall, A. D. 1990. Dynamic geography of marine fish populations. University of Washington, Washington Sea Grant Program, Seattle.

Manchester-Neesvig, J. B., A. W. Andren, and D. N. Edgington. 1996. Patterns of mass sedimentation and deposition of sediment contaminated by PCBs in Green Bay. Journal of Great Lakes Research 22:444–462.

Marsden, J. E., and S. R. Robillard. 2004. Decline of yellow perch in southwestern Lake Michigan, 1987–1997. North American Journal of Fisheries Management 24:952–966.

Marshall, C. T., and K. T. Frank. 1995. Density-dependent habitat selection by juvenile haddock (*Melanogrammus aeglefinus*) on the southwestern Scotian Shelf. Canadian Journal of Fisheries and Aquatic Sciences 52:1007–1017.

Matteson, S. W., P. W. Rasmussen, K. L. Stromborg, T. I. Meier, J. V. Stappen, and E. C. Nelson. 1999. Changes in the status, distribution, and management of double-crested cormorants in Wisconsin. U.S. Department of Agriculture Technical Bulletin 1879:27–45.

Mayer, C. M., A. VanDeValk, J. L. Forney, L. G. Rudstam, and E. L. Mills. 2000. Response of yellow perch (*Perca flavescens*) in Oneida Lake, New York, to the establishment of zebra mussels (*Dreissena polymorpha*). Canadian Journal of Fisheries and Aquatic Sciences 57:742–754.

Meadows, S. R. 2006. Double-crested cormorants in southern Green Bay: ecology and food habits with emphasis on the yellow perch fishery, dietary overlap with sympatric American white pelicans, and seasonal contaminant intake. Master's thesis. University of Wisconsin, Madison.

Nielsen, L. A. 1980. Effect of walleye (*Stizostedion vitreum vitreum*) predation on juvenile mortality and recruitment of yellow perch (*Perca flavescens*) in Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences 37:11–19.

Noble, R. L. 1975. Growth of young yellow perch (*Perca flavescens*) in relation to zooplankton populations. Transactions of the American Fisheries Society 104:718–725.

Paoli, T. 2009. Green Bay yellow perch. Pages 11–17 *in* W. Horns, editor. Lake Michigan management report 2009. Wisconsin Department of Natural Resources, Madison.

Post, J. R., M. R. S. Johannes, and D. J. McQueen. 1997. Evidence of density-dependent cohort splitting in age-0 yellow perch (*Perca flavescens*): potential behavioural mechanisms and population-level consequences. Canadian Journal of Fisheries and Aquatic Sciences 54:867–875.

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Reed, T., S. J. Wielgus, A. K. Barnes, J. J. Schiefelbein, and A. M. Fettes. 2004. Refugia and local controls: benthic invertebrate dynamics in lower Green Bay, Lake Michigan following zebra mussel invasion. Journal of Great Lakes Research 30:390–396.

Roberts, J. J., T. O. Hook, S. A. Ludsin, S. A. Pothoven, H. A. Venderploeg, and S. B. Brandt. 2009. Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch. Journal of Experimental Marine Biology and Ecology 381:132–142.

Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology 77:885–899.

Rudstam, L. G., A. J. VanDeValk, C. M. Adams, J. T. H. Coleman, J. L. Forney, and M. E. Richmond. 2004. Cormorant predation and the population dynamics of walleye and yellow perch in Oneida Lake. Ecological Applications 14:149–163.

Smith, O. H., and J. Van Oosten. 1940. Tagging experiments with lake trout, whitefish, and other species of fish from Lake Michigan. Transactions of the American Fisheries Society 69:63–84.

Swain, D. P., and A. F. Sinclair. 1994. Fish distribution and catchability: what is the appropriate measure of distribution? Canadian Journal of Fisheries and Aquatic Sciences 51:1046–1054.

VanDeValk, A. J., C. M. Adams, L. G. Rudstam, J. L. Forney, T. E. Brooking, M. A. Gerken, B. P. Young, and J. T. Hooper. 2002. Comparison of angler and cormorant harvest of walleye and yellow perch in Oneida Lake, New York. Transactions of the American Fisheries Society 131:27–39.

Venne, H., and P. Magnan. 1995. The impact of intra- and interspecific interactions on young-of-the-year brook char, in temperate lakes. Journal of Fish Biology 46:669–686.

Wells, L., and A. L. McLain. 1972. Lake Michigan: effects of exploitation, introductions, and eutrophication on the salmonid community. Journal of the Fisheries Research Board of Canada 29:889–898.

Wood, S. N. 2008. Fast stable direct fitting and smoothness selection for generalized additive models. Journal of the Royal Statistical Society Series B 70:495–518.

Wood, S. N. 2006. Generalized additive models: an introduction with R. CRC Press, Boca Raton, Florida.