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ARTICLE

Fish Growth Changes over Time in a Midwestern U.S. Lake

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Abstract
Growth of Walleyes *Sander vitreus*, Yellow Bass *Morone mississippiensis*, Common Carp *Cyprinus carpio*, and Black Bullheads *Ameiurus melas* was assessed in Clear Lake, Iowa, over several decades and in relation to environmental variables. Growth of Common Carp was positively correlated with phytoplankton concentration. Recent Black Bullhead growth was faster than in the 1950s and 1990s, which may be a consequence of their recent decline in abundance. Growth of Common Carp and Yellow Bass was faster in the 1940s than in more recent time periods. Relative to their entire range, Common Carp first-year growth was below average, whereas length at later ages was above average. Walleye relative growth showed a similar pattern. The large changes in growth over several decades suggest that as the Clear Lake ecosystem continues to change, growth rates of its important fish species are also likely to continue changing.

Growth is an important component of fish population dynamics, and knowledge of growth rates and understanding their determinants are essential to fisheries management (Summerfelt and Hall 1987; Weatherly and Gill 1987). Growth in the first year is important in determining eventual recruitment, as growth rate determines body size, which in turn has consequences for survival via size-dependent foraging success and vulnerability to predation (Miller et al. 1988; Chambers and Trippel 1997). Growth can be an indicator of potential management problems (e.g., overfishing, lack of food) and provide feedback on management actions, so understanding what factors influence growth is an important part of successful fishery management (Van Den Avyle and Hayward 1999). Several factors can influence fish growth, including temperature (Kelso 1972; Momot et al. 1977; Pauly 1980; Staggs and Otis 1996), food availability (Welker et al. 1994; DeVries et al. 1998; Bremigan et al. 2003), and competition (Ridenhour 1960; Welker et al. 1994).

Clear Lake is Iowa's third-largest natural lake and is a highly valued natural resource for angling, boating, and other outdoor recreation (Downing et al. 2001). More than 432,000 people visit Clear Lake annually, and economic value for vacation and recreational use exceeds US$43

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million annually (Center for Agriculture and Rural Development 2008). A recreational fishery, primarily for Yellow Bass *Morone mississippiensis* and Walleye *Sander vitreus*, is valued at \$1–2.5 million annually (Iowa Department of Natural Resources, unpublished data). In the past 60 years, Clear Lake has experienced increases in suspended sediment, nutrients, and phytoplankton concentrations, while water clarity, lake depth, and submerged macrophytes have all decreased (Downing et al. 2001; Anthony and Downing 2003; Egertson et al. 2004). Common Carp *Cyprinus carpio* have been present since the early 1900s (Bailey and Harrison 1945) but were not abundant until recent decades (Larscheid 2005; Colvin et al. 2010). Zebra mussels *Dreissena polymorpha* were first discovered in Clear Lake in 2005, and densities have since increased dramatically (Colvin et al. 2010). In response to long-term declines in water quality, management actions have been implemented to improve water quality and the fishery, including in-lake best management practices such as Common Carp removals (Colvin et al. 2012), dredging and shoreline stabilization, urban best-management practices such as native landscaping, permeable pavement and bioretention cells, and agricultural best-management practices such as cover crops, grassed waterways, terraces, and conversion of agricultural land to the Conservation Reserve Program (Iowa Department of Natural Resources 2008; Clear Lake Enhancement and Restoration Project 2016).

Two approaches were used for quantifying and comparing growth rates (size-specific) and lengths attained (age-specific) among years and time periods for four fish species in Clear Lake. Size-specific analyses relate growth to body size rather than age (Gutreuter 1987; Putman et al. 1995; Pierce et al. 2003; Shoup et al. 2007; Quist et al. 2012). Because fish of the same age can vary greatly in size, age-specific analyses can result in comparing growth rates among groups of fish that differ significantly in preferred prey, metabolic rates, habitat requirements, risk of predation, and other important factors (Larkin et al. 1956; Osenberg et al. 1988). Although they are often referred to as “growth,” age-specific analyses actually yield estimates of attained lengths, which are the sums of growth in all previous years and thus are not comparable with annual estimates of environmental variables as size-specific analyses are. Despite containing influences of different numbers of years, the length-at-age estimates resulting from age-specific analyses are useful because of their relative ease in computation, their widespread application in fisheries management, and their incorporation in quantitative methods such as the von Bertalanffy model and many associated techniques (Slipke and Maceina 2014). Although biases due to unknown yearly differences are likely when using age-specific analyses to make comparisons among adjacent years over short time frames, comparing time periods separated by longer intervals, such as in this analysis of historical data, reduces the effect of these biases and provides a useful way to compare growth among different periods widely separated in time (Millner and Whiting 1996). Similarly, Copp et al. (2004) demonstrated the utility of this approach for examining intercontinental growth differences in Pumpkinseed *Lepomis gibbosus*.

The purpose of this study was to examine growth changes of four common fish species in Clear Lake—Walleye, Yellow Bass, Common Carp, and Black Bullhead *Ameiurus melas*—over time. Common Carp, Yellow Bass, and Walleye are the three most abundant fish species in Clear Lake (Colvin et al. 2010). Black Bullheads were recently among the most abundant but have declined in the last two decades (Larscheid 2005). The first objective was to document annual growth rates over several years of the four fish species in their first year of life and at the length at which they are maturing. The second objective was to examine relationships between fish growth and environmental variables. The third objective was to compare recent growth of these fishes to historical growth documented in previous studies. The third objective was to provide insight into how fish growth has changed over time as habitats and water quality have changed.

METHODS

Study site.— Clear Lake is a shallow, eutrophic lake located in Cerro Gordo County in north-central Iowa (43°08′N, 93°22′W). It has a surface area of 1,474 ha, a watershed area of 4,888 ha, a mean depth of 3.1 m, and a maximum depth of 7.3 m. Inorganic substrates cover the vast majority of the bottom, with silt accounting for 92%, sand 4%, and rock 2% of the area. Historically, Clear Lake supported abundant aquatic vegetation, but due to poor water clarity in recent years, aquatic vegetation cover has been reduced to 2% of the bottom area and is also reduced in diversity (Downing et al. 2001; Egertson et al. 2004; Colvin et al. 2010).

The predominant fish species include Yellow Bass, Walleye, and Common Carp (Colvin et al. 2010). This is in sharp contrast to the historical fish community that contained abundant Largemouth Bass *Micropterus salmoides*, Bluegill *L. macrochirus*, and Northern Pike *Esox lucius* (Bailey and Harrison 1945). Walleyes have been stocked nearly every year since 1915 (Bailey and Harrison 1945; Carlander and Payne 1977). Fish species diversity has declined since 1945 when 43 species were recorded (Bailey and Harrison 1945), including several darter and cyprinid species that are no longer present. Currently, Clear Lake supports 23 fish species (Colvin et al. 2010).

Fish and aging structure collection.— Fish sampling was conducted as part of another study in 2007 and 2008 using a variety of methods (Colvin et al. 2010). A 132-m long beach seine, 3.5 m in depth with a 3.5-m^2 bag in the center and 6-mm square mesh, was used to sample the nearshore fish community in September. The offshore fish community was sampled using a semiballoon otter trawl with an 8-m head rope, 3.8-cm-stretch-mesh body, and 6.3-mm-mesh cod end, also in September. Night electrofishing was conducted in October and November to obtain a larger sample of Walleyes. Common Carp were captured by commercial fishers using seines in May and November of 2007 and June and November of 2008. Sex of collected fish was not determined.

Dorsal spines were used for aging and back-calculation of lengths at previous ages for Common Carp and Walleyes, pectoral spines for Black Bullheads, and sagittal otoliths for Yellow Bass based on criteria discussed in Quist et al. (2012). Upon capture, Common Carp, Walleyes, and Black Bullheads were measured for TL (mm), an aging structure was removed, and the fish were released alive. Yellow Bass were captured in greater numbers and were subsampled randomly within 2.5-cm length groups and frozen or preserved in formalin for later length measurement and extraction of aging structures. Common Carp and Walleye dorsal spines were removed by cutting the spine as close to the base as possible with a side cutter. Black Bullhead pectoral spines were removed by laying the spine flat against the fish's body and rotating it dorsally until the articulating process separated from the joint. Spines were placed singly in scale envelopes and allowed to air dry. Sagittal otoliths were removed from Yellow Bass in the lab by making a dorsoventral cut from the top of the head through the preopercle and bending the head away from the body to expose the otoliths (Secor et al. 1991). Otoliths were rinsed in water, placed in a scale envelope, and allowed to dry.

Aging structure preparation.— Spines were sectioned for viewing with a Buehler Isomet low speed saw (Lake Bluff, Illinois) at a thickness of 0.8–1.0 mm using a diamond wafering blade. Large Common Carp spines were sectioned without additional preparation beyond drying. Small Common Carp dorsal spines, Walleye dorsal spines, and Black Bullhead pectoral spines were mounted in epoxy for sectioning (Koch and Quist 2007).

Large Yellow Bass otoliths were broken in half along the dorsoventral axis and sanded, first with 400-grain sandpaper until the nucleus was reached, and then polished with 1200-grit sandpaper (Secor et al. 1991). The otolith half was pushed into black clay (polished surface up) and covered with a drop of immersion oil for viewing. Small Yellow Bass otoliths that were too small to break in half were mounted in epoxy as described above and sectioned as close to the nucleus as possible and polished, first with 400-grain sandpaper until the nucleus was reached and then with 1200-grain sandpaper (Secor et al. 1991). These were also pushed into black clay and covered with immersion oil for viewing.

Aging structure measurement and back-calculation.— Aging structures were examined under a dissecting microscope (8–115× magnification) fitted with a computerized video image analysis system (Image Pro 6.2; Media Cybernetics, Rockville, Maryland). A still image (2,560 × 1,920 pixels) of each structure was saved for aging and measurement. The structures were aged, and measurements of distance between annuli were made independently by two readers who had no knowledge of the size of the fish. Measurements were taken along the longest axis of the structure from the origin of the structure to the edge for dorsal and pectoral spines. Yellow Bass otoliths were measured from the nucleus to the edge along the sulcal groove. When there was a discrepancy between the two readers, the structure was viewed together and a consensus was reached. If a consensus could not be reached, the structure was excluded from the analysis.

Back-calculation of length at previous ages was done using the Dahl–Lee (direct proportion) method (Quist et al. 2012). The Dahl–Lee formula is

$$L_i = (S_i/S_c)L_c, \tag{1}$$

where L_i = back-calculated fish body length at age i, L_c = fish body length at capture, S_i = mean aging structure length at annulus i, and S_c = mean aging structure total length. Back-calculated lengths at age were thus the average from the two independent readers for each fish.

Size-specific analysis of growth.— A size-specific approach (Quist et al. 2012) was used to analyze growth of the four fish species. Annual growth for a given year was calculated as the difference between two back-calculated lengths at age from consecutive years. The year in which the aging structure was collected was excluded from the analysis because the fish had not yet experienced a full growing season. Annual growth was then plotted against length at the beginning of the growing season. Estimates of length at hatching were obtained from the literature (Holland-Bartels et al. 1990) and used as the length at the beginning of the growing season for fish in their first year of life. For Black Bullheads and Walleyes, 7 mm was used for length at hatching, for Common Carp 3.5 mm was used, and 3 mm was used for Yellow Bass. For older ages, back-calculated length at the beginning of the growing season was used. Locally weighted scatterplot smoothing (LOWESS) regression was used to fit curves to the annual growth estimates (Pierce et al. 2003). The "loess" function in Program R (R Development Core Team 2009) was used for these analyses. LOWESS is a nonparametric regression method appropriate where the data suggest no particular parametric model form (Cleveland 1979). After testing several different smoothing parameters (span in Program R) for LOWESS, a smoothing parameter that worked best for each species individually was used. For Common Carp and Yellow Bass a span of 1 and for

Walleyes and Black Bullheads a span of 1.2 were used. These parameters provided accurate fits to the data that represent the growth patterns in the data set, while not allowing the overpowering influence of individual variation and outliers.

Mean annual growth at age 0 (AG-0) and mean annual growth at length of maturation (AG-m) were chosen as expressions of growth for size-specific comparisons because they represent two important stages (AG-0) or events (AG-m) in the life cycle of fishes. The LOWESS regressions represent "average" annual growth of fish at all sizes in a given year, therefore allowing estimation of growth for any size fish in that year. Age-of-maturity estimates were obtained from the literature (Carlander 1969, 1997), and averaged back-calculated lengths at that age for each fish species were used to estimate length at maturity for each species. Ages at maturity used were age 3 for Black Bullheads and Walleyes and age 2 for Common Carp and Yellow Bass. Actual age and length at maturity can vary among sexes and water bodies and with changing environmental conditions, as well as with changes in exploitation (Hutchings and Jones 1998; Stearns 2000), so in nature they are not constants as literature-derived values imply. Therefore, we henceforth refer to our estimated "adult" growth rates as growth at length of maturation, rather than growth at length of maturity. Because age-0 fish begin growing at a fairly consistent length at hatching, age-specific growth and size-specific growth are essentially identical in the first year. Thus, AG-0 was estimated by averaging length at age 1. Estimates of AG-m were obtained from LOWESS regressions, solving for annual growth at length at maturation.

Growth relationships with environmental variables.— Five environmental variables were analyzed for relationships with growth. The annual number of degree-days where water temperature exceeded 5°C (hereafter referred to as degree-days) was used as an index of temperature because it encompasses most of the open-water season and the temperature range where most fish growth occurs. Walleyes do not gain weight at temperatures below 6°C (Hokanson 1977); thus, it was assumed that 5°C and greater should encompass temperature conditions favorable for growth of the four species. Air temperature data from the nearest station (Mason City, Iowa) were obtained from the National Oceanic and Atmospheric Administration (NOAA 2009), and from these data daily mean water temperatures were estimated using an air–water relationship developed for Clear Lake (Jacobsen 1968). Using 5°C as a base temperature, for each day that the daily mean water temperature exceeded 5°C in a given year, 5°C was subtracted from the daily mean temperature and these quantities were summed over days to give the annual degree-days. Mean water transparency, chlorophyll *a* concentration, phytoplankton concentration, and zooplankton concentration were obtained from the Iowa Lakes Information System (ILIS; Iowa Department of Natural Resources 2009) and were based on three sampling periods at approximately monthly intervals during the summer of each year. Water transparency is an indicator of overall water quality and lake productivity (Carlson 1977). Chlorophyll *a* concentration is an indicator of phytoplankton abundance, which is the trophic base of aquatic ecosystems (McCauley and Kalff 1981; Kalff 2002). Zooplankton are important in the diets of many fish species, especially young of the year (Chambers and Trippel 1997). Relationships between size-specific growth and environmental variables were examined using Pearson correlation coefficients.

Age-specific growth comparisons with historical data.— Recent fish growth estimated as described above in the 2000s (1990s–2000s for Common Carp) (hereafter referred to as "Recent") was compared with historical growth documented in previous time periods in the literature (Carlander 1969, 1997; Larscheid 2005; for details see Table S1 found online in the Supporting Information section at the end of the article). Literature data consisted of mean lengths at age with no estimates of error. Where only single studies were available from a time period (Black Bullhead, Common Carp), growth curves were plotted without estimates of error. For species where multiple years of length-at-age data were available for a time period (Walleye, Yellow Bass), means for each age were calculated by decade and a single growth curve with 95% CIs for each age was plotted. The estimated length at age 4 for Black Bullheads from 1955 was less than the age-3 estimate and was likely erroneous; this estimate was omitted from further analysis.

For each time period L_∞, k, and t_0 were estimated from the von Bertalanffy growth model,

$$L(t) = L_\infty\left[1 - e^{-k(t-t_0)}\right], \tag{2}$$

where L_∞ is the theoretical maximum length a fish will reach in the population, k is a growth constant, and t_0 is the time at which the fish's length is zero (Quist et al. 2012). In addition, ω, which is roughly equivalent to the product of L_∞ and k and corresponds to the growth rate near t_0, was estimated and is recommended for statistical comparisons (Gallucci and Quinn 1979) because of the strong negative correlation of L_∞ and k. The original von Bertalanffy growth model can be reparameterized using ω, and the equation is

$$L(t) = \omega/k[1 - e^{-k(t-t_0)}]. \tag{3}$$

The ω term was compared across time periods for each species using pairwise *t*-tests (Katzenmeyer 2010).

For Common Carp and Walleye the approach of Jackson et al. (2008) and Quist et al. (2003) was followed to convert lengths at age to the relative growth index (RGI).

This allowed comparisons of lengths attained in Clear Lake to the entire species' ranges, which may be useful for interpreting results in Clear Lake and elsewhere, as well as identifying factors contributing to slow growth and helping guide management actions (Jackson et al. 2008). The RGI analysis was not attempted for Black Bullhead and Yellow Bass because length-at-age standards have not been developed for these species.

RESULTS

Environmental Variables

Annual degree-days ranged from 2,372 to 2,892 (Table 1). Annual mean summer water transparency, chlorophyll *a*, and phytoplankton and zooplankton concentrations were not monitored before 2000, but from 2000 to 2007 transparency varied over threefold, ranging from 0.4 to 1.4 m, chlorophyll *a* concentration varied roughly fourfold, ranging from 20.7 to 82 μg/L, phytoplankton concentration varied by over two orders of magnitude, ranging from 14.6 to 3,112.7 mg/L, and zooplankton concentration varied by over an order of magnitude, ranging from 23.4 to 276.1 μg/L. Although there was substantial year-to-year variability in the five measured variables, no clear temporal trend was evident for any variable during the period when measurements were recorded.

Size-Specific Growth

Aging structures were examined from 408 Common Carp, 222 Walleyes, 102 Yellow Bass, and 61 Black Bullheads. Size-specific growth curves fit by LOWESS regression and resulting AG-0 and AG-m estimates are shown in Figures S1–S5 in the Supporting Information. Black Bullhead first-year growth (AG-0) ranged from 92 to 150 mm and annual growth at length at maturation (AG-m) ranged from 30 to 43 mm, Common Carp AG-0 ranged from 88 to 182 mm and AG-m ranged from 84 to 143 mm, Walleye AG-0 ranged from 111 to 212 mm and AG-m ranged from 43 to 64 mm, and Yellow Bass AG-0 ranged from 81 to 100 mm and AG-m ranged from 24 to 52 mm (Figure 1). First-year growth was greater than annual growth at length at maturation for Black Bullheads, Walleyes, and Yellow Bass, but was similar for both life cycle stages for Common Carp.

The AG-0 of Black Bullheads, Common Carp, and Yellow Bass gradually increased during the study, with an average increase of 58% over the years for which estimates were possible (Figure 1). Walleye AG-0 increased each year from 2002 through 2005 but then declined in the next 2 years. Common Carp and Yellow Bass AG-m mirrored their AG-0 trends, increasing an average of 50% over the years of available data. Although there was year-to-year variation there were no apparent trends in Black Bullhead and Walleye AG-m.

There were relatively few significant relationships for size-specific growth variables among species, and small sample sizes (i.e., years with corresponding annual growth estimates) for correlation analysis suggest interpreting these relationships with caution. Black Bullhead AG-0 was positively correlated with Walleye and Yellow Bass AG-0 (Table 2). Although not significant at $\alpha = 0.05$, Common Carp AG-0 and AG-m values appeared to be positively associated with corresponding Yellow Bass values, and Common Carp AG-m appeared to be negatively associated with Walleye AG-0 ($0.1 > P > 0.05$). Values

TABLE 1. Environmental variables in Clear Lake, Iowa, 1994–2007. Degree-days are annual totals; other variables are annual summertime averages. Empty cells indicate no data were available.

Year	Degree-days (°C)	Transparency (m)	Chlorophyll *a* (μg/L)	Phytoplankton (mg/L)	Zooplankton (μg/L)
1994	2,655				
1995	2,584				
1996	2,372				
1997	2,486				
1998	2,892				
1999	2,602				
2000	2,729	0.4	30.8	37.1	23.4
2001	2,688	0.7	70.7	14.6	124.3
2002	2,569	0.8	30.2	142.6	223.7
2003	2,518	1.4	20.7	66.6	101.9
2004	2,465	0.5	81.5	543.6	276.1
2005	2,836	0.5	82.0	305.3	39.3
2006	2,584	0.5	53.1	3,112.7	119.8
2007	2,878	1.2	22.4	40.9	66.5

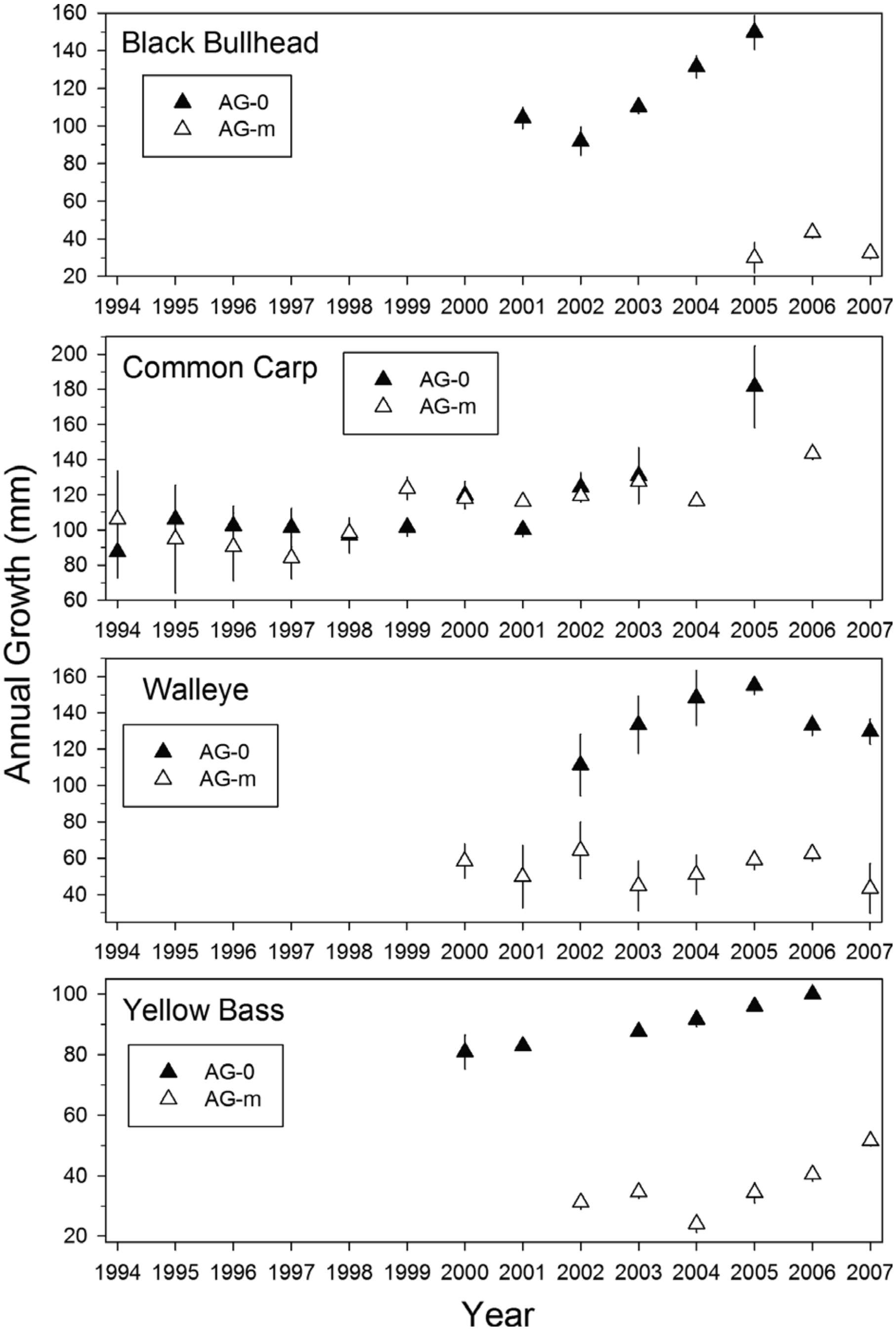

FIGURE 1. Annual growth (mm) at age 0 (AG-0) and at length at maturation (AG-m) (±1 SE) for Black Bullhead, Common Carp, Walleye, and Yellow Bass in Clear Lake, Iowa, 1994–2007. AG-0 values are mean back-calculated lengths at age 1; AG-m values were estimated from LOWESS regressions (Figures S1–S5).

for AG-0 and AG-m were not significantly correlated within any of the four species.

There were also relatively few significant relationships between growth variables and the environmental variables that were quantified, and caution due to small samples sizes applies here as well. Common Carp AG-0 and AG-m were positively correlated with phytoplankton concentration (Table 3). Although not significant at $\alpha = 0.05$, Walleye AG-0 appeared to be positively associated with chlorophyll *a*, Yellow Bass AG-0 was positively associated with phytoplankton concentration, and Walleye AG-m was negatively associated with transparency ($0.1 > P > 0.05$; Table 3).

TABLE 2. Correlations of annual growth (mm) at age 0 (AG-0) and at length at maturation (AG-m) of Black Bullhead, Common Carp, Walleye, and Yellow Bass in Clear Lake, Iowa. In each cell the top value is the Pearson correlation coefficient, the middle value is the P-value, and the bottom value is the sample size. Dashes (–) indicate sample sizes < 3.

Species	Black Bullhead AG-m	Common Carp		Walleye		Yellow Bass	
		AG-0	AG-m	AG-0	AG-m	AG-0	AG-m
Black Bullhead AG-0	–	0.88 0.122 4	−0.16 0.843 4	0.97 0.027 4	−0.03 0.962 5	0.97 0.030 4	−0.05 0.948 4
Black Bullhead AG-m		–	–	−0.55 0.626 3	0.49 0.671 3	–	0.01 0.991 3
Common Carp AG-0			0.55 0.101 10	−0.31 0.688 4	0.27 0.652 5	0.93 0.070 4	0.55 0.633 3
Common Carp AG-m				−0.82 0.087 5	0.29 0.584 6	0.81 0.100 5	0.93 0.071 4
Walleye AG-0					−0.19 0.723 6	0.07 0.931 4	−0.24 0.657 6
Walleye AG-m						0.48 0.331 6	−0.32 0.533 6
Yellow Bass AG-0							0.53 0.466 4

Age-Specific Growth Comparisons with Historical Data

Differences in lengths at age between study periods were evident to varying degrees for all four species (Figures 2, 3). Black Bullhead length at age was greater in the present study than in earlier studies (Figure 2), and this was supported by significantly larger ω values in the present study than in previous studies (Table 4). Common Carp length at age was much greater in the 1952 study than in the late 1990s or the present study, and this was supported by significantly larger ω (Table 4) and consistently higher RGI values (Figure 3) in the 1952 study than in the two later studies. The RGI values for age-2 and older fish were above 100% of "average" for Common Carp throughout its range, but RGI values for age-1 Common Carp were 30% to 50% lower than for older ages in all three time periods. Walleye lengths at age were broadly similar across the three time periods, although lengths increased fastest in years 2 and 3 in the present study, and lengths beyond age 6 in the 1948–1974 time period were slightly lower than in the other time periods (Figure 2). As expressed by ω, Walleye growth was significantly faster in the present study than in previous studies (Table 4), but this was largely due to faster early growth and a larger k in the present study and did not result in substantially greater lengths at age, especially compared with the 1940s (Figure 2). There was a general trend in all three time periods for the Walleye RGI to increase with age; younger ages had average or below average lengths and older ages had above average lengths for the species (Figure 3). Lengths of age-1 Walleyes in the present study were shorter than in the earlier time periods (Figure 3). Yellow Bass attained significantly greater lengths at older ages in the 1940s than in the two more recent time periods (Figure 2). In the present study growth in the first 2 years was rapid, resulting in the greatest lengths at age in the first 2 years among the three time periods, but thereafter growth slowed considerably, resulting in the shortest lengths at age among the three time periods in years 4 through 6 (Figure 2). As expressed by ω, Yellow Bass growth was significantly lower during the 1960s than during the 1940s and in the present study; growth in the latter two time periods did not differ (Table 4).

DISCUSSION

Patterns of Black Bullhead growth evident in both the age-specific and size-specific analyses suggest a potential role for density dependence. Black Bullheads grew more

TABLE 3. Correlations of annual growth (mm) at age 0 (AG-0) and at length at maturation (AG-m) of Black Bullhead, Common Carp, Walleye, and Yellow Bass with environmental variables in Clear Lake, Iowa. In each cell the top value is the Pearson correlation coefficient, the middle value is the *P*-value, and the bottom value is the sample size.

	Black Bullhead		Common Carp		Walleye		Yellow Bass	
Variable	AG-0	AG-m	AG-0	AG-m	AG-0	AG-m	AG-0	AG-m
Degree-days (°C)	0.44	−0.95	0.29	0.10	−0.24	-0.11	−0.11	0.72
	0.463	0.202	0.380	0.759	0.598	0.791	0.841	0.110
	5	3	11	12	7	8	6	6
Transparency (m)	−0.50	−0.33	−0.16	0.08	−0.41	−0.69	−0.18	0.44
	0.394	0.784	0.798	0.877	0.419	0.057	0.738	0.383
	5	3	5	6	6	8	6	6
Chlorophyll *a* (μg/L)	0.71	−0.17	0.40	−0.18	0.79	0.19	0.39	−0.54
	0.179	0.894	0.505	0.728	0.061	0.651	0.449	0.2733
	5	3	5	6	6	8	6	6
Phytoplankton (mg/L)	0.66	0.97	0.94	0.89	0.03	0.45	0.75	0.12
	0.222	0.167	0.018	0.018	0.953	0.266	0.085	0.826
	5	3	5	6	6	8	6	6
Zooplankton (μg/L)	−0.34	0.99	−0.39	−0.22	−0.24	0.10	0.20	−0.71
	0.573	0.099	0.513	0.671	0.647	0.818	0.706	0.116
	5	3	5	6	6	8	6	6

slowly in the 1950s and 1999 than was documented recently. Black Bullheads were described as being very abundant in the 1940s (Bailey and Harrison 1945) and 1950s (Forney 1955), and a quantitative study showed them to be the most abundant species in Clear Lake in 1959 with a biomass of 49 kg/ha (McCann 1960). In 1999, Black Bullhead biomass was estimated to be 336 kg/ha (Larscheid 2005). In sharp contrast, the biomass of Black Bullheads averaged only 10 kg/ha recently (Colvin et al. 2010). Lengths at age and ω from the three time periods were negatively related to biomass, suggesting the possibility of intraspecific competition. The recent precipitous decline in Black Bullhead biomass in Clear Lake could have released them from intraspecific competition for food and is a plausible explanation for the recent increase in their growth. The steady increase in first-year growth of Black Bullheads from the early to middle first decade of the 2000s is consistent with this interpretation. Previous studies in Iowa (Rose and Moen 1950), Oklahoma (Houser and Collins 1962), and South Dakota (Hanchin et al. 2002) have likewise concluded that Black Bullhead growth is strongly regulated by intraspecific competition, so it is possible that density dependence may frequently be an important determinant of Black Bullhead growth. Since the 1950s, numerous other factors have changed in Clear Lake (Downing et al. 2001; Egertson et al. 2004) that may have also played a role in the changes in Black Bullhead growth documented here.

Common Carp attained markedly greater lengths at age in the 1950s than in the two more recent time periods examined in this study. Unfortunately, no comparable data on Common Carp abundance and few data on environmental conditions exist across the three time periods, making interpretation difficult. Common Carp were described as "common" in the early 1940s (Bailey and Harrison 1945) and as "abundant" in the late 1940s and early 1950s (Parsons 1950; English 1951). Recent studies documented a highly abundant Common Carp population in the early 2000s (Larscheid 2005; Colvin et al. 2012). The largest annual removal of Common Carp since nuisance fish removals began in 1929 was 111,427 kg (76 kg/ha) removed in 1949 (Iowa Department of Natural Resources, unpublished data), which is roughly half of the average population biomass estimated during 2007 to 2010 (Colvin et al. 2012), and would most likely have reduced biomass of the remaining population significantly for a few years. The studies published in the 1950s, during the time that corresponded with the 1952 length-at-age estimates, speculated that Common Carp played a significant role in the declines of submerged vegetation and water clarity during that time period (Parsons 1950; English 1951). It is reasonable to further speculate that the more abundant vegetation and likely lower population density and biomass in the 1950s may have enabled faster growth of Common Carp than that observed in more recent time periods when reduced plant abundance and water transparency were the norm.

Clear Lake presents distinctly different growing conditions to juvenile and adult Common Carp relative to the rest of the species' range, as evidenced by the distinctly lower RGI values for age-1 Common Carp in all three time periods, implying slower first-year growth relative to populations elsewhere and contrasting faster relative

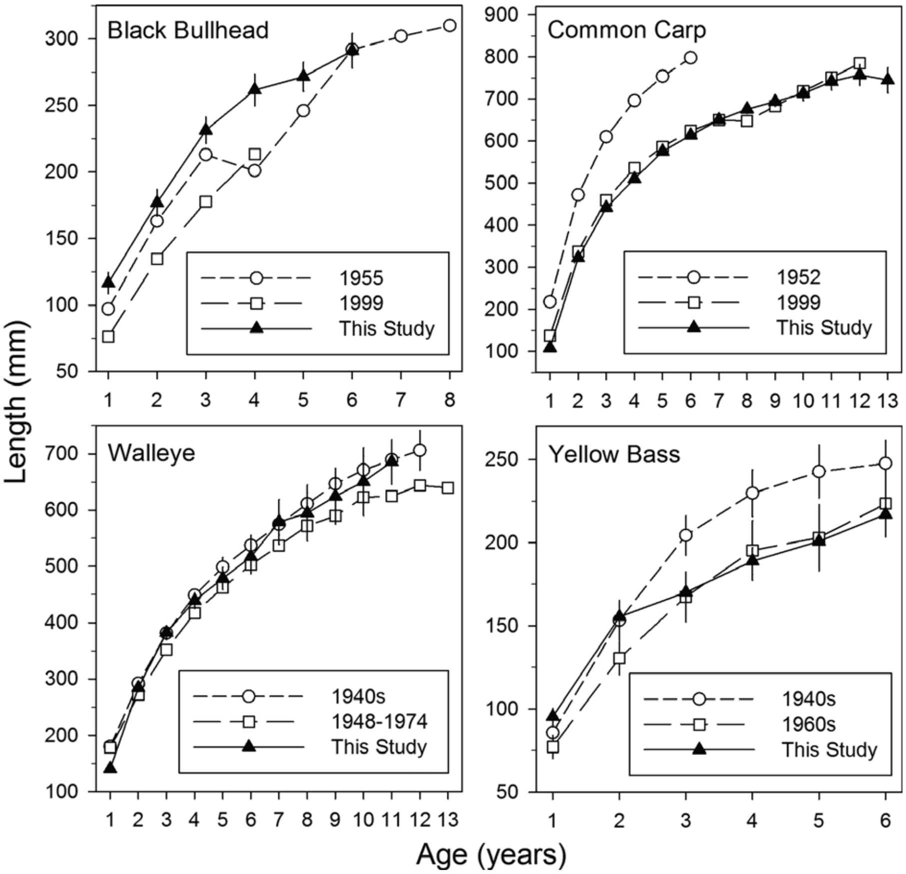

FIGURE 2. Mean back-calculated length at age (mm) (±95% CI) for Black Bullhead, Common Carp, Walleye, and Yellow Bass from studies conducted in different time periods in Clear Lake, Iowa.

growth experienced at older ages. Extensive areas of shallow, vegetated, marsh-like habitat, shown in other studies (Koehn 2004; Stuart and Jones 2006; Bajer and Sorensen 2009) to be important nursery habitat for juvenile Common Carp, are scarce in Clear Lake (Egertson et al. 2004; Penne and Pierce 2008), although juvenile Common Carp seek these limited shallow, vegetated areas (Penne and Pierce 2008). Relative to their growth elsewhere, the slow growth of Common Carp in their first year may indicate that the environment of Clear Lake, currently supporting limited shallow, vegetated habitat, is unfavorable for juvenile growth. In turn, the greater-than-average RGI values in subsequent years imply very fast growth in the second year and at least average growth in succeeding years. This dichotomy in growth conditions relative to the species' range between the first and subsequent years in the life history of Common Carp suggests that in addition to continuing efforts to reduce adult Common Carp biomass by commercial-scale netting (Colvin et al. 2012), we suggest that future comprehensive control strategies seek to exploit the poor growing conditions for juveniles.

Although our sampling and analytical methods had the potential to reveal patterns of annual growth with environmental variables, small sample sizes limited the power of many of these correlations and suggest that all should be interpreted with caution. The significant positive correlations between growth of both Common Carp life cycle stages and phytoplankton abundance suggest a relationship with algal production in the water column. In addition to contributing to Common Carp diets in the form of settled organic detritus (Panek 1987), phytoplankton abundance has been shown in a number of studies, to be positively correlated with benthic invertebrate abundance (Dermott et al. 1977; Davies 1980; Blumenshine et al. 1997), which typically make up the majority of Common Carp diets. Increased phytoplankton concentration is frequently observed when Common Carp invade new water bodies and become established (Weber and Brown 2009); thus, the initial ecosystem impacts of Common Carp invasion may serve as a positive feedback mechanism through enhanced growth.

Although the length-at-age plots for Walleyes in the three time periods examined are similar, growth as reflected by ω was faster in the present study than in the previous periods. The primary difference was much faster growth in the second year of life and a larger *k* in the

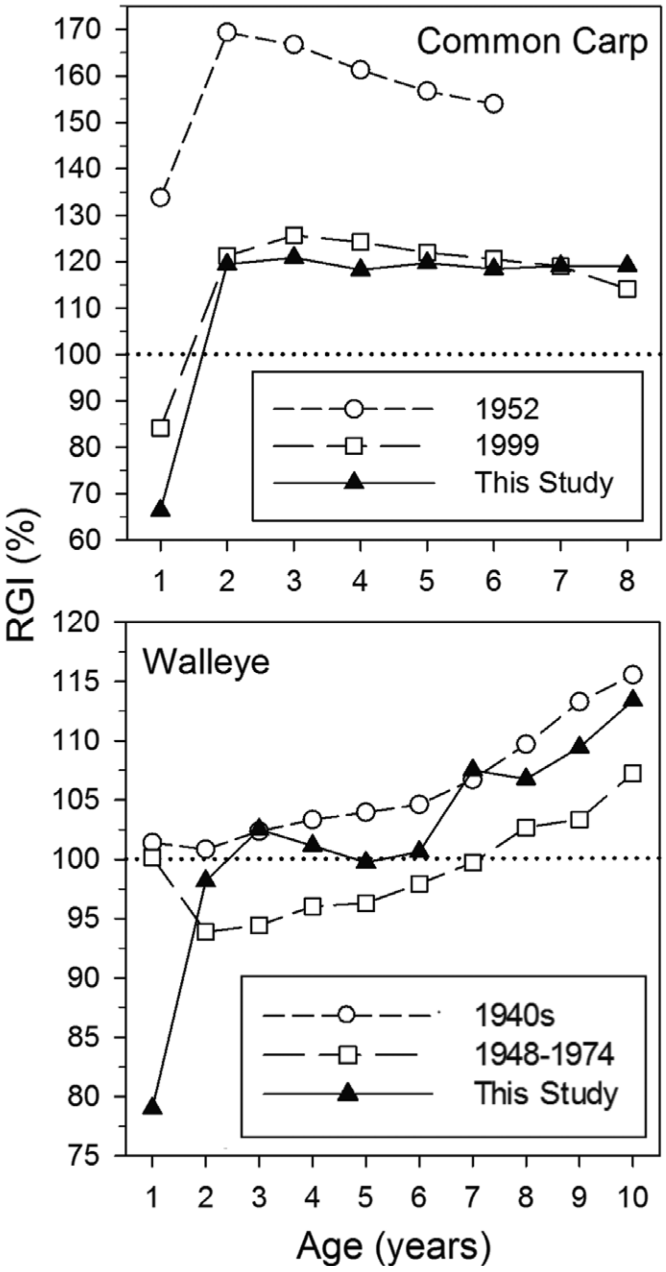

FIGURE 3. Relative growth index (RGI) (%) for Common Carp and Walleye from studies conducted in different time periods in Clear Lake, Iowa. Dotted horizontal lines represent the "average" length at age as predicted by the standardized growth model for each species.

present study. The explanation for this pattern is elusive, but in addition to natural influences, early growth phenomena exhibited by Walleyes in Clear Lake could also be consequences of stocking. Natural reproduction of Walleyes in Clear Lake is believed to be poor, and therefore Walleyes have been stocked nearly every year since 1915 (Bailey and Harrison 1945; Bulkley et al. 1976; Carlander and Payne 1977). Historically all Walleyes were stocked as fry (Carlander and Payne 1977), but in the last two decades Clear Lake has been stocked with large fingerlings (150–200 mm) as well as fry. Fish stocked at a larger size typically have higher survival and recruitment because they are less susceptible to predation and other stressors (Santucci and Wahl 1993). In Clear Lake, Walleye fry are stocked in the early spring and fingerlings are stocked in September and October. Fingerlings attain a much larger size (approximately 175–200 mm) at the end of the first growing season than do fry (approximately 100 mm). Pratt and Fox (2003) found that when two sizes of fingerlings were stocked, the two size-groups converged 4 years later. Also, the size difference can persist throughout life or the small fingerlings can grow faster (Olson et al. 2000; Brooks et al. 2002). Changes in stocking practices over time complicate comparisons of Walleye growth across time periods, especially in early age-classes. The results of this study suggest that young Walleyes are currently growing as fast or faster than in earlier times and are attaining adult sizes similar to or larger than in earlier times, although changes in stocking practices, differential survival of Walleyes stocked as fry and fingerlings between years, and differential growth of surviving stocked Walleye fry and fingerlings may account for some of these apparent differences.

Conditions for Walleye growth improve with age in Clear Lake relative to Walleyes throughout their range. This pattern was evident in all three time periods, suggesting that factors that enable Clear Lake Walleyes to grow increasingly better later in life than in many other locations have been at work for decades. Walleyes are maintained in Clear Lake through yearly, intensive stocking (Carlander and Payne 1977), and the fishery and its associated harvest of adults, occurring in both winter and summer, have been popular for over a century (Wahl 2001). Regardless of the current food web structure and in-lake nutrient dynamics, Clear Lake is located in one of the most nutrient-rich landscapes in the world (Downing et al. 2001). Our results suggest that future Walleye management strategies seek to enhance the survival of juvenile and early adult Walleyes to allow more fish to survive to older ages and capitalize on the inherently faster growth of older, larger fish.

The age-specific analysis showed that Yellow Bass growth has slowed since the 1940s in Clear Lake. Yellow Bass are native to the Mississippi River and its drainage (Harlan and Speaker 1987) but were likely introduced to Clear Lake in the 1920s, and they first showed up in anglers' catches in 1932 (Bailey and Harrison 1945). As is the case with many introduced species, Yellow Bass may have experienced their most rapid growth shortly after their introduction. Ridenhour (1960) found evidence of intraspecific competition among Yellow Bass in Clear Lake, showing that in years when abundance was greater, growth tended to be slower than in years when abundance was low. Presently, Yellow Bass are the most abundant fish species in Clear Lake (Colvin et al. 2010), and

TABLE 4. Growth parameter estimates and their SEs for Black Bullhead, Common Carp, Walleye, and Yellow Bass from studies conducted in different time periods in Clear Lake, Iowa. N is the sample size of fish examined in the recent time period, n is the number of studies used to calculate each parameter, and L_∞, k, t_0, and ω are parameters from the von Bertalanffy growth model. Significant differences among ω values within species are indicated by different letters; values with the same letters are not significantly different.

			L_∞		k		t_0		ω	
Time period	N	n	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Black Bullhead										
1955		1	343.7	26.61	0.28	0.07	−0.22	0.33	96.9 z	17.95
1999		1	331.2	16.47	0.26	0.02	−0.12	0.05	84.9 z	3.71
Recent	61	1	313.3	11.00	0.43	0.04	−0.02	0.05	136.0 y	7.16
Common Carp										
1952		1	844.1	13.02	0.49	0.03	0.39	0.04	416.8 z	17.16
1999		1	758.2	21.97	0.31	0.04	0.25	0.19	237.5 y	24.04
Recent	408	1	728.4	3.21	0.36	0.01	0.48	0.02	258.9 y	2.92
Walleye										
1940s		21	779.0	13.50	0.19	0.01	−0.49	0.10	144.7 z	5.43
1948–1974		1	694.4	7.40	0.20	0.01	−0.46	0.08	140.8 z	3.99
Recent	222	1	688.7	16.14	0.26	0.01	0.05	0.02	178.8 y	4.08
Yellow Bass										
1940s		9	262.8	6.10	0.54	0.05	0.28	0.08	140.8 z	10.51
1960s		9	245.3	10.95	0.38	0.06	0.01	0.14	94.0 y	9.71
Recent	102	1	229.2	2.91	0.54	0.02	−0.01	0.02	123.1 z	2.97

intraspecific competition likely contributes to their reduction in growth since the 1940s.

The potential value of the increased temporal resolution of size-specific analysis relative to age-specific analysis is illustrated by the recent trend in Yellow Bass annual growth. Although sufficient data to rigorously examine relationships of fish growth with zebra mussel abundance were lacking, the doubling in the annual growth at length at maturation observed in Yellow Bass during the first 3 years (2004–2007) of zebra mussel colonization in Clear Lake may have been related to the coinciding increase in zebra mussels (Colvin et al. 2010). Stewart et al. (1998) showed that increased benthic habitat provided by zebra mussel shells led to increases in several benthic macroinvertebrate taxa, including hydrids, turbellarians, gastropods, amphipods, and chironomids. Many of these taxa, especially amphipods and chironomids, commonly make up large proportions of the diet of Yellow Bass in Clear Lake (Welker 1963; Atchison 1967). Thus, increased zebra mussel abundance could have positively facilitated faster adult Yellow Bass growth through increased food availability, as has been demonstrated in Yellow Perch *Perca flavescens* (Thayer et al. 1997) and in several species in the Hudson River (Strayer et al. 2004).

The multiple species and life stages represented in the size-specific analyses provided the opportunity to test whether the species and life stages responded similarly to the unique set of growth conditions presented each year. Perhaps not surprisingly, growth in the first year and as fish were reaching maturation was not correlated in any of the four species. Ontogenetic changes in diet, preferred habitat, and numerous other characteristics occur in all fish species (Mittelbach and Osenberg 1993; Jobling 1995), and as conditions changed in Clear Lake from year to year the growth of the two life stages studied in each species responded asynchronously. Similarly, there were no significant correlations of adult growth among the four species studied, again suggesting that as conditions changed over time the adult growth of the four species responded uniquely. There were some positive relationships in first-year growth among species, and this is consistent with the general observation that diets are similar among fish species when they are young and diverge as they become older (Osenberg et al. 1988). As researchers seek to predict growth responses and managers seek to improve growth responses of fish populations to future environmental changes and management actions, it would be prudent to remember that responses will likely differ among species. Further complicating predictions of impacts of invasive species is the growing evidence that responses of both invaders and resident species may be population- specific rather than species-specific due to genetic and phenotypic variation among populations (Reichard et al. 2015).

In addition to previously mentioned cautions regarding small sample sizes and stocking of Walleyes, three reasons for caution when interpreting our results and their implications deserve mention. First, the sex of collected fish was not determined in either the recent or the historical studies (see Table S1 for one minor exception), which means that growth differences associated with sex, if any, were not accounted for and thus increased the variation in our analyses. The consequence of this is that differences evident in our analyses were probably conservative estimates, although it is conceivable that unknown gender bias in fish collections could have occurred and influenced apparent differences in unknown ways. Second, our use of literature-derived age of maturity for establishing common lengths within species for the purpose of estimating size-specific growth corresponding to the approximate onset of "adulthood" could have resulted in so-called "adult" growth that was in fact occurring during the transition to true adulthood or even before adulthood in some individual fish. Although it is important to be aware of this potential bias, it is not critical to the interpretation of results of this study. The more important consideration is that the size-specific approach we used ensured that growth rates occurring at consistent lengths were compared within each species, which in turn implies consistency of the comparison with respect to ecological and physiological characteristics such as preferred prey, metabolic rate, habitat requirements, risk of predation, as well as probable state of sexual maturation. Third, fish sampling methods and aging structures used differed between the historical and recent time periods. With up to a six-decade time span between the time periods from which we obtained data, advances in technology and changes in practices were inevitable. The methods used during each period were the best available at the time, and although their existence allows important temporal comparison, caution due to potential biases resulting from different methods is warranted.

Clear Lake has undergone significant changes in the past and is poised to change rapidly in the future. A 4-year food web modeling study highlighted large changes in biomass and trophic pathways during 2007–2010 associated with the roles of nonnative Common Carp, invading zebra mussels, and phytoplankton dynamics, all in the context of multiple management actions (Colvin et al. 2015). The most recent (2005–2007) of the annual growth rates measured in the present study occurred during the first few years of the zebra mussel invasion in Clear Lake, which may have been sufficient to allow glimpses of the eventual effects zebra mussels will have, but was not sufficient to permit a rigorous analysis of zebra mussel impacts. The large changes in growth documented over several decades and more recently suggest that as the Clear Lake ecosystem continues to change, growth rates of its important fish species are also likely to continue changing.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.

Supporting Information

Table S1. Supplemental information from historical studies in Clear Lake, Iowa, USA.

Species	Time Period	Data Source	Sampling Gear	Aging Structures	Sex
Black Bullhead	1955	Forney, J. L. 1955. Life history of the black bullhead, *Ameiurus melas*, in Clear Lake, Iowa. Iowa State College Journal of Science 30:145-162.	Gillnets, hoop nets, seines	Dorsal spines, vertebrae; gave similar results	No sex information
	1999	Larscheid, J. G. 2005. Population densities, biomass, and age-growth of common carp and blacl bullheads in Clear Lake and Ventura Marsh. Report F-160-R. Iowa Department of Natural Resources, Des Moines. Iowa	Bottom trawl, seines	Pectoral spines	No sex information
Common Carp	1952	English, T. S. 1952. Growth studies of the carp, Cyprinus carpio Linneaus, in Clear Lake, Iowa. Iowa State College Journal of Science 24:527-540.	Gillnets, seines	Opercles	No sex information
	1999	Larscheid, J. G. 2005. Population densities, biomass, and age-growth of common carp and blacl bullheads in Clear Lake and Ventura Marsh. Report F-160-R. Iowa Department of Natural Resources, Des Moines.	Bottom trawl, seines	Dorsal spines	No sex information
Walleye	1940s	Carlander, K. D. and R. R. Whitney. 1961. Age and growth of walleyes in Clear Lake, Iowa. Transactions of the American Fisheries Society 90:130-138.	Gillnets	Scales	No sex information
	1948-1974	Carlander, K. D. and P. M. Payne. 1977. Year-class abundance, population, and production of walleye (*Stizostedion vitreum vitreum*) in Clear Lake, Iowa, 1948-1974, with varied fry stocking rates.J. Fish. Res. Bd. Can. 34:1792-1799.	Gillnets	Scales	Fish not sexed except for 1953, when female growth was slightly faster in ages 3 through 6
Yellow Bass	1940s	Carlander, K. D., W. M. Lewis, C. E. Ruhr, and R. E. Cleary. 1953. Abundance, growth, and condition of yellow bass, *Morone interrupta* Gill, in Clear Lake, Iowa. Trans. Am. Fish Soc. 82:91-103.	Gillnets, hoop nets, wire traps, seines	Scales	No sex information
	1960s	Atchison, G. J. 1967. Contributions to the life history of the yellow bass, *Roccus mississippiensis*, in Clear Lake, Iowa. M.S. Thesis, Iowa State College, Ames.	Gillnets, electrofishing, seines	Scales	No sex information

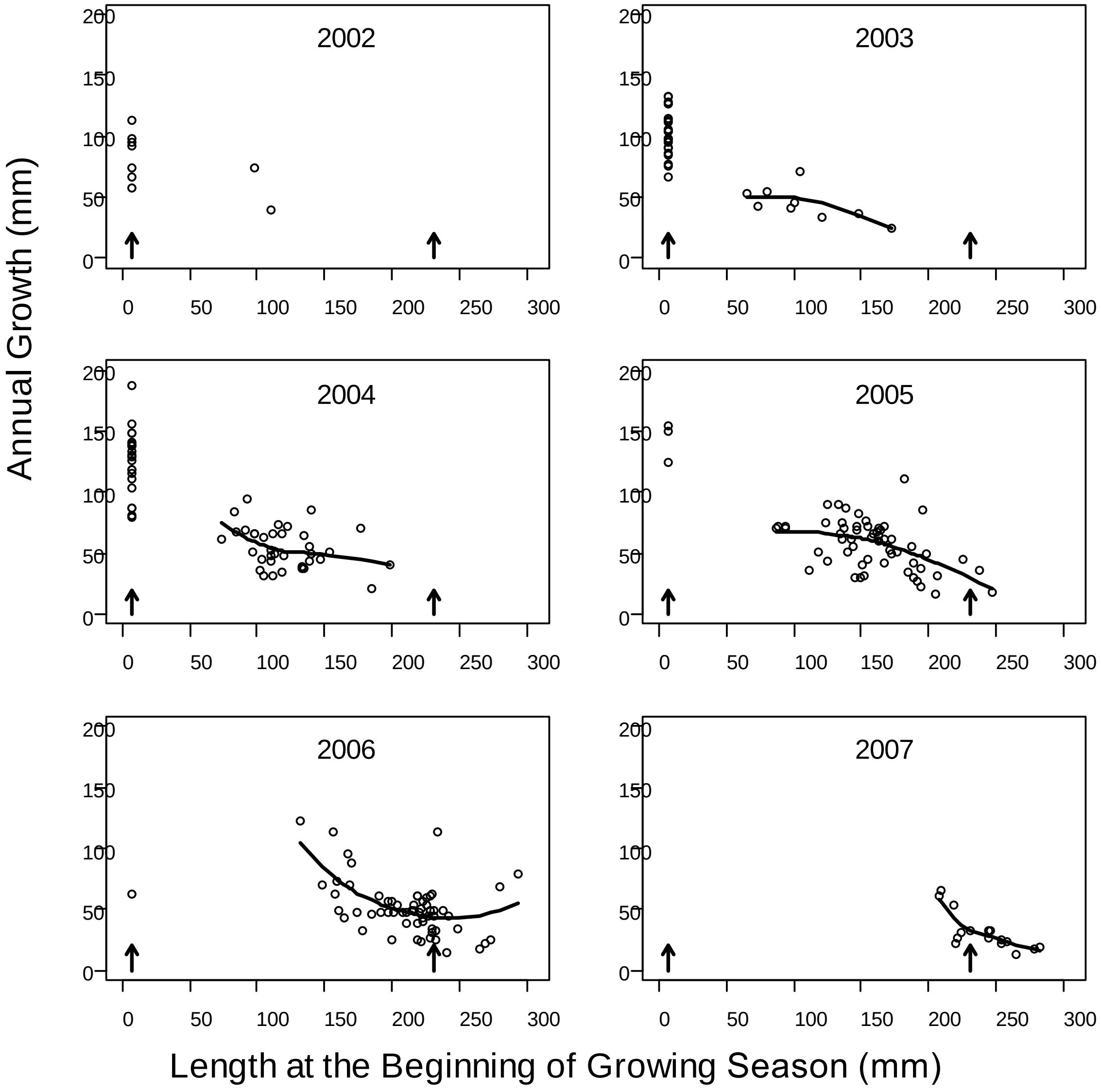

Figure S1. Size-specific growth curves for Black Bullhead in Clear Lake, Iowa, USA. Curves were fit to individual estimates of annual growth and length at the beginning of the growing season by year using LOWESS regression. Individual annual growth was estimated by back-calculating growth increments on pectoral spine cross sections. Arrows represent the two points within a fish’s life where growth estimates were made (AG-0 and AG-m).

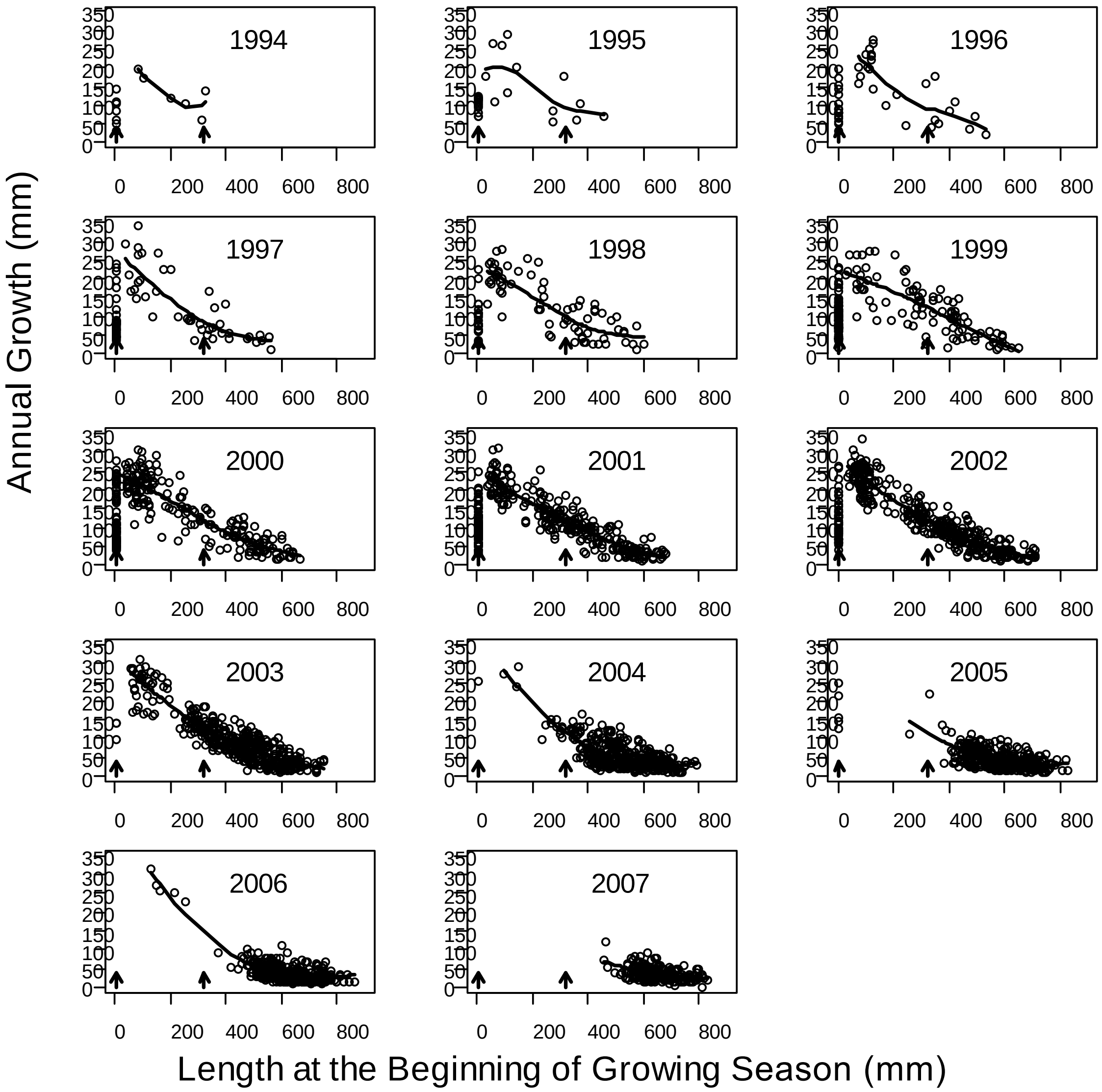

Figure S2. Size-specific growth curves for Common Carp in Clear Lake, Iowa, USA. Curves were fit to individual estimates of annual growth and length at the beginning of the growing season by year using LOWESS regression. Individual annual growth was estimated by back-calculating growth increments on dorsal spine cross sections. Arrows represent the two points within a fish's life where growth estimates were made (AG-0 and AG-m).

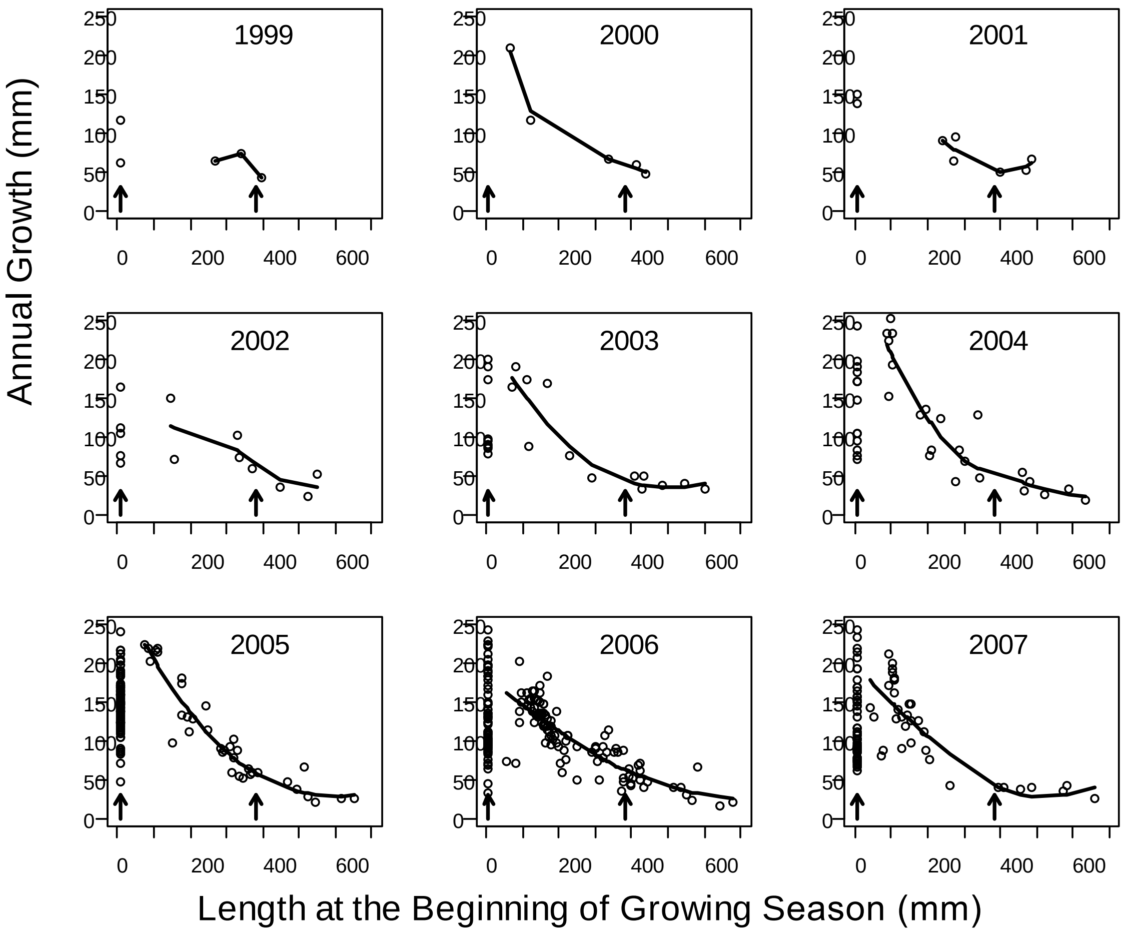

Figure S3. Size-specific growth curves for Walleye in Clear Lake, Iowa, USA. Curves were fit to individual estimates of annual growth and length at the beginning of the growing season by year using LOWESS regression. Individual annual growth was estimated by back-calculating growth increments on dorsal spine cross sections. Arrows represent the two points within a fish's life where growth estimates were made (AG-0 and AG-m).

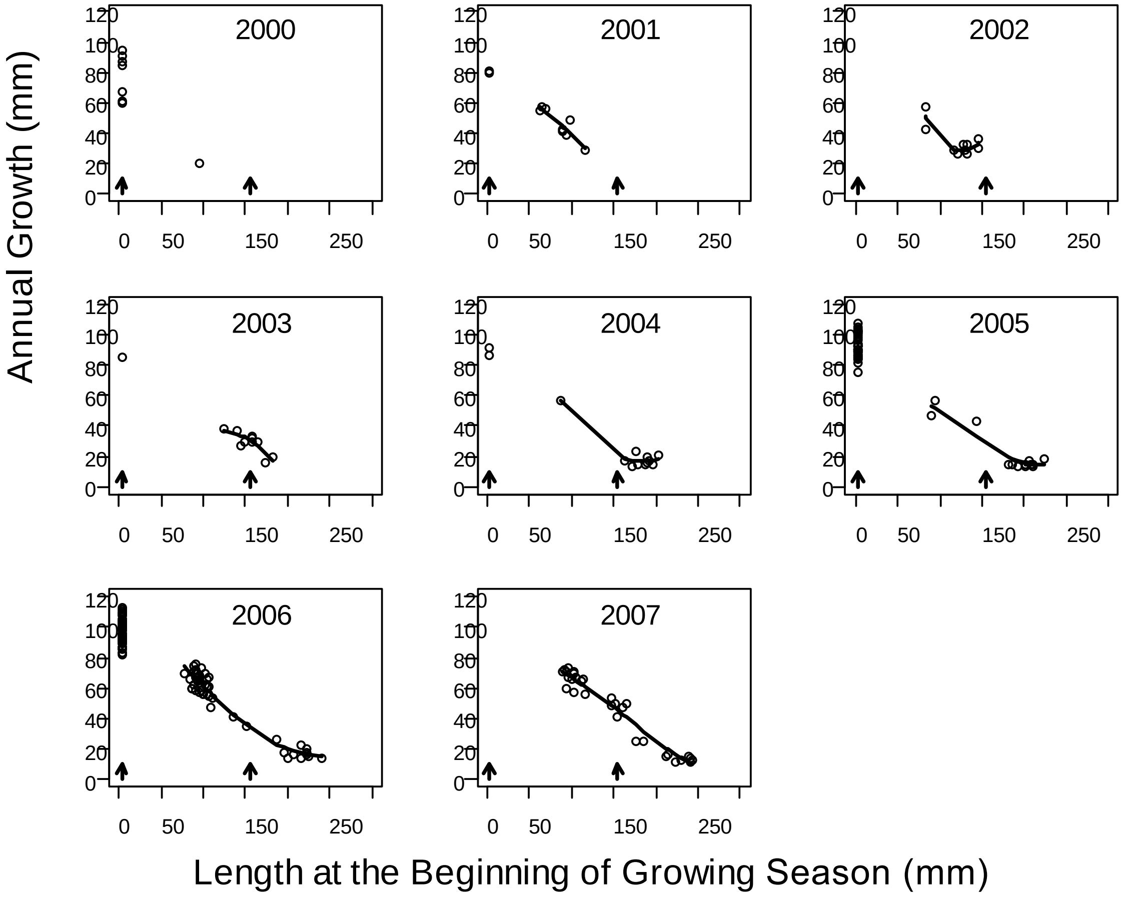

Figure S4. Size-specific growth curves for Yellow Bass in Clear Lake, Iowa, USA. Curves were fit to individual estimates of annual growth and length at the beginning of the growing season by year using LOWESS regression. Individual annual growth was estimated by back-calculating growth increments on otolith cross sections. Arrows represent the two points within a fish’s life where growth estimates were made (AG-0 and AG-m).

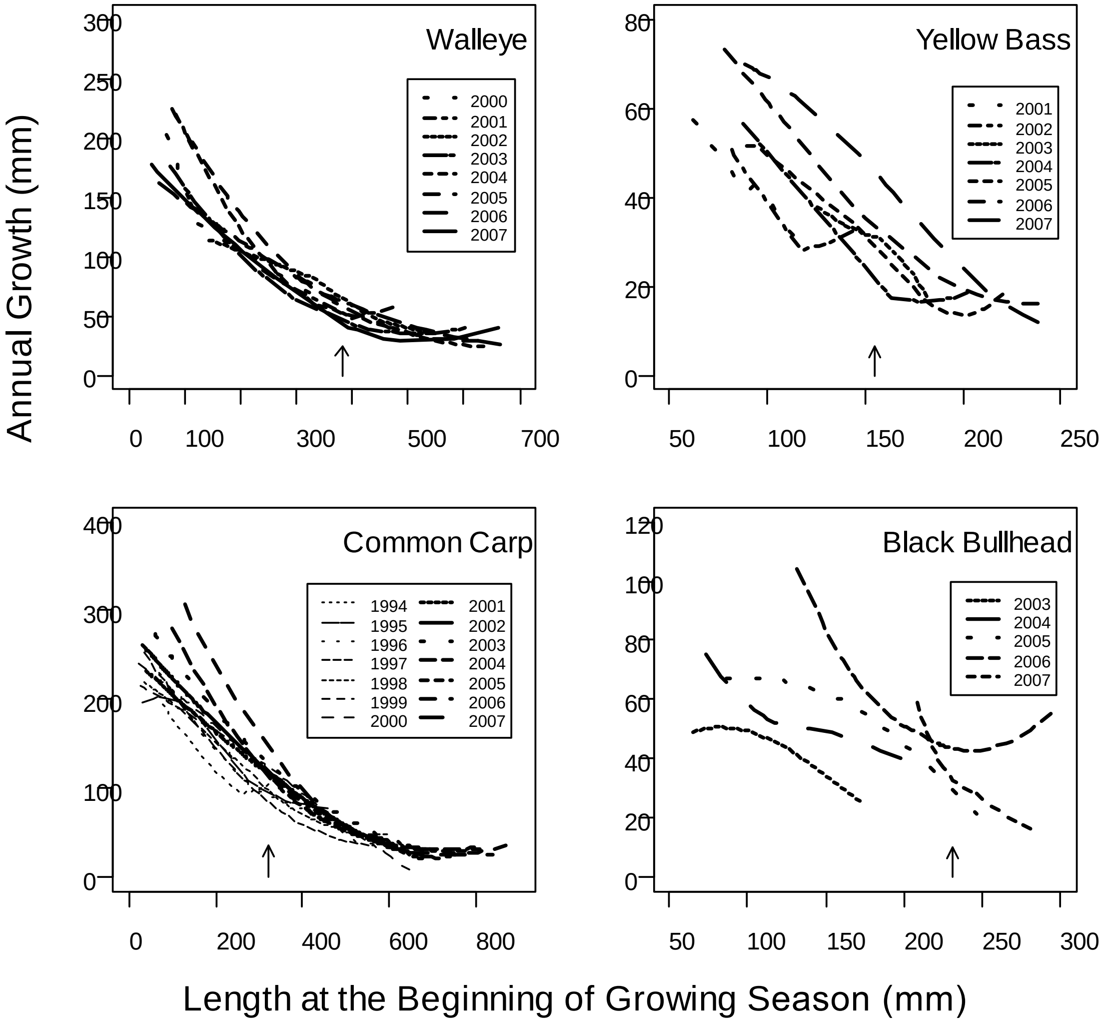

Figure S5. Size-specific growth curves by year for Walleye, Yellow Bass, Common Carp and Black Bullhead in Clear Lake, Iowa, USA. Curves depict growth beginning at age 1, and were fit using LOWESS regression. Arrows indicate length-at-maturation, which was the point where AG-m was estimated from each curve. First-year growth (AG-0) was omitted from these graphs for clarity; AG-0 values are shown in Figure 1.