Relationship of fish catch and composition to water quality in a suite of agriculturally eutrophic lakes

Christopher J. Egertson and John A. Downing

Abstract: We examined the fish community, water quality, and morphometry of 32 agriculturally eutrophic lakes. Our purpose was to explore the relationships between eutrophication and fish catch per unit effort by weight ($\mathrm{CPUE_w}$) and fish community composition of the six most important species in this suite of the world's most nutrient-rich lakes. We found that the $\mathrm{CPUE_w}$ of the sum of all species increased with lake trophic status measured as chlorophyll *a* ($r = 0.45$, $p < 0.009$). By dissecting total fish $\mathrm{CPUE_w}$ into individual species and functional groups, we found that only common carp (*Cyprinus carpio*) and benthivore $\mathrm{CPUE_w}$ increased significantly with trophic status ($p < 0.03$ and 0.001, respectively). Sport fish (principally piscivores) decreased as a proportion of total $\mathrm{CPUE_w}$ by approximately 50%, while benthivores, primarily common carp, increased by approximately 80% over an increase in cholorophyll *a* from 10 to 100 $\mu g \cdot L^{-1}$. Common carp $\mathrm{CPUE_w}$ was correlated with and may have a negative influence on $\mathrm{CPUE_w}$ of bluegill (*Lepomis macrochirus*) and black crappie (*Pomoxis nigromaculatus*) and a positive influence on white crappie (*Pomoxis annularis*). Our study suggests that species other than benthivores may be unable to exploit increased energy availability in hypereutrophic systems or are competitively excluded from using this increased production.

Résumé : Nous avons examiné la communauté de poissons, la qualité de l'eau et la morphométrie de 32 lacs rendus eutrophes par l'agriculture. Notre objectif est d'étudier la relation entre l'eutrophisation, la capture de poissons (en masse) par unité d'effort ($\mathrm{CPUE_w}$) et la composition de la communauté des six espèces dominantes de poissons dans cette série de lacs, parmi les plus enrichis au monde en nutriments. La somme des $\mathrm{CPUE_w}$ de toutes les espèces augmente avec le statut trophique du lac, déterminé par le dosage de la chlorophylle *a* (r = 0,45; p < 0,009). Lorsque la $\mathrm{CPUE_w}$ totale des poissons est réparti dans les différentes espèces et groupes fonctionnels, seules les $\mathrm{CPUE_w}$ de la carpe commune (*Cyprinus carpio*) et des poissons benthonophages augmentent de façon significative avec le statut trophique (p < 0,03 et 0,001, respectivement). La proportion des poissons sportifs, principalement des piscivores, dans la $\mathrm{CPUE_w}$ totale décline d'environ 50 %, alors que les benthonophages, surtout la carpe commune, s'accroissent d'environ 80 % sur une gamme d'augmentation de la chlorophylle *a* de 10–100 $\mu g \cdot L^{-1}$. Il existe une corrélation avec, semble-t-il, un effet négatif entre la $\mathrm{CPUE_w}$ de la carpe commune et les $\mathrm{CPUE_w}$ du crapet harlequin (*Lepomis macrochirus*) et de la marigane noire (*Pomoxis nigromaculatus*) et un effet positif sur la marigane blanche (*Pomoxis annularis*). Notre étude indique que les espèces non benthonophages n'arrivent pas à exploiter l'augmentation de l'énergie disponible dans les systèmes hypereutrophes ou alors qu'elles sont empêchées par la compétition d'utiliser cette production accrue.

[Traduit par la Rédaction]

Introduction

Eutrophication of fresh water lakes is a worldwide problem. Nutrients enter lakes from agricultural lands, animal feedlots, industry, wastewater treatment plants, and lawn fertilizers (Carpenter et al. 1998; Downing et al. 1999). This rapid increase in nutrients can cause great changes to lake ecosystems. One important resource that can change through eutrophication is the fish community (Persson et al. 1991).

Eutrophication can lead to increased energy supply to fish, but it can also lead to shifts in fish community composition. Trophic state variables such as primary production, chlorophyll *a*, total phosphorus, and total nitrogen have been shown to increase fish production (Hanson and Leggett 1982; Downing et al. 1990; Bachmann et al. 1996). However, as eutrophication increases, some studies have established a systematic loss of piscivorous fish (Bays and Crisman 1983; Persson et al. 1988; Jeppesen et al. 2000), while planktivorous (Yurk and Ney 1989; Bachmann et al. 1996) and benthivorous fish have been observed to increase (Persson et al. 1991; Jeppesen et al. 2000).

A benthivorous fish of particular interest in North America is the common carp (*Cyprinus carpio*). Carp is an invasive, exotic species and has often been associated with

Received 25 April 2003. Accepted 13 April 2004. Published on the NRC Research Press Web site at http://cjfas.nrc.ca on 24 November 2004.
J17489

C.J. Egertson. Oregon Natural Desert Association, Bend, OR 97701, USA.
J.A. Downing.[1] Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011-1020, USA.

[1] Corresponding author (e-mail: downing@iastate.edu).

doi: 10.1139/F04-109

degradation in water quality and biota. They may increase turbidity within the water column by resuspending sediment (Meijer et al. 1990; Breukelaar et al. 1994; Lougheed et al. 1998), and they can increase nutrient concentrations in lakes directly through excretion (Lamarra 1975) or indirectly through sediment resuspension (Andersson et al. 1978; Breukelaar et al. 1994). Carp may further impact the biota of the ecosystem by uprooting submerged macrophytes while feeding (Crivelli 1983; Ten Winkel and Meulemans 1984), by decreasing benthic invertebrates (Zieba and Szarowska 1987; Tatrai et al. 1994) and zooplankton (Kirk 1991; Lougheed et al. 1998), and by influencing fish species by disrupting nests or through modification of their habitat (Taylor et al. 1984; Harlan et al. 1987).

Because fish possess ecological, commercial, and recreational value, the influence of eutrophication on fish catch in lakes and reservoirs is of great significance to fisheries managers. Despite the notable impacts that carp and other benthivores may have on the fisheries of nutrient-rich lakes, few studies have attempted to analyze trends in fish abundance under highly eutrophic conditions and high abundances of benthivores. Several studies have examined lakes that span a broad range of trophic status (Kautz 1980; Bachmann et al. 1996; Jeppesen et al. 2000) and some have included lakes with benthivores such as bream (*Abramis brama*) and roach (*Rutilus rutilus*) (Persson et al. 1991; Jeppesen et al. 2000), but few have examined a range of lakes in which carp are abundant. Jones and Hoyer (1982) investigated nutrient-rich lakes where carp may have been present, but they only quantified sport fish abundances. Because carp are often implicated in the degradation of eutrophic lake ecosystems, it is important to know how both high nutrient supplies and carp abundances influence fisheries.

Our objectives therefore were to (*i*) examine agriculturally eutrophic lakes to find the best correlates of fish catch, (*ii*) determine how the fish communities change in composition across a gradient of high nutrient concentration, and (*iii*) explore correlations between carp abundance and the abundance and composition of fish communities. Lakes in highly agricultural Iowa, USA, are ideal for this analysis because they are among the worlds most nutrient rich (Arbuckle and Downing 2001), and they frequently have high densities of benthivorous carp.

Methods

The overall approach of our study was to seek correlations between fish catch per unit effort (CPUE) and lake ecosystem characteristics by collecting detailed information of fish CPUE and lake characteristics across 32 eutrophic to hypereutrophic lakes. Fish managers recollect significant management of only a few of these lakes in the 1980s, mostly to eliminate carp. As is typical in this region, none of these management activities altered the species composition for more than a few years. Water samples were collected monthly, May through July 2001, from eight natural and 24 impounded lakes (Fig. 1). Water quality variables that were estimated include chlorophyll *a*, arcsine-transformed percent algal biomass as Cyanobacteria, ammonia measured as the sum of ammonium and un-ionized ammonia, un-ionized ammonia, total nitrogen, total phosphorus, total suspended solids, water transparency, dissolved oxygen, temperature, and specific conductivity. All water samples were collected as integrated samples of the upper mixed zone of each lake. When a thermocline was not present, the entire water column was sampled. Collected water was kept at 4 °C and analyzed within 2 days. Macrophytes occur only sporadically and at very low densities in lakes, so they were not included in our water quality assessments.

Total phosphorus and ammonia were analyzed according to standard methods (American Public Health Association et al. 1998). Total nitrogen was analyzed using second-derivative spectroscopy (Crumpton et al. 1992). Laboratory analysis of chlorophyll *a* was conducted using a Turner Designs TD-700 laboratory fluorometer (Turner Designs Inc., Sunnyvale, California) with acetone and magnesium carbonate extraction (American Public Health Association et al. 1998). Mean estimates of temperature, specific conductivity, and dissolved oxygen were averaged from epilimnetic profiles and were obtained with a YSI 6-Series multiparameter water quality monitor (Yellow Springs Instrument Inc., Yellow Springs, Ohio). Transparency was estimated by Secchi disc depth.

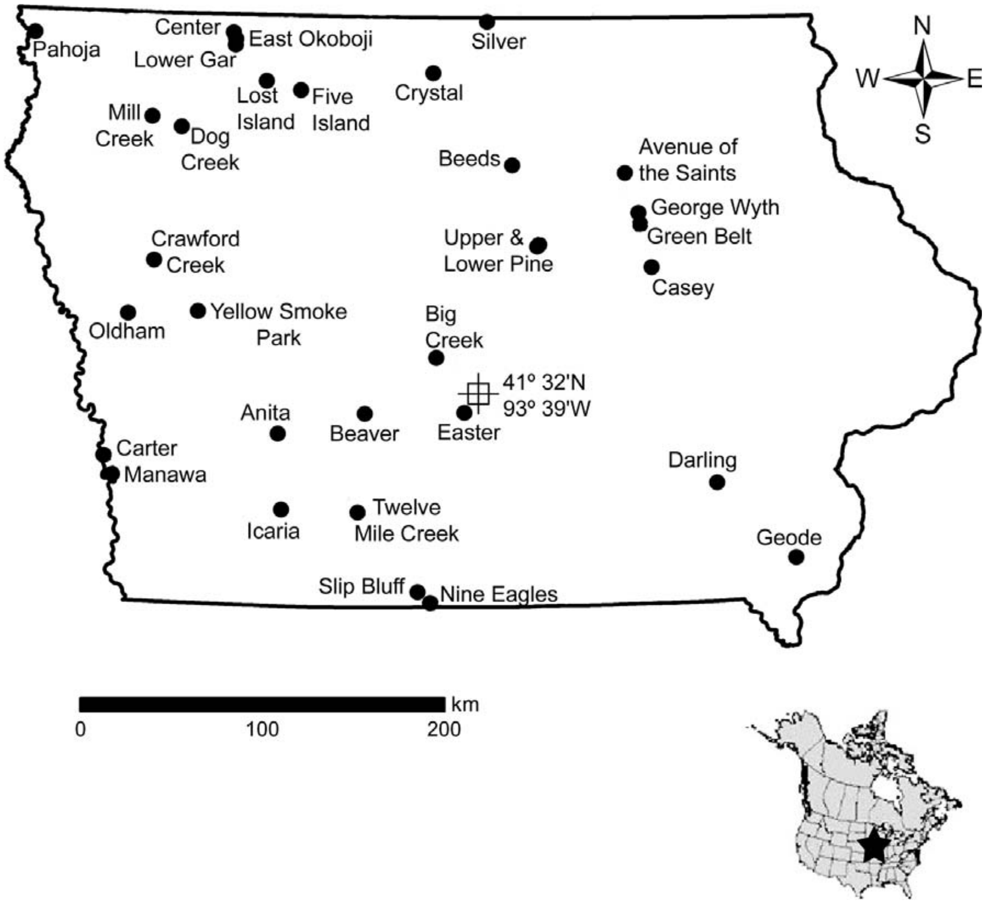
Morphometric variables were collected by Bachmann et al. (1994) and consisted of lake type, lake surface area, mean depth, watershed to lake area ratio, shoreline development index (using equations from Hutchinson 1957), and water residence time.

Fish CPUE estimates were collected by the Iowa Department of Natural Resources between September and October of 2001. Collection methods were standardized to allow comparisons of fish CPUE among lakes. Fyke nets with 12.2-m lead lines and constructed of 0.6 m × 1.2 m frames with seven 0.6-m-diameter hoops enclosed with 1.9-cm bar mesh netting were used to collect fish. These nets were placed randomly within the littoral zone where water measured up to 1.2 m. Nets were set for 24 h before collection and the amount of effort (net nights) varied with lake area and other factors. Three to 15 nets were set per night in lakes <40 ha, 5 to 20 nets were set per night in lakes ranging from 40 to 200 ha, and 7 to 28 nets were set per night in lakes >200 ha. The number of nets set per night in each lake was determined from past experience by local fisheries managers as the number required to obtain a reliable estimate of community composition. Because these lakes are very shallow (average mean depth 2.9 m), fyke nets set at approximately half this depth were assumed to obtain a good representation of fish species found in these lakes.

Fish of stock length (>8 cm for most species) or greater were retained because this is the approximate length that fish reach when mature and the length required for fish to be effectively sampled by gear (Murphy and Willis 1996). Length was measured to the nearest 2 mm, while weight was measured to the nearest 0.5 g. CPUE was determined as an estimate of fish abundance (Murphy and Willis 1996). From CPUE data and fish weights, we estimated fish catch in grams per net per night ($\mathrm{CPUE_w}$).

Fish data were analyzed by individual species $\mathrm{CPUE_w}$, total $\mathrm{CPUE_w}$, and $\mathrm{CPUE_w}$ of species grouped by functional categories, i.e., benthivores and sport fish (primarily piscivores). Total $\mathrm{CPUE_w}$ consisted of the summed $\mathrm{CPUE_w}$ of all species: black crappie (*Pomoxis nigromaculatus*), white crappie (*Pomoxis annularis*), bluegill (*Lepomis macrochirus*), chan-

Fig. 1. Location of 32 lakes sampled throughout the state of Iowa, USA. The star on the map of the United States and Canada indicates the position of the state of Iowa on the continent.



nel catfish (*Ictalurus punctatus*), black bullhead (*Ameiurus melas*), common carp, largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), yellow bass (*Morone mississippiensis*), northern pike (*Esox lucius*), walleye (*Stizostedion vitreum*), yellow perch (*Perca flavescens*), green sunfish (*Lepomis cyanellus*), redear sunfish (*Lepomis microlophus*), freshwater drum (*Aplodinotus grunniens*), and yellow bullhead (*Ameiurus natalis*). Only trends in the first six species were analyzed individually because they were most abundant in these lakes (Harlan et al. 1987), constituted the majority of the fish CPUE$_w$, and could therefore be estimated with confidence. The species caught more sporadically, precluding systematic analysis of trends in catch, were freshwater drum, northern pike, yellow bullhead, green sunfish, redear sunfish, largemouth bass, smallmouth bass, yellow bass, yellow perch, and walleye. These species constituted <13% of the total CPUE$_w$ in most lakes. The sport fish group included black crappie, white crappie, bluegill, and channel catfish. These four species were grouped together because they are important sport fish (Harlan et al. 1987), they are primarily piscivores, and they are not commonly thought to degrade water quality. The benthivore category consisted of common carp and black bullhead. These fish are benthivorous (Harlan et al. 1987) and have been known to degrade water quality through rooting in sediments for food (Keen and Gagliardi 1981; Breukelaar et al. 1994). Although channel catfish are also benthivorous fish, they were not included in this category because they primarily eat fish (Pflieger et al. 1975), they do not root in the sediments for invertebrates, and they are not commonly categorized as a habitat-degrading species.

Because both natural and impounded lakes were combined in the data set, we used bivariate regression analysis to determine whether water quality, morphometric variables, and CPUE$_w$ varied systematically between natural and impounded lakes. Differences in CPUE$_w$ that were found between natural lakes and impoundments were principally attributable to differences in lake morphometry and nutrients. This allowed us to combine both types of lakes and perform bivariate regression analysis between all water quality and morphometric variables and fish CPUE$_w$. The two lake types are distinguished by different symbols in graphical analysis and residuals were examined for homoscedasticity with respect to independent variables and outliers (Gujarati 1995).

Correlation, regression, and variable deletion

Correlations among CPUE$_w$ and independent variables were determined as simple Pearson correlation coefficients (Gujarati 1995). Although correlation analyses were performed using several measures of environmental characteristics, we report the calculated p values without altering them in consideration of multiple comparisons (e.g., Bonferroni correction). There is considerable debate in the statistical literature concerning the necessity or meaning of these corrections in exploratory studies such as this (e.g., Perneger 1998; Moran 2003); thus, we follow the advice of Bender and Lange (1999) in labeling our results as exploratory. We also attempted to limit the number of independent variables to those that might logically be expected to influence fish abundance.

Trends in CPUE_w were characterized using ordinary least squares regression analysis. We used ordinary least squares rather than orthogonal or "robust" regression (sensu Draper and Smith 1998), because variances in fyke net estimates of fish catch are very high compared with the variances in independent variables considered here. Results of ordinary least squares and orthogonal regression converge when ratios of variance in dependent to independent variables are large.

Our study lakes are distributed across the landscape, so there is the potential for spatial autocorrelation or spatial patterns altering the interpretation of statistical analyses (Legendre et al. 2002). We did not employ special spatial statistics in this study because spatial variograms indicated no significant spatial structure in the CPUE_w estimates. Indeed, some lakes with the highest CPUE_w were near lakes with very low CPUE_w.

Because the list of independent variables suggested to effect fish yield is extensive, the number of variables was decreased to minimize the number of potential comparisons and seriousness of multicollinearity. A correlation matrix (see Appendix A) was examined to discard variables that were highly correlated ($r > 0.70$) (Gujarati 1995). Water residence time was removed because it was correlated with watershed to lake area ratio ($r = 0.89$), and Secchi transparency and ammonia (as the sum of un-ionized ammonia and ammonium) were both removed because of close correlations with total suspended solids ($r = 0.84$ and 0.75, respectively). As a result, we reduced our number of independent variables from 16 to 13.

All variables were $\log_{10}$ transformed to stabilize the variances, linearize the responses, and normalize the residuals (Draper and Smith 1998). CPUE_w data were $\log_{10}(x + 1)$ transformed to allow zeros to be included in regressions. Using JMP 5.0® (SAS Institute Inc., Cary, North Carolina), bivariate and multiple regression (using stepwise selection) analyses were performed between individual species CPUE_w, total CPUE_w, and CPUE_w of fish categories (i.e., sport fish, benthivores) and all remaining independent variables.

Species composition

To examine changes in fish composition with eutrophication, we performed simple regression analyses between the CPUE_w of individual species, sport fish, and benthivorous categories and chlorophyll *a*. Chlorophyll *a* was used as an overall measurement of eutrophication because it has been shown to be positively correlated with nutrient concentration (e.g., Jones and Bachmann 1976) and photosynthetic production (e.g., Smith 1979) and provides an index of lake trophic state (e.g., Carlson 1977).

We determined the relative importance of individual species, sport fish, and benthivores in the fish community by examining the relationship between the fraction of total CPUE_w for each and chlorophyll *a* concentration. The percentages were arcsine transformed using $\sin^{-1}(\sqrt{x})$ (where x is the percent composition of fish CPUE_w) to prevent the data from being skewed toward 0% or 100% (Quinn and Keough 2002).

Carp influences on catch of other species

Because the fisheries literature suggests that carp can have deleterious effects on other fish species (Taylor et al. 1984; Harlan et al. 1987), bivariate and multiple regression analyses were performed to compare the CPUE_w of individual fish and sport fish with carp CPUE_w in all lakes and in lakes containing carp.

Results

Lakes surveyed were in the most fertile range of nutrients worldwide (e.g., Downing and McCauley 1992). Most independent variables spanned a range of more than an order of magnitude (chlorophyll *a*, un-ionized ammonia, total nitrogen, total phosphorus, total suspended solids, and watershed to lake area ratio) and lake surface area ranged over two orders of magnitude (Appendix B). Because lake mean depth averaged 2.9 m and total phosphorus ranged from 27 to 300 $\mu\mathrm{g}\cdot\mathrm{L}^{-1}$, these lakes can be classified as shallow, nutrient-rich lakes.

Predictors of fish CPUE_w

The ranges of CPUE_w for all fish and fish categories are given in Appendix C. As others have found, our study revealed a significant, positive correlation between fish catch and lake trophic status as measured by chlorophyll *a* (Fig. 2). Chlorophyll *a* was a strong correlate ($p < 0.01$) of total fish CPUE_w in bivariate analyses ($r = 0.45$) (Table 1). Other independent variables correlating with the CPUE_w of the six major fish species included lake surface area and mean depth ($r = 0.50$ and –0.37, respectively) (Table 1). There were no multivariate relationships of total CPUE_w and environmental characteristics that accounted for significantly more variation than the bivariate regressions.

The best correlates of individual species and fish group CPUE_w varied with a diversity of lake characteristics. Bluegill CPUE_w tended to be highest in small lakes, while the largest CPUE_w of carp was found in large lakes ($r = -0.39$ and 0.53, respectively). Black bullhead and the benthivore group both yielded higher CPUE_w in shallow lakes ($r = -0.40$ and –0.58, respectively). Black crappie and channel catfish CPUE_w increased and decreased, respectively, with specific conductivity ($r = 0.40$ and –0.39, respectively), while the CPUE_w of white crappie increased with total suspended solids ($r = 0.37$) and the sport fish group CPUE_w decreased with dissolved oxygen ($r = -0.37$) (Table 2).

Stepwise analyses to determine the best predictors of CPUE_w for each fish species and fish category yielded results similar to those found in bivariate analyses for black crappie, white crappie, and channel catfish, while the best predictor for black bullhead switched from mean depth to specific conductivity ($r = 0.37$) (Table 2). Carp and benthivore CPUE_w were the only fish for which the stepwise analyses yielded significant multiple regressions. Carp CPUE_w was highest in large, shallow, highly conductive lakes, while benthivore CPUE_w was highest in large, shallow lakes with high chlorophyll *a* concentrations (Table 3).

Fig. 2. Relationship between total fish catch per unit effort by weight ($CPUE_w$) ($g \cdot net^{-1} \cdot night^{-1}$) and chlorophyll *a* ($\mu g \cdot L^{-1}$) ($r = 0.45$, $p < 0.01$). "Total" means the summed catch of all species caught in fyke nets. Solid circles, impounded lakes; open circles, natural lakes.

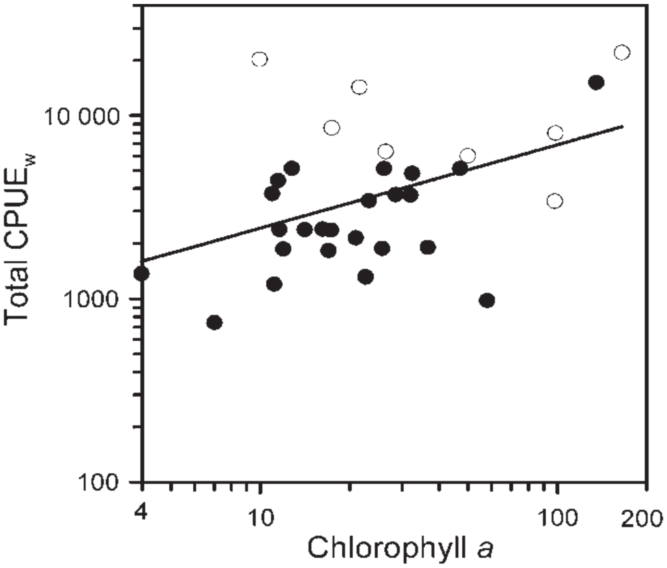


Table 1. Regression equations of variables correlated with the log_{10} of total fish catch per unit effort by weight ($CPUE_w$) ($g \cdot net^{-1} \cdot night^{-1}$).

Bivariate regression	*n*	*r*	*p*
2.93 + 0.31 (log_{10} SA)	32	0.50	0.003
2.93 + 0.46 (log_{10} Chl *a*)	32	0.45	0.009
3.89 – 0.78 ($log_{10}\bar{Z}$)	30	–0.37	0.043

Note: SA, lake surface area (ha); Chl *a*, chlorophyll *a* concentration ($\mu g \cdot L^{-1}$); $\bar{Z}$, mean depth (m).

Variables related to a gradient of eutrophication were seldom correlated with fish $CPUE_w$. In fact, carp, white crappie, and benthivores were the only fish groups that responded positively to indices of lake trophic status. Chlorophyll *a* and total nitrogen were positively correlated with carp $CPUE_w$, while total suspended solids correlated positively with the $CPUE_w$ of white crappie (r = 0.38, 0.35, and 0.37, respectively) (Table 2). Carp were also partially responsible for the positive correlation between total phosphorus and benthivorous fish ($r = 0.40$) because carp made up an average 70% of the $CPUE_w$ for this group.

Species composition

Benthivore and carp $CPUE_w$ increased significantly across a gradient of chlorophyll *a* ($p < 0.001$ and 0.03, respectively) (Fig. 3), while no other species or groups of fish were significantly related to lake trophic status. These results changed when we examined the relative importance of individual species and functional categories, expressed as a percentage of total $CPUE_w$ across a chlorophyll *a* gradient. Benthivore $CPUE_w$, expressed as a fraction of the total $CPUE_w$ increased significantly with chlorophyll *a*, while percent bluegill and sport fish $CPUE_w$ decreased significantly ($p < 0.05$, 0.01, and 0.03, respectively) (Fig. 4).

Carp influences on catch of other species

Because carp $CPUE_w$ became dominant as total fish $CPUE_w$ increased (Fig. 5), there may be a possibility that carp can have deleterious impacts on other fish species. Bivariate analyses revealed a significant increase in white crappie $CPUE_w$ and a significant decrease in bluegill $CPUE_w$ with carp $CPUE_w$ ($p < 0.03$ and 0.05, respectively) (Fig. 6). Stepwise selection analyses indicated that carp $CPUE_w$ was not a strong predictor of any individual fish $CPUE_w$.

Because deleterious effects of carp would be expected to be most apparent at high carp standing stock, we also analyzed the relationships between carp and other species in the lakes containing carp. Results of regression analyses from lakes with carp indicated that only black crappie decreased significantly ($p < 0.03$) (Fig. 6). Further, stepwise selection analyses found that carp explained a significant additional amount of variance in only the $CPUE_w$ of black crappie ($R^2 = 0.59$, $p > 0.005$) (Table 3).

Discussion

Overall, our study showed that total fish $CPUE_w$ increased with lake trophic status, but with weaker correlations and with fewer trophic status variables showing significant trends than other studies. Chlorophyll *a* was the water quality variable that was best correlated with the total $CPUE_w$ ($r = 0.45$). This result is similar to the results of Oglesby (1977), Bays and Crisman (1983), and Bachmann et al. (1996). They have found total fish catch to increase systematically with chlorophyll *a* (r = 0.92, 0.67, and 0.52, respectively) in lakes with cholorophyll *a* ranges similar to ours (1 to >130 $\mu g \cdot L^{-1}$). Increased fish catch with chlorophyll *a* is expected because algal primary production fuels the base of the trophic pyramid in these nearly macrophyte-free lakes. This production can benefit all trophic levels above it, including fish. Surprisingly, other variables related to lake trophic status, such as total phosphorus and total nitrogen, were not correlated with total fish $CPUE_w$. This result differs from those of Hanson and Leggett (1982), Downing et al. (1990), and Bachmann et al. (1996), who found that these variables were positively correlated with fish catch, biomass, or production.

The weak correlation with chlorophyll *a* and lack of correlations with nutrient concentrations may result from several factors. The most likely explanation is due to decoupling of high concentrations of the nutrients nitrogen and phosphorus from production in these lakes receiving high inputs from agricultural land. Because nutrients are so abundant, nitrogen and phosphorus may no longer be primary production limiting resources (Arbuckle and Downing 2001). Instead, suspended solids may lead to light limitation in some lakes, while nutrients may limit phytoplankton in others. Studies of both algal biomass (Watson et al. 1992) and fish catch (Jeppesen et al. 1997) have suggested production approaching an asymptote in nutrient-rich systems. In place of nitrogen and phosphorus as the limiting resources in these lakes, other variables such as lake surface area and mean depth could become stronger correlates of total fish $CPUE_w$. This

Table 2. Significant correlation coefficients (r) between independent variables and catch per unit effort by weight ($\mathrm{CPUE_w}$) ($\mathrm{g \cdot net^{-1} \cdot night^{-1}}$) of individual and grouped fish species.

	BLG	BLC	WHC	CARP	BBHD	CCF	SPORT	BENTH
LType	–0.44			+0.51	+0.68		–0.42	+0.61
$\bar{Z}$				–0.46	–0.40			–0.58
SA	–0.39			+0.53				+0.47
Cond		+0.40		+0.48	+0.37	–0.39		+0.37
DO							–0.37	
Chl *a*				+0.39				+0.57
TN				+0.35				
TP								+0.40
TSS			+0.37					

Note: LType, lake type; $\bar{Z}$, mean depth (m); SA, lake surface area (ha); Cond, specific conductivity ($\mathrm{mS \cdot cm^{-1}}$); DO, dissolved oxygen concentration ($\mathrm{mg \cdot L^{-1}}$); Chl *a*, chlorophyll *a* concentration ($\mathrm{\mu g \cdot L^{-1}}$); TN, total nitrogen concentration ($\mathrm{mg \cdot L^{-1}}$ as N); TP, total phosphorus concentration ($\mathrm{\mu g \cdot L^{-1}}$ as P); TSS, total suspended solids concentration ($\mathrm{mg \cdot L^{-1}}$); BLG, bluegill; BLC, black crappie; WHC, white crappie; CARP, common carp; BBHD, black bullhead; CCF, channel catfish; SPORT, sport fish group: summed $\mathrm{CPUE_w}$ of BLG, BLC, WHC, and CCF; BENTH, benthivore group: summed $\mathrm{CPUE_w}$ of CARP and BBHD. The slope of the regression line is indicated as "+" for positive and "–" for negative. Only significant correlations ($p < 0.05$) are listed. Independent variables showing no correlation with fish $\mathrm{CPUE_w}$ were temperature, un-ionized ammonia, arcsine-transformed percent algal biomass made up of Cyanobacteria, watershed to lake area ratio, and shoreline development index (Murphy and Willis 1996).

Table 3. Regression models showing the best predictors for species-specific and species group catch per unit effort by weight ($\mathrm{CPUE_w}$) ($\mathrm{g \cdot net^{-1} \cdot night^{-1}}$) and regression models obtained when common carp $\mathrm{CPUE_w}$ was added to the list of independent variables in lakes with high carp $\mathrm{CPUE_w}$ (>180 $\mathrm{g \cdot net^{-1} \cdot night^{-1}}$).

Multiple regression	n	R^2	p
CARP = 2.75 + 3.76(Cond) – 3.08($\bar{Z}$) + 1.15(SA)	30	0.54	<0.001
BENTH = 2.89 + 3.17(Cond) – 2.48($\bar{Z}$) + 1.47(Chl *a*)	30	0.61	<0.0001
CARP included as independent variable: BLC = 9.01 – 1.86(TP) – 0.86(CARP)	15	0.59	<0.005

Note: Stepwise selection of independent variables was used to obtain the models. Cond, specific conductivity ($\mathrm{mS \cdot cm^{-1}}$); $\bar{Z}$, mean depth (m); SA, lake surface area (ha); Chl *a*, chlorophyll *a* concentration ($\mathrm{\mu g \cdot L^{-1}}$); TP, total phosphorus concentration ($\mathrm{\mu g \cdot L^{-1}}$ as P); CARP, common carp; BLC, black crappie. BENTH, benthivore group: summed $\mathrm{CPUE_w}$ of BBHD (black bullhead) and CARP. Only statistically significant multiple regressions ($p < 0.05$) are shown.

implies that although we see an increase in total fish $\mathrm{CPUE_w}$ with lake trophic status as measured by chlorophyll *a*, increases in fish $\mathrm{CPUE_w}$ may not be as simple as others have found. This may be especially true in agriculturally enriched hypereutrophic lakes where production may be limited by suspended solids, nitrogen, or phosphorus, depending on the configuration of the lake and its watershed.

Other potential reasons for lack of correlations between total fish $\mathrm{CPUE_w}$ and nutrients could be due to the near lack of macrophytes in these lakes or to low statistical power resulting from well-known high within-lake error in estimation of fish catch. Macrophytes add complexity to the lake ecosystem and allow multiple pathways for nutrients to increase habitat and food for fish (Scheffer 1998). Spatial distributions of fish or errors introduced during collection can increase variability of catch data (Murphy and Willis 1996) and cause low statistical power (Draper and Smith 1998) for the detection of statistical trends.

Correlations of total fish $\mathrm{CPUE_w}$ with other variables considered to be important to fish were infrequent. Water quality and morphometric variables such as water temperature, dissolved oxygen concentration, Cyanobacteria, un-ionized ammonia, and the shoreline development index may influence fish (Alabaster and Lloyd 1982; Guy and Willis 1995; Paerl et al. 2001), but we did not observe significant correlations between total fish $\mathrm{CPUE_w}$ and these variables. This is likely due to shifts in the fish community toward species tolerant of poor water quality as ecosystems became enriched.

Taxon-specific $\mathrm{CPUE_w}$ and community composition

The only fish that appeared to capture increased energy from increased lake trophic status were carp and the benthivore group. The $\mathrm{CPUE_w}$ of carp and benthivores (consisting of an average of 70% carp) were both strongly correlated with chlorophyll *a*. Carp $\mathrm{CPUE_w}$ was also correlated with total nitrogen, while benthivore group $\mathrm{CPUE_w}$ was correlated with total phosphorus. White crappie catch may also increase somewhat with lake trophic status, as indicated by the increase in $\mathrm{CPUE_w}$ with total suspended solids. These results suggest that only a few taxa respond positively to eutrophication in these lakes and that catches of species that are more economically and socially desirable (i.e., bluegill, black crappie, and channel catfish) do not increase with hypereutrophication.

As eutrophication, measured by chlorophyll *a*, increased in these lakes, a systematic shift in fish species composition from the desirable sport fish (primarily piscivores) to less desirable benthivores occurred. The $\mathrm{CPUE_w}$ of carp and other benthivores increased systematically across a chlorophyll *a* gradient, while sport fish $\mathrm{CPUE_w}$ showed lit-

Fig. 3. Variation in community composition (estimated from catch per unit effort by weight ($CPUE_w$) ($g \cdot net^{-1} \cdot night^{-1}$)) with increasing lake trophic status estimated from chlorophyll *a* ($\mu g \cdot L^{-1}$). Solid lines indicate significant regression slopes ($p < 0.05$), while broken lines indicate nonsignificant relationships ($p > 0.05$). BLC, black crappie; BLG, bluegill; WHC, white crappie; CCF, channel catfish; CARP, common carp; BBHD, black bullhead; SPORT, sport fish group (i.e., sum of BLC, WHC, BLG, and CCF); BENTH, benthivore group (i.e., sum of BBHD and CARP); Total, total fish (i.e., the summed catch of the all species caught by fyke nets in these lakes). Individual data points are not shown to avoid confusion.

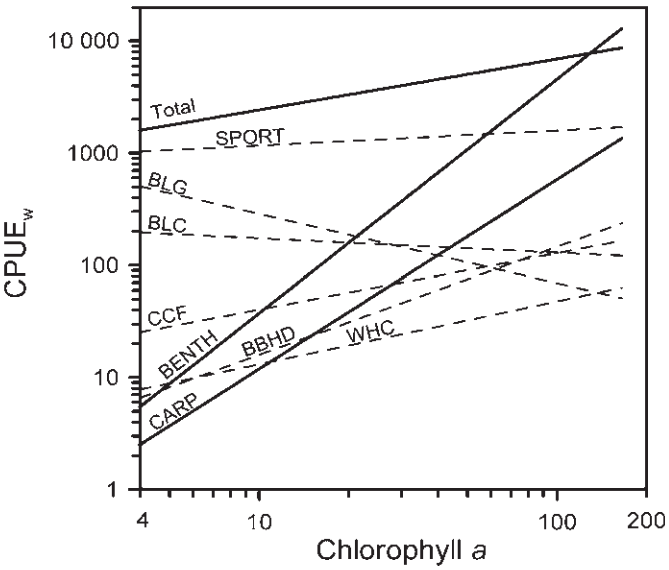


Fig. 4. Variation in relative importance (arcsine-transformed fraction of total fish catch per unit effort by weight ($CPUE_w$) ($g \cdot net^{-1} \cdot night^{-1}$)) of bluegill (BLG), sport fish (SPORT), and benthivores (BENTH) plotted against chlorophyll *a* ($\mu g \cdot L^{-1}$) ($p < 0.002$, 0.03, and 0.01, respectively). The units on the right *y* axis represent approximate percentages of fish $CPUE_w$ when the units on the left *y* axis are untransformed. Individual data points were not shown to avoid confusion.

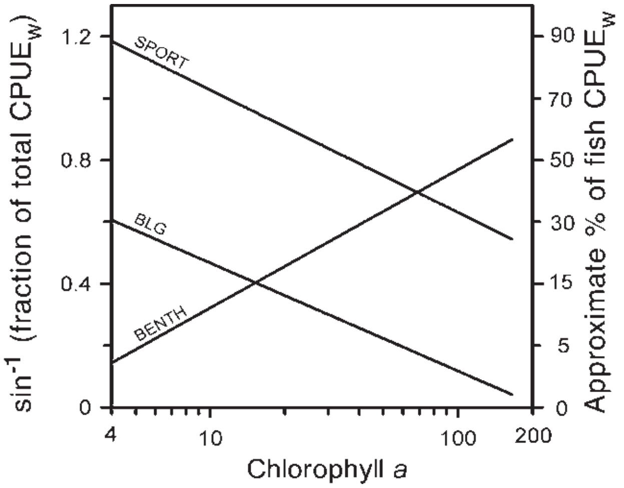
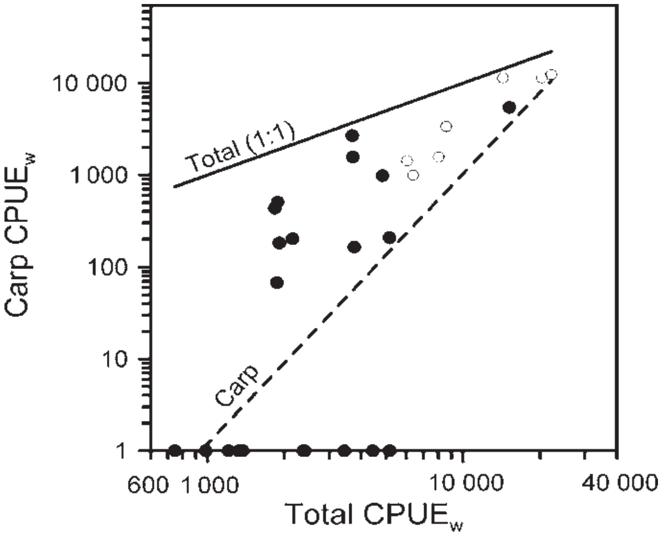


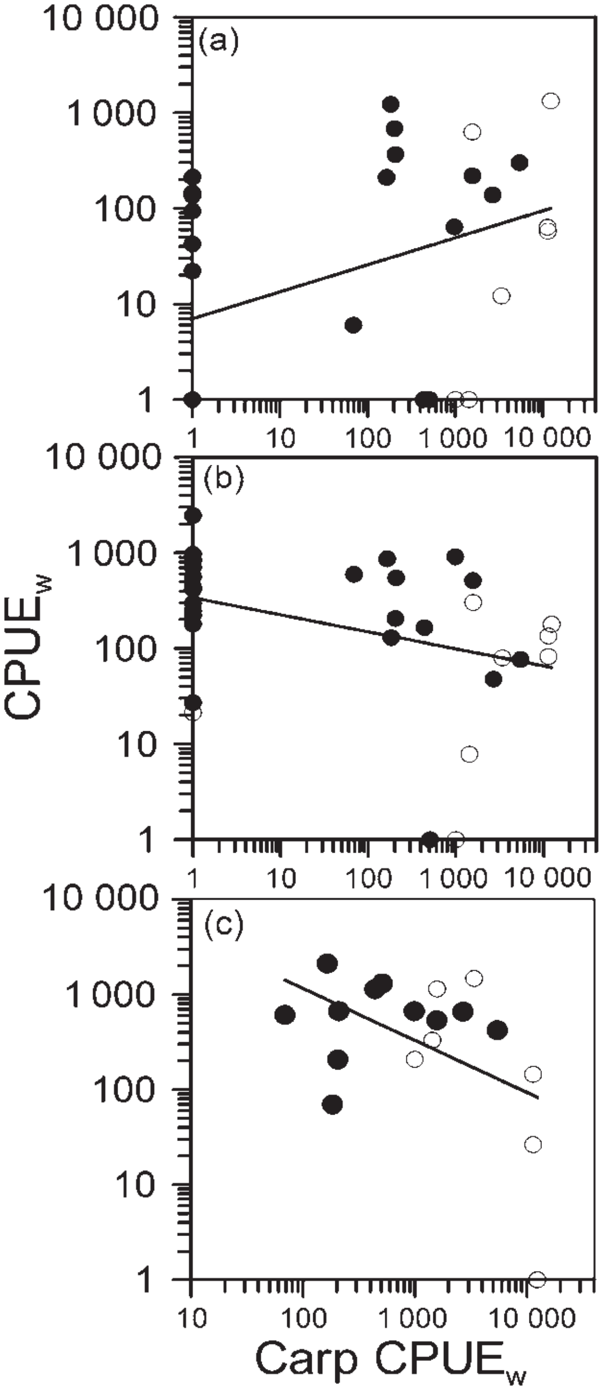
Fig. 5. Relationship between common carp and total fish catch per unit effort by weight ($CPUE_w$) ($g \cdot net^{-1} \cdot night^{-1}$) showing carp dominating total fish $CPUE_w$ at high biomass. The solid line indicates a 1:1 relationship of total fish $CPUE_w$, while the broken line represents an ordinary least squares regression of the relationship between total fish and carp $CPUE_w$. Solid circles, impounded lakes; open circles, natural lakes.



tle systematic change. Carp and benthivore $CPUE_w$ increased by approximately 100% over a chlorophyll *a* range of 10–100 $\mu g \cdot L^{-1}$. The relative importance (fraction of total $CPUE_w$) of species also showed that benthivore $CPUE_w$ increased by 80% over a range of chlorophyll *a* of 10–100 $\mu g \cdot L^{-1}$. However, the sport fish and bluegill fraction of total biomass decreased by approximately 50% and 80%, respectively, across the same range of chlorophyll *a*. Such a shift from sport fish (primarily piscivores) to benthivores agrees with Persson et al. (1991) who found that benthivores (roach and bream) replaced piscivores and eventually dominated ecosystems over a similar chlorophyll *a* gradient in Europe.

Jones and Hoyer's (1982) results differed from ours in that they found that the yield of sport fish increased systematically across a similar chlorophyll *a* gradient ($r = 0.91$). Our yields of sport fish did not increase systematically with chlorophyll *a*. Detailed analysis of our data indicated that Silver Lake was a strong outlier that was very high in chlorophyll *a* (100 $\mu g \cdot L^{-1}$) but yielded few fish other than black bullhead. If we categorize black bullhead as a sport fish, as done by Jones and Hoyer (1982), we also see a positive correlation with chlorophyll *a* ($r = 0.41$, $p < 0.02$). This regression may reveal a species shift from piscivores to benthivores, however, more than an increase in sport fish with increased lake trophic status. Silver Lake has an extremely high concentration of un-ionized ammonia (415 $\mu g \cdot L^{-1}$), which can be toxic to intolerant fish such as piscivores at concentrations >200 $\mu g \cdot L^{-1}$ (Alabaster and Lloyd 1982). Because black bullheads are more tolerant than piscivores of decreases in water quality, they appear to replace piscivores and make up the entire catch in this lake. Because Jones and Hoyer (1982) did not indicate the fish species yields along the entire trophic gradient, their regres-

Fig. 6. Relationship between common carp catch per unit effort by weight ($\mathrm{CPUE_w}$) ($\mathrm{g \cdot net^{-1} \cdot night^{-1}}$) and the $\mathrm{CPUE_w}$ of (*a*) white crappie ($r = 0.40$, $p < 0.03$), (*b*) bluegill ($r = -0.36$, $p < 0.05$), and (*c*) black crappie ($r = -0.49$, $p < 0.03$). White crappie and bluegill figures represent a regression using all lakes, while that of black crappie represents a regression from lakes with carp. Solid circles, impounded lakes; open circles, natural lakes. Note the scale change between bluegill and black crappie figures.



sion may not suggest that the most desirable fish will offer high yields in the most eutrophic lakes. Our data indicate that the only species benefiting substantially from increases in lake trophic status are the benthivores.

There are many possible reasons for this shift from sport fish to benthivores in eutrophic lakes. Sport fish (primarily picivores) depend on clear water because they are principally visual feeders (Bruton 1985). Young-of-the-year piscivores typically rely on zooplankton as a food source, but because large zooplankton are often rare in turbid eutrophic lakes (Jeppesen et al. 2000), food shortages may limit piscivore growth and recruitment. Benthivores, especially carp, are not limited by turbid water because they are tolerant of great levels of turbidity (>200 $\mathrm{g \cdot L^{-1}}$; Alabaster and Lloyd 1982). They also may not encounter food shortages because zoobenthos may be less impacted than zooplankton under hypereutrophic conditions (Scheffer 1998). Some sport fish depend on aquatic macrophytes for habitat (Grimm and Backx 1990), whereas macrophytes often decrease with increased eutrophication (Egertson et al. 2004) and carp abundance (Crivelli 1983). Hypereutrophic ecosystems may therefore represent very poor habitat for sport fish.

Carp influences on other species

Carp $\mathrm{CPUE_w}$ was strongly correlated with $\mathrm{CPUE_w}$ of white crappie and bluegill when analyzed across all lakes and with black crappie $\mathrm{CPUE_w}$ when considering only lakes with carp. This may indicate some antagonism between these species or potential competitive exclusion. The positive correlation between white crappie $\mathrm{CPUE_w}$ and carp $\mathrm{CPUE_w}$ may result from white crappies' good adaptation to turbid, shallow waters (Carlander 1977). On the other hand, bluegills and black crappies, some of the most important sport fishes in the highly eutrophic lakes of the Midwest USA (Harlan et al. 1987), are both intolerant of continuous high turbidity and siltation and grow best in clear water (Pflieger 1975; Harlan et al. 1987).

Although the relationship found between bluegill, black crappie, and carp $\mathrm{CPUE_w}$ could simply be chance correlations owing to contrasting habitat requirements, carp may directly impact these fish by interfering with reproduction and growth. Both bluegill and black crappie build nests in shallow waters (<0.5–2 m; Harlan et al. 1987) where carp are typically found (Pflieger 1975). Nests may therefore be in jeopardy of disruption by the benthos-feeding carp. Because white crappie can spawn in deeper waters (1–3 m; Harlan et al. 1987), their nests may be able to escape this disturbance. Carp may also impact bluegill and black crappie by decreasing habitat through uprooting macrophytes (Crivelli 1983), by outcompeting young-of-the-year fish by decreasing zooplankton and aquatic insects (Tatrai et al. 1994; Lougheed et al. 1998), and by resuspending sediment (Breukelaar et al. 1994), limiting the ability of bluegill and black crappie to see prey. It is therefore plausible that carp may experience differential success in hypereutrophic ecosystems not only because of their resistance to poor water quality conditions but also because they may competitively exclude other species.

In conclusion, counter to the results of other studies, we found that benthivorous fish were the principal beneficiaries of increased eutrophication in these agriculturally enriched lakes. Benthivorous carp become so dominant that their responses to lake conditions determine the trends of total fish $\mathrm{CPUE_w}$. Our study indicates that, with the tremendous increase in eutrophication and carp abundance, species other than benthivores seem unable to exploit the increased energy available in hypereutrophic systems. Thus, fisheries responses to hypereutrophication are characterized by the shunting of resources to benthivorous fish, with little net gain in biomass for sport fish (primarily piscivores), in these very fertile lakes.

Acknowledgments

We thank Joe Larschied, Larry Mitzner, Jim Wahl, Jim Christianson, Don Klein, Mike McGhee, Brian Hayes, Jerry Hudson, Lannie Miller, and Dick McWilliams for collecting the fish data. We also thank Joy Ramstack, Rebecca Anthony, Nicole Eckles, Kristian Haapa-aho, Kendra Lee, and the many people on the lakes survey crews that helped with water quality data collection and analysis. The Iowa Department of Natural Resources funded this project. We are also grateful to Clay Pierce and Richard Schultz for their comments and suggestions.

References

Alabaster, J.S., and Lloyd, R. 1982. Water quality criteria for freshwater fish. 2nd ed. Cambridge University Press, Cambridge, UK.

American Public Health Association, American Water Works Association, and Water Environmental Federation. 1998. Standard methods for the examination of water and wastewater. 20th ed. American Public Health Association, Washington, D.C.

Andersson, G., Berggren, H., Crondberg, G., and Gelin, C. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemisty in eutrophic lakes. Hydrobiologia, **59**: 9–15.

Arbuckle, K., and Downing, J.A. 2001. The influence of watershed land use on lake N:P in a predominantly agricultural landscape. Limnol. Oceanogr. **464**: 970–975.

Bachmann, R.W., Hoyman, T., Hatch, L., and Hutchins, B. 1994. A classification of Iowa's lakes for restoration. A final report. Iowa Department of Natural Resources, Des Moines, Iowa.

Bachmann, R.W., Jones, B.L., Fox, D.D., Hoyer, M., Bull, L.A., and Canfield, D.E., Jr. 1996. Relations between trophic state indicators and fish in Florida (U.S.A.) lakes. Can. J. Fish. Aquat. Sci. **53**: 842–855.

Bays, J.S., and Crisman, T.L. 1983. Zooplankton and trophic state relationships in Florida lakes. Can. J. Fish. Aquat. Sci. **40**: 1813–1819.

Bender, R., and Lange, S. 1999. Multiple test procedures other than Bonferroni's deserve wider use. Br. Med. J. **318**: 600.

Breukelaar, A.W., Lammens, E.H.R.R., Klein Breteler, J.G.P., and Tatrai, I. 1994. Effects of benthivorous bream (*Abramis brama*) and carp (*Cyprinus carpio*) on sediment resuspensions and concentrations of nutrients and chlorophyll *a*. Freshw. Biol. **32**: 113–121.

Bruton, N.M. 1985. The effects of suspensoids on fish. Hydrobiologia, **125**: 221–241.

Carlander, K.D. 1977. Handbook of freshwater fishery biology. Iowa State University Press, Ames.

Carlson, R.E. 1977. A trophic state index for lakes. Limnol. Oceanogr. **49**: 155–160.

Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., and Smith, V.H. 1998. Non-point pollution of surface waters with phosphorus and nitrogen. Ecol. Appl. **8**: 559–568.

Crivelli, V.J. 1983. The destruction of aquatic vegetation by carp. Hydrobiologia, **106**: 37–41.

Crumpton, W.G., Isenhart, T.M., and Mitchell, P.D. 1992. Nitrate and organic N analyses with second-derivative spectroscopy. Limnol. Oceanogr. **37**: 907–913.

Downing, J.A., and McCauley, E. 1992. The nitrogen:phosphorus relationship in lakes. Limnol. Oceanogr. **37**: 936–945.

Downing, J.A., Plante, C., and Lalonde, S. 1990. Fish production correlated with primary productivity, not the morphoedaphic index. Can. J. Fish. Aquat. Sci. **47**: 1929–1936.

Downing, J.A., Rabalais, N.N., Diaz, R.J., Zimmerman, R.J., Baker, J.L., and Prato, T. 1999. Gulf of Mexico Hypoxia: land and sea interactions. Council for Agricultural Science and Technology Task Force Report. Council for Agricultural Science and Technology, Ames, Iowa.

Draper, N.R., and Smith, H. 1998. Applied regression analysis. 3rd ed. Wiley, New York.

Egertson, C.J., Kopaska, J.A., and Downing, J.A. 2004. A century of change in macrophyte abundance and composition in response to agricultural eutrophication. Hydrobiologia, **524**: 145–156.

Grimm, M.P., and Backx, J.J.G.M. 1990. The restoration of shallow eutrophic lakes, and the role of northern pike, aquatic vegetation and nutrient concentration. Hydrobiologia, **200/201**: 557–566.

Gujarati, D.N. 1995. Basic econometrics. 3rd ed. McGraw-Hill, New York.

Guy, C., and Willis, D.W. 1995. Population characteristics of black crappies in South Dakota waters: a case for ecosystem-specific management. N. Am. J. Fish. Manag. **15**: 754–765.

Hanson, J.M., and Leggett, W.C. 1982. Emprical predictions of fish biomass and yield. Can. J. Fish. Aquat. Sci. **39**: 257–263.

Harlan, J.R., Speaker, E.B., and Mayhew, J. 1987. Iowa fish and fishing. Iowa Department of Natural Resources, Des Moines, Iowa.

Hutchinson, G.E. 1957. A treatise on limnology. Wiley, New York.

Jeppesen, E., Jensen, J.P., Sondergaard, M., Lauridsen, T., Pedersen, L.J., and Jensen, L. 1997. Top-down control in freshwater lakes: the role of nutrient state, submerged macrophytes and water depth. Hydrobiologia, **342/343**: 151–164.

Jeppesen, E., Jensen, J.P., Sondergaard, M., Lauridsen, T., and Landkildehus, F. 2000. Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. Freshw. Biol. **45**: 201–218.

Jones, J.R., and Bachmann, R.W. 1976. Prediction of phosphorus and chlorophyll levels in lakes. J. Water Pollut. Control Fed. **48**: 2176–2182.

Jones, J.R., and Hoyer, M.V. 1982. Sportfish harvest predicted by summer chlorophyll-*a* concentration in midwestern lakes and reservoirs. Trans. Am. Fish. Soc. **111**: 176–179.

Kautz, R.S. 1980. Effects of eutrophication on the fish communities of Florida lakes. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies, **34**: 67–80.

Keen, W.H., and Gagliardi, J. 1981. Effect of brown bullheads on release of phosphorus in sediment and water systems. Prog. Fish-Cult. **43**: 181–185.

Kirk, K.L. 1991. Inorganic particles alter competition in grazing plankton: the role of selective feeding. Ecology, **72**: 915–923.

Lamarra, V.A., Jr. 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. Verh. Int. Ver. Limnol. **19**: 2461–2468.

Legendre, P., Dale, M.R.T., Fortin, M.-J., Gurevitch, J., Hohn, M., and Myers, D. 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. Ecography, **25**: 601–615.

Lougheed, V.L., Crosbie, B., and Chow-Fraser, P. 1998. Predictions on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes wetland. Can. J. Fish. Aquat. Sci. **55**: 1189–1197.

Meijer, M.L., de Haan, M.W., Breukelaar, A.W., and Buiteveld, H. 1990. Is reduction of the benthivorous fish an important cause of high trasparency following biomanipulation in shallow lakes? Hydrobiologia, **200/201**: 303–315.

Moran, M.D. 2003. Arguments for rejecting the sequential Bonferroni in ecological studies. Oikos, **100**: 403–405.

Murphy, B.R., and Willis, D.W. 1996. Fisheries techniques. 2nd ed. American Fisheries Society, Bethesda, Md.

Oglesby, R.T. 1977. Relationships of fish yield to lake phytoplankton standing crop, production, and morphoedaphic factors. J. Fish. Res. Board Can. **34**: 2271–2279.

Paerl, H.W., Fulton, R.S., and Moisander, P.H. 2001. Harmful freshwater algal blooms, with an emphasis on Cyanobacteria. Sci. World, **1**: 76–113.

Perneger, T.V. 1998. What's wrong with Bonferroni adjustments. Br. Med. J. **316**: 1236–1238.

Persson, L., Diehl, S., Johansson, L., Andersson, G., and Hamrin, S.F. 1988. Predation regulation and primary production along the productivity gradient of temperate lake ecosystems. *In* Complex interactions in lake communities. *Edited by* S.R. Carpenter. Springer, New York. pp. 45–65.

Persson, L., Diehl, S., Johansson, L., and Andersson, G. 1991. Shifts in fish communities along the productivity gradient of temperate lakes: patterns and the importance of size-structured interactions. J. Fish Biol. **38**: 281–294.

Pflieger, W.L. 1975. The fishes of Missouri. Missouri Department of Conservation, Columbus, Mo.

Quinn, G.P., and Keough, M.J. 2002. Experimental design and data analysis for biologists. 1st ed. Cambridge University Press, Cambridge, UK.

Scheffer, M. 1998. Ecology of shallow lakes. Chapman and Hall, London, UK.

Smith, V.H. 1979. Nutrient dependence of primary productivity in lakes. Limnol. Oceanogr. **24**: 1051–1064.

Tatrai, I., Lammens, E.H., Breukelaar, A.W., and Klein Breteler, J.G.P. 1994. The impact of mature cyprinid fish on the composition and biomass of benthic macroinvertebrates. Arch. Hydrobiol. **131**: 309–320.

Taylor, J.N., Courtenay, W.R., Jr., and McCann, J.A. 1984. Known impacts of exotic fishes in the continental United States. *In* Distribution, biology, and management of exotic fishes. *Edited by* W.R. Courtenay, Jr. and J.R. Stauffer, Jr. Johns Hopkins University Press, Baltimore, Md. pp. 322–373.

Ten Winkel, E.H., and Meulemans, J.T. 1984. Effects of fish upon submerged vegetation. Hydrobiol. Bull. **18**: 157–158.

Watson, S., McCauley, E., and Downing, J.A. 1992. Sigmoid relationships between phosphorus, algal biomass, and algal community structure. Can. J. Fish. Aquat. Sci. **49**: 2605–2610.

Yurk, J.J., and Ney, J.J. 1989. Phosphorus – fish community biomass relationships in southern Appalachian reservoirs: can lakes be too clean for fish? Lake Reservoir Manag. **5**: 83–90.

Zieba, J., and Szarowska, M. 1987. Macrobenthos of productive carp ponds with different levels of intensification of second year carp rearing. Acta Hydrobiol. **29**: 465–477.

Appendices appear on the following pages.

Appendix A

Table A1. Correlation matrix of all independent variables.

	°C	Cond	DO	Chl *a*	NH3	TN	TP	TSS	BG	W:L	$\bar{Z}$	SA	SDI	RT	NH4	Secchi
°C	—	–0.20	0.39	0.11	0.63	–0.39	–0.10	0.34	0.10	–0.35	–0.18	0.10	–0.20	0.10	0.34	–0.40
Cond	–0.20	—	0.07	0.12	–0.10	0.22	0.00	–0.15	0.23	0.20	–0.27	0.11	0.00	0.00	–0.25	0.25
DO	0.39	0.10	—	0.14	0.41	–0.28	–0.18	0.04	0.16	–0.27	–0.10	0.12	–0.20	0.22	0.14	–0.14
Chl *a*	0.11	0.12	0.14	—	0.44	0.32	0.55	0.49	0.32	0.00	–0.37	0.44	–0.30	–0.10	0.28	–0.64
NH3	0.63	–0.10	0.41	0.44	—	–0.15	0.31	0.52	0.45	–0.33	–0.30	0.20	–0.30	0.17	0.55	–0.52
TN	–0.40	0.22	–0.28	0.32	–0.20	—	0.50	0.00	–0.10	0.55	0.06	0.16	0.10	–0.50	–0.10	0.00
TP	0.00	0.00	–0.18	0.55	0.31	0.50	—	0.62	0.29	0.20	–0.17	0.30	–0.30	–0.30	0.62	–0.64
TSS	0.34	–0.20	0.04	0.49	0.52	0.00	0.62	—	0.19	–0.24	–0.54	0.33	–0.40	0.00	0.75	–0.84
BG	0.10	0.23	0.16	0.32	0.45	–0.10	0.29	0.19	—	–0.19	–0.12	0.25	–0.30	0.26	0.21	–0.10
W:L	–0.40	0.20	–0.27	0.00	–0.30	0.55	0.20	–0.24	–0.19	—	0.19	–0.30	0.23	–0.90	–0.20	0.18
$\bar{Z}$	–0.20	–0.30	–0.10	–0.37	–0.30	0.06	–0.17	–0.54	–0.12	0.19	—	0.00	0.59	0.10	–0.10	0.44
SA	0.10	0.11	0.12	0.44	0.20	0.16	0.30	0.33	0.25	–0.34	–0.10	—	0.14	0.35	0.24	–0.29
SDI	–0.20	0.00	–0.15	–0.29	–0.30	0.07	–0.27	–0.39	–0.30	0.23	0.59	0.14	—	0.00	–0.13	0.31
RT	0.10	0.00	0.22	–0.12	0.17	–0.48	–0.27	0.01	0.26	–0.89	0.07	0.35	0.00	—	0.12	0.08
NH4	0.34	–0.30	0.14	0.28	0.55	–0.10	0.62	0.75	0.21	–0.20	–0.10	0.24	–0.10	0.12	—	–0.70
Secchi	–0.40	0.25	–0.14	–0.64	–0.50	0.00	–0.64	–0.84	–0.10	0.18	0.44	–0.30	0.31	0.10	–0.70	—

Note: Values are correlation coefficients (*r*) and a dash indicates the correlation of a variable with itself. °C, mean summer temperature; Cond, specific conductivity (mS·cm^{-1}); DO, dissolved oxygen concentration (mg·L^{-1}); Chl *a*, chlorophyll *a* concentration (µg·L^{-1}); NH3, un-ionized ammonia concentration (µg·L^{-1} as N); TN, total nitrogen concentration (mg·L^{-1} as N); TP, total phosphorus concentration (µg·L^{-1} as P); TSS, total suspended solids concentration (mg·L^{-1}); BG, arcsine-transformed percentage of algae biomass made up of Cyanobacteria; W:L, ratio of watershed to lake area; $\bar{Z}$, mean depth (m); SA, lake surface area (ha); SDI, shoreline development index (Murphy and Willis 1996); RT, water residence time (years); NH4, ammonia (as the sum of un-ionized ammonia and ammonium, NH_3 + NH_4); Secchi, Secchi disc transparency (m).

Appendix B

Table B1. Lake characteristics of 32 lakes surveyed during the summer of 2001.

Lake	LType	°C	Cond	DO	Chl *a*	NH3	TN	TP	TSS	BG	W:L	$\bar{Z}$	SA	SDI
Avenue of the Saints Lake	I	23.2	0.2	6.3	47	67	1.8	115.8	17.4	0.8	na	na	12.1	na
Beaver Lake	I	24.6	0.3	7.8	11.6	36.6	1.9	67	5.4	–0.1	29.5	2.9	14.1	2.5
Beeds Lake	I	19.1	0.5	8.2	32.4	7	13.8	164.4	7.2	–1.1	187.2	2.6	41	2.1
Big Creek Lake	I	21.4	0.4	7.1	11.9	16.7	9.3	88.9	5.9	–0.4	55	5.4	357.4	5.1
Carter Lake	N	24.2	0.6	8.3	98.5	49.0	2	181.2	21.4	1.7	36.8	2.5	128	2.7
Casey Lake	I	22.4	0.3	5.9	14.1	85.1	1.9	123.3	6.4	1.2	13.6	3.1	22	2.4
Center Lake	N	22.4	0.6	10.2	50	26.6	2	113.3	6.7	1.7	2.7	2.9	110	2
Crawford Creek	I	22.1	0.5	na	12.8	35.1	1	43	10.7	0.1	38.3	3.4	25	2.3
Crystal Lake	N	23.8	0.3	9	165	89	3.1	300.6	40	0.9	6.8	1.4	108.6	1.2
Dog Creek Lake	I	20.6	0.6	5.3	17.3	30.1	5.2	154.4	11.6	0.7	105.5	3	11	2
East Okoboji Lake	N	21.8	0.5	8.8	9.9	16.9	1.1	59.4	3.9	1.1	6.7	3.2	743	2.8
Easter Lake	I	25.1	0.5	12.4	26.1	209.9	1.3	87.5	13.5	–0.1	51.7	3.3	70	3.6
Five Island Lake	N	22.8	0.4	8.2	17.4	50.9	2.7	59.2	16.5	0	8.9	1.4	384.9	3.3
George Wyth Lake	I	24.7	0.4	6.9	11	31.3	1	27.5	10.1	0.1	12.5	2.7	21	1.6
Green Belt Lake	I	24.9	0.5	7.2	11.5	31	0.7	26.5	5.8	2.1	na	na	8.9	na
Lake Anita	I	23.3	0.2	8.2	58	49.4	1.4	51.1	13	–0.2	na	3.7	74	4.1
Lake Darling	I	24.9	0.2	7.1	20.9	58.9	5.2	252.4	57.2	0.1	40.7	2.7	121	3.4
Lake Geode	I	23.8	0.3	11.5	16.2	67.6	4.4	71	4.2	0.9	52.2	7.2	76.5	3.1
Lake Icaria	I	23.1	0.2	6.2	23.2	32.1	2.8	67	14.9	–0.7	25	3.4	270.9	4.7
Lake Manawa	I	24.3	0.5	10.7	36.6	94.2	1.2	89.5	17.4	0	3.5	1.9	289.1	2.1
Lake Pahoja	I	21.1	0.8	8.8	17	47.8	6.9	87.4	7.4	1.2	62.5	3.2	25.6	2.9
Lower Gar Lake	N	23.8	0.5	9.3	21.5	40.1	1.2	91.3	25.8	0.3	47	1.1	97.9	1.8
Lost Island Lake	N	22.7	0.4	10.7	26.4	64	2.2	110	19.7	0.9	4	3.1	464.3	1.5
Lower Pine Lake	I	24.2	0.3	6.9	32	72	7.8	104	11.9	–1.1	16.9	2	20	1.5
Mill Creek (Lake)	I	22.6	0.5	6.8	25.7	35	2.3	59.9	7.9	0.6	123.3	1.5	12	1.7
Nine Eagles Lake	I	22.6	0.2	8.6	7	16.1	0.6	37.4	6.8	–0.3	19	4.2	25.4	2.3
Oldham Lake	I	21.6	0.4	11.5	22.6	31.9	1.2	57.9	6.8	–0.3	46.5	3	6	3.3
Silver Lake	N	24.3	0.2	13.3	98	414.7	1.6	119.9	33.8	1.3	8.1	1.4	128	1
Slip Bluff Lake	I	21.9	0.2	7.4	4	17.6	0.9	94.2	15.4	–0.6	15.5	3.8	6	2.3
Twelve Mile Creek Lake	I	22.7	0.3	8.1	135.4	30.2	2.6	59.6	7.5	0	21.3	4.6	267.3	3.9
Upper Pine Lake	I	22.4	0.4	9.3	28.5	17.7	11.4	67.9	6.2	0.1	120.1	2.2	28	2.2
Yellow Smoke Park Lake	I	22.5	0.4	6.4	11.1	22.2	1.3	46.7	5.3	–0.7	50.5	3.4	11.7	3.6

Note: All concentrations are the mean summer concentrations from the upper mixed zone. LType, lake type: I indicates an impounded lake, N indicates a natural lake; °C, mean summer temperature; Cond, specific conductivity ($mS \cdot cm^{-1}$); DO, dissolved oxygen concentration ($mg \cdot L^{-1}$); Chl *a*, chlorophyll *a* concentration ($\mu g \cdot L^{-1}$); NH3, un-ionized ammonia concentration ($\mu g \cdot L^{-1}$ as N); TN, total nitrogen concentration ($mg \cdot L^{-1}$ as N); TP, total phosphorus concentration ($\mu g \cdot L^{-1}$ as P); TSS, total suspended solids concentration ($mg \cdot L^{-1}$); BG, arcsine-transformed percentage of algae biomass made up of Cyanobacteria; W:L, ratio of watershed to lake area; $\bar{Z}$, mean depth (m); SA, lake surface area (ha); SDI, shoreline development index (Murphy and Willis 1996); na, missing datum.

Appendix C

Table C1. Catch per unit effort by weight ($CPUE_w$) ($g \cdot net^{-1} \cdot night^{-1}$) from 32 lakes surveyed in the fall of 2001.

Lake	LType	Nets	BBHD	CARP	BLC	WHC	BLG	CCF	SPORT	BENTH	Total
Avenue of the Saints Lake	I	6	62	0	1216	0	701	2987	4904	62	5 150
Beaver Lake	I	8	169	0	282	0	438	1497	2217	169	2 390
Beeds Lake	I	6	1314	980	666	63	912	799	2440	2 294	4 834
Big Creek Lake	I	24	0	68	610	5	594	0	1209	68	1 868
Carter Lake	N	16	743	1 573	1140	631	303	3442	5515	2 315	8 035
Casey Lake	I	6	0	0	696	94	855	671	2315	0	2 392
Center Lake	N	20	4272	1 424	330	0	7	0	337	5 696	6 033
Crawford Creek	I	6	0	0	1442	145	2465	1012	5063	0	5 162
Crystal Lake	N	6	131	12 355	0	1333	178	7699	9210	12 485	22 131
Dog Creek (Lake)	I	10	1567	0	530	0	248	0	778	1 567	2 373
East Okoboji Lake	N	14	7559	11 391	25	57	81	0	163	18 950	20 333
Easter Lake	I	16	57	207	666	367	547	1678	3258	264	5 153
Five Island Lake	N	15	343	3 371	1470	11	79	0	1560	3 714	8 587
George Wyth Lake	I	6	157	164	2111	210	864	227	3412	320	3 755
Green Belt Lake	I	5	0	0	81	0	970	3383	4434	0	4 434
Lake Anita	I	12	77	0	289	21	418	54	782	77	983
Lake Darling	I	12	0	202	206	686	205	83	1180	202	2 149
Lake Geode	I	8	0	0	35	0	296	1152	1482	0	2 400
Lake Icaria	I	9	62	0	0	136	26	1931	2093	62	3 434
Lake Manawa	I	16	0	181	69	1232	129	48	1478	181	1 907
Lake Pahoja	I	18	22	435	1133	0	164	0	1297	457	1 831
Lost Island Lake	N	10	3105	996	207	0	0	0	207	4 101	6 373
Lower Gar Lake	N	10	1255	11 381	144	63	135	0	341	12 636	14 311
Lower Pine Lake	I	6	0	2 683	659	138	47	157	1001	2 683	3 683
Mill Creek (Lake)	I	10	69	506	1307	0	0	0	1307	574	1 881
Nine Eagles Lake	I	9	0	0	4	42	222	186	455	0	746
Oldham Lake	I	5	111	0	588	0	565	0	1153	111	1 323
Silver Lake	N	6	2015	0	0	0	20	0	20	2 015	3 416
Slip Bluff Lake	I	9	0	0	34	212	823	304	1373	0	1 374
Twelve Mile Creek Lake	I	9	0	5 449	419	301	76	7578	8373	5 449	15 173
Upper Pine Lake	I	6	0	1 568	535	219	512	0	1265	1 568	3 705
Yellow Smoke Park Lake	I	6	72	0	0	0	179	882	1061	72	1 208

Note: LType, lake type: I indicates an impounded lake, N indicates a natural lake; Nets, effort in net-nights; BBHD, black bullhead; CARP, common carp; BLC, black crappie; WHC, white crappie; BLG, bluegill; CCF, channel catfish; SPORT, sport fish group: summed $CPUE_w$ of BLC, WHC, BLG, and CCF; BENTH, benthivore group: summed $CPUE_w$ of BBHD and CARP; Total, summed $CPUE_w$ of all species caught.