

**LENGTH AT AGE ESTIMATES OF BLACK CRAPPIE AND WHITE CRAPPIE
AMONG LAKE CLASSES, RESERVOIRS, IMPOUNDMENTS, AND RIVERS
IN MINNESOTA**

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Abstract: We estimated lengths at ages 1 through 5 of black crappies from 964 water bodies (natural lakes, reservoirs, impoundments, and rivers) and white crappies from 76 water bodies in Minnesota. We report herein mean lengths at ages 1 through 5 of both species by lake class, reservoirs (man-made and natural), impoundments, and rivers. Mean lengths at ages 1 through 5 of black crappies differed significantly ($P < 0.0001$) among 32 lake classes, reservoirs, impoundments, and rivers. Conversely, white crappie lengths at the same ages did not differ as strongly (P ranged from 0.0002 to 0.0609) among nine lake classes, reservoirs, and impoundments. White crappie lengths frequently exceeded black crappie lengths at the same ages, but the opposite did not occur. Lengths at age 1 of both species increased from north to south, and appeared related to spawning and hatching times. However, longer lengths at older ages of both crappie species occurred in more productive waters, longer lengths at older ages of black crappies occurred in lakes and reservoirs with higher gill net catch per unit effort (CPUE) of walleye, and longer lengths at older ages of white crappies occurred in lakes with very low trap net CPUE of pumpkinseed. Increased lengths at age of one or both species also occurred in waters with low CPUE of bluegill, bowfin, and northern pike; high CPUE of black bullhead and yellow perch; and in lakes or reservoirs with low aquatic plant diversity or abundance. Diet of both species consisted of primarily dipterans, but fish became more important forage as crappie sizes increased. Lastly, black crappie lengths at ages 4 and 5 in lakes declined with increasing angling pressure.

Introduction

Knowledge of factors affecting growth of black crappie *Pomoxis nigromaculatus* in Minnesota waters is rather limited, and essentially nothing has been documented on growth of white crappie *P. annularis*. First-year growth of black crappies in the southern half of Minnesota increased with decreasing lake depth and peaked when chlorophyll-*a* concentrations reached around 100 µg/L (McInerny and Cross 1999). However, the number of years black crappies needed to reach 200 mm TL increased with increasing gill net catch per unit effort (CPUE) but did not change with increasing trap net CPUE (McInerny and Cross 1999). Furthermore, first-year growth did not affect the number of years to reach 200 mm. In South Dakota and Wisconsin, both at similar latitudes as Minnesota, growth decreases with increasing density of black crappies (Hanson et al. 1983; Snow and Staggs 1994; Guy and Willis 1995b; Galinet et al. 2002). In South Dakota, white crappies grew faster in natural lakes than in reservoirs (Guy and Willis (1995a), but we know of no other study on white crappie growth at similar latitudes as Minnesota.

We hypothesized that length at age of crappies is influenced by the fish species composition of the water body because other fish may prey on young crappies and affect abundance, provide sources of fish prey for adult crappies, or directly compete for food or cover. Snow and Staggs (1994) reported that growth of black crappies in northwestern Wisconsin lakes increased with increasing CPUE of adult rock bass *Ambloplites rupestris*, bluegill *Lepomis macrochirus*, walleye *Sander vitreus*, and young brown bullhead *Ameiurus nebulosus*. Growth and size structure of black crappies in a South Dakota lake improved after saugeye *Sander vitreus* x *S. canadensis* introductions, primarily because predation by saugeye reduced density of black crappies (Galinet et al. 2002). Smaller (< 200 mm TL) black crappies and white crappies in north temperate waters feed mostly on small insects or crustaceans (*Hyaella* spp., *Chaoborus* spp., and *Chironomus* spp.) (Scidmore and Woods 1959; Seaburg and Moyle 1964; Guy and Willis 1993; Sheik et al. 1998) as do bluegills,

pumpkinseed *Lepomis gibbosus*, and yellow perch *Perca flavescens* (Seaburg and Moyle 1964). Larger black crappies in Midwestern waters feed on several fish species including yellow perch, sunfish *Lepomis* spp., black crappies, largemouth bass *Micropterus salmoides*, and darters *Percina* spp. (Seaburg and Moyle 1964; Liao et al. 2004). We know larger white crappies feed on fish (Guy and Willis 1993; Sheik et al. 1998), but we do not know which species they likely consume.

Aquatic plant communities could affect length at age of crappies. Higher trap net CPUE of black crappies occurred in lakes with aquatic plant communities with low diversity and density, communities with the exotic *Potamogeton crispus*, and communities with relatively high occurrences of cattails *Typha* spp. (Cross and McInerny 2006). Conversely, low CPUE of black crappies occurred in lakes with communities having wild rice *Zizania palustris* or high occurrences of bulrushes *Scirpus* spp. Furthermore, CPUE of other fish species differed among aquatic plant communities. Thus, increased density of crappies linked with few aquatic macrophytes could result in decreased length at age, and variable density of other fish species could directly or indirectly affect length at age via predation, providing prey, or competition for food and space.

Diet also affects growth of crappies; however, information on diet from Minnesota waters is limited. Heidinger et al. (1985) reported that white crappies feeding mostly on fish grew faster than white crappies feeding mostly on invertebrates in an Illinois reservoir. In a Nebraska impoundment, white crappies longer than 200 mm TL grew faster and survived better than black crappies, primarily because they began feeding on fish whereas black crappies still fed on invertebrates (Ellison 1984). Seaburg and Moyle (1964) observed that individual black crappies from a slower growing, more dense population ate fewer organisms than a faster growing, less dense population in western Minnesota. For Minnesota, we found diet information from four lakes for black crappie and only two lakes for white crappie. Black crappies fed mostly on dipterans and fish, and white crappies fed

mostly on zooplankton (Scidmore and Woods 1959; Seaburg and Moyle 1964)

Angling mortality can also potentially affect length at age estimates of crappies. Angling mortality is size-selective, and this size-selective mortality can alter length at age estimates in fish. Most crappies harvested by Minnesota anglers range from 180 to 250 mm TL (Cook and Younk 1998). Miranda and Dorr (2000) reported that anglers in Mississippi harvest smaller proportions of the very smallest and the very largest crappies in the population compared to intermediate-sized individuals. We do not know if the same trends occur in Minnesota waters.

Since the early 1990s, fisheries staff of the Minnesota Department of Natural Resources (MNDNR) have regularly used a lake classification system to aid them in managing fisheries. This classification system is based on physical and chemical variables. The initial system consisted of 44 lake classes (Schupp 1992), but revisions of this system reduced to 43 the number of classes (D. H. Schupp, personal communication). To help identify potential problems in a given fish population, MNDNR fisheries staff compare their gill net and trap net catch per unit effort data with interquartile ranges of CPUE (derived from statewide gill net and trap net catch data) from the appropriate lake class. Besides collecting CPUE data, length at age data are also collected from all game fishes (MNDNR 1993). Length at age data are likely more sensitive than CPUE for detecting effects from a management action or other environmental change (Carpenter et al. 1995). However, except for bluegill (Tomcko and Pierce 1997), data on length at age by lake class are not available to MNDNR staff.

We examined some factors that may affect growth of both crappie species throughout Minnesota. One objective of this project was to determine lengths at age of black crappies from each lake class where they are commonly found. However, because growth potentially differs between natural and man-made waters (Guy and Willis 1995a; 1995b), we also classified into separate categories reservoirs and impoundments. Crappie fisheries also occur in rivers; thus we gathered information from some of those systems as well. This report

provides mean back-calculated lengths at age for black crappies and white crappies sampled from these lake classes, plus reservoirs, impoundments, and rivers. We also determined if lengths at age differ among water body types, with changing CPUE of common fish species, among different aquatic plant communities, and with angling pressure. Lastly, we present general information on diet of both crappie species, which could explain links between length at age and the other independent variables tested.

Methods

Scale samples of both crappie species were obtained from each MNDNR area office. Acetate strips with scale impressions and data files with scale increment measurements were also obtained from most area offices. These samples and data came from crappies collected with either trap netting or gill netting during special assessments, population assessments, or lake surveys done between 1998 and 2002. Scale samples were usually collected from up to five individuals per 1-cm length group (MNDNR 1993).

At least one scale impression from each crappie was read with the aid of a microfiche reader. Scale impressions were made for those samples that did not come with acetate strips. One experienced reader (MCM) read each scale impression, estimated age, and measured increments between the center of the scale focus and each annulus and between the focus and scale edge along the longest axis in the middle of the scale. Initial scale increment measurements made by area office staff were usually used when the initial scale age agreed with the scale age determined by MCM, but increments measured by MCM were used when scale ages differed. To aid in consistency, increments measured by MCM were also used if measurements made by office staff differed substantially from those made by MCM.

To minimize positive bias in black crappie length at age estimates caused by hybridization, length-frequency distributions of all year classes of black crappies captured in trap nets set in water bodies with white crappies were examined for outliers and right skew-

ness. An age-length key was used to assign ages to unaged black crappies captured in trap nets in these water bodies. About 81% of the outliers in length distributions of selected year classes of black crappies were F_1 hybrids, which grow faster than black crappies in Minnesota waters (Miller et al. In press.). Although rarely observed, hybridization also accounts for strong right-skewness observed in some year classes (Miller et al. In press.). Thus, scale increment measurements of outliers and individuals causing strong right-skewness were removed from the data set. Hybridization does not affect white crappie growth estimates (Miller et al. In press.).

We calculated a mean back-calculated length for each age (1 through 5) of each species from each water body. We used the Fraser-Lee method with a standard intercept of 20 mm for estimating back-calculated lengths at age (MNDNR 1993). We back-calculated lengths at age from crappies we aged 1 to 5 years old because scale age became less reliable for aging crappies older than age 5 (McInerney et al., in preparation). To calculate a mean length at age for a water body, we first calculated mean lengths at age for each year class if two or more individuals were sampled. Then we calculated the mean length at age of all year classes sampled in the given water body.

Because distributions of mean lengths of each age were essentially normal, we calculated means and standard deviations for ages 1 through 5 of each species for each lake class, plus for reservoirs, impoundments, and rivers. We separated reservoirs and impoundments (usually assigned a lake class number) from natural lakes because growth rates of both crappie species from natural lakes differed from those observed in impoundments and reservoirs in South Dakota (Guy and Willis 1995a; 1995b). We defined as reservoirs those water bodies formed by natural or man-made damming of a river or stream, or wide regions of a river where a substantial portion of the energy appears to come from allochthonous sources. We defined impoundments as man-made water bodies that seldom discharge water. We used aerial photographs, MNDNR lake survey reports, and for one water body a plot of chlorophyll-*a* as a function of total

phosphorus (abnormally low chlorophyll-*a* relative to total phosphorus concentration) to aid in separating reservoirs and impoundments from naturally formed lakes.

We tested if length at age differed among classes of water bodies. For each species, we used one-way analysis of variance (ANOVA) to determine if mean lengths at age (each age group separately) differed ($P < 0.05$) among lake classes, reservoirs, impoundments, and rivers. If $P < 0.05$, then we used Tukey's Honestly Significant Difference (HSD) tests to identify which means differed significantly. For each ANOVA model, sample size per water body type equaled or exceeded two.

We used two analytical methods to test if lengths at ages 1 through 5 were linked with the independent variable lake class (analysis of natural lakes only), linked with the physical and chemical variables (lake surface area, maximum depth, percent littoral area, Secchi depth, total alkalinity, and UTM coordinates) used to develop lake classes (reservoirs and impoundments only), or linked with relative abundance of the most frequently sampled fishes (all waters except rivers and impoundments). First, we used regression tree analyses (RTA) to identify the independent variables (categorical and continuous) most strongly linked with lengths at age (McCune and Grace 2002). Results of RTA consist of a series of two-way splits of the independent variable explaining the most variation (i.e. high vs. low CPUE of a species) at that level of the split. This analysis is analogous to dichotomous keys; the output reports where in the distribution of the independent variable the split occurs and reports the means of the dependent variable (length at age data) within each of the two groups (Iverson and Prasad 1998). Regression trees also use continuous and categorical data simultaneously and are useful for identifying key variables when no other prior model exists (SAS 2002). Because regression trees are nonparametric, data transformations are unnecessary (McCune and Grace 2002). We used JMP software to generate all regression trees (SAS 2002). We continued splitting as long as R^2 values of the entire model increased by at least 0.05 or until sample sizes after splitting dropped below 10. Because RTA is conservative (i.e. may not reveal all

potential variables linked with length at age), we also calculated Pearson correlation coefficients between length at age and all continuous variables we collected. These continuous variables include relative abundance of each fish species, Secchi depth (m), total alkalinity (mg/L), lake surface area (hectares), maximum depth (m), percent littoral area (area of lake < 4.6 m deep/lake surface area), and Universal Transverse Mercator (UTM) northing and easting (m). We used gill net CPUE as an index of relative abundance of northern pike *Esox lucius*, black bullhead *Ameiurus melas*, yellow bullhead *A. natalis*, cisco *Coregonus artedii* (for analysis of black crappie length at age only), white sucker *Catostomus commersonii*, yellow perch, and walleye, and trap net CPUE as an index of abundance of bowfin *Amia calva*, common carp *Cyprinus carpio*, rock bass, green sunfish *Lepomis cyanellus*, pumpkinseed, bluegill, black crappie, and white crappie (for analysis of white crappie length at age only). All CPUE data were collected at the same time as scale samples and were gathered from the MNDNR statewide fisheries database. We used lake surface area and maximum depth from lake survey reports, and we used Landview Version 4.3.7 to obtain UTM coordinates. We gathered data on Secchi depth and total alkalinity from the MNDNR statewide fisheries database and calculated a mean value from all years available through 2001; we did not evaluate for temporal trends.

For natural lakes, we included in RTA lake class and excluded lake surface area, maximum depth, percent littoral area, Secchi depth, total alkalinity, and UTM coordinates because these variables are used to determine lake class and geographic centers of lake classes differ (Schupp 1992; Cook and Younk 1998). For reservoirs, we excluded from RTA lake class and included lake surface area, maximum depth, percent littoral area, Secchi depth, total alkalinity, and UTM coordinates. All RTA models included CPUE of the most common fish species sampled during lake surveys or assessments.

For correlation analysis, we excluded water bodies lacking a complete set of independent variables. However, for water bodies with small sample sizes (impoundments), we removed independent variables that were

missing from most waters. UTM northing and easting were the only independent variables acquired for rivers. To improve normality of data distributions, we \log_e transformed CPUE (CPUE + 1) of all fish species, \log_{10} transformed lake surface area, and we arcsine transformed percent littoral area. Lastly, we applied Bonferroni techniques by dividing P (we defined $P < 0.05$ as significant in this report) by the number of independent variables in the data sets (Trippel and Hubert 1990).

To test the effects of aquatic plant communities on length at age of crappies, we used the nine-category classification system by Reschke et al. (2006) to characterize aquatic plant communities in each lake. This aquatic plant classification is based on frequency of occurrence data among transects sampled during MNDNR lake surveys (MNDNR 1993), and the categories are numbered as 1, 3, 16, 40, 42, 59, 66, 117, and 134 (Reschke et al. 2006). Lakes with plant community types 1, 3, and 16 have the most diverse plant communities, but the most common plant taxa differ among these types (Appendix 1). Lakes characterized as type 40 have high plant diversity, but the exotic Eurasian milfoil *Myriophyllum spicatum* is common. Type 42 lakes have the least diverse plant communities and are sometimes ringed with broadleaf cattail *Typha latifolia*, and type 59 lakes are ringed with sedges *Carex* spp. Algae, sago pondweed *Potamogeton pectinatus*, northern milfoil *Myriophyllum sibiricum*, and coontail *Ceratophyllum demersum* compose most of the plants in lakes characterized as type 66, and lakes characterized as types 117 or 134 have fewer plant taxa and the exotic curly-leaf pondweed *Potamogeton crispus* is common (Reschke et al. 2006; Appendix 1). Reschke et al. (2006) found different aquatic plant communities in lakes with low (< 100 mg/L) alkalinity than in lakes with high alkalinity. We used one-way ANOVA to test if length at age differed among plant community types in natural lakes, reservoirs, and impoundments. Separate analyses were done for low-alkalinity and high-alkalinity waters. We used Tukey's HSD tests to identify the specific means that differed ($P < 0.05$) when ANOVA models were significant.

Because diet affects growth, we gathered data on crappie diets from individual lakes throughout Minnesota. Staff from most area offices sent to us samples of crappies collected during their routine surveys and population assessments. We measured total length in millimeters and examined stomach contents of each individual fish. We identified to the nearest practical taxon (usually to the nearest order) all invertebrates (using Pennak [1978] as a guide) and all fish. We classified diet into four groups, loosely based on size of the organisms: small crustaceans (Cladocera, Copepoda, Amphipoda), small insects (< 20 mm TL), large insects (\geq 20 mm TL), and fish. For each 1-cm length group (all samples combined) of each crappie species, we calculated the percentage of stomachs containing each group of food items. For each species of crappie, we plotted as a function of 1-cm length group the percentage of stomachs containing each group of food items. We also measured total length (mm) of fish prey consumed by crappies and plotted prey length as a function of length of each crappie species (all samples combined for each species). We used Pearson correlations to test for associations between prey length and crappie length.

To test if estimates of length at age are potentially affected by angling, we plotted mean length at age estimated for each lake class as a function of mean summer angling pressure among these same lake classes. We used summer angling pressure data by lake class reported in Cook and Younk (2001). We then used Pearson correlation coefficients to show associations between length at age and pressure estimates. Because the black crappie is more widely distributed in Minnesota, we limited this analysis to just black crappie and used only lake classes where sample size of length at age estimates equaled or exceeded two.

Results

Black crappie

We estimated length at age of 32,751 black crappies from 895 lakes from 36 lake classes, 57 reservoirs, six impoundments (Figure 1), and six rivers. Rivers sampled included the Rainy (Lake of the Woods County), Red Lake (one location in Pennington and two lo-

cations in Polk County), Thief (Pennington County), St. Louis (St. Louis County), Red (Wilkin County), and Vermillion (Goodhue County). We calculated mean lengths at age with standard deviations for 32 of the 36 lake classes, plus reservoirs, impoundments, and rivers (Table 1). Mean lengths at age 1 ($F = 19.20$; $df = 34, 927$; $P < 0.0001$), age 2 ($F = 13.19$; $df = 34, 896$; $P < 0.0001$), age 3 ($F = 8.09$; $df = 34, 845$; $P < 0.0001$), age 4 ($F = 7.76$; $df = 34, 699$; $P < 0.0001$), and age 5 ($F = 6.18$; $df = 33, 415$; $P < 0.0001$) differed among classes of water bodies. The longest mean lengths for all ages came from class 43 lakes, and black crappies from class 41 lakes were also consistently long at all ages (Table 1). Conversely, lengths at ages 1 through 5 in lake classes 11 and 37 were comparatively short (Table 1). Lengths at age 1 from classes 22 and 27 were relatively short, but lengths at ages 4 and 5 were among the longest (Table 1). On the other hand, mean lengths in class 24 and 38 lakes were relatively high at ages 1 and 2 but were among the shortest at ages 4 and 5 (Table 1). Lengths at ages 1 through 5 in reservoirs also ranked relatively high compared to those of natural lakes, but lengths in impoundments were relatively short after age 2.

Regression tree analyses suggested that lake class and CPUE of black bullhead, pumpkinseed, and walleye affected lengths at age in natural lakes (Table 2). Lengths at age 1 in a set of eight lake classes exceeded lengths in the other larger set of lake classes. Longer lengths at age 2 occurred in lakes with higher CPUE of black bullheads coupled with low CPUE of pumpkinseeds, and shorter lengths occurred in lakes with low CPUE of black bullheads coupled with low CPUE of walleyes. Longer lengths at ages 3 through 5 occurred in lakes with higher CPUE of walleyes.

Correlation analysis suggests that lengths at age in natural lakes differed geographically, and, depending on age, changed with changing CPUE of black bullhead, common carp, and walleye, and increased with increasing total alkalinity (Table 3). Lengths at age 1 decreased with increasing UTM northing, increasing CPUE of black bullhead, and increasing CPUE of common carp. Lengths at age 2 increased with increasing CPUE of black bullheads and increasing total alkalinity.

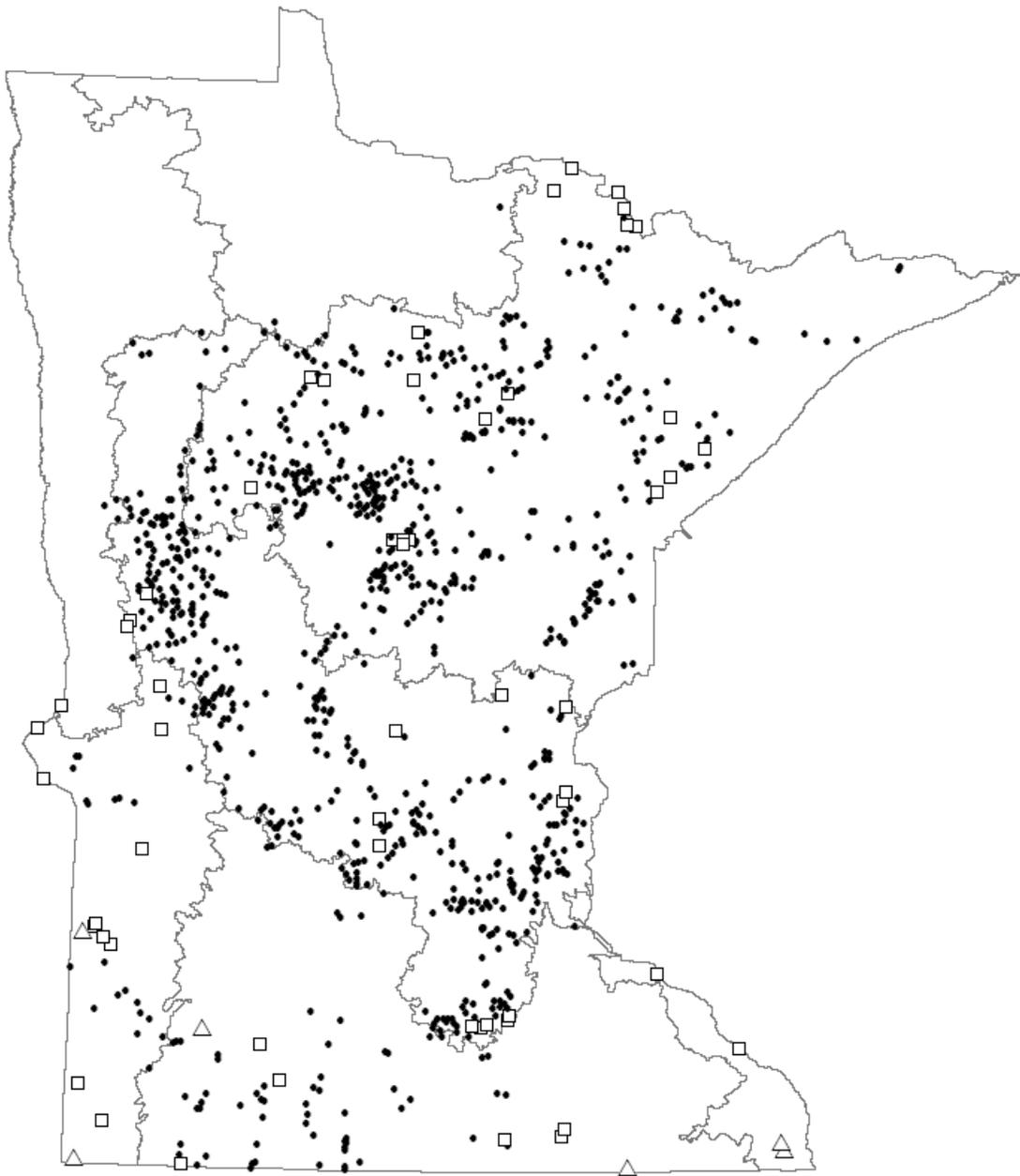


Figure 1. Locations of lakes (solid circles), reservoirs (open squares), and impoundments (open triangles) where scale samples from black crappies were collected.

Table 1. Mean (s.d.) back-calculated total lengths (mm) at ages 1 through 5 of black crappie from 36 lake classes plus reservoirs, impoundments, and rivers across Minnesota (columns with same superscripted letter denote that means did not differ [$P > 0.05$]; Tukey's Honestly Significant Difference tests).

Lake class	n	Lengths at age (mm)				
		Age 1	Age 2	Age 3	Age 4	Age 5
2	1	52	113	186	234	268
5	11	45 (4) ^g	102 (15) ^{f-i}	172 (24) ^{b-i}	219 (26) ^{a-g}	248 (26) ^{a-f}
6	1	53	118	193	241	
7	7	52 (6) ^{d-g}	109 (19) ^{d-i}	176 (29) ^{a-i}	219 (26) ^{a-g}	252 (23) ^{a-f}
8	1	73	136	196	230	252
10	5	44 (1) ^{fg}	90 (17) ^{f-i}	144 (36) ^{e-i}	197 (45) ^{a-g}	222 (49) ^{a-f}
11	14	50 (11) ^{fg}	102 (26) ⁱ	156 (28) ^{g-i}	191 (21) ^{a-g}	213 (20) ^{c-f}
12	9	48 (3) ^{fg}	105 (20) ^{e-i}	171 (33) ^{b-i}	215 (32) ^{a-g}	237 (5) ^{a-f}
13	5	48 (3) ^{e-g}	97 (10) ^{e-i}	156 (26) ^{c-i}	195 (36) ^{a-g}	203 (29) ^{a-f}
14	2	53 (8) ^{a-g}	134 (1) ^{a-i}	224 (28) ^{a-i}	265 (20) ^{a-g}	289
16	8	48 (5) ^{fg}	106 (26) ^{e-i}	169 (36) ^{b-i}	212 (38) ^{a-g}	225 (28) ^{a-f}
18	1	65	145	198		
19	14	52 (9) ^{e-g}	113 (22) ^{d-i}	188 (33) ^{a-i}	226 (25) ^{a-g}	263 (17) ^{a-e}
20	11	54 (17) ^{d-g}	100 (11) ⁱ	158 (24) ^{e-i}	187 (10) ^{e-g}	219 (15) ^{a-f}
21	9	52 (5) ^{e-g}	99 (8) ^{hi}	150 (12) ^{hi}	187 (15) ^{e-g}	214 (12) ^{c-f}
22	44	56 (6) ^{e-g}	129 (19) ^{d-i}	197 (18) ^{a-e}	243 (18) ^{a-c}	271 (23) ^{ab}
23	42	50 (5) ^g	119 (19) ^{e-i}	190 (27) ^{b-h}	231 (30) ^{a-f}	253 (31) ^{a-e}
24	86	65 (11) ^{b-d}	133 (21) ^{de}	183 (29) ^{d-i}	212 (33) ^{e-g}	225 (33) ^{d,f}
25	66	52 (7) ^{fg}	116 (21) ^{f-i}	184 (29) ^{c-i}	226 (30) ^{b-f}	252 (33) ^{a-c, e}
27	72	56 (8) ^{fg}	133 (22) ^{c-e}	203 (24) ^{a-c}	248 (25) ^{ab}	273 (28) ^a
28	22	52 (8) ^{fg}	117 (27) ^{e-i}	176 (30) ^{c-i}	221 (27) ^{a-g}	241 (26) ^{a-f}
29	42	53 (6) ^{fg}	112 (19) ^{f-i}	171 (29) ^{f-i}	210 (35) ^{e-g}	232 (36) ^{b-f}
30	35	63 (11) ^{b-e}	127 (22) ^{f-i}	175 (27) ^{e-i}	201(28) ^{fg}	221 (31) ^{d-f}
31	74	54 (6) ^{fg}	121 (20) ^{e-i}	188 (27) ^{b-h}	229 (29) ^{a-e}	254 (26) ^{a-c, e}
32	27	52 (5) ^{fg}	109 (17) ^{g,i}	163 (29) ^{g-i}	200 (36) ^{e-g}	211 (37) ^{d,f}
33	9	56 (11) ^{c-g}	117 (30) ^{d-i}	171 (40) ^{b-i}	200 (40) ^{b-g}	224 (39) ^{a-f}
34	49	57 (9) ^{e-g}	130 (23) ^{d-f, h}	193 (34) ^{b-f}	230 (35) ^{a-f}	259 (37) ^{a-c, e}
35	12	53 (10) ^{e-g}	115 (34) ^{d-i}	172 (46) ^{c-i}	200 (43) ^{d-g}	221 (40) ^{a-f}
36	18	58 (13) ^{c-g}	119 (29) ^{d-i}	170 (38) ^{e-i}	193 (43) ^{e-g}	221 (48) ^{b-f}
37	19	57 (10) ^{d-g}	116 (32) ^{e-i}	156 (31) ⁱ	184 (36) ^g	185 (26) ^f
38	25	67 (16) ^{b-d}	133 (25) ^{b-g}	183 (29) ^{b-i}	210 (29) ^{c-g}	224 (33) ^{b-f}
39	29	60 (11) ^{c-f}	132 (26) ^{c-h}	194 (29) ^{a-g}	234 (33) ^{a-f}	256 (36) ^{a-e}
40	11	74 (10) ^{ab}	136 (29) ^{b-i}	176 (41) ^{b-i}	198 (50) ^{d-g}	219 (70) ^{a-f}
41	30	69 (13) ^{a-c}	152 (25) ^{a-c}	211 (28) ^{ab}	245 (26) ^{a-c}	264 (25) ^{a-c}
42	19	73 (14) ^{ab}	159 (29) ^{ab}	212 (36) ^{a-d}	233 (42) ^{a-g}	233 (51) ^{a-f}
43	65	77 (11) ^a	165 (25) ^a	217 (28) ^a	252 (32) ^a	272 (32) ^a
Reservoirs	57	66 (15) ^{b-d}	141 (29) ^{b-d}	202 (32) ^{a-d}	237 (29) ^{a-d}	262 (34) ^{a-c}
Impoundments	6	67 (11) ^{a-f}	126 (19) ^{b-i}	155 (16) ^{c-i}	179 (15) ^{e-g}	209 (12) ^{a-f}
Rivers	8	57 (10) ^{c-g}	127 (19) ^{b-i}	185 (22) ^{a-i}	230 (17) ^{a-g}	263 (13) ^{a-e}

Table 2. Mean (s.d.) back-calculated total lengths at ages 1 through 5 of black crappie as a function of lake class, gill net catch per unit effort (number per lift; CPUE) of black bullhead and walleye, and trap net CPUE of pumpkinseed among natural lakes in Minnesota (based on regression tree analysis; r^2 listed on the first couplet of each split denotes the amount of variation explained).

Length at age 1 (Total $R^2 = 0.347$)	
Lake class (8,18,24,30,38,40,41,42,43) (Length = 68 (11) mm; n = 248); $r^2 = 0.347$	
Lake class (5,6,7,10,11,12,14,19,20,21,22,23,25,27,28,29,31,32,33,34,35,36,37,39) (Length = 54 (8) mm; n = 603)	
Length at age 2 (Total $R^2 = 0.381$)	
Black bullhead CPUE ≥ 3.7 per lift (Length = 145 (27) mm; n = 262); $r^2 = 0.225$	
Pumpkinseed CPUE ≥ 0.2 per lift (Length = 136 (25) mm; n = 177); $r^2 = 0.076$	
Pumpkinseed CPUE < 0.2 per lift (Length = 164 (22) mm; n = 85)	
Black bullhead CPUE < 3.7 per lift (Length = 117 (22) mm; n = 568)	
Walleye CPUE ≥ 2.7 per lift (Length = 128 (21) mm; n = 251); $r^2 = 0.080$	
Walleye CPUE < 2.3 per lift (Length = 109 (18) mm; n = 317)	
Length at age 3 (Total $R^2 = 0.211$)	
Walleye CPUE ≥ 3.0 per lift (Length = 203 (27) mm; n = 340); $r^2 = 0.211$	
Walleye CPUE < 3.0 per lift (Length = 173 (30) mm; n = 444)	
Length at age 4 (Total $R^2 = 0.253$)	
Walleye CPUE ≥ 2.7 per lift (Length = 242 (29) mm; n = 291); $r^2 = 0.253$	
Walleye CPUE < 2.7 per lift (Length = 206 (32) mm; n = 360)	
Length at age 5 (Total $R^2 = 0.290$)	
Walleye CPUE ≥ 2.7 per lift (Length = 266 (31) mm; n = 171); $r^2 = 0.290$	
Walleye CPUE < 2.7 per lift (Length = 225 (33) mm; n = 236)	

Table 3. Correlation coefficients between mean back-calculated total lengths at ages 1 through 5 of black crappie and Universal Transverse Mercator (UTM) northing and easting; lake surface area (ha), maximum depth (m), and percent littoral area of lakes; Secchi depth (m) and total alkalinity (mg/L); gill net catch per unit effort (CPUE) of black bullhead, yellow bullhead, white sucker, northern pike, cisco, yellow perch, and walleye; and trap net CPUE of bowfin, common carp, rock bass, green sunfish, pumpkinseed, bluegill, and black crappie among natural lakes in Minnesota (* denotes correlation coefficient differs [$P \leq 0.05$ adjusted with Bonferroni techniques] from zero).

Variable	Age				
	1	2	3	4	5
UTM Northing	-0.60*	-0.44*	-0.20*	-0.07	0.03
UTM Easting	-0.16*	-0.38*	-0.42*	-0.42*	-0.47*
Lake surface area	0.02	0.19*	0.30*	0.37*	0.43*
Maximum depth	-0.31*	-0.24*	-0.06	0.04	0.05
Percent littoral area	0.35*	0.28*	0.12*	0.03	-0.02
Secchi depth	-0.43*	-0.34*	-0.17*	-0.07	-0.03
Total alkalinity	0.31*	0.47*	0.46*	0.44*	0.45*
Gill net CPUE					
Black bullhead	0.56*	0.52*	0.32*	0.20*	0.18*
Yellow bullhead	-0.19*	-0.13*	-0.05	0.00	0.04
White sucker	-0.04	0.12*	0.24*	0.28*	0.25*
Northern pike	-0.31*	-0.26*	-0.13*	-0.07	-0.04
Cisco	-0.20*	-0.09	0.02	0.11	0.15
Yellow perch	0.30*	0.35*	0.30*	0.24*	0.24*
Walleye	0.19*	0.41*	0.50*	0.53*	0.55*
Trap net CPUE					
Bowfin	-0.07	-0.01	0.05	0.09	0.11
Common carp	0.49*	0.41*	0.27*	0.20*	0.19*
Rock bass	-0.27*	-0.11	0.08	0.19*	0.29*
Green sunfish	0.06	0.02	0.01	-0.02	-0.05
Pumpkinseed	-0.31*	-0.22*	-0.14*	-0.11	-0.09
Bluegill	-0.17*	-0.33*	-0.31*	-0.30*	-0.30*
Black crappie	0.38*	0.14*	-0.04	-0.11	-0.13
n	749	729	690	570	342

Lengths at ages 3, 4, and 5 increased with increasing CPUE of walleye and increasing total alkalinity, and lengths at ages 4 and 5 decreased with increasing UTM easting and increased with increasing lake surface area. Lengths at ages 1 and 2 were negatively linked with Secchi depth and maximum depth and positively linked with percent littoral area, while lengths at ages 2 through 5 were negatively linked with bluegill CPUE.

Length at age of black crappie in reservoirs was linked with geographic location; lake surface area; gill net CPUE of walleye, white sucker, and yellow perch; and trap net CPUE of common carp and rock bass (Tables 4 and 5). With RTA, the first splits for lengths at ages 1 and 2 were a function of UTM northing, which approximated a line bisecting Mille Lacs. Lengths south of this line exceeded lengths at the same ages north of this line (Table 4). Lengths at ages 1 and 2 south of Mille Lacs were also longer in reservoirs with higher gill net CPUE of walleye. Lengths at ages 3 and 4 in reservoirs with higher gill net CPUE of walleye exceeded lengths of the same respective ages in reservoirs with lower CPUE of walleye. In reservoirs with lower gill net CPUE of walleye, lengths at age 3 were longer in reservoirs with lower gill net CPUE of white sucker. In reservoirs with higher CPUE of white sucker, lengths at age 3 in more westerly (line from Mankato to the east shore of Lake Winnibigoshish) reservoirs exceeded lengths in easterly reservoirs. In these westerly reservoirs with higher CPUE of white sucker, lengths at age 3 were longer in reservoirs with higher gill net CPUE of walleye. Lengths at age 4 west of a line between Grand Rapids and Waseca exceeded lengths east of this line in reservoirs with lower gill net CPUE of walleye. Lengths at age 4 of these westerly populations were longer in reservoirs with higher gill net CPUE of yellow perch. The shortest lengths occurred in the most easterly reservoirs. The longer lengths at age 5 occurred in the larger reservoirs (Table 4). Correlation analysis generally reflected RTA; however, lengths at ages 1 through 3 increased with increasing total alkalinity, and lengths at age 1 increased with decreasing maximum depth, increasing trap net CPUE of common

carp, and decreasing trap net CPUE of rock bass (Table 5).

Lengths at age in impoundments were unrelated to UTM northing and easting, percent littoral area, maximum depth and surface area; however, sample size was also low (Table 6). Gill net samples were collected in only one impoundment; thus we did not test for effects associated with relative abundance of fish. Lengths at ages 1 through 4 in rivers increased with decreasing UTM northing but were not linked with UTM easting (Table 6). We did not conduct RTA on impoundments or rivers because we lacked sufficient sample sizes.

Lengths at age differed in lakes and reservoirs with differing plant community types. Lengths at most ages were shorter in natural lakes with plant community type 3 (highly diverse plant communities but with no clear dominant taxa) regardless of alkalinity (Table 7). In low-alkalinity lakes, lengths at ages 2 through 4 in lakes classified as plant community type 16 (highly diverse plant community but with high frequency of occurrence/abundance of *Chara* spp., bushy pondweed *Najas flexilis*, flatstem pondweed *Potamogeton zosteriformis*, coontail, and northern milfoil; Appendix 1) exceeded lengths at the same ages in type 3 lakes. In high-alkalinity lakes, the longest lengths at all ages occurred in type 134 (relatively low diversity with high frequency of occurrence/abundance of sago pondweed and curly-leaf pondweed) lakes. Lengths at age 1 in reservoirs with type 66 (high frequency of occurrence/abundance of algae, sago pondweed, northern milfoil, coontail, and flatstem pondweed) plant communities exceeded lengths at age 1 in type 16 reservoirs (Table 7). Too few samples came from low-alkalinity reservoirs to address plant community effects.

Diet of 1,298 black crappies from 90 lakes was diverse (Table 8), but most fed on small aquatic insects. Essentially all (98%) of the identifiable small insect prey consisted of larvae and pupae of Chaoborinae and Chironomidae. We found small insects in over half of the stomachs (all lakes combined) in most length groups between 100 and 290 mm TL (Figure 2). Small crustaceans occurred in

Table 4. Mean (s.d.) back-calculated total lengths at ages 1 through 5 of black crappie as a function of Universal Transverse Mercator (UTM) northing and easting coordinates; lake surface area (ha); and gill net catch per unit effort (number per lift; CPUE) of white sucker, yellow perch, and walleye among reservoirs in Minnesota (based on regression tree analysis; r^2 listed on the first couplet of each split denotes the amount of variation explained).

Length at age 1 (Total $R^2 = 0.755$)

UTM Northing ≥ 5126122 (Length = 53 (7) mm; n = 18); $r^2 = 0.647$

UTM Northing < 5126122 (Length = 77 (10) mm; n = 22)

Walleye CPUE ≥ 11.5 per lift (Length = 85 (8) mm; n = 8); $r^2 = 0.108$

Walleye CPUE < 11.5 per lift (Length = 72 (9) mm; n = 14)

Length at age 2 (Total $R^2 = 0.756$)

UTM Northing ≥ 5123144 (Length = 121 (16) mm; n = 18); $r^2 = 0.552$

UTM Northing < 5123144 (Length = 166 (25) mm; n = 19)

Walleye CPUE ≥ 12.3 per lift (Length = 192 (10) mm; n = 7); $r^2 = 0.204$

Walleye CPUE < 12.3 per lift (Length = 152 (19) mm; n = 12)

Length at age 3 (Total $R^2 = 0.708$)

Walleye CPUE ≥ 15.2 per lift (Length = 251 (10) mm; n = 6); $r^2 = 0.371$

Walleye CPUE < 15.2 per lift (Length = 197 (29) mm; n = 31)

White sucker CPUE ≥ 1.0 per lift (Length = 190 (25) mm; n = 24); $r^2 = 0.147$

UTM Easting ≥ 421209 (Length = 174 (21) mm; n = 11); $r^2 = 0.124$

UTM Easting < 421209 (Length = 203 (21) mm; n = 13)

Walleye CPUE ≥ 4.3 per lift (Length = 221 (24) mm; n = 5); $r^2 = 0.066$

Walleye CPUE < 4.3 per lift (Length = 192 (7) mm; n = 8)

White sucker CPUE < 1.0 per lift (Length = 222 (26) mm; n = 7)

Length at age 4 (Total $R^2 = 0.714$)

Walleye CPUE ≥ 12.7 per lift (Length = 282 (17) mm; n = 5); $r^2 = 0.336$

Walleye CPUE < 12.7 per lift (Length = 232 (28) mm; n = 26)

UTM Easting ≥ 459421 (Length = 216 (26) mm; n = 10); $r^2 = 0.144$

UTM Easting ≥ 504345 (Length = 235 (17) mm; n = 5); $r^2 = 0.122$

UTM Easting < 504345 (Length = 196 (18) mm; n = 5)

UTM Easting < 459421 (Length = 242 (24) mm; n = 16)

Yellow perch CPUE ≥ 13.3 per lift (Length = 259 (22) mm; n = 7); $r^2 = 0.112$

Yellow perch CPUE < 13.3 per lift (Length = 229 (17) mm; n = 9)

Length at age 5 (Total $R^2 = 0.406$)

Lake surface area ≥ 664 ha (Length = 283 (24) mm; n = 9); $r^2 = 0.406$

Lake surface area < 664 ha (Length = 240 (31) mm; n = 9)

Table 5. Correlation coefficients between mean back-calculated total lengths at ages 1 through 5 of black crappie and Universal Transverse Mercator (UTM) northing and easting; lake surface area (ha), maximum depth (m), and percent littoral area of reservoirs; Secchi depth (m) and total alkalinity (mg/L); gill net catch per unit effort (CPUE) of black bullhead, yellow bullhead, white sucker, northern pike, cisco, yellow perch, and walleye; and trap net CPUE of bowfin, common carp, rock bass, green sunfish, pumpkinseed, bluegill, and black crappie among Minnesota reservoirs (* denotes correlation coefficient differs [$P \leq 0.05$ adjusted with Bonferroni techniques] from zero).

Variable	Age				
	1	2	3	4	5
UTM Northing	-0.68*	-0.61*	-0.43	-0.12	-0.24
UTM Easting	-0.64*	-0.62*	-0.57*	-0.49	-0.57
Lake surface area	-0.00	0.01	0.10	0.38	0.47
Maximum depth	-0.53*	-0.50	-0.26	-0.00	0.06
Percent littoral area	0.48	0.51	0.34	0.14	0.06
Secchi depth	-0.48	-0.47	-0.24	0.02	0.12
Total alkalinity	0.74*	0.71*	0.61*	0.38	0.38
Gill net CPUE					
Black bullhead	0.40	0.40	0.29	0.12	0.19
Yellow bullhead	-0.17	-0.18	0.02	0.10	0.23
White sucker	0.06	0.20	0.15	0.39	0.19
Northern pike	-0.47	-0.48	-0.26	-0.13	-0.07
Cisco	-0.49	-0.43	-0.25	-0.07	0.03
Yellow perch	0.40	0.51	0.40	0.38	0.34
Walleye	0.37	0.59*	0.57*	0.56*	0.51
Trap net CPUE					
Bowfin	-0.17	-0.33	0.39	-0.43	-0.51
Common carp	0.51*	0.49	0.32	0.01	0.06
Rock bass	-0.55*	-0.42	-0.17	0.13	0.29
Green sunfish	0.13	0.11	0.06	-0.07	-0.04
Pumpkinseed	-0.31	-0.43	-0.24	-0.03	0.02
Bluegill	0.00	-0.22	-0.08	0.01	0.13
Black crappie	0.38	0.31	0.12	-0.13	0.03
n	35	32	32	27	15

Table 6. Correlation coefficients between mean back-calculated total lengths at ages 1 through 5 of black crappie in impoundments and Universal Transverse Mercator (UTM) northing and easting; lake surface area (ha), maximum depth (m), and percent littoral area; and mean lengths at ages 1 through 5 of black crappie in rivers and UTM northing and easting (* denotes correlation coefficient differs [$P \leq 0.05$ adjusted with Bonferroni techniques] from zero).

Variable	Age					
	1	2	3	4	5	
		Impoundments				
UTM Northing	0.72	0.65	-0.46	-0.08		
UTM Easting	-0.84	-0.55	0.30	0.29		
Lake surface area	0.49	0.74	0.53	0.80		
Maximum depth	0.15	-0.03	-0.45	-0.07		
Percent littoral area	-0.33	-0.03	0.54	0.20		
n	6	6	5	5	3	
		Rivers				
UTM Northing	-0.80*	-0.79*	-0.81*	-0.89*	-0.73	
UTM Easting	0.03	0.20	0.41	0.60	0.75	
n	8	8	8	7	6	

Table 7. Mean (s.e.) back-calculated total lengths (mm) at ages 1 through 5 of black crappie among nine aquatic plant community types (Reschke 2006) in lakes and reservoirs with low (< 100 mg/L) and high (\geq 100 mg/L) total alkalinity, and mean lengths at ages 1 through 5 of white crappie among seven aquatic plant community types in lakes with high total alkalinity (columns within groups with same superscripted letters denote means did not differ [$P > 0.05$]; Tukey's Honestly Significant Difference tests).

Plant community type	Mean lengths at age (s.e.)				
	1	2	3	4	5
Black crappie in low-alkalinity lakes (n = 187)					
1	56 (2) ^b	113 (3) ^{ab}	168 (5) ^{ab}	201 (6) ^{ab}	225 (8) ^a
3	51 (1) ^b	103 (2) ^b	160 (3) ^b	199 (4) ^b	220 (5) ^a
16	54 (2) ^b	117 (3) ^a	182 (5) ^a	222 (6) ^a	240 (8) ^a
40	69 (4) ^a	135 (7) ^a	180 (11) ^{ab}	202 (13) ^{ab}	227 (15) ^a
59	52 (4) ^b	117 (7) ^{ab}	186 (11) ^{ab}	222 (14) ^{ab}	207 (26) ^a
66	58 (5) ^{ab}	109 (11) ^{ab}	161 (17) ^{ab}	178 (25) ^{ab}	
117	69 (4) ^a	127 (7) ^{ab}	174 (12) ^{ab}	204 (14) ^{ab}	221 (19) ^a
Black crappie in high-alkalinity lakes (n = 378)					
1	55 (1) ^d	126 (2) ^d	192 (3) ^{bcd}	234 (3) ^b	256 (5) ^{ab}
3	61 (2) ^{cd}	125 (6) ^d	173 (7) ^d	204 (8) ^c	218 (10) ^c
16	54 (1) ^d	127 (2) ^d	195 (3) ^{bcd}	238 (3) ^{ab}	265 (4) ^{ab}
40	67 (1) ^{bc}	133 (4) ^{cd}	182 (4) ^{cd}	213 (5) ^c	227 (6) ^c
42	73 (2) ^{ab}	158 (6) ^{ab}	211 (7) ^{ab}	242 (8) ^{ab}	264 (10) ^{ab}
66	67 (1) ^{bc}	151 (3) ^{bc}	211 (4) ^a	243 (5) ^{ab}	275 (7) ^{ab}
117	75 (2) ^{ab}	153 (6) ^{abc}	205 (8) ^{abc}	233 (11) ^{abc}	226 (15) ^{bc}
134	76 (2) ^a	170 (5) ^a	225 (6) ^a	261 (7) ^a	285 (11) ^a
Black crappie in high-alkalinity reservoirs (n = 23)					
16	58 (7) ^b	128 (15) ^a	207 (20) ^a		
40	76 (4) ^{ab}	154 (11) ^a	208 (14) ^a	229 (16) ^a	227 (23) ^a
42	68 (8) ^{ab}	149 (19) ^a	204 (24) ^a	223 (25) ^a	
66	84 (5) ^a	183 (12) ^a	240 (15) ^a	275 (18) ^a	291 (19) ^a
White crappie in high-alkalinity lakes (n = 44)					
3	62 (9) ^{ab}	124 (16) ^c	183 (15) ^a	217 (20) ^a	
16	58 (5) ^b	143 (9) ^{bc}	203 (10) ^a	240 (14) ^a	
40	67 (5) ^{ab}	158 (9) ^{abc}	195 (11) ^a	239 (17) ^a	
42	83 (5) ^a	173 (10) ^{abc}	222 (11) ^a	246 (14) ^a	
66	75 (6) ^{ab}	195 (11) ^a			
117	79 (5) ^{ab}	173 (8) ^{abc}	223 (8) ^a	258 (20) ^a	
134	84 (5) ^a	185 (10) ^{ab}	223 (10) ^a	250 (14) ^a	

Table 8. Invertebrate (small crustaceans, small insects, large insects, other invertebrates) and fish taxa consumed by black crappie and white crappie in Minnesota lakes.

Black crappie	White crappie
	Small crustaceans
Cladocera	Cladocera
<i>Daphnia</i> spp.	<i>Daphnia</i> spp.
Copepoda	Copepoda
Amphipoda	Amphipoda
<i>Gammarus</i> spp.	<i>Gammarus</i> spp.
	Small insects (< 20 mm TL)
Diptera	Diptera
Chaoborinae	Chaoborinae
<i>Chaoborus</i> spp.	<i>Chaoborus</i> spp.
Chironomidae	Chironomidae
	Large insects (> 20 mm TL)
Ephemeroptera	Ephemeroptera
<i>Hexagenia</i> spp.	<i>Hexagenia</i> spp.
Odonata	Odonata
Anisoptera	Anisoptera
Zygoptera	Zygoptera
Chironomidae	Chironomidae
	Other invertebrates
Hirudinea	Gastropoda
Gastropoda	
Decapoda	
	Fish
Dace <i>Phoxinus</i> spp.	White sucker
Shiners	Bluntnose minnow <i>Pimephales notatus</i>
Other Cyprinidae	Shiners
Bullhead <i>Ameiurus</i> spp.	Other Cyprinidae
Brook stickleback <i>Culaea inconstans</i>	Yellow perch
Sunfish <i>Lepomis</i> spp.	
Largemouth bass	
Crappie <i>Pomoxis</i> spp.	
Johnny darter <i>Etheostoma nigrum</i>	
Yellow perch	
Walleye	
Freshwater drum <i>Aplodinotus grunniens</i>	

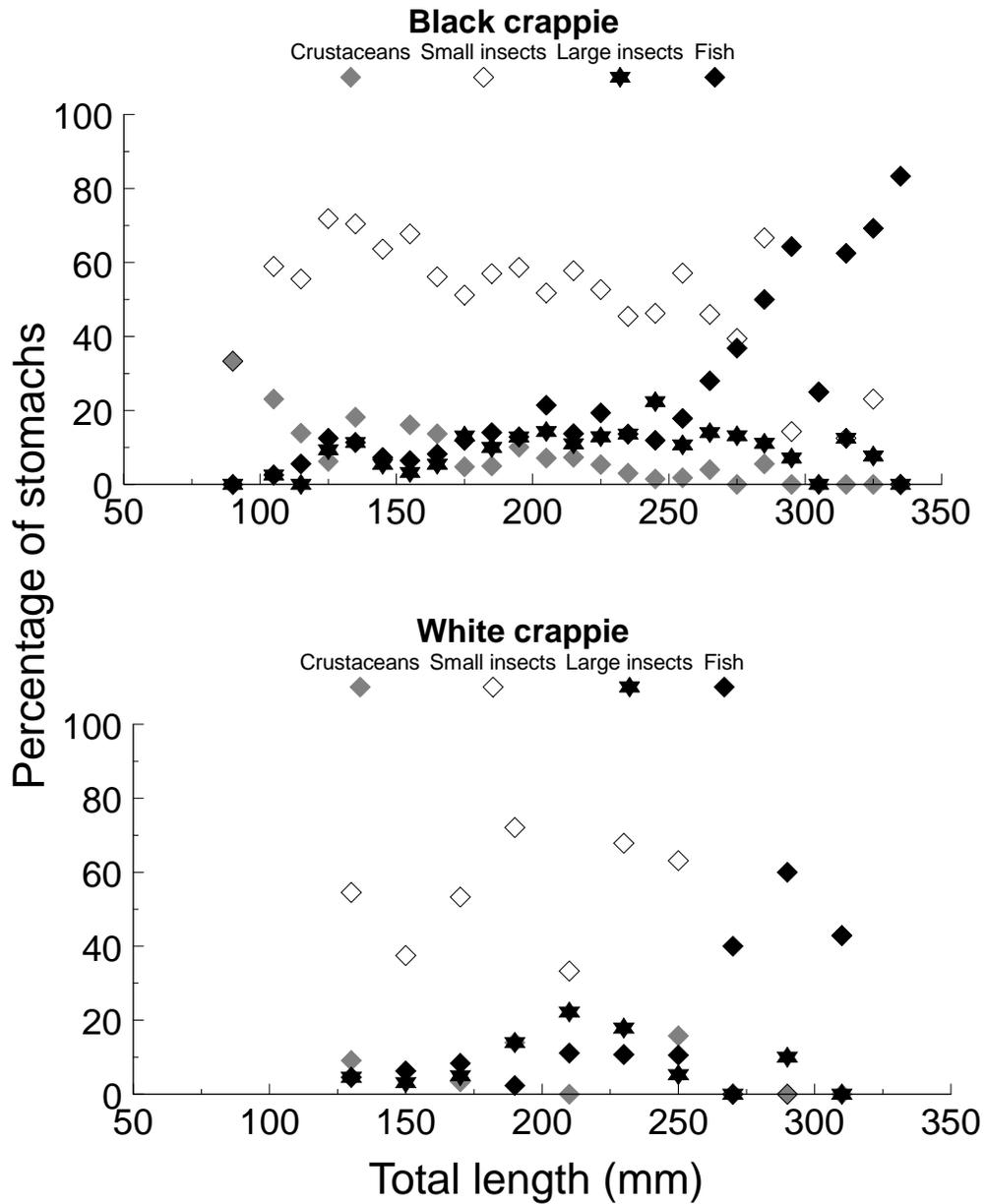


Figure 2. Percentage of black crappie and white crappie stomachs containing small crustaceans, small insects (< 20 mm TL), large insects (\geq 20 mm TL), and fish from Minnesota lakes.

over 20% of the stomachs of black crappies < 110 mm TL, but rarely occurred in longer individuals. Large insects occurred in 10-15 % of the stomachs of individuals 200 mm TL and longer. Black crappies as small as 100 mm TL consumed fish, but only after black crappies exceeded 260 mm TL did fish occur in at least 20% of the stomachs (Figure 2). Fish prey length ranged from 10 to 102 mm TL and increased gradually ($r = 0.40$; $n = 255$; $P < 0.0001$) with increasing length of black crappie (Figure 3). Yellow perch (25% of combined identifiable fish prey in stomachs; 17% of lakes) and sunfish (30% of combined identifiable fish prey in stomachs; 10% of lakes) were the most common identifiable fish prey items found in black crappie stomachs. Black crappie 173 to 331 mm TL fed on yellow perch 25 to 93 mm TL, but prey lengths did not change with changing length of black crappie ($r = 0.16$; $n = 42$; $P = 0.3186$; Figure 3). Sunfish 10 to 66 mm TL were found in stomachs of black crappie 134 to 285 mm TL, and sunfish prey length increased with increasing length of black crappie ($r = 0.56$; $n = 50$; $P < 0.0001$; Figure 3).

Length at age of black crappie in some populations could be affected by excessive angler harvest. Lengths at ages 1 ($r = 0.17$; $P = 0.3944$), 2 ($r = -0.05$; $P = 0.7812$), and 3 ($r = -0.27$; $P = 0.1639$) among 28 lake classes did not change with increasing angling pressure during the open-water period (Figure 4). However, lengths at ages 4 ($r = -0.45$; $P = 0.0161$) and 5 ($r = -0.37$; $P = 0.0512$) declined with increasing summer angling pressure among lake classes.

White crappie

We determined length at age of 1,895 white crappies from 76 water bodies, which included 13 lake classes, 13 reservoirs, two impoundments (Figure 5), and one river (Vermillion River, Goodhue County). Mean lengths at age 1 were not strongly different among classes of water bodies ($F = 1.91$; $df = 10,60$; $P = 0.0609$; Table 9). Mean lengths at age 2 ($F = 4.36$; $df = 10,53$; $P = 0.0002$), age 3 ($F = 4.92$; $df = 9,40$; $P = 0.0002$), age 4 ($F = 3.41$; $df = 7, 26$; $P = 0.0102$), and age 5 ($F = 4.03$; $df = 4,12$; $P = 0.0267$) differed more strongly among water body types. Pairwise

comparisons showed that mean lengths at ages 2 and 3 were shorter in class 24 than in class 43 lakes, and mean lengths at ages 3 and 4 were shorter in classes 24 and 38 than in reservoirs (Table 9). The longest lengths at age 5 occurred in reservoirs.

White crappies are frequently longer than black crappies of the same age within the same waters. Lengths at ages 1 through 5 of white crappies either equaled or exceeded lengths at the same ages of black crappie (Figure 6). When differences occurred, lengths of white crappies exceeded lengths of black crappies by an average of 21 (range = 15-28) mm at age 1, 41 (range = 20-70) mm at age 2, 40 (range = 22-75) mm at age 3, 51 (range = 21-96) mm at age 4, and 62 (range = 48-77) mm at age 5.

Length at age of white crappies varied by geographic location, maximum depth, and percent littoral area along with CPUE of several fish species. Based on RTA, variation in length at age of white crappies in natural lakes appeared most affected by CPUE of pumpkinseed; however, RTA also revealed splits associated with CPUE of bowfin, black bullhead, northern pike, white sucker, green sunfish, bluegill, black crappie, white crappie, and walleye and lake class (Table 10). Longer lengths at all ages except 2 occurred in lakes with low CPUE of pumpkinseed, the first split in all four age groups. Longer lengths at age 2 occurred in lakes with lower CPUE of bluegill. Regardless of where secondary splits occurred within age groups, lower lengths at age occurred in lakes with higher CPUE of green sunfish, bowfin, northern pike, and white crappie and with lower CPUE of black bullhead, white sucker, walleye, and black crappie. In lakes with low CPUE of bluegill, longer lengths at age 2 occurred in lake classes 42 and 43 than in classes 24, 40, and 41. Correlation analysis suggested that lengths at ages 1 and 2 decreased with increasing maximum depth and decreasing percent littoral area (Table 11). Lengths at age 1 also decreased with increasing northing, and lengths at age 2 increased with decreasing UTM easting. Lengths at ages 1 through 3 decreased with increasing CPUE of bluegill, but, unlike results found with RTA, lengths at age were not

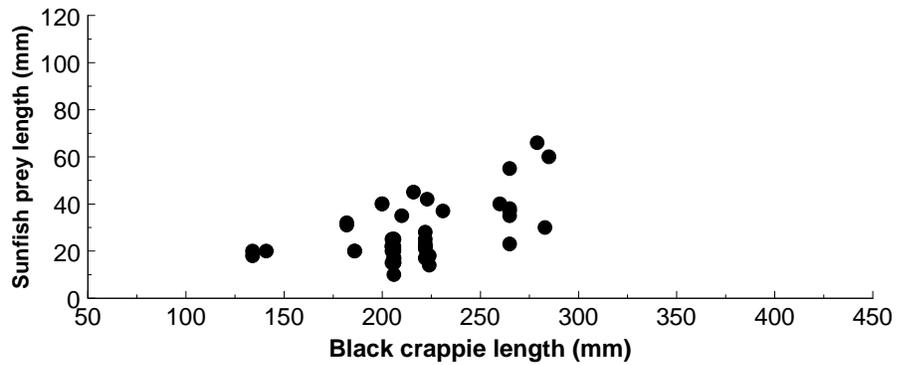
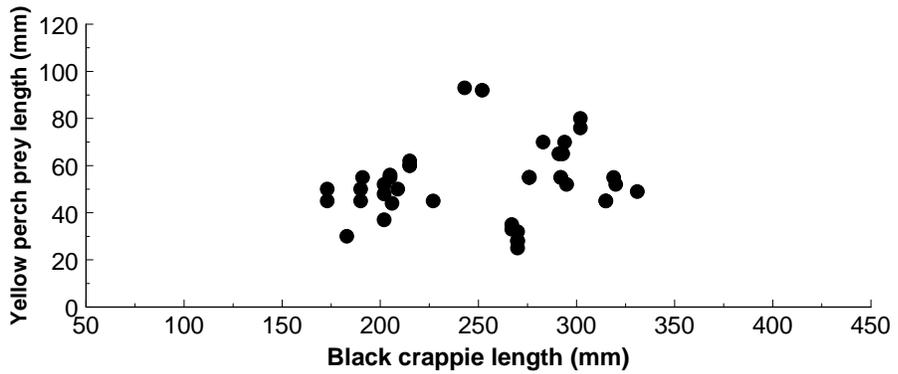
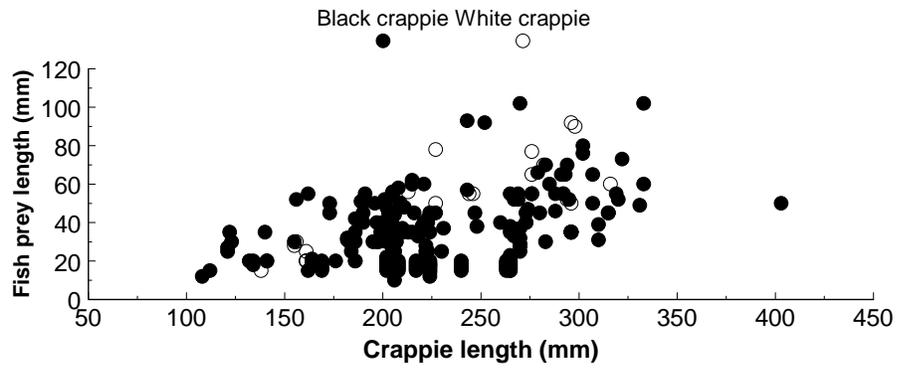


Figure 3. Total lengths of all fish eaten by black crappies and white crappies as a function of crappie length, and length of yellow perch and sunfish *Lepomis* spp. eaten by black crappies as a function of black crappie length in Minnesota lakes.

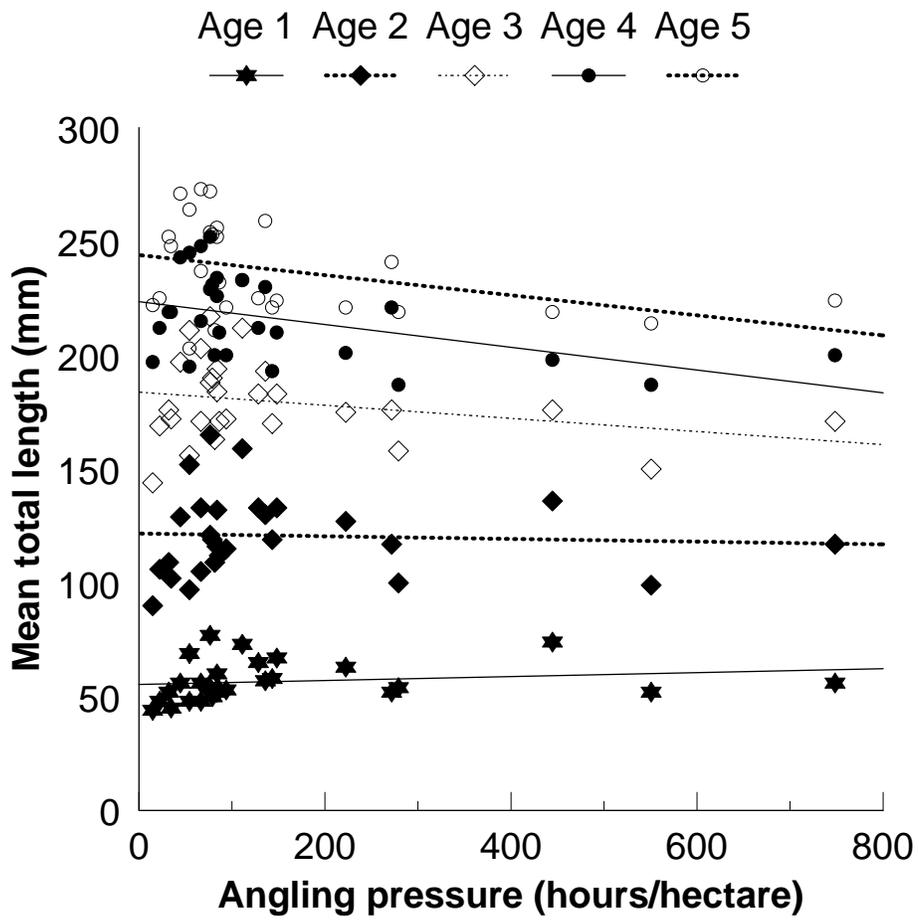


Figure 4. Mean total lengths at ages 1 through 5 of black crappies as a function of angling pressure estimates during summer among 28 lake classes throughout Minnesota.

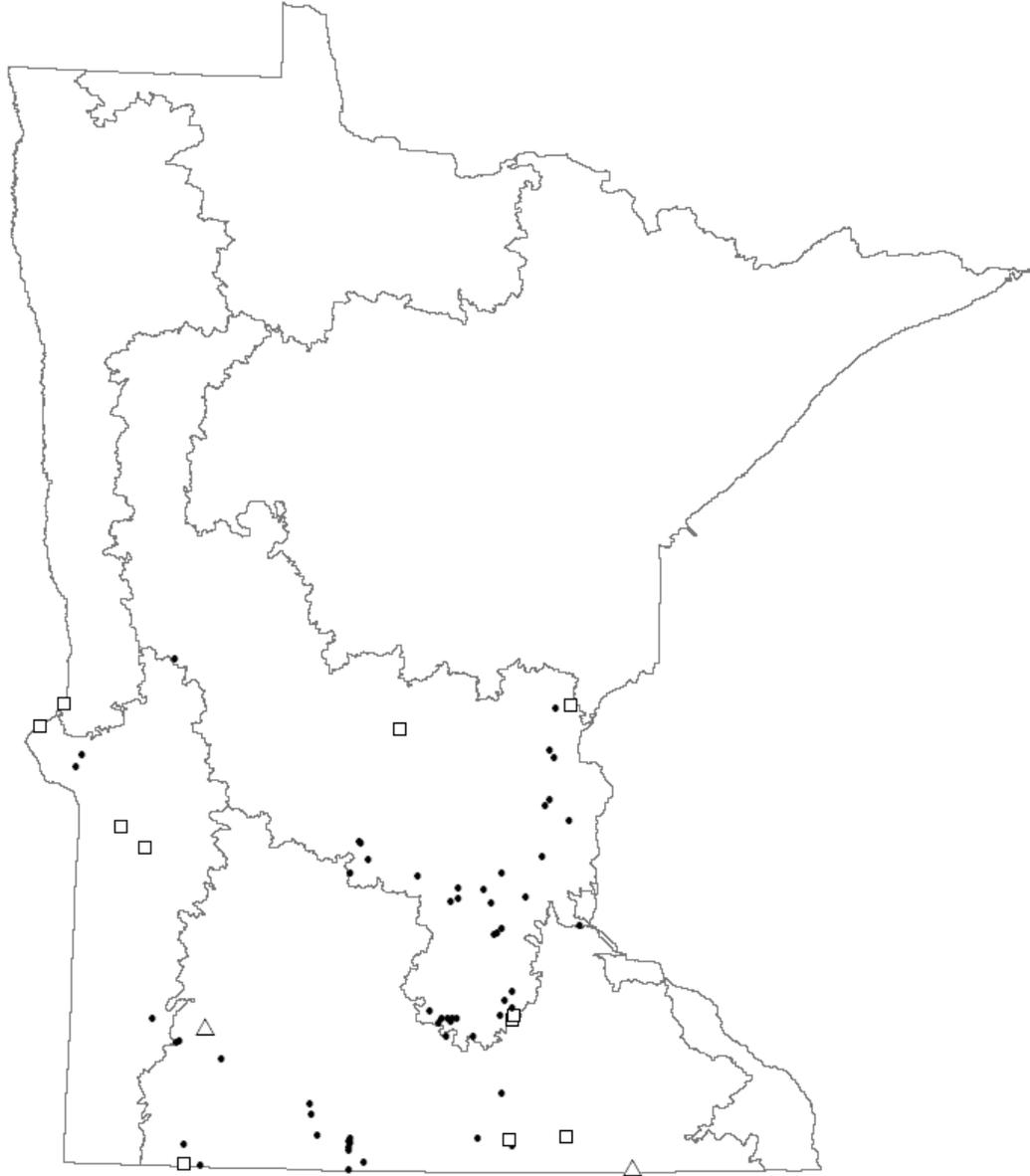


Figure 5. Locations of lakes (solid circles), reservoirs (open squares), and impoundments (open triangles) where scale samples from white crappies were collected.

Table 9. Mean (s.d.) back-calculated total lengths (mm) at ages 1 through 5 of white crappie from 13 lake classes plus reservoirs, impoundments, and rivers across Minnesota (columns with same superscripted letter denote that means did not differ [$P > 0.05$]; Tukey's Honestly Significant Difference tests).

Lake class	n	Lengths at age (mm)				
		Age 1	Age 2	Age 3	Age 4	Age 5
22	1	62	97	118		
24	21	68 (13) ^a	153 (26) ^b	208 (23) ^b	236 (26) ^b	251 (34) ^b
25	1	66	127	201	226	
27	2	74 (1) ^a	168 (10) ^{ab}	227 (21) ^{ab}	242 (23) ^{ab}	275
29	1	54	110	165	206	242
30	3	63 (14) ^a	142 (12) ^{ab}	209 (31) ^{ab}	269 (8) ^{ab}	282
33	1	62	144	220	232	
34	2	65 (12) ^a	175 (2) ^{ab}	236	281	300
38	2	69 (7) ^a	135 (13) ^{ab}	185 (5) ^b	215 (17) ^b	237
40	3	88 (10) ^a	174 (53) ^{ab}	192 (29) ^{ab}		
41	8	76 (19) ^a	174 (22) ^{ab}	226 (23) ^{ab}	256 (27) ^{ab}	294 (22) ^{ab}
42	3	87 (12) ^a	193 (33) ^{ab}	241 (23) ^{ab}	275 (27) ^{ab}	302 (22) ^{ab}
43	12	81 (12) ^a	192 (23) ^a	239 (21) ^a	264 (23) ^{ab}	288 (18) ^{ab}
Reservoirs	13	81 (16) ^a	193 (22) ^{ab}	254 (21) ^a	292 (8) ^a	316 (7) ^a
Impoundments	2	64 (15) ^a	121 (5) ^b	164 (18) ^b	205	
Rivers	1	60	183	259	287	313

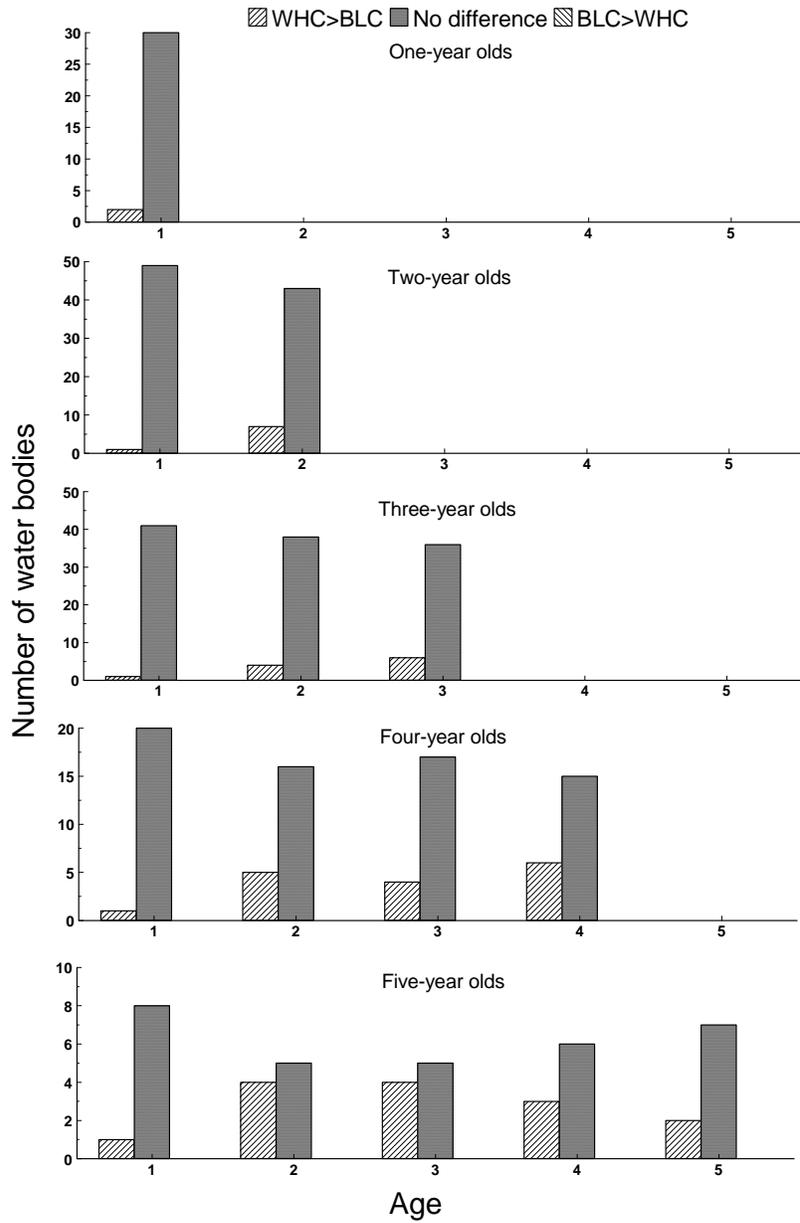


Figure 6. Number of water bodies in Minnesota where total lengths at ages 1 through 5 of white crappie exceeded ($P < 0.05$; Tukey's Honestly Significant Difference tests) lengths of black crappie of the same ages, where lengths of black crappie at ages 1 through 5 exceeded lengths of white crappies of the same ages, and where lengths at age did not differ between the two species.

Table 10. Mean (s.d.) back-calculated total lengths at ages 1 through 5 of white crappie as a function of lake class; gill net catch per unit effort (number per lift; CPUE) of black bullhead, white sucker, northern pike, and walleye; and trap net CPUE of bowfin, green sunfish, pumpkinseed, bluegill, white crappie, and black crappie among natural lakes in Minnesota (based on regression tree analysis; r^2 listed on the first couplet of each split denotes the amount of variation explained).

Length at age 1 (Total $R^2 = 0.518$)	
Pumpkinseed CPUE ≥ 0.05 per lift (Length = 65 (11) mm; n =29); $r^2 = 0.320$	
Black crappie CPUE ≥ 16.75 per lift (Length = 73 (11) mm; n = 10); $r^2 = 0.102$	
Black crappie CPUE < 16.75 per lift (Length = 61 (9) mm; n = 19)	
Pumpkinseed CPUE < 0.05 per lift (Length = 82 (13) mm; n =21)	
Northern pike CPUE ≥ 1.5 per lift (Length = 74 (13) mm; n =10); $r^2 = 0.096$	
Northern pike CPUE < 1.5 per lift (Length = 88 (9) mm; n = 11)	
Length at age 2 (Total $R^2 = 0.754$)	
Bluegill CPUE ≥ 5.0 per lift (Length = 152 (24) mm; n = 36); $r^2 = 0.426$	
Green sunfish CPUE ≥ 0.1 per lift (Length = 133 (24) mm; n =13); $r^2 = 0.160$	
Black bullhead CPUE ≥ 4.6 per lift (Length = 152 (23) mm; n = 6); $r^2 = 0.095$	
Black bullhead CPUE < 4.6 per lift (Length = 117 (8) mm; n = 7)	
Green sunfish CPUE < 0.1 per lift (Length = 162 (16) mm; n =23)	
Bluegill CPUE < 5.0 per lift (Length = 196 (21) mm; n = 13)	
Lake class (24, 40, 41) (Length = 179 (9) mm; n = 6); $r^2 = 0.073$	
Lake class (42, 43) (Length = 210 (18) mm; n = 7)	
Length at age 3 (Total $R^2 = 0.505$)	
Pumpkinseed CPUE ≥ 0.1 per lift (Length = 204 (25) mm; n = 24); $r^2 = 0.285$	
Green sunfish CPUE ≥ 0.1 per lift (Length = 190 (25) mm; n =10); $r^2 = 0.110$	
Green sunfish CPUE < 0.1 per lift (Length = 214 (21) mm; n = 14)	
Pumpkinseed CPUE < 0.1 per lift (Length = 232 (20) mm; n =18)	
White sucker CPUE ≥ 1.1 per lift (Length = 249 (22) mm; n = 7); $r^2 = 0.110$	
White sucker CPUE < 1.1 per lift (Length = 222 (9) mm; n = 11)	
Length at age 4 (Total $R^2 = 0.522$)	
Pumpkinseed CPUE ≥ 0.1 per lift (Length = 233 (24) mm; n = 19); $r^2 = 0.270$	
White crappie CPUE ≥ 2.4 per lift (Length = 217 (16) mm; n = 5); $r^2 = 0.075$	
White crappie CPUE < 2.4 per lift (Length = 239 (25) mm; n = 14)	
Bowfin CPUE ≥ 0.3 per lift (Length = 228 (19) mm; n =7); $r^2 = 0.068$	
Bowfin CPUE < 0.3 per lift (Length = 250 (26) mm; n = 7)	
Pumpkinseed CPUE < 0.1 per lift (Length = 263 (24) mm; n = 13)	
Black bullhead CPUE ≥ 34.7 per lift (Length = 278 (19) mm; n = 6); $r^2 = 0.109$	
Black bullhead CPUE < 34.7 per lift (Length = 249 (22) mm; n = 7)	
Length at age 5 (Total $R^2 = 0.575$)	
Pumpkinseed CPUE ≥ 1.1 per lift (Length = 242 (25) mm; n = 5); $r^2 = 0.455$	
Pumpkinseed CPUE < 1.1 per lift (Length = 287 (24) mm; n = 12)	
Walleye CPUE ≥ 2.3 per lift (Length = 302 (18) mm; n = 5); $r^2 = 0.120$	
Walleye CPUE < 2.3 per lift (Length = 276 (23) mm; n = 7)	

Table 11. Correlation coefficients between mean back-calculated total lengths at ages 1 through 5 of white crappie and Universal Transverse Mercator (UTM) northing and easting; lake surface area (ha), maximum depth (m), and percent littoral area of lakes; Secchi depth (m) and total alkalinity (mg/L); gill net catch per unit effort (CPUE) of black bullhead, yellow bullhead, white sucker, northern pike, yellow perch, and walleye; and trap net CPUE of bowfin, common carp, green sunfish, pumpkinseed, bluegill, white crappie, and black crappie among natural lakes in Minnesota (* denotes correlation coefficient differs from zero [$P \leq 0.05$]; adjusted with Bonferroni techniques).

Variable	Age				
	1	2	3	4	5
UTM Northing	-0.51*	-0.40	-0.14	0.03	-0.08
UTM Easting	-0.43	-0.56*	-0.48	-0.34	-0.48
Lake surface area	0.10	-0.01	0.02	-0.38	-0.05
Maximum depth	-0.56*	-0.64*	-0.48	-0.23	-0.20
Percent littoral area	0.51*	0.63*	0.40	0.18	0.36
Secchi depth	-0.36	-0.42	-0.27	-0.09	-0.17
Total alkalinity	0.05	0.27	0.23	0.10	0.05
Gill net CPUE					
Black bullhead	0.04	0.33	0.22	0.07	0.17
Yellow bullhead	-0.27	-0.42	-0.29	-0.11	-0.11
White sucker	0.18	0.44	0.48	0.42	0.34
Northern pike	-0.37	-0.22	0.02	0.14	-0.15
Yellow perch	0.15	0.10	0.00	-0.16	0.36
Walleye	0.26	0.34	0.30	0.20	0.56
Trap net CPUE					
Bowfin	-0.22	-0.36	-0.32	-0.28	-0.47
Common carp	0.22	0.20	0.14	0.02	-0.21
Green sunfish	-0.15	0.16	0.17	0.22	-0.20
Pumpkinseed	-0.27	-0.31	-0.46	-0.29	-0.51
Bluegill	-0.52*	-0.69*	-0.65*	-0.40	-0.28
White crappie	0.26	0.26	0.26	0.11	-0.09
Black crappie	0.39	0.24	0.28	0.30	0.39
n	37	36	31	23	11

strongly associated with CPUE of the other fish species (Table 11).

We did not run RTA on length at age data for white crappies in reservoirs because of insufficient sample size (≤ 10). Lengths at age 1 were not correlated with any continuous variable we collected ($r > 0.05$; Bonferroni adjusted; $n = 9$). We did not conduct correlation analysis on lengths at ages 2, 3, 4, or 5 because sample sizes were too small (≤ 5).

Lengths at ages 1 and 2 differed among some plant community types, but lengths at ages 3 and 4 did not (Table 7). Similarly to black crappie, longer lengths at early ages occurred in lakes with the less diverse plant communities. We lacked data to test for plant community effects on lengths at age in reservoirs.

We found several different taxa in stomachs of 244 white crappies from 20 water bodies (Table 8). Small aquatic insects, primarily larvae and pupae from Chaoborinae and Chironomidae, occurred most frequently in stomachs of white crappie 115 to 265 mm TL, and fish generally dominated the diet of the largest white crappies (Figure 2). Small crustaceans and large insects were relatively uncommon. White crappies fed on several fish species but data were insufficient to determine if they fed more frequently on any particular species (Table 8). Fish prey length ranged from 15 to 92 mm TL and increased with increasing length of white crappie ($r = 0.84$; $n = 20$; $P < 0.0001$; Figure 3).

Discussion

This study design cannot determine cause and effect, but we hypothesize that growing season, primary productivity, intra- and interspecific competition, and common habitat preferences with other fish species contributed to variations in lengths at age of both crappie species in Minnesota waters. Many of the independent variables including lakes class differ spatially across Minnesota, which prevents us from isolating the effects of these variables on length at age estimates. For example, growing season and lake productivity increase with decreasing latitude, and plant communities in northern waters differ from

those in southern waters (Baker et al. 1985; Heiskary and Wilson 1989; Cross and McInerney 2006).

Earlier hatching times, lengths of growing seasons, and lake productivity probably contributed to longer lengths at age 1 of both crappie species, but lake productivity, and not growing season length, probably contributed to longer lengths of older crappies. Growing season increases with decreasing latitude (synonymous with decreasing UTM northing) in Minnesota (Baker et al. 1985), which coincides with increasing lengths at age 1 from north to south. Geographic centers of lake classes 24, 30, 38, 40, 41, 42, and 43, where we observed longer lengths at age-1 black crappies in RTA, are also located well south of the other lake classes where we observed shorter lengths (Cook and Younk 1998). The longer lengths at age-1 black crappies observed in classes 8 and 18 (northeastern Minnesota) were likely anomalies because only one population from each class was sampled. Earlier warming of lakes in southern Minnesota likely contributed to earlier spawning of adult crappies and earlier hatching of age-0 crappies than in northern waters. Total alkalinity, which reflects photosynthetic activity (Cole 1979), increases from east to west ($r = -0.70$ between UTM easting and total alkalinity) more so than from north to south ($r = -0.44$ between UTM northing and total alkalinity) based on data gathered in this study ($n = 836$). Concentrations of total phosphorus and chlorophyll-*a* increase and maximum depth and Secchi depth decrease from northeast to southwest Minnesota (Heiskary and Wilson 1989) and are other indicators of lake productivity. These trends in lake productivity could also explain the longer lengths at age 1 crappies observed in southern waters. However, because correlation coefficients between length at age 1 and northing exceeded correlation coefficients between length at age 1 and easting, length at age appears more influenced by growing season/earlier hatching than by lake productivity. Conversely, lake productivity differences between eastern and western Minnesota could explain longer lengths at age of older crappies.

Sufficient predation by walleyes probably contributed to longer lengths at older age black crappies because walleyes feed on age-0 black crappies when their densities are high. This predation essentially eliminates intraspecific density-dependent effects on black crappie growth. Reduced abundance or faster growth of black crappies in Richmond Lake, South Dakota, and Boyd Reservoir, Colorado, occurred after introduction of walleye or saugeye (Puttmann and Weber 1980; Galinet et al. 2002). Saugeyes > 200 mm TL in Richmond Lake fed on age-0 black crappies in early June, late July and early August, and early October (Galinet et al. 2002). Davis (1975) reported that 3 to 12% of stomachs from walleyes > 400 mm TL in Belle Lake, Meeker County, contained black crappies, but black crappies were rarely found in stomachs of shorter walleyes. High population density of black crappies occurred in Richmond Lake before saugeye introductions, and high densities frequently occur at Belle Lake (MNDNR, statewide database). Conversely, walleyes fed primarily on yellow perch in Spirit Lake, Iowa (Liao et al. 2002) and fed mostly on white bass *Morone chrysops* and yellow perch in Shadehill Reservoir, South Dakota (Slipke and Duffy 1997). Population size of adult yellow perch in Spirit Lake exceeded that of black crappie by 25 to 51 times (Liao et al. 2004), but abundance estimates of fishes in Shadehill Reservoir were not known. All of these diet studies were conducted during open-water periods, but we also found black crappies < 100 mm TL in stomachs of walleyes caught by anglers during winter (personal observations).

The association between higher lengths at age of black crappies in reservoirs and higher CPUE of yellow perch and lower CPUE of white suckers, and that between higher lengths at age of white crappies and lower CPUE of northern pike, also appear linked to density-dependent mechanisms associated with predation. We know that yellow perch feed on black crappies < 100 mm TL in Minnesota lakes during winter (personal observations). Furthermore, Schneider and Breck (1996) demonstrated that yellow perch are capable of consuming high numbers of small bluegills during winter. Thus, yellow perch appear capable of suppressing age-0 black

crappies. Low CPUE of white suckers results from adequate densities of piscivores, which in turn could also be feeding on crappies. White suckers provide forage to numerous species including walleye, northern pike, and basses *Micropterus* spp. (Becker 1983). Lastly, excessive numbers of northern pike can decrease abundances of yellow perch and walleye (Anderson and Schupp 1986). Thus, assuming that walleye and yellow perch are key predators of age-0 crappies, the reduction of these predators via northern pike predation could lead to increased densities and suppressed lengths at age of crappies.

Lack of direct evidence showing intraspecific density-dependent effects on length at age was likely due to the inability of trap nets to sample crappies during summer. Only for lengths at age-3 white crappies, did lower lengths at age occur with higher trap net CPUE. We know lake survey trap nets do not effectively sample black crappie < 200 mm TL in spring or fall (McInerny and Cross 2006), but we do not know how well trap nets sample this size group in summer. Furthermore, trap net CPUE of black crappies \geq 200 mm TL in June and July did not increase with increasing population density among seven south-central Minnesota lakes (McInerny et al., unpublished manuscript). We know of no evaluation of trap netting on white crappie in natural lakes. Because abiotic and biotic factors differ among water bodies, we also hypothesize that density thresholds (densities when growth becomes suppressed) also differ among water bodies.

Interspecific competition for food resources could explain shorter lengths at age of black crappie when CPUE of white suckers were high and shorter lengths of both species when CPUE of bluegills was high. Similarly to black crappies, white suckers feed on chironomids (Hayes 1990), and dipterans compose much of the diet of bluegills in Minnesota waters (Etnier 1971; Cross et al. 1989). Therefore, crappies could be competing with bluegills and white suckers for the same food resources.

Habitat preferences could explain associations between lengths at age and other fish species. Rock bass, green sunfish, pumpkinseed, bluegill, and northern pike exhibit strong preferences for aquatic plants (Hall and

Werner 1977; Werner and Hall 1979; Cross and McInerney 2006), habitats where crappies exhibit shorter lengths at age. Conversely, abundance of black bullhead, common carp, and walleye generally decrease with increasing aquatic plant diversity (Cross and McInerney 2006).

We hypothesize that below-optimum forage and predator densities occur more often in smaller water bodies, which would explain the strong relationships between surface area and lengths at age of black crappies and shorter lengths at older ages of black crappies in impoundments. Surface area of impoundments in this study (with comparatively shorter lengths at older ages) averaged 6 ha (range = 1 to 12 ha) compared to 270 ha (range = 3 to 16,420 ha) for natural lakes, and 3,000 ha (range = 6 to 89,400 ha) for reservoirs.

Even though black crappies frequently feed on sunfish, the energy costs expended to catch young sunfish may contribute to shorter lengths at older ages in lakes with high CPUE of bluegills. Conversely, longer lengths at age occurred in lakes with higher CPUE of yellow perch, a bioenergetically less costly prey. In experiments with northern pike, largemouth bass, and walleye, bluegill were less vulnerable or harder to catch than were fusiform fish prey including yellow perch (Lewis and Helms 1964; Mauck and Coble 1971; Einfalt and Wahl 1997).

We suspect that white crappies are more piscivorous than black crappies in many Minnesota lakes because when length differences occurred, white crappies were always longer. Ellison (1984) found in a Nebraska impoundment that white crappies become more piscivorous than do black crappies. Although white crappies are more fusiform than black crappies and are slightly longer at the same weight, length differences between the two species were greater than body shape could explain. Although other studies suggest that growth of crappies increases if they feed on fish rather than invertebrates, we could not verify this trend for Minnesota populations. Diet information gathered in this study is also consistent with that found in other studies in the Midwest and southern Canada (Seaburg and Moyle 1964; Keast 1968; Hanson and

Qadri 1980; Keast and Fox 1992), suggesting that both species are opportunistic and rather generalist.

Selective angling mortality could affect length at age of older black crappies in lake classes receiving relatively heavy angling pressure. Because Minnesota lakes provide diverse fisheries, we do not know how much angling pressure was directed at crappies. However, crappies ranked among the top three taxa harvested by anglers in five (class 40, 30, 38, 34, and 24) of the 10 lake classes receiving the highest angling pressures; harvest by taxa data were lacking for the other five classes (33, 21, 20, 28, and 36) (Cook and Younk 1998; 2001). Thus, we cannot rule out selective angling mortality from contributing to shorter lengths for older black crappies.

Management Implications

Lake class appears valuable for explaining lengths at age of black crappies; thus, managers can use length at age data to help characterize the black crappie population in a lake (Table 1). We recommend managers characterize as fast growing those populations with length at ages exceeding one standard error of the mean. Conversely, populations with length at ages exceeding one standard error below the mean should be characterized as slow growing. We do not recommend using lake class for interpreting lengths at age of white crappies because, except for class 24, we sampled relatively few lakes from each lake class.

The value of length at age data decreases with increasing age because of greater odds of aging error. For black crappie, mean agreement rates between the MNDNR fisheries staff who read scales and ages we used in this study equaled 93% (n = 236 comparisons when sample size ≥ 5) for age 1, 86% (n = 456) for age 2, 79% (n = 487) for age 3, 71% (n = 418) for age 4, and 60% (n = 208) for age 5. Similarly, mean agreement for white crappie was 96% (n = 19) for age 1, 86% (n = 31) for age 2, 75% (n = 27) for age 3, 62% (n = 14) for age 4, and 38% (n = 5) for age 5.

Comparisons between back-calculated lengths at age in this report and those from other studies may not be meaningful because

intercept values used in other studies probably differ. For example, the standard intercept most likely used for back-calculating lengths at age in other studies is 35 mm (Carlander 1982), 15 mm longer than the one used by MNDNR staff (MNDNR 1993). Thus, lengths at younger ages reported herein will likely be shorter than those reported elsewhere.

Lastly, we recommend that estimated lengths at age by water body type be periodically updated. Our data came from samples collected in 1998 through 2002, and environmental factors affecting lengths at age will likely change with time.

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Appendix 1. Sum of importance values (importance = percent occurrence x mean abundance based on MNDNR aquatic plant surveys) of each plant taxon, total number of native taxa, and the most common aquatic plant taxa (importance values ≥ 10 ; importance value of each taxon in parentheses) within each of the nine types of plant communities described by Reschke et al. (2006).

Type	Sum of Importance values	Total number of native taxa	Most common taxa (importance value of taxa)				
1	396	98	Coontail (47)	Flatstem pondweed (37)	<i>Chara</i> spp. (27)	<i>Nuphar</i> spp. (25)	Northern milfoil (20)
3	220	100	<i>Carex</i> spp. (15)	<i>Nymphaea</i> spp. (14)	<i>Nuphar</i> spp. (14)	Bushy pondweed (11)	Water shield (10)
16	255	99	<i>Chara</i> spp. (45)	Bushy pondweed (20)	Flatstem pondweed (18)	Coontail (18)	Northern milfoil (17)
40	215	87	Coontail (56)	<i>Elodea</i> spp. (15)	Broadleaf cattail (15)	Lesser duckweed (12)	Eurasian milfoil (12)
42	37	43	Broadleaf cattail (14)				
59	121	90	<i>Carex</i> spp. (36)				
66	148	86	Algae (20)	Sago pondweed (19)	Northern milfoil (14)	Coontail (14)	
117	97	66	<i>Elodea</i> spp. (25)	Curly-leaf pondweed (18)			
134	79	50	Sago pondweed (30)	Curly-leaf pondweed (11)			