

**Recruitment of Bluegill and Yellow Perch in Nebraska Sandhills Lakes: Integrating
Multiple Life Stages**

By

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Life Stage Approach**

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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Abstract

Recruitment of Bluegill and Yellow Perch in Nebraska Sandhills Lakes: Integrating Multiple Life Stages

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Bluegill *Lepomis macrochirus* and yellow perch *Perca flavescens* are important, native sport fishes to Nebraska Sandhills lakes. Recruitment dynamics of the fish populations within a given community will ultimately structure the fish communities. I conducted a multiple life-stage investigation of bluegill and yellow perch recruitment in Nebraska Sandhills lakes. I focused on four topics, 1) the effect of climate on year-class strength of multiple populations broadly across a series of Nebraska Sandhills lakes, 2) larval prey selection and match- mismatch regulation of recruitment, 3) age-0 dynamics and the potential effect of abiotic and biotic variables on recruitment, and, 4) potential predation by yellow perch on age-0 bluegill. Results from this study contribute to the understanding of ecology of bluegill and yellow perch and management related to recruitment.

I collected adult population samples of bluegill and yellow perch from several Sandhills lakes and estimated ages using sagittal otoliths. Residuals from catch-curves were used to assess the relation between climatological variables and year-class strength. Recruitment was relatively consistent for both species (no missing year classes detected)

and asynchronous. The lack of synchrony in yellow perch and bluegill population year-class strength suggests that climate does not act similarly broadly across a series of Nebraska Sandhills lakes and that individual variability among lakes is equally or more important in influencing year-class strength for these two species in the Nebraska Sandhills ecoregion. I did find support for the concept of climate influence on bluegill and yellow perch recruitment. Spring temperature, precipitation, and winter severity appeared to be the most supported metrics governing recruitment of these species.

Food availability is believed to regulate fish recruitment, both directly and indirectly. The availability of zooplankton, especially to newly hatched larvae, is thought to be particularly crucial. I examined stomach contents of larval bluegill and yellow perch larvae in Pelican Lake and Cameron Lake for two years. I also determined zooplankton availability from environmental samples and calculated prey selection using Chesson's alpha. In addition, I investigated potential match-mismatch regulation of recruitment. Copepod nauplii and *Bosmina* spp. were commonly used by bluegill and copepods were commonly used by yellow perch. There were abundant zooplankton populations available for consumption. Matches in larval bluegill and yellow perch abundance and zooplankton abundance were detected in all years; exact matches were common. No mismatches in predator and prey production were observed. It is unknown if relatively large mismatches may lead to decreased recruitment for these two fish species. No predation by age-0 yellow perch on age-0 bluegill was observed, even though yellow perch hatched two months prior to bluegill. Given that zooplankton were abundant and well-timed to larval fish abundance over the time span of this study, the

match-mismatch hypothesis alone may not fully account for observed recruitment variability in the populations that I studied.

Recruitment dynamics of fish populations ultimately structure fish communities and may be regulated by abiotic and biotic factors both directly and indirectly. I documented age-0 dynamics of bluegill and yellow perch for four years in Pelican Lake and two years in Cameron Lake. I indexed larval densities, abundance of juveniles in the fall, abundance of the same cohorts the following spring, and abundance of age-2 bluegill and age-1 yellow perch to investigate recruitment to the adult population. Age was estimated for larval fishes using sagittal otoliths to determine hatching date. I also assembled an environmental dataset including temporal trends in zooplankton, benthic macroinvertebrates, vegetation coverage, and physical and biological water quality parameters. Peak larval densities of bluegill and yellow perch were variable although it appeared that recruitment was relatively consistent as some individuals of each cohort survived to recruit to the adult populations each year. A single peak in larval bluegill abundance was observed in most years, which is a finding contrary to the long-held assumption of multiple spawning bouts within a season. The bluegill spawning season was protracted, as previously reported, lasting approximately 2 months and the timing of hatch was relatively similar each year. Growth of later-hatched bluegill was faster than that of their earlier-hatched counterparts in most years. In addition, growth of late-hatched bluegill was correlated to catch of juveniles in the fall, suggesting that these fish may contribute more to eventual recruitment. No evidence of size-selective overwinter mortality was detected for bluegill. The yellow perch spawning season was truncated, a

finding consistent with previous research. There was some evidence of size-selective overwinter mortality of yellow perch in only one instance. My estimates of larval density for both species were a poor predictor of later season catches or recruitment to the adult population. My exploratory analyses indicated that temperature, winter severity, and growth rates may be important determinants of survival and ultimate recruitment to the adult population.

Seasonal food habits of adult yellow perch were investigated in West Long Lake. Benthic macroinvertebrates were a primary diet item. Specifically, chironomids, amphipods, and odonates were common diet items. Predation on age-0 bluegill was observed in the fall, and increased predation in the winter suggested potential ability of yellow perch to affect recruitment of bluegill.

My study provides some of the first ecosystem-wide information on the dynamics of age-0 bluegill and yellow perch. I found, over the years examined, that no single factor appears to affect bluegill and yellow perch recruitment. Instead, a suite of factors, interacting in complex ways may ultimately govern the recruitment of these species. My results should be interpreted with caution as they are based on four years of data collection and the addition of more years of observation in this ongoing project may improve our ability to determine abiotic and biotic factors that influence recruitment of these two important species.

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List of Abbreviations

AIC.....	Akaike's information criterion
AICc.....	Akaike's information criterion corrected for small sample size
Δ AIC.....	difference in AICc between each model and the most supported model
Apr.	April
Aug.....	August
C.....	Celsius
cm.....	centimeter
d.....	day
df.....	degrees of freedom
DO.....	dissolved oxygen
h.....	hour
ha.....	hectare
Jul.....	July
Jun.....	June
k.....	number of model paramters
km.....	kilometers
L.....	liter
m.....	meter
m ³	cubic meter
mm.....	millimeter
μg.....	microgram

μm	micrometer
n	sample size
p	probability level
PC	principal component
PCA	principal components analysis
QQ	quantile-quantile
r	Pearson correlation coefficient
SE	standard error
Spp	species
TDS	total dissolved solids
TL	total length
TOTP	total phosphorous
US	United States

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Chapter 1.

Introduction

The challenge of explaining observed patterns of population dynamics and community organization is often crucial to solving practical problems posed by human impacts on natural communities or achieving management goals. A broader understanding of processes within a community may enable a better approach to diverse management objectives through a more holistic view of the community. Specifically, several lakes within the Valentine National Wildlife Refuge in the Nebraska Sandhills ecoregion have been stocked with sport fishes and are managed for recreational angling, while other lakes are closed to the public and managed primarily for waterfowl and shorebird production. Traditional approaches to diverse management goals may not necessarily be mutually beneficial and a better understanding of the fish population and community ecology in Sandhills lakes may result in better management strategies for these and similar systems.

An important component influencing the community ecology of an ecosystem is recruitment dynamics of the populations within a given community, which, ultimately structure the fish communities (Diana 1995). Several factors are believed to regulate fish recruitment, both directly and indirectly. These include abiotic factors such as physical habitat, temperature, and weather (Beard 1982; Pope et al. 1996; Jackson and Noble 2000; Casselman et al. 2002), and biotic factors such as food availability and competition

(Prout et al. 1990; Welker et al. 1994; Ludsin and DeVries 1997; Bunnell et al. 2003), and predation (Forney 1971; Houde 1987; Rice et al. 1987b; Santucci and Wahl 2003).

High mortality during the first winter of life may also reduce survival of age-0 fishes in temperate regions. This effect is often size-specific (Oliver et al. 1979; Post and Evans 1989; Johnson and Evans 1991; Thompson et al. 1991), with smaller individuals experiencing higher mortality rates than larger ones. Starvation due to inadequate lipid reserves is often cited as the direct cause of high overwinter mortality (Oliver et al. 1979; Adams et al. 1982; Miranda and Hubbard 1994). Starvation can also influence mortality indirectly by increasing predation risk (Miller et al. 1988; Jonas and Wahl 1998) via reduced swimming capabilities (Rice et al. 1987a) and/or reduced growth rates (Werner and Gilliam 1984; Post and Prankevicius 1987). Large age-0 sizes have been reported to increase the probability of winter survival (Post and Evans 1989; Miranda and Hubbard 1994; Garvey et al. 1998). In addition, factors determining growth rates such as timing of hatching, food availability, and competition may have important implications for recruitment of temperate-latitude fishes.

The bluegill *Lepomis macrochirus* is typically considered a colonial, fractional-spawning fish (Werner 1969; Gross and MacMillan 1981) with a small percentage displaying solitary nesting activities (Gross and MacMillan 1981; Neff et al. 2004). In addition, the bluegill spawning season is protracted, often extending over several summer months (Beard 1982; Cargnelli and Gross 1996; Garvey et al. 2002). Protracted

spawning in bluegill may be considered a form of bet-hedging whereby reproductive output is distributed over several reproductive bouts because larval and juvenile survival is highly variable (Winemiller 2005) depending on variable, albeit broadly predictable, environmental conditions. Finally, nest guarding is regarded as a major behavioral adaptation associated with elevated predation levels on larvae (Balon 1975) and is well developed in bluegills (Avila 1976, Dominey 1981). The protracted spawning season considered typical for this species was documented in Crane Lake, Indiana, where larval bluegills were collected from early June to early September (Werner 1969). Beard (1982) reported bluegill spawning-season lengths ranging from 31 d (four spawning bouts) to 112 d (11 spawning bouts) in three Wisconsin lakes. Garvey et al. (2002) reported that inshore densities of larval bluegills were bimodal, peaking once in late May and again in early July in Lake Opinicon, Ontario. Chvala (2000), who evaluated the reproductive biology of bluegill in two Nebraska Sandhills lakes, found that while larvae were first collected in both lakes during June, the spawning season was comparatively extended in one lake compared with the other. Newly hatched (i.e., 4–6 mm) larvae were collected at Cozad Lake between June 5 and July 24, while newly hatched larvae were only collected from Pelican Lake between June 25 and July 9. Egg-diameter distributions from bluegill ovaries in both lakes had multiple modes, indicating multiple-spawning (i.e., fractional spawning) capabilities. Temporal variability in hatching date may have consequences for growth, and ultimately recruitment, of age-0 bluegill to age 1.

Large age-0 size often increases the probability of winter survival in temperate latitudes (Post and Evans 1989; Miranda and Hubbard 1994). Differences in the timing of hatching may affect the growth of gape-limited fish, thereby affecting their ability to consume larger-sized prey, increasing their energy intake, and ultimately reaching a large size before onset of winter (Goodgame and Miranda 1993; Phillips et al. 1995; Post 2003). Although early hatching is commonly assumed to lead to a large size and decreased mortality before the onset of the first winter, some studies have identified factors that can result in higher mortality for early-hatched fish compared with late-hatched fish. Garvey et al. (2002) found that age-0 bluegill hatched earlier in the year commonly did not survive to the juvenile stage due to high larval mortality. Santucci and Wahl (2003) reported that early-hatched bluegill were also subjected to higher mortality through predation by largemouth bass *Micropterus salmoides* in Illinois.

Previous research in South Dakota indicated that bluegill recruitment was asynchronous among four small impoundments (Edwards et al. 2007) and the authors suggested that biotic factors likely affected bluegill recruitment. Although bluegill recruitment is generally consistent (i.e., missing year classes are rare) in Nebraska Sandhills lakes there appears to be a moderate level of variability in relative year class strength among years (Paukert et al. 2002a). Furthermore, the effects of environmental control and predator regulation of recruitment of bluegill in Nebraska Sandhills lakes have not been separated (Paukert et al. 2002b).

Like bluegill, variable recruitment commonly occurs in percid populations (Koonce et al. 1977; Willemsen 1977; Hackney and Holbrook 1978; Newsome and Aalto 1987) and numerous studies have documented these patterns in yellow perch *Perca flavescens*, an economically important percid species (e.g., Forney 1971; Koonce et al. 1977; Mills et al. 1989). Critical time periods, or bottlenecks, of high mortality may exist for some species (Hjort 1914; May 1974) and researchers commonly incorporate this factor when describing the recruitment processes (Marr 1956). This critical period is thought to occur early in age-0 yellow perch cohort development (Forney 1971; Clady 1976; Anderson et al. 1998). Alternatively, several studies reported that year-class strengths of walleye *Sander vitreus* (another percid) in Oneida Lake (Forney 1976) and largemouth bass (a centrarchid) in southern reservoirs (Novinger 1988; Sammons and Bettoli 1998) are determined later in development, although larval mortality events may still be important as they can substantially affect cohort size. In addition, Houde (1989) reported that subtle shifts in daily mortality and growth may be ultimately responsible for influencing recruitment. Describing the type and relative importance of mortality factors during this critical period is difficult (Marr 1956; Braum 1978) because mechanisms influencing recruitment may differ both spatially and temporally, and may be species specific.

Several studies related variability in yellow perch recruitment to environmental variables (Craig et al. 1979; Kallemeyn 1987; Treasurer 1989; Pope et al. 1996; Ward et

al. 2004), but agreement among researchers regarding factors influencing these trends is low (Koonce et al. 1977), suggesting that recruitment regulation may vary among systems or is regulated by more complex factors. Size-selective overwinter mortality has been documented for yellow perch (Post and Prankevicius 1987; Post and Evans 1989; Johnson and Evans 1991), but the effect of overwinter mortality on perch recruitment has not been well analyzed. However, Post and Evans (1989) predicted that overwinter starvation mortality of yellow perch could greatly influence year-class strength.

The availability of prey when larval fish begin exogenous feeding has been proposed as a potential regulator of recruitment variability (match-mismatch hypothesis; Cushing 1975; 1990). The match-mismatch hypothesis consists of two assumptions: first, that fish at temperate latitudes spawn at approximately the same time each year and, secondly, that the larvae emerge during the spring or autumn peaks in plankton production (Cushing 1990). The match-mismatch hypothesis has been documented to varying degrees for age-0 threadfin shad *Dorosoma petenense* (Betsill and Van Den Avyle 1997), striped bass *Morone saxatilis* (Chick and Van Den Avyle 1999), and yellow perch (Fitzgerald et al. 2001). Poor survival may occur in year-classes of fish that have poor synchrony between hatching and food availability due to starvation and predation (May 1974; Houde 1987; Miller et al. 1988; Mills et al. 1989). Although food resources can be important to larval fish, predation may also affect recruitment.

Yellow perch as a predator can influence prey fish populations. Based on field studies, yellow perch experience an ontogenetic diet shift during their first year of life (Whiteside et al. 1985). Yellow perch initially feed on small zooplankton and gradually shift to larger zooplankton as fish size increases (Mills et al. 1989; Graeb et al. 2004). Yellow perch continue to feed on zooplankton and gradually shift to feeding on benthic invertebrates after reaching a total length of about 40 mm (Pycha and Smith 1955; Ney and Smith 1975). As yellow perch attain larger sizes (TL > 150 mm), food habits studies indicate they often shift to a diet of fish prey (Keast 1985; Fullhart et al. 2002). Older yellow perch will cannibalize younger perch (Seaburg and Moyle 1964; Clady 1974). Direct predation by yellow perch on small bluegills has also been reported (Reed and Parsons 1996; Fullhart et al. 2002). However, fish did not compose a substantial portion of the diet for larger (TL >200 mm) perch in Michigan (Laarman and Schneider 1972) or eastern South Dakota (Lott et al. 1996).

Biologists have often proposed that a dietary shift from macroinvertebrates to fish occurs when yellow perch attain a total length of 150-200 mm (Clady 1974; Fullhart et al. 2002) which is often mediated by gape limitation (Bremigan and Stein 1994). Other factors such as predation risk (Werner and Hall 1988), foraging efficiency (Wu and Culver 1992; Hjelm et al. 2003), food availability, and prey size (Hansen and Wahl 1981) can also influence diet shifts. However, yellow perch may be capable of switching to piscivory at 80 mm TL (Graeb et al. 2006). However, Graeb et al. (2004) reported that

the yellow perch switch to piscivory was facultative rather than obligate. In natural systems, availability of prey fish is often dependent on the timing of hatch for particular prey species. For example, in Lake Opinicon, Ontario, the timing of hatch of many prey fish species was similar to yellow perch (Keast 1980). Hence, by the time yellow perch reached a size at which they could shift to piscivory (i.e. 80 mm) prey fish may have outgrown the window of vulnerability to yellow perch predation. Although the food habits of age-0 yellow perch have been extensively studied in Midwestern waters (e.g. Fisher and Willis 1997), comparatively less attention has been focused on food habits of juvenile (i.e., age 1 and age 2) yellow perch.

The overall goal of this research is to better understand biotic and abiotic influences on the recruitment processes of bluegill and yellow perch in Nebraska Sandhills lakes by examining multiple life stages. Survival of age-0 fish to age 1 has been explained in two different ways that are not entirely mutually exclusive. One hypothesis is that predator regulation largely controls survival to age 1. Although predatory effects limiting bluegill recruitment have been inferred (Paukert et al. 2002b), questions remain about the extent of predatory and environmental influence in bluegill populations (DeBates et al. 2003; Paukert et al. 2003). A second hypothesis is that environmental factors (e.g. climate, habitat, prey availability) influence survival. This study will attempt to address the second hypothesis and identify environmental factors that may influence survival. Many previous studies have addressed growth and survival

during isolated life stages, which can make understanding and prediction of recruitment variability difficult (Ludsin and DeVries 1997). A recruitment assessment coupled with modeling procedures to identify important abiotic and biotic factors related to year-class strength is needed at this time. Specific mechanisms driving these relationships also need to be identified. Thus, to reach this goal, I conducted a series of field research projects examining multiple life stages combined with modeling techniques to address the following questions.

1. Are climate patterns (e.g., precipitation, wind, and temperature) related to year-class strength of adult bluegill and yellow perch populations broadly across a series of Nebraska Sandhills lakes?
2. Does the match-mismatch (i.e., zooplankton abundance) hypothesis predict recruitment of age-0 bluegill and yellow perch in two Sandhills lakes?
3. Can an examination of multiple life stages of age-0 bluegill and yellow perch coupled with a long term environmental database identify factors related to recruitment?
4. What is the extent of predation by yellow perch on age-0 bluegill in one Sandhills lake?

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Chapter 2.

Adult population structure and relations between climatological variables and year-class strength of yellow perch and bluegill populations in Nebraska Sandhills lakes

Year-class strength of fish populations is often determined in the first year of life. During this critical early life period several factors are believed to regulate fish recruitment, both directly and indirectly (Hjort 1914; May 1974). Physical habitat, temperature, and weather (Beard 1982; Pope et al. 1996; Jackson and Noble 2000; Casselman et al. 2002), food availability and competition (Prout et al. 1990; Welker et al. 1994; Ludsin and DeVries 1997; Bunnell et al. 2003), and predation (Forney 1971; Houde 1987; Rice et al. 1987; Santucci and Wahl 2003) can affect recruitment. Size-dependent overwinter mortality can also be significant (Oliver et al. 1979; Post and Evans 1989; Johnson and Evans 1991; Thompson et al. 1991), with smaller individuals often experiencing higher mortality rates than larger ones. Starvation is often cited as the direct cause of high overwinter mortality (Oliver et al. 1979; Adams et al. 1982; Miranda and Hubbard 1994).

Variable recruitment is often observed in bluegill populations. Previous research in South Dakota indicated that bluegill recruitment was asynchronous among four small impoundments (Edwards et al. 2007) and the authors suggested that biotic factors likely

affected bluegill recruitment. Although bluegill recruitment is generally consistent (i.e., missing year classes are rare) in Nebraska Sandhills lakes, there appears to be a moderate level of variability in relative year-class strength among years (Paukert et al. 2002a). Furthermore, the effects of environmental control and predator regulation of bluegill recruitment in Nebraska Sandhills lakes have not been separated (Paukert et al. 2002b). In addition, larval bluegill dynamics varied widely from year to year in Pelican Lake, Nebraska (Jolley et al. 2009).

Although bluegill recruitment is generally considered to be governed by lake-specific biotic factors, environmental factors may also have direct and/or indirect effects on recruitment. Lake water level may influence centrarchid recruitment (McDonough and Buchanan 1991; Mitzner 1991; Bonvechio and Allen 2005). Water level may also influence aquatic vegetation coverage, which may indirectly influence bluegill and yellow perch populations. Overabundant submergent vegetation may limit predation on bluegill and yellow perch, with the resulting increased abundance potentially leading to increased intraspecific competition and slower growth (Theiling 1990; Lott 1991; Engel 1995; Treibitz et al. 1997; Olson et al. 1998). Conversely, Schneider (1999) reported quality bluegill populations in lakes with dense aquatic vegetation and Paukert et al. (2002b) found that emergent vegetation was positively related to panfish population quality in Sandhills lakes. Aquatic vegetation coverage may be negatively affected in

cooler years (Barko and Smart 1981; Barko et al. 1982; Spencer 1986) as lower temperatures slow macrophyte growth (Scheffer 2004).

Water temperature may indirectly affect larval fish via its influence on the food chain in addition to directly mediating spawning and hatching (Beard 1982). Water temperature influences phytoplankton and zooplankton growth (Sommer et al. 1986; Taylor et al. 1987). Phytoplankton abundance thereby influences zooplankton growth which is an important prey item of larval fish. Thus, suitable growth and prey conditions for larval fish are largely determined by the physical environment (e.g., water temperature). In addition, Miner and Stein (1993) experimentally found that increased turbidity levels reduced consumption of zooplankton by larval bluegill.

Variable recruitment commonly occurs in yellow perch populations (Forney 1971; Koonce et al. 1977; Mills et al. 1989). The critical period is thought to occur early in age-0 yellow perch cohort development (Forney 1971; Clady 1976; Anderson et al. 1998). In addition, Houde (1989) reported that subtle shifts in daily mortality and growth may be ultimately responsible for influencing recruitment. Describing the type and relative importance of mortality factors during this critical period is difficult (Marr 1956; Braum 1978) because mechanisms influencing recruitment may differ both spatially and temporally, and may be species specific.

Several studies related variability in yellow perch recruitment to environmental variables (Craig et al. 1979; Kallemeyn 1987; Treasurer 1989; Pope et al. 1996; Ward et

al. 2004), but agreement among researchers regarding factors influencing these trends is low (Koonce et al. 1977), suggesting that recruitment regulation may vary among systems or is regulated by more complex factors. Post and Evans (1989) predicted that first-winter starvation mortality of yellow perch could greatly influence year-class strength. Considering the potential influences of climate on bluegill and yellow perch year-class strength a need remains to assess the potential effects of environmental (i.e., climatological) variables on recruitment.

My objectives were to describe age structure of bluegill and yellow perch populations and to quantify climatological factors related to recruitment in Nebraska Sandhills lakes. Previous age-structured assessments of bluegill and yellow perch populations in Nebraska Sandhills lakes have been conducted (Paukert et al. 2002b) but those researchers aged fish using scales, a less accurate and precise aging structure. Although sagittal otoliths have not been validated as aging structures for yellow perch, they have been validated for other percids (Erickson 1983; Heidinger and Clodfelter 1987) and for bluegill (Hales and Belk 1992). More precise ages have been obtained using otoliths compared with scales for yellow perch (Robillard and Marsden 1996; Niewinski and Ferri 1999; Maceina and Sammons 2006) and for bluegill (Hoxmeier et al. 2001). An accurate and precise population structure could then be assessed to determine environmental influence on year-class strength (Maceina 1997; Maceina and

Stimpert 1998). Studies reporting the effects of environmental influences on year-class strength abound for yellow perch and bluegill although these effects have not been clearly demonstrated in Nebraska Sandhill lakes. These studies guided *a priori* model formation and allowed me to compare recruitment of bluegill and yellow perch populations to other water bodies and also to model abiotic factors (e.g., climatological) influencing recruitment of these populations. Understanding factors related to year-class strength is crucial to managing these important sport fish populations and also to understanding the basic underlying ecology and potential mechanisms governing recruitment.

Methods

Study area

Six lakes were sampled for bluegill and seven lakes were sampled for yellow perch in the Sandhills region of north-central Nebraska from 2004 to 2007 (Table 2-1). Water levels in these lakes are primarily governed by groundwater; surface runoff is minimal (Ginsberg 1985; Rundquist et al. 1987). Winterkills are rare due to flowing springs even though ice coverage may last up to three months (McCarragher 1977). The watersheds are primarily mixed- and tall-grass prairie and livestock grazing is the principal land use (Bleed and Flowerday 1989). Lakes varied in surface area from 15 to 907 ha, were shallow (maximum depth 1.2-4.3 m), and almost entirely littoral (mean

depth 0.6-2.9 m). Submergent vegetation coverage in Sandhills lakes is variable, ranging from approximately 15 to nearly 100%. Common fish species present in the lakes included largemouth bass, northern pike *Esox lucius*, common carp *Cyprinus carpio*, golden shiner *Notemigonus crysoleucas*, fathead minnow *Pimephales promelas*, black bullhead *Ameiurus melas*, and green sunfish *L. cyanellus*. Angler exploitation was presumably minimal (Paukert et al. 2002a) although Cameron and Linke lakes were commercially harvested for adult yellow perch by the landowner, likely mimicking substantial angler exploitation. Four lakes were closed to fishing and most of the lakes were difficult to access.

Population structure and recruitment patterns

Adult bluegill and yellow perch were collected once from each lake using randomly-located, overnight sets of double-throated trap (i.e., modified fyke) nets with 16-mm bar measure mesh, 1.1- by 1.5-m frames, and 22-m leads during late-May to early-June from 2004 to 2007. Catch per unit effort (CPUE) in trap nets was expressed as the mean number of fish (all sizes) captured per net night. Total sampling effort was variable depending on lake size and ability to obtain reasonable sample sizes of fish.

Collected bluegill and yellow perch were counted, measured (TL in mm), and transported to the laboratory for processing. The size structure of the bluegill and yellow perch populations was indexed using proportional size distribution (PSD; the number of

quality length and longer fish/number of stock length and longer fish x 100) (Guy et al. 2007) and proportional size distribution of preferred-length fish (PSD-P; the number of preferred-length and longer fish/number of stock length and longer fish x 100) (Guy et al. 2007). Minimum stock, quality, and preferred lengths are 8, 15 and 20 cm for bluegill and 13, 20 and 25 cm for yellow perch (Gabelhouse 1984). The 95% confidence intervals for PSD and PSD-P were determined following Fleiss (1981).

Sagittal otoliths were removed for aging. Age was estimated by two independent readers viewing the otolith in whole view for fish of ages 4 and younger. Otoliths from age 5 and older fish were cracked, sanded, placed in clay, and viewed with a fiber optic light under a binocular microscope at 40X magnification to estimate age. Discrepancies in age estimates were reconciled by reading the otolith in concert. If agreement could not be achieved, the otolith was omitted from the analysis. Age-frequency histograms were constructed for each population. Quantification of year-class strength followed the residual method proposed by Maceina (1997) and modified by Maceina (2003). Catch-curve analyses (Ricker 1975) were performed on age-structure data that had been collected with trap nets by regressing the natural logarithm of the number caught in each year class against age. Catch-curve analyses were performed for each species by individual lake. Age 1 and older yellow perch and age 2 and older bluegill were assumed recruited to the trap nets and the population in this study. I assumed residuals of the catch curve were representative of recruitment variability among years and were an index

of relative year-class strength (Maceina 1997; Isermann et al. 2002). Year-class strength was then compared by species and among populations with correlation analysis to determine recruitment synchrony within species.

Population model

Weaker and stronger year classes for bluegill and yellow perch were identified and related to abiotic variables. Climatological data were obtained from National Oceanic and Atmospheric Administration (NOAA) weather stations located closest to the lakes. I selected air temperature, precipitation, wind speed, and winter severity as important variables to examine. I constructed biologically meaningful combinations of these variables into competing models and fit each model with regression. For bluegill I examined six models constructed to represent important life stages or hypothesized influential variables (Table 2-2). Total annual precipitation, cumulative warming days for March through May (total number of days when mean daily air temperature was $\geq 4.4^{\circ}\text{C}$), cumulative warming days for June (total number of days when mean daily air temperature was $\geq 22^{\circ}\text{C}$ in June), and winter severity (cumulative number of days when mean daily air temperature was $\leq 0^{\circ}\text{C}$ over the entire winter period) were examined. I constructed biologically meaningful combinations of these variables into competing models and fit each model with regression. Models were compared using Akaike's

information criterion (AIC_c , corrected for small sample sizes; Burnham and Anderson 1998). Rankings were made of *a priori* models based on level of support to explain variation in year-class strength of yellow perch and bluegill in Nebraska Sandhills lakes. The number of parameters (main factors plus error and intercept) was designated as K , ΔAIC_c is the difference in AIC_c between each model and the most supported model, and AIC_c weight is the relative weight of evidence for each model. Ranks were designated by ΔAIC_c and AIC_c weights (smaller ΔAIC_c and larger values of AIC_c weights indicate highest support).

For yellow perch I examined five models constructed to represent important life stages in a similar manner to that previously described for bluegills (Table 2-2). Total annual precipitation, cumulative warming degree days for March through May (number of days when mean daily air temperature $\geq 4.4^\circ\text{C}$), mean summer air temperature (i.e., June, July, and August), a wind magnitude index during spawning and hatching (i.e., April, May, and June), and winter severity. The wind magnitude (W_m) index is given by:

$$W_m = \text{mean lake fetch (km)} / \text{mean wind velocity (km/h)}$$

where the mean lake fetch is calculated as the average fetch of four transects of the lake at a given wind vector. Wind vectors were categorized into eight cardinal direction categories (i.e., north, northeast, east, southeast, south, southwest, west, and northwest).

Thus, this index takes into account the waterbody size (fetch) at a given wind vector and wind velocity as wind likely has a larger effect at greater fetches.

Post-hoc exploratory analyses were conducted to further identify potential relationships between year-class strength and climatological variables. Correlation and multiple-regression analyses were conducted using residuals from the catch-curve regressions as the dependent variable for the regression models. The monthly mean of the average daily wind speed, total monthly precipitation, and monthly mean of the average daily temperature were used in my analyses. Statistical significance was set *a priori* at $\alpha=0.10$ because this was an exploratory exercise with a low number of observations (i.e., years) for most lakes.

Results

I examined 454 bluegills of broad ranges of size (22 to 293 mm TL) and age (age 1 to 11) from six Sandhills lakes (Table 2-3). Mean CPUE was generally low and size structure of bluegills was variable with one lake (i.e., Cottonwood Lake) having a moderate number of smaller individuals while others contained a relatively higher proportion of larger individuals (Table 2-3). In addition, age structure was variable among populations. Some lakes had a truncated age structure dominated by younger individuals while others had an extended age structure (Figure 2-1). Missing year classes

were rare. Recruitment of bluegill was asynchronous (i.e., similar strong/weak year classes were not consistently observed) across study lakes ($n=13$ year classes, $r = 0.01$, $P=0.99$; Figure 2-2) and among study lakes. All between-lake correlations of year-class strength indices (i.e., residuals) were not significant (Table 2-4). The highest correlation coefficient was between Cottonwood Lake and Dewey Lake ($r = 0.71$) but most correlation coefficients were low and year-class strength was negatively correlated in several pairs of lakes.

I examined 689 yellow perch over a broad range in size (68 to 361 mm TL) and ages (age 0 to 11) from seven Sandhills lakes (Table 2-5). Relative abundance (i.e., mean CPUE) was generally low and size structure of yellow perch was variable with some lakes containing populations dominated by smaller individuals while others contained a relatively higher proportion of larger individuals (Table 2-5). Age structure was variable among populations. Some lakes had a truncated age structure dominated by younger individuals while others had an extended age structure (Figure 2-3). Missing year classes were rare. Recruitment of yellow perch was asynchronous across study lakes ($n = 13$ year-classes). Between-lake correlations of year-class strength indices (i.e., residuals) indicated two significant comparisons (i.e., Cameron Lake*Linke Lake $r=-0.98$; Dewey Lake*Marsh Lake $r=-1.00$; Table 2-4). The correlation coefficients were both negative

for these comparisons, which is the opposite of the predicted pattern that would indicate synchronous recruitment patterns.

Among the *a priori* models examined for bluegill, year-class strength appeared to be influenced by a combination of factors. Four models had ΔAIC_c values less than 2.0. The most supported model for bluegill was warming degree days for the period prior to spawning (Table 2-6). Three single variable models (i.e., June warming degree days, total annual precipitation, and winter severity) were also supported. Positive relationships were found for total annual precipitation and winter severity and year-class strength (Figure 2-5). A negative relationship was found for June warming degree days, and year-class strength (Figure 2-5). All other additive models were much less supported.

Among the *a priori* models examined for yellow perch, year-class strength appeared to be influenced by winter severity, spring warming degree days, and total annual precipitation. The most supported model for yellow perch was winter severity which had a positive relationship to year-class strength (Table 2-6). The second and third most supported models (spring warming rate and total annual precipitation, respectively) also warrant strong consideration as the level of support was less than one AIC_c distance from the most supported model and both had positive relationships to year-class strength. The fourth most supported model (mean summer air temperature + winter severity) had

marginal support ($\Delta AIC_c = 2.5$) but corroborates the strength of winter severity as an important variable influencing year-class strength of yellow perch (Figure 2-6). All other additive models were much less supported.

Discussion

Recruitment patterns for bluegill and yellow perch were asynchronous in Nebraska Sandhills lakes. The lack of synchrony in yellow perch and bluegill population year-class strength suggests that climate does not act similarly broadly across a series of Nebraska Sandhills lakes and that individual variability among lakes is equally or more important in influencing year-class strength for these two species in the Nebraska Sandhills ecoregion. Recruitment synchrony has been documented to varying degrees for several freshwater species, including yellow perch (Myers et al. 1997; Thomas and Haas 2004) Eurasian perch *Perca fluviatilis* (Lehtonen and Lappalainen 1995; Paxton et al. 2004), roach *Rutilus rutilus* (Grenouillet et al. 2001), common carp (Phelps et al. 2008), walleye *Sander vitreus* (Colby et al. 1979; Myers et al. 1997; Schupp 2002), common whitefish *Coregonus lavaretus* (Ranta et al. 1995), and vendace *Coregonus albula* (Marjömaki et al. 2004). Conversely, recruitment was asynchronous among several populations of bluegill in South Dakota glacial lakes (Edwards et al. 2007).

Recruitment synchrony may be an uncommon event. Myers et al. (1997) found that the spatial scale of recruitment correlations for several freshwater fish species (including walleye and yellow perch) was less than 50 km. This contradicts the findings of synchronous recruitment over large spatial scales for walleye (e.g., 1,000 km; Colby et al. 1979) and roach (e.g., 150 km; Grenouillet et al. 2001). My study lakes spanned a spatial scale of 195 km. In addition, Myers (1998) reported that environment-recruitment correlations were more likely to be confirmed for populations at the geographical limit of the species range. For example, Koonce et al. (1977) suggested that temperature may only directly limit year-class strength under severe climatic regimes which likely occur most commonly at the northern and southern edge of the percid range. In addition, Lehtonen and Lappalainen (1995) reported that temperature was positively correlated with recruitment for populations of Eurasian perch at the northern edge of their range. Bluegill and yellow perch in the Nebraska Sandhills are within their native range and have been extensively introduced successfully in other areas; the climatic conditions typical of the area are well-within their tolerance limits.

Bluegill models containing spring warming temperature, June warming degree days, total annual precipitation, and winter severity and yellow perch models based individually on winter severity, spring warming rate, and total annual precipitation were all supported by the data. These metrics were similarly supported based on their respective AIC_c weights. Thus, based solely on this analysis of climate variables, I did

find some support for the concept of climatic influence on bluegill and yellow perch recruitment.

Environmental factors related to recruitment of bluegill and yellow perch showed the common positive effect of spring warming and precipitation. Formation of stronger year classes in years with warmer growing season periods is also a shared result of previous research on bluegill (Beard 1982; Tomcko and Pierce 2005) and yellow perch (Clady 1976; Koonce et al. 1977; Craig et al. 1979; Ward et al. 2004). Craig et al. (1979) found a significant positive relation between year-class strength of Eurasian perch and summer temperature, although Ridenhour (1960) and Schneider (1971) found no relationship between bluegill year-class strength and air temperature. Water temperature may directly affect bluegill spawning and hatching. Beard (1982) reported that years when water temperatures fluctuated about 21 C led to a protracted bluegill spawning season in northern Wisconsin lakes. He also reported that the later a successful hatch occurred, the smaller the resulting year class was and that spawning after the first week in July always resulted in a weak year class. Edwards et al. (2007) reported that growing season temperature was positively related to bluegill year-class strength in South Dakota impoundments although the relationship was weak. Cargnelli and Gross (1996) also reported higher survival of earlier hatched bluegills. Conversely, Garvey et al. (2002) identified lower survival of earlier hatched cohorts and Santucci and Wahl (2003)

reported that the earliest hatched bluegills experienced higher mortality through increased predation by largemouth bass. I found a negative relationship between June air temperature and bluegill year-class strength, which is a counter-intuitive result. The exploratory nature of my analysis may have identified environmental variables related to recruitment that may be indirect and challenging to fully elucidate without further, in-depth examination of potential mechanisms.

Warmer, more stable spring temperatures have been linked to stronger yellow perch year classes (Kallemeyn 1987) and increased age-0 abundance (Pope et al. 1996) as well as warmer summer temperatures (Eurasian perch, Craig et al. 1979). Sandhills lakes are typically shallow and wind-swept, facilitating relatively rapid responses of the lake water temperature to the ambient air temperature via mixing. Erratic temperature fluctuations in the spring, characteristic of the Great Plains climate, could negatively affect yellow perch recruitment. For example, Hokanson and Kleiner (1974) reported that a higher abundance of yellow perch swim-up larvae were produced when water temperatures gradually increased and led to a shorter hatching period with fewer abnormalities in larvae. In addition, Longhenry (2006) attributed the lack of larval yellow perch abundance in semi-permanent wetlands in South Dakota to a cold-front that decreased the water temperature from 12°C to 8°C in 24 h. Conversely, Jansen (2008)

reported that rapid declines in water temperature had little effect on yellow perch egg survival in experimental tanks.

Temperature may be a proximate factor representing other variables but identification of these variables was beyond the scope of my study. A cooler spring may have indirect influences on recruitment if water temperature indirectly affects larval fish via its influence on the food chain. Suitable growth conditions for zooplankton are largely determined by the physical environment (e.g., water temperature), which in turn influences phytoplankton growth (Sommer et al. 1986; Taylor et al. 1987). Decreased prey abundance in the spring may lead to lower body condition of adults prior to nesting and spawning activities. Cooler water temperatures may also suppress the vegetative community (Barko and Smart 1981; Barko et al. 1982; Spencer 1986) by slowing growth (Scheffer 2004); Schneider (1999) linked dense vegetation to quality bluegill populations in Michigan. Tomcko and Pierce (2005) found that Secchi depth was negatively related to back-calculated length at age-3 for bluegill in Minnesota, suggesting the importance of productivity. This may be anecdotal evidence that depressed spring temperatures, limiting productivity, may have negative effects on bluegills and yellow perch and the direct mechanisms may remain unknown. Several other factors associated with temperature may operate in the systems I studied. For example, temperature may mediate egg maturation rate, growth rate of larvae and juveniles, food availability, and

production of potential competitors (Koonce et al. 1977; Madenjian et al. 1996; Hansen et al. 1998).

Higher precipitation has also been related to higher recruitment of bluegill (Gaboury and Patalas 1984; Paller 1997) and yellow perch (Clady 1976; Gillet and Dubois 1995; Pope et al. 1996; Ward et al. 2004). The Nebraska Sandhills ecoregion has experienced a recent period of below average annual precipitation (Svoboda 2008) that has led to lower water levels in many lakes (M. Lindvall, Valentine National Wildlife Refuge, personal communication). Because the prevailing landscape feature of the Sandhills ecoregion is a vast expanse of sand dunes stabilized by a thin veneer of grass cover there is essentially no runoff due to the sandy soil. Precipitation events generally lead to rapid and extensive recharge of the underlying aquifer (Rundquist et al. 1987). In addition, Rundquist et al. (1987) suggested that the precipitation lag to lake-size reaction is potentially of long duration (> 90 days). In addition, although lake surface area minimum were generally in the fall, lakes within the refuge experienced additional minima in early summer, likely when bluegill, in particular, are spawning. If water levels are related to recruitment of bluegill and yellow perch populations then it is logical that annual precipitation was identified in my most supported models. Years with increased precipitation may have led to relatively stronger year classes in several lakes. Lake water levels may have several effects on bluegill recruitment. Bonvechio and Allen (2005) reported a positive relationship between year-class strength of combined bluegill and

redbreast sunfish *Lepomis auritus* populations and pre-spawn water levels in three Florida rivers, suggesting that potential inundation of spawning habitat increases year-class strength. Year-class strength in another centrarchid, crappies *Pomoxis* spp., was positively related to water level in reservoirs (McDonough and Buchanan 1991; Mitzner 1991). Conversely, Pope et al. (1996) found a negative relationship between black crappie *Pomoxis nigromaculatus* year-class strength and precipitation (as a surrogate for water level) in a South Dakota natural lake but suggested a potential biological interaction between age-0 yellow perch abundance as abundances for these two species were negatively correlated. Ward et al. (2004) found that April precipitation and May temperatures were positively correlated with larval yellow perch abundance in eastern South Dakota glacial lakes but that the relative importance of those climate variables was lake-specific and not consistently statistically significant over all lakes.

Winter severity was positively related to year-class strength of bluegill and yellow perch, which may initially seem counter intuitive as longer/colder winters may lead to increased overwinter starvation mortality. However, colder or longer winters may have a positive effect on year-class strength if increased overwinter mortality of juvenile fish leads to a less dense cohort, through increased starvation mortality, which, through a density-dependent release, is able to produce a relatively stronger year-class. The survivors would then experience less competition and therefore be more likely to recruit. Size-selective overwinter mortality may not be a frequent occurrence in bluegill

populations (see chapter 3; Toney and Coble 1979). Edwards et al. (2007) identified a weak relationship between winter severity and recruitment in bluegill populations in eastern South Dakota lakes. Size-selective overwinter mortality has been documented for yellow perch (Post and Prankevicius 1987; Post and Evans 1989; Johnson and Evans 1991), but the effect of overwinter mortality on perch recruitment has not been well analyzed. Overwinter starvation mortality of yellow perch can greatly influence year-class strength (Post and Evans 1989) and this topic warrants further examination.

Based on my analysis of climate variables, some evidence for the concept of climatic influence on bluegill and yellow perch recruitment was found. The addition of additional Sandhill lake population age structures of bluegill and yellow perch may increase the ability to detect climatic influences over a broadly across a series of Nebraska Sandhills lakes. Attempts were made to sample several additional lakes for adult bluegill and yellow perch but catches were often extremely low ($n < 10$). Adult fish collections were made over a period of several years. Many yellow perch population age structures were truncated; thus, population samples collected in different years may contain very few overlapping year classes from which to directly compare and contrast among one another. Finally, biotic factors such as predation (Forney 1971; Mills et al. 1987; Treasurer 1989; Mason and Brandt 1996; Santucci and Wahl 2003), competition (Werner and Hall 1979), and food availability (Dettmers et al. 2003) may influence recruitment in these systems.

Other climatic influences on yellow perch have been described in the past to varying degrees. Isermann and Willis (2008) documented prevalent short hatching durations of yellow perch in eastern South Dakota lakes and suggested an increased probability of catastrophic losses when environmental conditions were not conducive to yellow perch reproduction and subsequent survival. Although wind was not documented as influencing year-class strength in my study, several researchers have implicated wind as negatively influencing age-0 percid survival (Clady 1976; Treasurer 1989; Aalto and Newsome 1993; Pope et al. 1996; Ward et al. 2004). Sandhills lakes typically have moderate to high levels of submergent and emergent vegetation coverage likely providing ample yellow perch spawning surfaces and reducing the need to spawn directly on the lake substrate. The vegetation availability may buffer the negative effect that wind can have on embryos that are deposited directly on the lake bottom by providing some increased protection. In addition, Aalto and Newsome (1993) suggested that yellow perch embryos are negatively affected by winds that cause upwelling of cold water from beneath the thermocline. These temperature shocks may kill or result in deformed larvae. Sandhills lakes are typically not stratified; thus, this effect should be minimal or nonexistent in my study lakes. In addition, Miner and Stein (1993) reported that increased turbidity reduced larval bluegill consumption of zooplankton in experimental enclosures. Given the potential impact of wind on recruitment of bluegill and yellow

perch, coupled with the fact that high winds are a pervasive climatic feature of the Great Plains, the effects of wind on recruitment should not be discounted in future studies.

Many of my results are correlative and thus not necessarily cause-and-effect. Nevertheless my results are corroborated to a degree by the findings of other researchers and suggest that environmental effects on yellow perch and bluegill recruitment are ubiquitous but complex and likely difficult to elucidate. In addition, high population fecundity and/or protracted spawning in these populations may alleviate the abiotic (i.e., climatic) factors that influence the recruitment of other freshwater fishes.

An in-depth examination of year-class production (i.e., recruitment) within specific systems is warranted to further understand the mechanisms related to year-class strength. Specifically, direct field observations of the timing of larval appearance coupled with empirical data on abiotic and biotic conditions and subsequent temporal tracking of cohorts through their first year could provide valuable insights into recruitment mechanisms. Laboratory experiments involving the effects of temperature fluctuations on egg and larval survival also may reveal further information relating to this critical time period.

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Table 2-1. Legal description and physical characteristics of Nebraska Sandhills lakes sampled for adult bluegill and yellow perch in 2004-2007.

Lake	County	Latitude	Longitude	Surface area (ha)	Mean depth (m)	Maximum depth (m)	Maximum fetch (km)
Cameron	Rock	42.38	99.42	39	1.8	2.9	1.1
Clear	Cherry	42.56	100.62	172	2.9	4.3	2.8
Cottonwood	Cherry	42.91	101.67	15	2.7	1.4	0.7
Dewey	Cherry	42.54	100.63	223	1.9	2.8	4.0
Duck	Cherry	42.54	100.73	27	1.7	3.3	0.7
Linke	Rock	42.40	99.40	31	0.6	1.2	0.5
Marsh	Cherry	42.53	100.51	907	1.2	1.9	3.4
Pelican	Cherry	42.53	100.67	332	1.3	2.8	5.0
Watts	Cherry	42.58	100.69	93	1.3	1.8	2.6
West Long	Cherry	42.53	100.72	25	1.3	1.8	1.8

Table 2-2. Climatological variables used to assess models for bluegill and yellow perch recruitment. The predicted relationship to recruitment (negative “–” or positive “+”), potential mechanism, and literature source are for each variable.

Species	Variable	Predicted relationship	Potential mechanism	Source
Bluegill	Spring/summer warming rate	+	Increased larval survival and growth	Beard 1982 Tomcko and Pierce 1997, 2005
	Winter severity	--	Increased and/or size selective overwinter mortality	Miranda and Hubbard 1994 Garvey et al. 2002
	Precipitation	+	Increased spawning habitat	Gaboury and Patalas 1984 Paller 1987
Yellow perch	Spring wind index	--	Physical egg destruction Increased turbidity Reduced foraging	Clady 1976 Aalto and Newsome 1993 Pope et al. 1996 Ward et al. 2004
	Spring warming rate/ summer air temperature	+	Increased larval survival and growth	Clady 1976 Koonce et al. 1977 Craig et al. 1979 Ward et al. 2004
	Winter severity	--	Increased and/or size selective overwinter mortality	Post and Prankevicius 1987 Post and Evans 1989
	Precipitation	+	Increased spawning habitat	Clady 1976 Gillet and Dubois 1995 Pope et al. 1996 Ward et al. 2004

Table 2-3. Number of bluegill aged, mean catch per unit effort (CPUE, number of fish [all sizes] per trap-net night), proportional size distribution (PSD), and proportional size distribution of preferred-length fish (PSD-P) in six Sandhills lakes. Values in parentheses are standard errors for CPUE and 95% confidence intervals for PSD and PSD-P.

Lake	Number	CPUE	PSD	PSD-P
Cottonwood	111	138 (38)	22 (50, 12-36)	0 (50, 0-9)
Dewey	38	2.2 (0.82)	30 (38, 17-47)	0 (38, 0-11)
Duck	25	3 (1)	17 (24, 6-39)	13 (24, 4-34)
Pelican	137	2 (1)	84 (115, 76-90)	51 (115, 42-60)
Watts	10	1 (0.4)	60 (10, 27-86)	20 (10, 4-56)
West Long	133	17 (3)	21 (108, 14-30)	16 (108, 10-25)

Table 2-4. Bivariate correlations of bluegill population year class strength among different pairs of Sandhills lakes.

Species	Comparison	n	<i>r</i>	<i>P</i>
Yellow perch	Cameron*Dewey	3	0.66	0.55
	Cameron*West Long	3	-0.30	0.80
	Cameron*Linke	4	-0.98	0.02
	Cameron*Marsh	4	-0.60	0.40
	Dewey*West Long	3	0.92	0.26
	Dewey*Linke	3	-0.46	0.70
	Dewey*Marsh	3	-1.00	0.05
	West Long*Linke	4	0.05	0.95
	West Long*Marsh	5	0.73	0.16
	Linke*Marsh	5	0.37	0.54
Bluegill	Cottonwood*Dewey	3	0.71	0.50
	Cottonwood*Duck	5	-0.34	0.57
	Cottonwood*Pelican	5	0.31	0.61
	Cottonwood*West Long	7	0.42	0.35
	Dewey*Duck	3	0.58	0.61
	Dewey*Pelican	3	-0.36	0.77
	Dewey*West Long	3	0.05	0.97
	Duck*Pelican	4	-0.52	0.48
	Duck*West Long	5	-0.65	0.24
	Pelican*West Long	7	0.32	0.49

Table 2-5. Number of yellow perch aged, mean catch per unit effort (CPUE, number of fish [all sizes] per trap-net night), proportional size distribution (PSD), and proportional size distribution of preferred-length fish (PSD-P) in seven Sandhills lakes. Values in parentheses are standard errors for CPUE and 95% confidence intervals for PSD and PSD-P.

Lake	Number	CPUE	PSD	PSD-P
Cameron	79	-*	85 (79, 75-92)	33 (79, 23-100)
Dewey	99	196 (107.48)	42 (99, 32-52)	10 (99, 5-18)
Linke	155	-*	30 (155, 23-38)	0 (155, 0-3)
Marsh	141	9.5 (1.9)	84 (132, 76-90)	61 (132, 52-69)
Pelican	29	0.7 (1)	14 (7, 1-58)	14 (7, 1-58)
Watts	37	4 (1)	50 (12, 22-77)	0 (12, 0-30)
West Long	149	3 (1)	80 (149, 72-86)	38 (149, 30-46)

*Individual trap-net effort was unavailable

Table 2-6. Rankings of *a priori* models based on level of support to explain variation in year-class strength of yellow perch and bluegill in Nebraska Sandhills lakes. The number of parameters (main factors plus error and intercept) is designated as K, Akaike's Information Criterion corrected for small sample size (ΔAIC_c), ΔAIC_c is the difference in AIC_c between each model and the most supported model, and AIC_c weight is the relative weight of evidence for each model. Ranks were designated by ΔAIC_c and AIC_c weights (smaller ΔAIC_c and larger values of AIC_c weights indicate highest support). Winter severity represents the total number of days when air temperature was $\leq 0^\circ C$ for the first winter of life. Total precip represents total annual precipitation.

Species	Model	K	AIC_c	ΔAIC_c	AIC_c weight
Yellow perch	Winter severity	3	6.22	0.00	0.33
	Spring warming	3	6.29	0.07	0.31
	Total precip	3	6.82	0.60	0.24
	Summer temp, winter severity	4	8.67	2.45	0.10
	Total precip, AMJ wind, spring warming	5	11.49	5.27	0.02
	Global	7	16.66	10.44	0.00
Bluegill	Spring warming	3	-11.57	0.00	0.29
	June warming	3	-11.40	0.17	0.27
	Total precip	3	-10.75	0.82	0.19
	Winter severity	3	-10.20	1.37	0.15
	Total precip, June warming	4	-9.06	2.50	0.08
	Global	6	-4.90	6.67	0.01

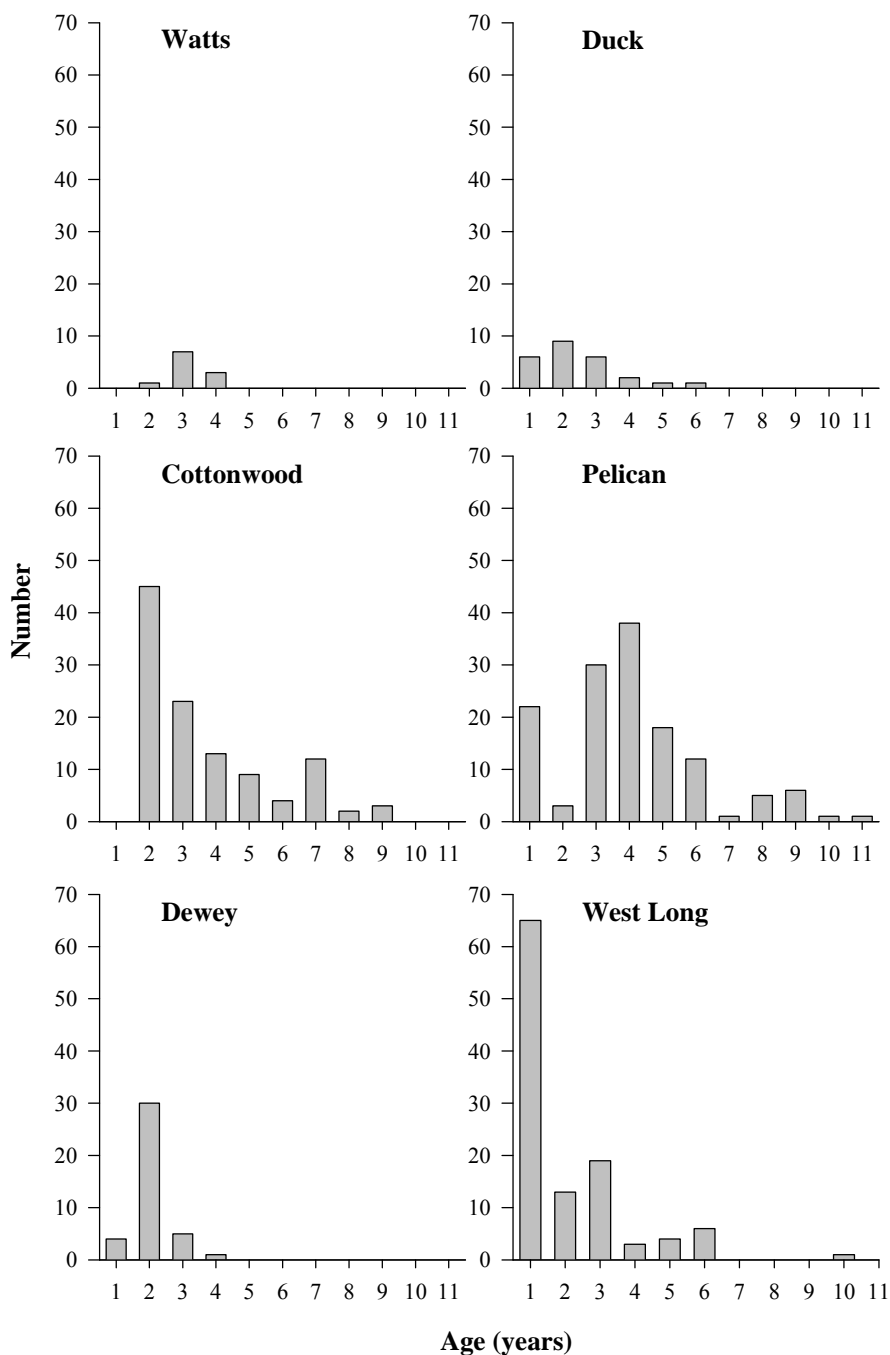


Figure 2-1. Age-frequency histograms of bluegills collected from six Nebraska Sandhills lakes, 2004-2007.

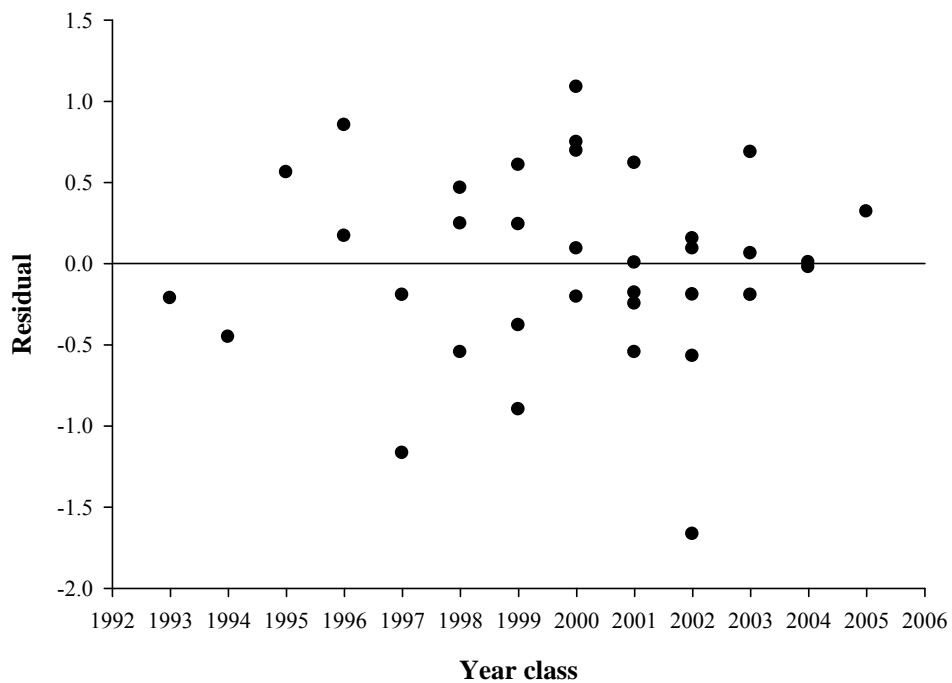


Figure 2-2. Year-class strength (as indexed by catch-curve residuals) of bluegills from six Nebraska Sandhills lakes.

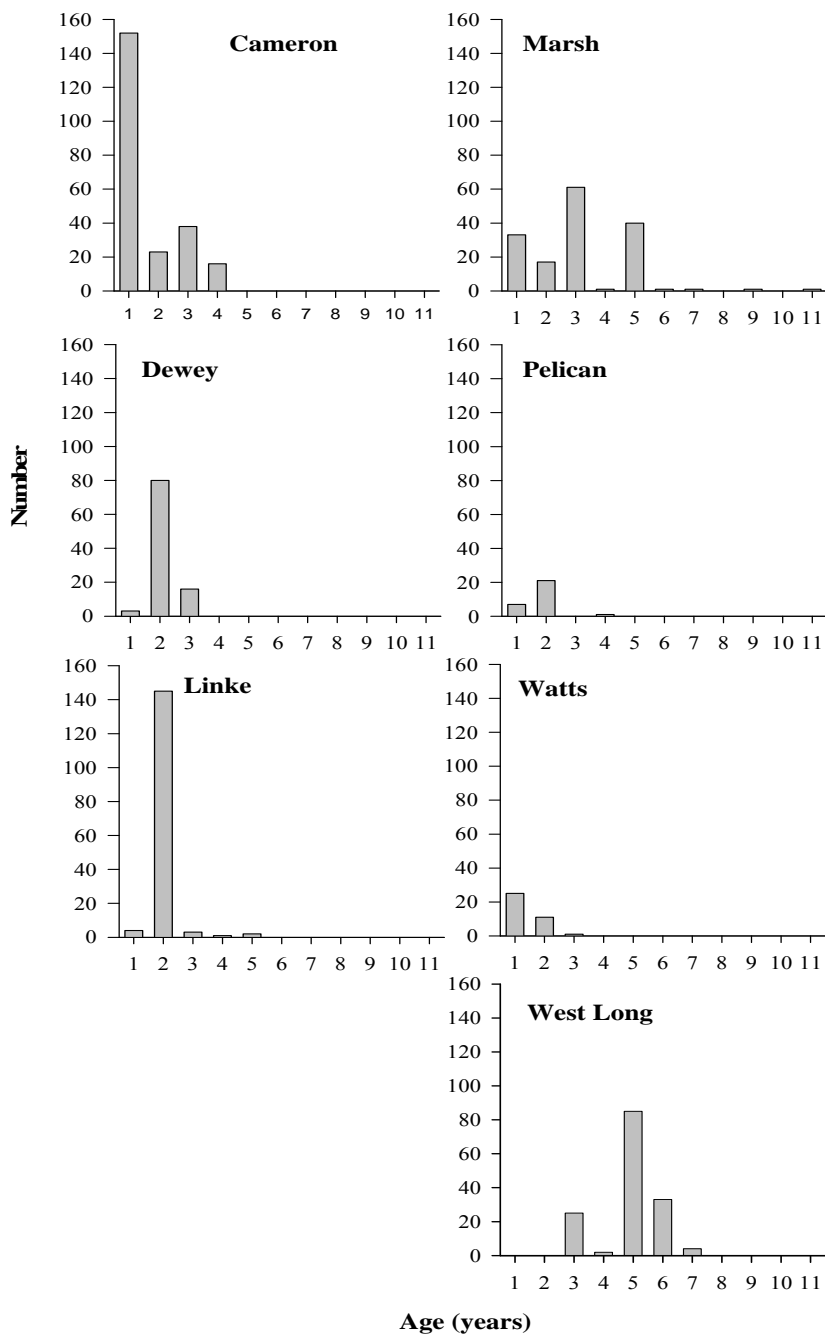


Figure 2-3. Age-frequency histograms of yellow perch collected from seven Nebraska Sandhills lakes.

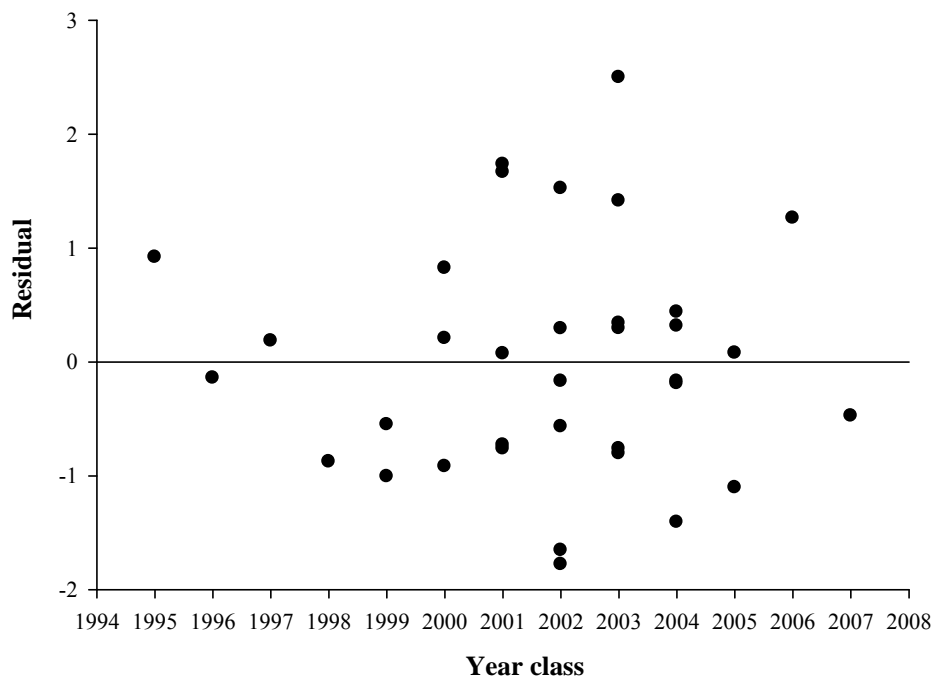


Figure 2-4. Year-class strength (as indexed by catch-curve residuals) of yellow perch from seven Nebraska Sandhills lakes.

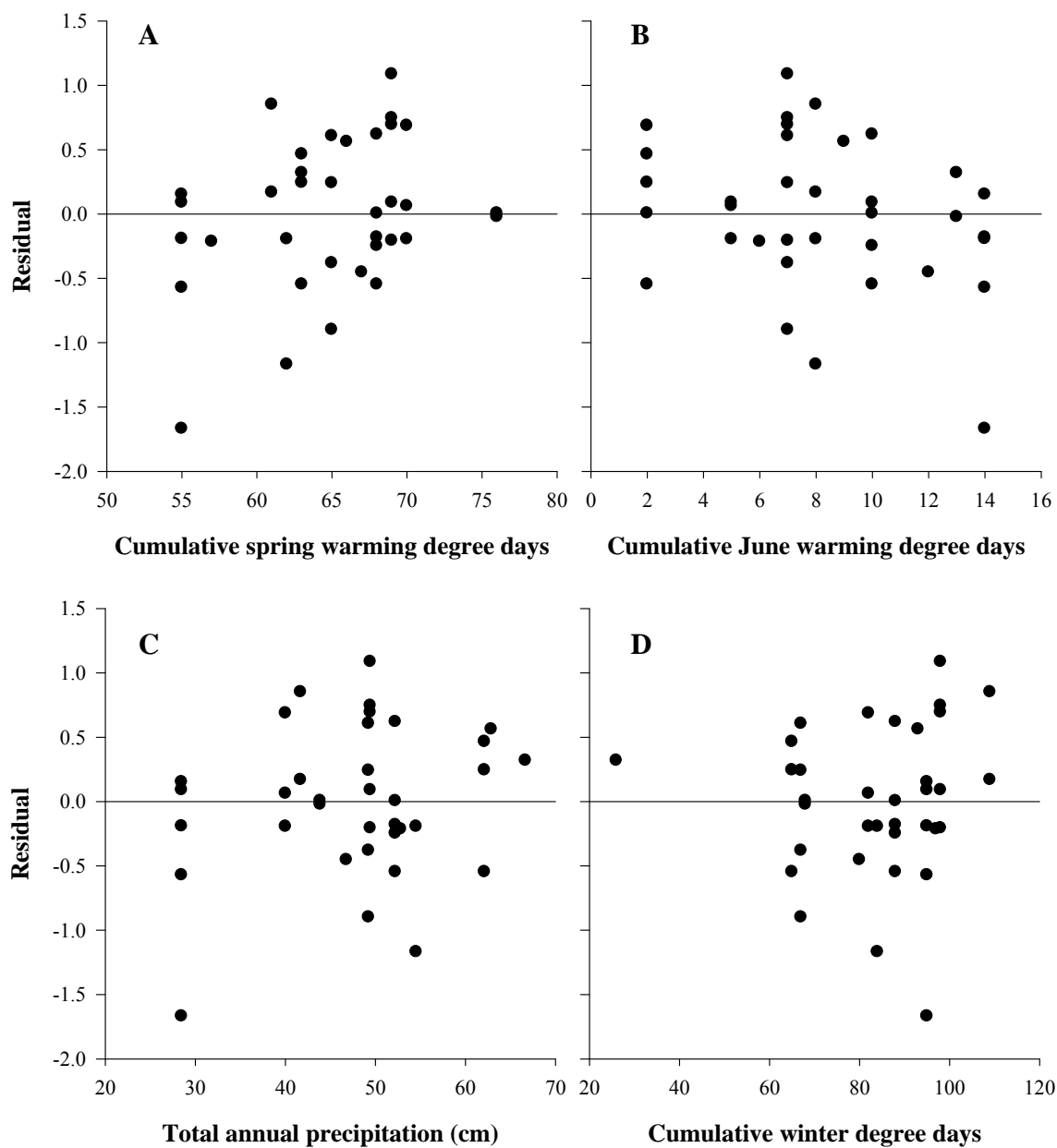


Figure 2-5. Relation between year-class strength (as indexed by catch-curve residuals) of bluegills and cumulative spring warming degree days (A), cumulative June warming degree days (B), total annual precipitation (C), and cumulative winter degree days (D)

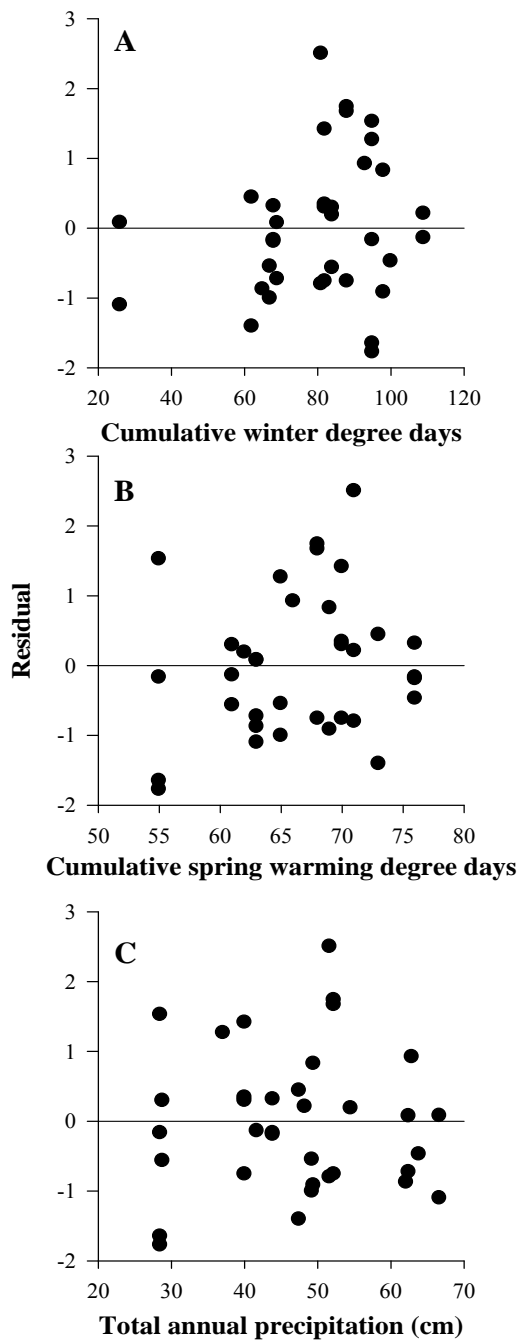


Figure 2-6. Relation between year-class strength (as indexed by catch-curve residuals) of yellow perch and cumulative winter degree days (A), cumulative spring warming degree days (B), and total annual precipitation (C).

Chapter 3.

Prey selection and an examination of potential match-mismatch regulation by larval bluegill and yellow perch in Pelican Lake and Cameron Lake, Nebraska

An important component influencing the community ecology of an ecosystem is recruitment dynamics of the populations within a given community, which ultimately structure the fish communities (Diana 1995). Biotic factors such as food availability and competition (Prout et al. 1990; Welker et al. 1994; Ludsin and DeVries 1997; Bunnell et al. 2003), and predation (Forney 1971; Houde 1987; Rice et al. 1987; Santucci and Wahl 2003) are believed to regulate fish recruitment, both directly and indirectly.

Variable recruitment commonly occurs in yellow perch (Forney 1971; Koonce et al. 1977; Mills et al. 1989) and bluegill (Ricker 1945; Edwards et al. 2007) populations. Although bluegill recruitment is generally consistent (i.e., missing year classes are rare) in Nebraska Sandhills lakes there appears to be a moderate level of variability in relative year class strength among years (Paukert et al. 2002). Early survival and subsequent recruitment of fishes is often affected by availability of appropriately sized zooplankton and benthic invertebrate prey items to age-0 fishes.

The availability of prey when larval fish begin exogenous feeding has been proposed as a potential regulator of recruitment variability (match-mismatch hypothesis; Cushing 1975, 1990). The match-mismatch hypothesis consists of two assumptions: first, that fish at temperate latitudes spawn at approximately the same time each year and, second, that the larvae are released during the spring or autumn peaks in plankton

production (Cushing 1990). A match occurs when production of fish larvae and their prey is synchronous or nearly so; conversely, a mismatch occurs when there is a large temporal difference in these two variables (Figure 3-1; Cushing 1990).

Although the food habits of age-0 yellow perch have been extensively studied in Midwestern waters (e.g. Weber and Les 1982; Wahl et al. 1993; Fisher and Willis 1997), lake-specific prey selection patterns in the face of variable prey densities is a topic of importance. Similarly, age-0 bluegill food habits are well-studied (Werner 1969; Mittelbach 1981; Werner and Hall 1988), although data specific to Sandhills lakes have not been collected. The objectives of this study were to 1) describe prey selection for larval and juvenile yellow perch and bluegill in Cameron and Pelican lakes, Nebraska to better understand the prey utilization in these lakes and 2) examine potential match-mismatch regulation of bluegill and yellow perch recruitment.

Methods

Study areas

Cameron Lake is a 39-ha, shallow (mean depth = 1.2 m) natural lake in Rock County of the Sandhills region of north central Nebraska (McCarragher 1977). Submergent and emergent vegetation coverage was low (< 17% total coverage, see Table 4-7) in 2004 and 2005. The fish community is also simple, primarily comprised of yellow perch, green sunfish, black bullhead, common carp, fathead minnow, and golden shiner *Notemigonus crysoleucas*. The lake was closed to angling for over 12 months preceding our study, with little fishing effort for the previous three years (personal communication,

R. Lackaff, property owner). The lake is used for commercial harvest of yellow perch (total length [TL] > ~ 76 mm). The lake watershed is mostly mid and tall-grass prairie and primarily used for livestock grazing (Bleed and Flowerday 1989).

Pelican Lake is a 332-ha, shallow (mean depth = 1.3 m) natural lake in Cherry County of the Sandhills region of north central Nebraska within the Valentine National Wildlife Refuge (McCarragher 1977). Total vegetation coverage (emergent and submergent) ranged from 40 to 52% in 2004 and 2005 (see Table 4-7). The fish community is relatively simple, comprised primarily of bluegill, largemouth bass, yellow perch, northern pike, black bullhead, common carp, and fathead minnow. The lake watershed is mostly mid and tall-grass prairie and limited livestock grazing is allowed. Detailed lake descriptions are provided in Table 2-1.

Field methods

Larval yellow perch were obtained from Pelican and Cameron lakes and larval bluegill were obtained from Pelican Lake using a surface trawl with a 0.76-m diameter and 1,000- μ m mesh (bar measure). Isermann et al. (2002) found no difference in yellow perch density estimates between a 500- and 1,000- μ m mesh trawl, although the 1,000- μ m size was less likely to become fouled with algae and zooplankton. Larval sampling occurred approximately every 10 d from late-April to early September in Pelican Lake and from late-April to mid-June in Cameron Lake. In Pelican Lake, five randomly chosen locations within the lake were trawled on each occasion. Each random location was paired as an inshore (<100 m from emergent, littoral vegetation) and an offshore

(>100 m from emergent, littoral vegetation) site for a total of 10 trawling locations per occasion. In Cameron Lake, four randomly chosen locations within the lake were trawled on each occasion and paired as described above for a total of eight trawling locations per occasion. The number of recently hatched (e.g., ≤ 13 mm) bluegill and yellow perch larvae in the lakes were indexed using a flowmeter (Ocean Test Equipment, Inc.) in the mouth of the trawl, which allowed determination of water volume towed. All larval samples were preserved in 90% ethanol and transported to laboratory for identification and diet analysis.

Juvenile bluegill and yellow perch were collected from Pelican Lake in August or September 2004-2008 and juvenile yellow perch were collected from Cameron Lake in August, using cloverleaf traps and placed in 90% ethanol in the same years as trawling collections were made. The same cohorts were sampled the following April or May as age-1 fish. Each three-lobed cloverleaf trap was constructed of galvanized 6.4-mm bar mesh, with three 12.7-mm wide openings between lobes to accommodate entrance of small yellow perch (Brown and St. Sauver 2002). Each lobe was 50-cm in diameter and 41-cm height. Adult bluegill (i.e., age 2) and yellow perch (i.e., age 1) were collected and aged using otoliths (described in Chapter 2). Mean CPUE of age-1 yellow perch and age-2 bluegill were selected as lifestages recruited to the adult population.

Zooplankton and benthic macroinvertebrates were collected at the time of each trawling sample. Zooplankton was collected during the daytime as two replicates at each site using a 2-m long tube sampler (Rabeni 1996). Samples were filtered through a 65- μ m mesh net and stored in 90% ethanol. Benthic macroinvertebrates were sampled at the

same time and sites using a 231-cm² Ekman grab sampler. Two replicate benthic macroinvertebrate samples were collected at each site, strained through a 583- μ m mesh sieve in the field, and stored in 90% ethanol. Replicate samples were collected and processed separately.

Laboratory methods

Larval fish samples were sorted and identified in the laboratory using identification keys (Auer 1982; Holland-Bartels et al. 1990). All larvae were counted and up to 200 fish per sample were measured (mm TL) from each site. Digestive tracts were removed from up to 30 randomly selected larvae of each species per sampling occasion. Diet items were identified under a microscope, counted, and measured (mm TL). Zooplankton were enumerated and identified to family for cladocerans (i.e., Bosminidae, Chydoridae, Daphnidae, and Sididae), and as cyclopoid or calanoid copepods, copepod nauplii, ostracods, and rotifers. Other uncommon taxa were also noted. Each sample was diluted with water to a measured volume of 30 mL. Three subsamples were then taken with a 5-mL Hensen-Stempel pipette and placed in a Ward counting wheel. Up to 20 individuals of each category were measured (mm TL) and all individuals were counted. The total number of zooplankton of each taxon in a sample was calculated by dividing the number of organisms counted by the proportion of the sample volume processed. Density was then calculated by dividing the number of zooplankters of each taxon by the volume of the water filtered with the tube sampler.

Macroinvertebrates were typically identified to order and enumerated using a dissecting microscope in the laboratory. Up to 20 individuals of each taxon were measured (mm TL) and all individuals were counted. Density and standard error was then calculated by dividing the number of benthic invertebrates of each taxon by the area sampled with the Ekman dredge.

To determine prey selectivity, mean Chesson's (1983) coefficient of selectivity (α) was calculated for individual larval bluegill and yellow perch from each sampling occasion in 2004 and 2005:

$$\alpha = \frac{r_i/n_i}{\sum_{i=1}^m r_i/n_i}$$

where r_i is the number of food type i in the predator diet, n_i is the number of food type i in the environment, and m is the number of prey types available. Chesson's α was calculated separately for zooplankton and macroinvertebrate prey items. Mean α values (\pm 95% confidence intervals) were compared with random feeding ($1/m$) to determine selectivity.

Temporal density curves for yellow perch larvae and copepods and bluegill larvae and combined nauplii and *Bosmina* were constructed for each year and the mean and standard deviation of the peak density for predators and their prey were calculated. The aforementioned zooplankton taxa were chosen based on patterns of positive prey selection. In addition, newly hatched fish larvae consume zooplankton and do not consume benthic invertebrates until later in life, thus benthic invertebrates were not considered in the match-mismatch analyses. The width and overlap of the density curves

for predator and prey were calculated. Methods outlined by Mertz and Myers (1994) and Johnson (2000) were utilized for my analysis. The following parameters were first calculated:

t_0 = timing between peaks of larval production and food supply (days);

Δt_0 = annual differences in (t_0) from its mean value;

δ = one-half width of the density curve for larvae; and

σ = one-half width of the density curve for zooplankton.

These parameters were used to calculate 1) variability in peak timing from the mean for individual species (σ and δ), 2) variability in timing between larval abundance and peak zooplankton production (t_0), and 3) year-to-year variability in peak spawning and production (Δt_0). When $t_0 = 0$, the match between the peak larval abundance and abundance of zooplankton prey is exact (Mertz and Myers 1994). A mismatch occurs when one-half the width of the larval density curve does not overlap one-half the width of the zooplankton density curve. Correlation analysis was used to examine the relationship between predator-prey overlap (t_0) and indices of fish recruitment (i.e., larval abundance, juvenile abundance, and adult abundance) for yellow perch and bluegill in Pelican Lake. Yellow perch from Cameron Lake were omitted from this analysis due to inadequate sample size ($N=2$). Fall (age 0) and spring (age 1) juvenile abundance was indexed as the mean number per cloverleaf trap night. Adult yellow perch and bluegill abundance was indexed as the mean number of age-1 or age-2 fish, respectively, captured per trap net night in May or June during annual surveys. Detailed collection methods for juvenile and adult fishes are presented in detail in Chapter 4.

Results

Cameron lake contained eight taxa of zooplankters (Table 3-1) and nine taxa of benthic invertebrates (Table 3-2); Chesson's alpha values >0.125 and >0.111 indicated positive prey selection for zooplankton and benthic invertebrates, respectively, for yellow perch and bluegill. Temporal patterns of negative, neutral, and positive prey selection were found for yellow perch in Cameron Lake (Figure 3-2) and Pelican Lake (Figure 3-3) in 2004 and 2005. In Cameron Lake in both years, the most abundant zooplankters were generally daphnids, copepods, and rotifers (Table 3-1) and most abundant benthic invertebrates were dipterans (i.e. Chironomidae, Diptera pupae, and Ceratopogonidae; Table 3-2). In Cameron Lake, stomachs from 120 yellow perch larvae stomachs were examined in 2004 and 60 were examined in 2005 during May and June for prey items (Table 3-3). Copepods and daphnids were consistently the most abundant prey item found in stomachs by both percent of occurrence and percent by number (Table 3-4). In 2004, yellow perch selected copepods earlier in the season while shifting later to cladoceran prey. In 2005, copepods were consistently the positively selected prey item (Figure 3-2). Empty stomachs were not encountered in either year and nauplii were not observed in stomachs in any year. Benthic invertebrates were not consumed by yellow perch in Cameron Lake over the range of perch lengths examined (4.2 – 30.0 mm TL).

In Pelican Lake in 2004, the most abundant zooplankters were generally daphnids, copepods, and nauplii (Table 3-5) while chironomids were overwhelmingly the most abundant benthic invertebrate (Table 3-6). In 2005, the most abundant

zooplankters were generally cladocerans (i.e. daphnids, chydorids, and bosminids; Table 3-2) while chironomids were again the most abundant benthic invertebrate (Table 3-6). In Pelican Lake, 238 yellow perch larvae were examined from May through August for prey items (Table 3-3). Seven empty stomachs were encountered (3%). In 2005, larval yellow perch were only captured on 3 May in very low numbers. All larvae examined ($N = 16$) had empty stomachs. In 2004, copepods, daphnids, and chydorids were the most abundant prey items found in yellow perch stomachs by occurrence and by number (Table 3-7).

Yellow perch prey selection

Yellow perch selected copepods early in the season, shifted to cladocerans, and later exhibited neutral prey selection for most prey items (Figure 3-3). Nauplii were not consumed by yellow perch in this study and rotifers were uncommon in yellow perch diets. Benthic invertebrates were first consumed on 6 June (yellow perch mean TL = 23.1) indicating the beginning of an ontogenetic diet shift, although benthic invertebrates and zooplankton were both consumed through 26 August. Yellow perch consumed a variety of benthic invertebrates with corixids (Hemiptera), chironomids, and odonates generally displaying the highest percent occurrence and percent by number in diets (Table 3-8). Odonates and hemipterans were selected through June while neutral selection was observed for all benthic invertebrates throughout the rest of the season indicating opportunistic feeding patterns.

Bluegill prey selection

Temporal patterns of negative, neutral, and positive prey selection were found for bluegill consuming zooplankton in Pelican Lake in 2004 and 2005 (Figure 3-5). In 2004, 225 bluegill larvae were examined and 33 empty stomachs were encountered (15%). In 2005, 189 bluegill larvae were examined and 9 empty stomachs (5%) were encountered (Table 3-3). In 2004, age-0 bluegill consumed cladocerans, copepods, nauplii, ostracods, and rotifers. Nauplii and rotifers were common in smaller bluegill stomachs while cladocerans and copepods became more common later in the season (Table 3-9). Although the smallest bluegills (mean TL = 9.1 mm) consumed primarily nauplii and rotifers, these invertebrates were neutrally selected. Eventually, bluegill preferred cladocerans followed by copepods as prey items. Rotifers and ostracods were consistently neutrally or negatively selected (Figure 3-5) indicating opportunistic feeding on these prey items. Bluegill (mean TL = 19.1 mm) began to consume benthic invertebrates in low numbers on 16 August 2004 initiating an ontogenetic diet shift (Figure 3-6). Chironomids were positively selected on two occasions. Diptera pupae, ephemeropterans, and odonates were also consumed (Table 3-10) but displayed neutral selection while amphipods were avoided (Figure 3-6). In 2005, only one chironomid was observed in a bluegill stomach throughout the sizes examined (7.2 – 18.4 mm TL).

Yellow perch match-mismatch analyses

Copepods were chosen as an important prey item for first-feeding yellow perch based on the above results. The duration of larval yellow perch (TL < 13 mm) abundance

varied from 1 to 39 d. Duration was longest in Cameron Lake in 2004 (Figure 3-7) and shortest in Pelican Lake in 2005, when larvae were only collected on one day (3 May). The duration of peak copepod abundance varied from 9 to 38 d. Duration was longest in Pelican Lake in 2004 (Figure 3-8) and shortest in Cameron Lake in 2005 (Figure 3-7). The mean annual difference in peak abundance date for yellow perch predators and their copepod prey (t_0) was 7.2 d. Copepods peaked before yellow perch larvae in two instances, peaked after larvae in two instances, and exactly matched in two instances (Figure 3-7, 3-8; Table 3-11).

Bluegill match-mismatch analyses

The combined abundance of nauplii and *Bosmina* were chosen as an important prey item for first-feeding bluegill. The duration of larval bluegill abundance in Pelican Lake ranged from 51 to 71 d. Duration was longest in 2004 and shortest in 2007 (Figure 3-9). The duration of peak nauplii/*Bosmina* abundance ranged from 42 to 72 d. Duration was longest in 2004 and shortest in 2006 (Figure 3-9). The mean annual difference in peak abundance date for bluegill predators and their prey (t_0) was 10.3 d. The peak of larval bluegill and their prey was an exact match in two instances and prey peaked after larvae in one year. In 2004, there were two peaks in larval bluegill abundance and zooplankton prey peaked between these two dates (Figure 3-9, Table 3-11).

Examinations of matches and mismatches of zooplankton prey and larval abundance by the occurrence of width displacements from larvae (δ) and prey (σ) indicated matches in all years examined for both species (Table 3-11). In fact, there were

exact matches (i.e., $t_0=0$) in two years for both yellow perch and bluegill. To examine the relationship between predator-prey overlap and year-class strength, differences between predator and prey peaks versus indices of recruitment were examined (Table 3-12).

Correlation analyses between predator-prey overlap (t_0) and recruitment indices indicated no relationships for yellow perch ($P > 0.05$). Predator-prey overlap (t_0) was negatively correlated to mean CPUE of age-2 bluegill ($r = -0.95$, $P = 0.05$, $N = 4$). All other correlations were not significant ($P > 0.05$). For both species the highest observed abundance occurred in a year where the predators temporally matched or very closely match their prey (Table 3-11). Recruitment dynamics of bluegill and yellow perch are further explored in Chapter 4.

Discussion

Copepod densities were high in both of my study lakes relative to published findings for other water bodies (Kratz et al. 1987; Schael et al. 1991; Kim and DeVries 2000; Dettmers et al. 2003), although higher densities were reported in one year in an eastern South Dakota lake (Fisher 1996) when yellow perch larvae were present. Furthermore, copepod densities in Cameron Lake were actually higher in 2005 when we documented a weaker yellow perch year class than in 2004. Pelican Lake had a lower density of copepods in 2005 when yellow perch larvae were collected (mean = 23/L), although the density of copepods was higher than that typically reported at other

locations (Schael et al. 1991; Dettmers et al. 2003). Increased predation on daphnids by larger (i.e., 30 mm) yellow perch has been previously reported (Whiteside et al. 1985; Prout et al. 1990) and positive selection for these diet items has been shown (Mills et al. 1984; Schael et al. 1991). My observations corroborate such findings although daphnids were first consumed when yellow perch were between 15 and 17 mm TL. Wahl et al. (1993) reported consumption of daphnids by larval yellow perch at 9 mm TL. Although nauplii and rotifers have also been reported (Whiteside et al. 1985; Schael et al. 1991; Wahl et al. 1993; Fisher and Willis 1997) as a preferred prey item of newly hatched yellow perch, I found rare consumption of these taxa despite their availability.

Cladocerans and copepods generally appeared to be the most important zooplankton diet item for larval yellow perch and bluegill among years and lakes. I could not assess prey selection patterns for yellow perch in Pelican Lake in 2005 as all fish examined (N = 16) had empty stomachs. This appeared to be a weak year class or year class failure of yellow perch (see Chapter 4) and adequate zooplankton densities of appropriate sizes were available for consumption when larvae began exogenous feeding. My results agree with findings that copepods are a common prey item for newly hatched yellow perch (Weber and Les 1982; Whiteside et al. 1985; Fisher and Willis 1997) and are positively selected (Schael et al. 1991; Wahl et al. 1993).

Yellow perch in Pelican Lake in 2004 began a gradual ontogenetic diet shift from zooplankton to benthic invertebrates when they began positively selecting hemipterans on 16 June at a mean perch TL of 32.2 mm, although one individual of 26 mm TL positively selected odonates on 6 June. Yellow perch gradually shift to feeding on benthic

invertebrates after reaching a total length of 40 mm (Pycha and Smith 1955; Ney and Smith 1975; Wu and Culver 1992) although Whiteside et al. (1985) reported yellow perch began to feed on benthic invertebrates between 20 and 27 mm TL. Yellow perch also continued feeding on zooplankton throughout the summer, which was also reported by Whiteside et al. (1985).

Yellow perch hatched two months prior to bluegill and thus had the potential to either prey upon or compete with bluegill larvae. I did not observe any larval bluegill consumed by juvenile yellow perch in this study. I examined yellow perch up to 74 mm TL, which is likely an inadequate size to efficiently consume fish prey. Although Graeb et al. (2006) demonstrated experimentally that yellow perch begin a shift to fish prey at 80 mm TL, most field studies do not report consistent piscivory by yellow perch until they attain 130-150 mm TL (Clady 1974; Keast 1985; Fullhart et al. 2002).

Copepods and daphnids were also common prey items for age-0 bluegill, which corroborates findings by other researchers (Werner 1969; Beard 1982; Partridge and DeVries 1999). The smallest bluegill larvae (i.e., recently hatched) consumed *Bosmina* and copepod nauplii in 2004 but prey selection was neutral for these items. Total zooplankton densities were low on the first day that bluegill larvae were collected. Only trace amounts of *Bosmina* ($< 1/L$) were detected and nauplii were also in low abundance, which may explain the lack of positive prey selection for any particular group of zooplankton by newly hatched bluegill larvae in 2004. In 2005, *Bosmina* were positively selected by small bluegill larvae although they were low in availability. *Bosmina* consumption increased over time in both years and larval bluegill also began to positively

select *Daphnia* as prey. In 2004, copepods eventually became a positively selected prey item, which did not occur in 2005. Copepods were more abundant in environmental samples in 2004 but 2005 densities appeared to be at adequate densities and higher than published densities at other geographic locations (Kratz et al. 1987; Schael et al. 1991). Similar densities were reported for Pelican Lake (Paukert and Willis 2000), although higher densities were observed in several South Dakota lakes (Fisher 1996; Pope and Willis 1998). Daphnids were more abundant in 2005, which may have led to increased selection by larval bluegill in 2005. In addition, as previously indicated, I documented the potential weak year class of yellow perch in 2005. Decreased abundance of larval yellow perch may have allowed persistence of an abundant *Daphnia* population in the absence of elevated predation. Partridge and DeVries (1999) noted a high proportion of rotifers in larval bluegill diets, which may lead to suboptimal bluegill growth. Rotifers were rarely consumed in my study and the yellow perch never displayed positive prey selection for them although the rotifers were remarkably abundant in Pelican Lake in 2004 and remarkably sparse in 2005. The availability of energetically profitable prey (i.e., copepods and cladocerans) likely precluded bluegill larvae from consuming rotifers.

Bluegill in Pelican Lake in 2004 began a gradual ontogenetic diet shift to benthic invertebrates when they began positively selecting chironomids on 16 August at a mean TL of 19.1 mm. Chironomids were occasionally consumed throughout the remainder of the 2004 season. In 2005, one bluegill (13.4 mm TL) was observed with one chironomid in its stomach. Ontogenetic diet shifts have been reported to begin at a size of ~20 mm TL and chironomids have commonly been reported as a preferred prey item of bluegill

(Beard 1982; Harrel and Dibble 2001) and were abundant in Pelican Lake in both years. My observation of limited benthic invertebrate consumption by bluegill in this study was likely explained by the smaller-sized fish (mostly <30 mm TL) that were examined for food items. These fish likely had not attained a size where predation on benthic invertebrates became energetically profitable. Chironomids were common diet items for larger bluegills in Cozad and Watts lakes, Nebraska during 2000 (Olson et al. 2003).

Sparse prey resources for first-feeding fish larvae have been commonly implicated as a cause of high mortality (Cushing 1975; Cushing 1990; May 1974; Hart and Werner 1987) and Toetz (1966) experimentally reported mass starvation of larval bluegill between 5 and 6 mm TL, which corresponded to initiation of exogenous feeding. Prey densities in my study were adequate for larval yellow perch and bluegill. Although a low number of yellow perch were detected in both lakes in 2005, prey was available for consumption. The observation of all larval yellow perch collected on one day with empty stomachs in 2005 in Pelican Lake is puzzling as these fish should have been feeding. I do not know if these fish were already in a stressed condition upon their collection, and had already reached a point of inability to adequately seek prey items. Houde (1994) predicted that starvation of larval fishes in freshwater environments was less likely to occur than in marine environments because freshwater fish larvae are generally larger, thus conferring greater energy reserves and resistance to starvation (Miller et al 1988). Garvey et al. (2002) reported that zooplankton biomass was unrelated to larval bluegill survival. Pope and Willis (1998) found no relations between zooplankton abundance or size-structure and larval black crappie *Pomoxis nigromaculatus* abundance, while

Bunnell et al. (2003) reported that zooplankton biomass was correlated to early growth for crappie *Pomoxis* spp. but was not correlated to later growth or recruitment to the juvenile stage. These results are contrary to multiple experimental studies in which survival of larval fishes is most influenced by zooplankton biomass (Hart and Werner 1987; Welker et al. 1994).

No mismatches in predator and prey abundance were detected over the years examined in my study; thus, I cannot determine if severe mismatches in the appearance of fish larvae and their zooplankton prey would lead to depressed survival of age-0 bluegill and yellow perch in Nebraska Sandhills lakes. Density of larval fish and zooplankton was variable among years and the effect of zooplankton density on recruitment warrants investigation (see Chapter 4). Exact matches occurred frequently for bluegill (50%) and yellow perch (33%). Although zooplankton density can vary spatially (Folt and Schulze 1993) leading to potential spatial mismatches (Chick and Van Den Avyle 1999) I did not find differences in zooplankton densities between inshore and offshore strata (see Chapter 4).

The life history and reproductive and spawning behavior of many fishes have been selected for in ecosystems where environmental variability is predictable (Winemiller and Rose 1993). Many environmental factors that are important to larval survival (e.g., prey availability and temperature) are often stochastic and unpredictable. Recruitment variability as predicted by the match-mismatch hypothesis is thought to be a result of this environmental variability. A combination of factors may interact in complex ways to affect larval fish survival, growth, and recruitment (Fitzgerald et al.

2001). In addition, Houde (1989) reported that subtle shifts in daily mortality and growth may be ultimately responsible for influencing recruitment. Many studies that provide support for the match-mismatch hypothesis involved marine species and systems (Cushing 1990; Fortier and Gagné 1990; Leggett and Deblois 1994; Gotceitas et al. 1996; Wright and Bailey 1996; Johnson 2000). Some studies from temperate freshwater systems have also supported the match-mismatch hypothesis including landlocked striped bass *Morone saxatilis* (Chick and Van Den Avyle 1999), threadfin shad *Dorosoma petenense* (Betsill and Van Den Avyle 1997) and yellow perch (Fitzgerald et al. 2001). Houde (1994) compared properties of marine and freshwater fish larvae critical to recruitment. He found marine larvae may be more susceptible to starvation mortality due to their high metabolic demand and small size at hatch. These traits may be related to the common support of the match-mismatch hypothesis for marine fish. Houde (1994) found that freshwater fish larvae may be more susceptible to episodic mortalities that affect recruitment but that the juvenile stage may be equally important in regulating and controlling recruitment. In light of these complexities, and given that zooplankton were abundant and well-timed to larval fish abundance over the initial years of this study, the match-mismatch hypothesis alone may not be able to fully account for observed recruitment variability in the populations that I studied. Therefore, examination of later life-stages (e.g., juveniles) of bluegill and yellow perch may be necessary.

Given the importance of copepods, nauplii, daphnids, and bosminids as prey for larval yellow perch and bluegill, more in-depth examination of these relationships is warranted. Abundance indices of these zooplankton taxa may be used as surrogates for

prey availability. In addition, the dynamic nature of zooplankton populations may suggest important consequences via timing (e.g., match-mismatch regulation; Cushing 1974, 1990) which could be further explored. Our sampling interval of 10 d may lack the required resolution to fully understand the relation between zooplankton and larval bluegill and yellow perch recruitment. If catastrophic mortality events happen in a short time (Hjort 1914; May 1974) then more frequent sampling may be required to pinpoint the time and reason for it. Stage specific investigations of the relationship of zooplankton to larval fish growth and recruitment may produce important insights into the dynamics of bluegill and yellow perch in Nebraska Sandhills lakes.

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Table 3-1. Mean density and associated standard errors for zooplankton (number/L) in Cameron Lake, Nebraska in 2004 and 2005. Trace densities of less than 1/L are denoted “tr”.

Date	Bosminidae	Chydoridae	Daphnidae	Sididae	Copepoda	Nauplii	Ostracoda	Rotifera
2004								
13-May	181 (16)	641 (35)	786 (29)	0	49 (2)	45 (10)	tr	206 (14)
18-May	186 (13)	757 (71)	773 (118)	0	50 (6)	25 (6)	5 (2)	50 (7)
27-May	99 (19)	201 (21)	411 (53)	0	18 (6)	7 (4)	4 (1)	4 (1)
7-Jun	14 (3)	121 (6)	112 (36)	0	20 (4)	16 (2)	1 (0)	46 (6)
2005								
15-May	2 (1)	3 (1)	627 (92)	0	97 (20)	66 (11)	2 (1)	95 (16)
24-May	7 (2)	19 (4)	453 (66)	0	53 (5)	49 (6)	16 (7)	28 (8)
2-Jun	20 (3)	34 (4)	464 (52)	0	78 (8)	17 (3)	3 (1)	51 (10)

Table 3-2. Abundance (number/m²) and standard error of common benthic invertebrates in Cameron Lake, 2004-2005.

Date	Amphipoda	Ceratopogonidae	Chironomidae	Diptera pupae	Ephemeroptera	Gastropoda	Hemiptera	Odonata	Trichoptera
2004									
13-May	0	17 (13)	1304 (225)	48 (16)	0	0	17 (13)	0	4 (4)
18-May	3 (3)	136 (85)	1190 (205)	101 (29)	3 (3)	0	5 (4)	0	3 (3)
27-May	0	30 (15)	353 (85)	22 (8)	0	0	0	0	5 (5)
7-Jun	3 (3)	125 (46)	394 (141)	33 (15)	0	0	0	3 (3)	0
2005									
15-May	0	49 (29)	420 (84)	24 (9)	0	0	0	0	0
24-May	16 (16)	24 (22)	359 (85)	11 (4)	0	0	0	0	3 (3)
2-Jun	0	27 (24)	652 (117)	0	0	0	0	0	0

Table 3-3. Number (Num) and mean total length (TL; mm) of yellow perch and bluegill examined for food items from Cameron and Pelican lakes, Nebraska, 2004-2005.

Lake	Date	Num (with prey)	Total examined	Mean TL	SE	Range	% Empty
Cameron							
Yellow perch							
2004	13-May	30	30	11.5	0.2	9.9 - 13.1	0
	18-May	30	30	12.5	0.2	9.1 - 14.9	0
	27-May	30	30	15.7	0.5	10.0 - 19.6	0
	7-Jun	30	30	25.0	0.5	19.4 - 30.0	0
2005	15-May	18	18	8.3	0.4	4.2 - 12.8	0
	24-May	30	30	14.5	0.2	12.2 - 18.3	0
	2-Jun	12	12	19.0	0.6	16.0 - 23.1	0
Pelican							
Yellow perch							
2004	8-May	30	35	8.8	0.2	6.8 - 13.8	14
	17-May	30	30	12.7	0.2	10.4 - 14.5	0
	26-May	30	30	17.1	0.4	12.7 - 20.6	0
	6-Jun	23	24	23.1	0.5	18.1 - 26.9	4
	16-Jun	30	31	32.2	0.7	19.5 - 37.3	3
	26-Jun	17	17	28.0	1.7	18.9 - 39.5	0
	7-Jul	7	7	31.8	2.5	22.0 - 36.8	0
	17-Jul	3	3	41.8	3.7	34.6 - 46.5	0
	27-Jul	9	9	49.3	1.0	46.0 - 53.0	0
	6-Aug	14	14	57.6	2.3	40.2 - 69.5	0
	16-Aug	13	13	59.8	0.9	56.2 - 67.1	0
	26-Aug	9	9	59.9	2.6	44.6 - 74.1	0
2005	3-May	16	16	5.4	0.1	4.2 - 6.5	100
Pelican Bluegill							
2004	26-Jun	3	11	7.5	0.4	6.6 - 11.0	73
	7-Jul	9	14	9.1	0.6	6.1 - 12.4	36
	17-Jul	30	47	10.8	0.4	3.8 - 15.5	36
	27-Jul	30	30	15.0	0.3	8.6 - 18.5	0
	6-Aug	30	32	15.0	0.6	7.3 - 23.3	6
	16-Aug	30	30	19.1	1.0	10.9 - 29.1	0
	27-Aug	30	30	20.7	1.0	7.9 - 29.3	0
	5-Sep	30	31	19.5	1.5	11.2 - 40.1	3
2005	30-Jun	30	32	8.3	0.2	7.2 - 12.3	6
	11-Jul	30	31	10.7	0.4	7.8 - 14.7	3
	21-Jul	30	31	10.4	0.4	7.4 - 14.1	3
	1-Aug	30	35	11.4	0.4	8.0 - 15.6	14
	11-Aug	30	30	11.2	0.4	7.3 - 15.3	0
	22-Aug	30	30	12.9	0.4	9.8 - 18.4	0

Table 3-4. Percent occurrence and percent by number for zooplankton prey items found in larval yellow perch stomachs in Cameron Lake, Nebraska in 2004 and 2005.

Taxon	2004				2005		
	13-May	18-May	27-May	7-Jun	15-May	24-May	2-Jun
Percent occurrence							
Bosminidae	3.3	33.3	30.0	20.0	0	3.3	16.7
Chydoridae	6.7	20.0	26.7	66.7	0	0	16.7
Daphnidae	86.7	100.0	100.0	100.0	33.3	90.0	100.0
Sididae	0	23.3	30.0	0.0	0	0	0
Copepoda	100.0	96.7	66.7	60.0	94.4	100.0	91.7
Nauplii	0	0	0	0	0	0	0
Ostracoda	0	3.3	0	3.3	0	0	0
Rotifera	33.3	66.7	3.3	0	0	0	0
Percent by number							
Bosminidae	0.2	2.3	2.5	0.3	0	0.2	0.3
Chydoridae	0.5	1.5	1.1	34.4	0	0	0.5
Daphnidae	26.8	37.5	81.7	60.2	24.4	28.8	38.6
Sididae	0	1.3	2.5	0	0	0	0
Copepoda	61.1	33.2	12.1	5.1	75.6	71.0	60.6
Nauplii	0	0	0	0	0	0	0
Ostracoda	0	0.2	0	0.1	0	0	0
Rotifera	11.3	24.1	0.1	0	0	0	0

Table 3-5. Mean density and associated standard errors for zooplankton (number/L) in Pelican Lake, Nebraska in 2004 and 2005. Trace densities of less than 1/L are denoted “tr”.

Date	Bosminidae	Chydoridae	Daphnidae	Sididae	Copepoda	Nauplii	Ostracoda	Rotifera
2004								
8-May	1 (1)	1 (0)	69 (12)	0	56 (10)	3 (1)	1 (1)	1 (1)
17-May	tr	1 (1)	76 (23)	0	21 (5)	10 (1)	3 (2)	1 (0)
26-May	0.00	1 (0)	63 (23)	0	9 (2)	13 (5)	4 (2)	50 (45)
6-Jun	tr	1 (0)	9 (2)	0	15 (2)	41 (7)	5 (1)	75 (14)
16-Jun	0	4 (1)	tr	0	43 (10)	11 (1)	27 (9)	218 (42)
26-Jun	tr	3 (0)	0	0	11 (3)	12 (3)	17 (5)	528 (214)
7-Jul	5 (1)	6 (1)	3 (1)	tr	23 (4)	13 (2)	10 (3)	231 (26)
17-Jul	126 (24)	12 (3)	28 (5)	2 (1)	23 (4)	42 (7)	11 (4)	143 (30)
27-Jul	731 (104)	25 (5)	107 (13)	8 (2)	85 (8)	40 (8)	5 (1)	190 (41)
6-Aug	1443 (106)	66 (14)	74 (8)	6 (1)	48 (5)	41 (5)	9 (2)	39 (6)
16-Aug	662 (116)	131 (18)	78 (11)	6 (1)	62 (7)	68 (7)	2 (1)	102 (12)
26-Aug	370 (62)	101 (18)	65 (8)	4 (1)	42 (4)	64 (5)	4 (1)	2 (1)
5-Sep	1084 (234)	273 (73)	78 (16)	2 (1)	50 (10)	54 (9)	2 (1)	8 (5)
2005								
3-May	84 (27)	115 (36)	172 (33)	0	23 (9)	28 (7)	2 (0)	9 (2)
14-May	75 (9)	215 (49)	80 (8)	tr	22 (3)	26 (9)	2 (1)	13 (5)
23-May	40 (7)	80 (14)	135 (23)	0	10 (2)	31 (10)	6 (1)	26 (12)
2-Jun	10 (3)	15 (5)	87 (15)	0	9 (2)	16 (4)	1 (1)	13 (4)
13-Jun	1 (0)	8 (2)	78 (15)	0	18 (3)	7 (1)	6 (2)	6 (4)
22-Jun	tr	5 (2)	43 (8)	0	20 (3)	7 (2)	12 (3)	3 (1)
30-Jun	3 (1)	3 (1)	20 (3)	0	17 (3)	10 (2)	8 (3)	1 (0)
11-Jul	14 (3)	21 (4)	95 (8)	0	12 (2)	5 (1)	7 (1)	1 (0)
21-Jul	28 (3)	44 (9)	49 (7)	0	20 (3)	18 (5)	2 (1)	1 (0)
1-Aug	65 (11)	67 (10)	164 (25)	0	8 (1)	4 (1)	1 (0)	tr
11-Aug	114 (15)	58 (12)	166 (27)	0	20 (2)	15 (2)	3 (1)	tr
22-Aug	122 (13)	55 (10)	72 (16)	1 (1)	13 (1)	7 (1)	3 (1)	0

Table 3-6. Abundance (number/m²) and standard error of common benthic invertebrates in Pelican Lake, 2004-2005.

Date	Amphipoda	Ceratopogonidae	Chironomidae	Diptera pupae	Ephemeroptera	Gastropoda	Hemiptera	Odonata	Trichoptera
2004									
8-May	0	7 (7)	612 (112)	11 (7)	7 (5)	0	0	0	0
17-May	83 (79)	22 (14)	634 (133)	0	11 (11)	0	0	0	0
26-May	7 (7)	14 (10)	737 (131)	10 (5)	7 (7)	0	0	5 (3)	0
6-Jun	26 (19)	13 (6)	898 (282)	3 (3)	1 (1)	0	0	0	0
16-Jun	230 (172)	87 (57)	994 (319)	4 (3)	13 (7)	11 (5)	13 (11)	2 (2)	0
26-Jun	9 (7)	65 (35)	2720 (653)	13 (5)	0	0	0	0	2 (2)
7-Jul	24 (13)	15 (10)	1828 (447)	4 (3)	0	0	2 (2)	0	0
17-Jul	239 (225)	4 (3)	907 (195)	4 (3)	0	2 (2)	0	0	2 (2)
27-Jul	841 (832)	7 (5)	839 (252)	11 (9)	39 (33)	9 (5)	0	0	43 (41)
6-Aug	24 (22)	14 (9)	682 (150)	5 (5)	79 (79)	14 (14)	0	2 (2)	76 (73)
16-Aug	22 (22)	20 (20)	461 (138)	13 (5)	2 (2)	2 (2)	0	11 (11)	4 (3)
26-Aug	2 (2)	7 (3)	352 (98)	2 (2)	0	4 (4)	0	4 (3)	11 (11)
5-Sep	1280 (828)	0	1375 (658)	8 (6)	27 (27)	14 (11)	0	478 (255)	16 (9)
2005									
3-May	46 (27)	0	1702 (287)	0	2 (2)	15 (15)	0	0	0
14-May	59 (42)	0	604 (160)	17 (11)	2 (2)	11 (11)	0	0	13 (9)
23-May	76 (37)	0	541 (116)	9 (5)	7 (7)	70 (60)	0	7 (5)	0
2-Jun	13 (11)	0	200 (59)	0	0	4 (3)	0	0	2 (2)
13-Jun	106 (54)	0	674 (336)	0	14 (11)	11 (11)	0	16 (9)	0
22-Jun	41 (19)	2 (2)	574 (189)	0	0	2 (2)	0	0	0
30-Jun	30 (15)	0	639 (261)	4 (3)	4 (4)	0	0	0	0
11-Jul	107 (62)	0	1548 (246)	0	9 (6)	0	0	0	0
21-Jul	2 (2)	0	1274 (411)	0	0	0	0	0	0
1-Aug	20 (9)	2 (2)	1750 (270)	15 (7)	2 (2)	2 (2)	0	0	2 (2)
11-Aug	470 (453)	0	496 (130)	11 (7)	2 (2)	2 (2)	0	15 (15)	0
22-Aug	7 (5)	0	615 (247)	13 (7)	0	0	0	0	0

Table 3-7. Percent occurrence and percent by number for zooplankter prey items found in larval yellow perch stomachs in Pelican Lake, Nebraska in 2004.

Taxon	8-May	17-May	26-May	6-Jun	16-Jun	26-Jun	7-Jul	17-Jul	27-Jul	6-Aug	16-Aug	26-Aug
Percent occurrence												
Bosminidae	0	0	0	0	0	0	14.3	33.3	37.5	57.1	100.0	77.8
Chydoridae	0	3.3	0	0	50.0	64.7	71.4	66.7	75.0	50.0	100.0	77.8
Daphnidae	0	70.0	100.0	100.0	26.7	41.2	42.9	33.3	62.5	42.9	100.0	77.8
Sididae	0	0	0	0	0	0	0	0	12.5	21.4	76.9	0
Copepoda	100.0	100.0	13.3	17.4	70.0	58.8	71.4	66.7	75.0	57.1	76.9	22.2
Nauplii	0	6.7	0	0	0	0	0	0	0	0	0	0
Ostracoda	0	0	0	0	50.0	47.1	14.3	0	62.5	57.1	38.5	11.1
Rotifera	0	0	0	0	0	0	0	0	0	0	0	0
Percent by number												
Bosminidae	0	0	0	0	0	0	0.6	19.2	39.5	74.0	84.8	73.0
Chydoridae	0	0.8	0	0	10.3	44.5	19.5	28.3	10.2	3.3	4.5	9.5
Daphnidae	0	15.5	97.0	98.8	2.3	33.2	18.5	12.1	31.3	14.1	9.3	16.9
Sididae	0	0	0	0	0	0	0	0	0.8	1.2	0.1	0
Copepoda	100.0	83.0	3.0	1.2	50.1	15.0	60.8	40.4	16.4	6.6	1.3	0.6
Nauplii	0	0.8	0	0	0	0	0	0	0	0	0	0
Ostracoda	0	0	0	0	37.3	7.4	0.6	0	1.8	0.8	0	0
Rotifera	0	0	0	0	0	0	0	0	0	0	0	0

Table 3-8. Percent occurrence and percent by number for benthic invertebrate prey items found in age-0 yellow perch stomachs in Pelican Lake, Nebraska in 2004.

Taxon	6-Jun	16-Jun	26-Jun	7-Jul	17-Jul	27-Jul	6-Aug	16-Aug	27-Aug
Percent occurrence									
Amphipoda	0	13.3	5.9	42.9	0	25.0	14.3	0	11.1
Ceratopogonidae	0	0	0	0	0	12.5	0	0	0
Chironomidae	0	30.0	23.5	42.9	66.7	25.0	35.7	23.1	11.1
Corixidae	0	63.3	29.4	0	33.3	0	14.3	0	0
Diptera pupae	0	6.7	11.8	28.6	0	0	7.1	7.7	11.1
Ephemeroptera	0	6.7	0	14.3	0	25.0	14.3	7.7	22.2
Gastropoda	0	0	0	14.3	0	0	0	0	0
Odonata	4.3	3.3	0	0	0	37.5	0	0	11.1
Trichoptera	0	0	0	0	33.3	0	0	0	0
Percent by number									
Amphipoda	0	10.5	6.4	13.3	0	22.4	18.6	0	9.1
Ceratopogonidae	0	0	0	0	0	3.9	0	0	0
Chironomidae	0	5.2	25.5	33.3	13.3	31.6	54.2	44.4	9.1
Corixidae	0	69.7	27.7	0	33.3	0	15.3	0	0
Diptera pupae	0	1.1	17.0	6.7	0	0	1.7	11.1	9.1
Ephemeroptera	0	1.5	0	33.3	0	10.5	10.2	22.2	18.2
Gastropoda	0	0	0	6.7	0	0	0	0	0
Odonata	100.0	0.7	0	0	0	26.3	0	0	54.5
Trichoptera	0	0	0	0	6.7	0	0	0	0

Table 3-9. Percent occurrence and percent by number for zooplankton prey items found in age-0 bluegill stomachs in Pelican Lake, Nebraska in 2004-2005.

Taxon	2004							2005						
	26-Jun	7-Jul	17-Jul	27-Jul	6-Aug	16-Aug	27-Aug	5-Sep	30-Jun	11-Jul	21-Jul	1-Aug	11-Aug	22-Aug
Percent occurrence														
Bosminidae	0	0	63.3	50.0	80.0	83.3	96.7	83.3	46.7	60.0	60.0	76.7	63.3	70.0
Chydoridae	0	22.2	10.0	3.3	6.7	40.0	53.3	60.0	6.7	56.7	63.3	33.3	40.0	50.0
Daphnidae	0	0	46.7	83.3	60.0	83.3	96.7	80.0	26.7	63.3	76.7	60.0	96.7	83.3
Sididae	0	0	0	3.3	3.3	13.3	10.0	43.3	0	0.0	3.3	6.7	3.3	43.3
Copepoda	33.3	11.1	30.0	96.7	76.7	83.3	86.7	90.0	60.0	33.3	36.7	20.0	23.3	63.3
Nauplii	66.7	44.4	10.0	3.3	3.3	10.0	6.7	6.7	40.0	6.7	16.7	0	3.3	0
Ostracoda	0	0	3.3	0	0	0	0	6.7	10.0	6.7	3.3	0	0	0
Rotifera	0	66.7	16.7	0	0	3.3	0	3.3	0	20.0	0	0	10.0	0
Percent by number														
Bosminidae	0	0	46.7	15.3	42.6	46.2	47.9	34.6	21.7	28.3	32.9	51.2	44.5	32.8
Chydoridae	0	8.8	3.5	0.2	0.5	9.3	5.3	19.2	1.6	22.7	23.9	5.7	14.6	12.9
Daphnidae	0	0	38.1	21.9	22.7	12.9	18.4	23.4	10.1	34.0	31.2	39.2	33.0	28.9
Sididae	0	0	0	0.2	0.2	0.7	0.2	3.2	0	0	0.4	1.0	0.2	3.6
Copepoda	10.0	5.9	5.4	61.9	33.6	30.4	28.0	19.0	34.1	11.5	9.0	2.9	6.4	21.8
Nauplii	90.0	20.6	1.6	0.4	0.5	0.3	0.2	0.4	27.9	0.4	2.1	0	0.2	0
Ostracoda	0	0	0.4	0	0	0	0	0.2	4.7	0.7	0.4	0	0	0
Rotifera	0	64.7	4.3	0	0	0.1	0	0.1	0	2.4	0	0	1.1	0

Table 3-10. Percent occurrence and percent by number for benthic invertebrate prey items found in larval bluegill stomachs in Pelican Lake, Nebraska in 2004-2005.

Taxon	2004			2005
	16-Aug	27-Aug	5-Sep	11-Aug
Percent occurrence				
Amphipoda	0	0	3.3	0
Chironomidae	20.0	6.7	6.7	3.3
Diptera pupae	0	0	3.3	0
Ephemeroptera	3.3	0	0	0
Odonata	0	0	3.3	0
Percent by number				
Amphipoda	0	0	7.1	0
Chironomidae	92.3	100.0	42.9	100.0
Diptera pupae	0	0	42.9	0
Ephemeroptera	7.7	0	0	0
Odonata	0	0	7.1	0

Table 3-11. Mean peak larval abundance ($n/100\text{ m}^3$), parameters used in match-mismatch examination and result for yellow perch and copepods in Cameron and Pelican Lake, Nebraska and for bluegill and combined nauplii/*Bosmina* in Pelican Lake, Nebraska 2004-2007. Parameters are t_0 (timing between peaks of larval production and food supply in days), Δt_0 (annual differences in $[t_0]$ from its mean value), δ (one-half width of the production period for larvae), and σ (one-half width of the production period for zooplankton). In addition, a represents the first peak in larval bluegill abundance and b represents the second peak in larval bluegill abundance in 2004.

Lake	Predator-prey combination	Year	Peak larval abundance	Parameter				Result
				t_0	Δt_0	δ	σ	
Cameron	Yellow perch - copepods	2004	1,685	5	2.2	19.5	7	match
		2005	17	9	1.8	9	4.5	match
Pelican	Yellow perch - copepods	2004	185	0	7.2	9	19	exact match
		2005	5	0	7.2	0.5	10	exact match
		2006	211	21	13.8	15	16	match
		2007	523	8	0.8	12	9	match
		Bluegill - nauplii/ <i>Bosmina</i>	2004 _a	116	20	9.8	35.5	36
	2004 _b	144	10	0.2	35.5	36	match	
	2005	924	21	10.8	26.5	26.5	match	
	2006	1,764	0	10.2	31.5	21	exact match	
2007	732	0	10.2	25.5	26	exact match		

^a First peak in larval bluegill abundance

^b Second peak in larval bluegill abundance

Table 3-12. Bivariate correlations between predator-prey overlap (t_o) and fish abundance indices for yellow perch and bluegill. Abundance indices are peak larval abundance (mean number/m³), fall and spring juvenile CPUE (mean number/cloverleaf trap night), and age-1 and age-2 CPUE (mean number/ trap net night).

Independent variable	<u>Yellow perch</u>			<u>Bluegill</u>		
	<i>N</i>	<i>r</i>	<i>P</i>	<i>N</i>	<i>r</i>	<i>P</i>
Peak larval abundance	4	0.30	0.70	5	-0.51	0.34
Fall juvenile CPUE	4	0.11	0.89	5	0.03	0.96
Spring juvenile CPUE	4	0.46	0.54	5	-0.44	0.46
Age 1 CPUE	4	0.86	0.14	-	-	-
Age 2 CPUE	-	-	-	4	-0.82	0.18

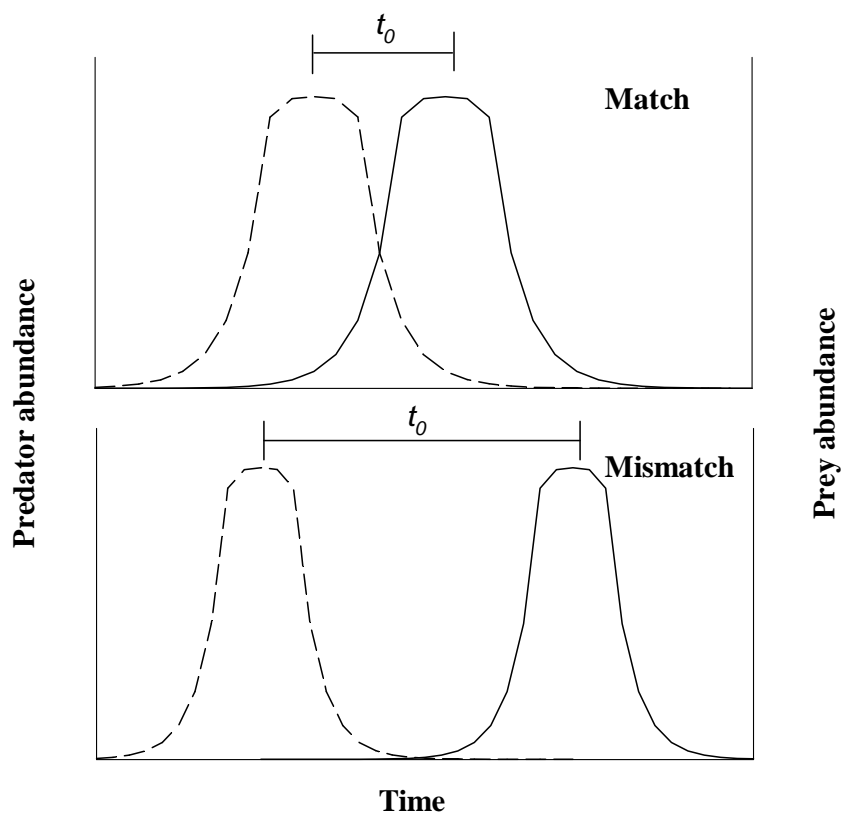


Figure 3-1. Theoretical examples of a match (top panel) represented by close overlap of predator (solid line) and prey (broken line) abundance curves and a mismatch (bottom panel) represented by a lag in time between production of predators and prey. The temporal difference between peak abundance curves of predators and their prey is represented by t_0 . Figure adapted from Cushing (1990).

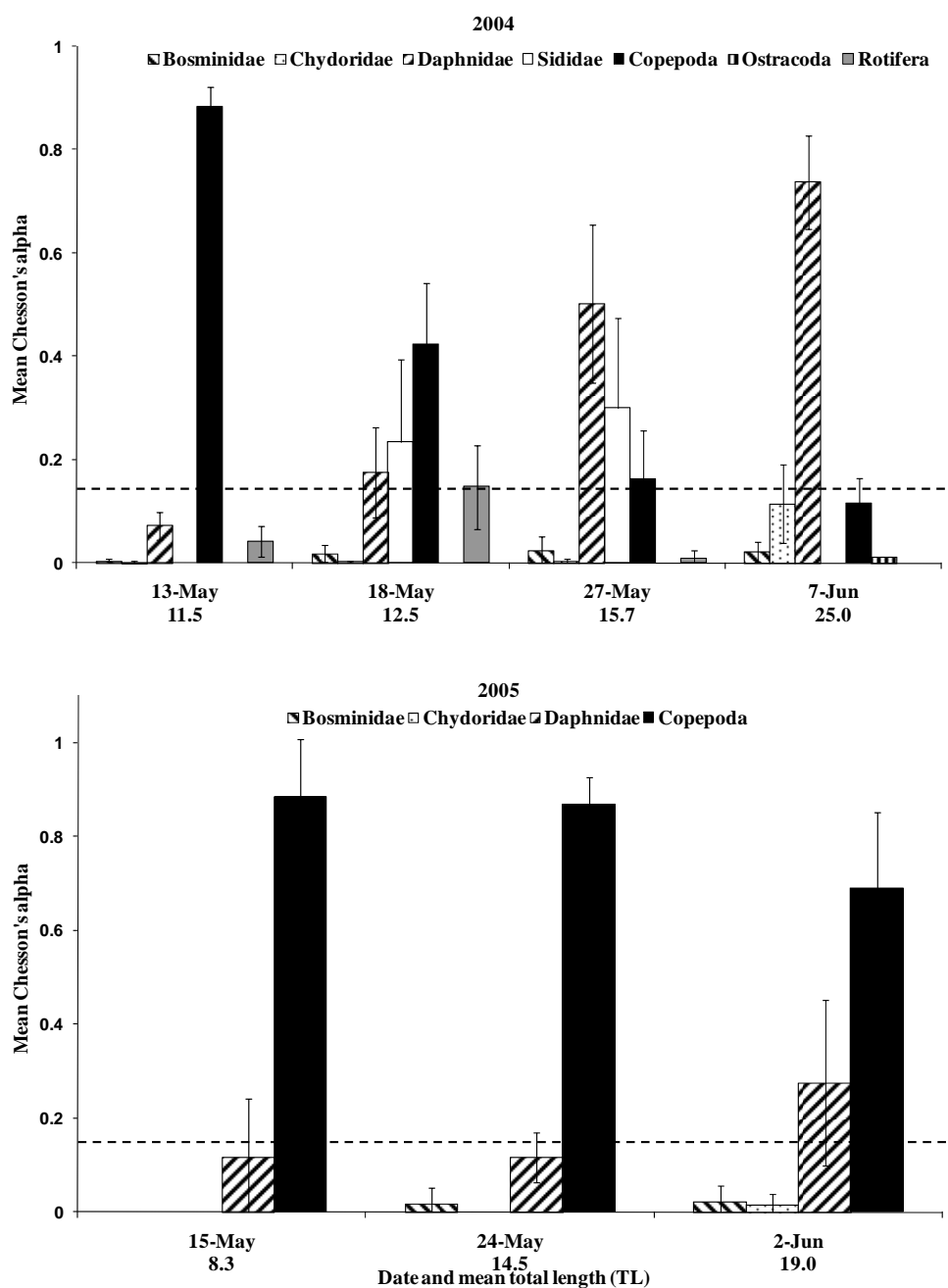


Figure 3-2. Mean (95% confidence intervals) prey selection (Chesson's α) by yellow perch in Cameron Lake, Nebraska 2004-2005 by prey category of zooplankton. Confidence intervals above the random feeding (dashed) line indicate positive selection, values below the line indicate negative selection, and values overlapping the line indicate neutral selection. Mean total length (mm) of yellow perch examined by date are given.

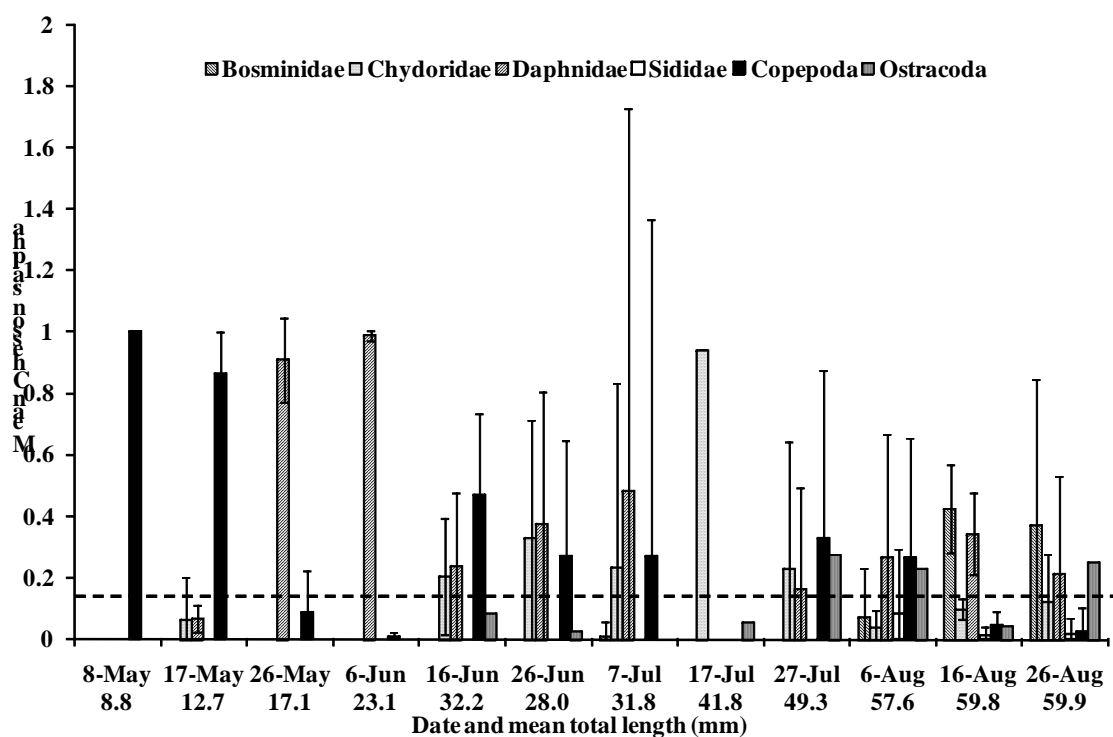


Figure 3-3. Mean (95% confidence intervals) prey selection (Chesson's α) by yellow perch in Pelican Lake, Nebraska, 2004 by prey category of zooplankton. Confidence intervals above the random feeding (dashed) line indicate positive selection, values below the line indicate negative selection, and values overlapping the line indicate neutral selection.

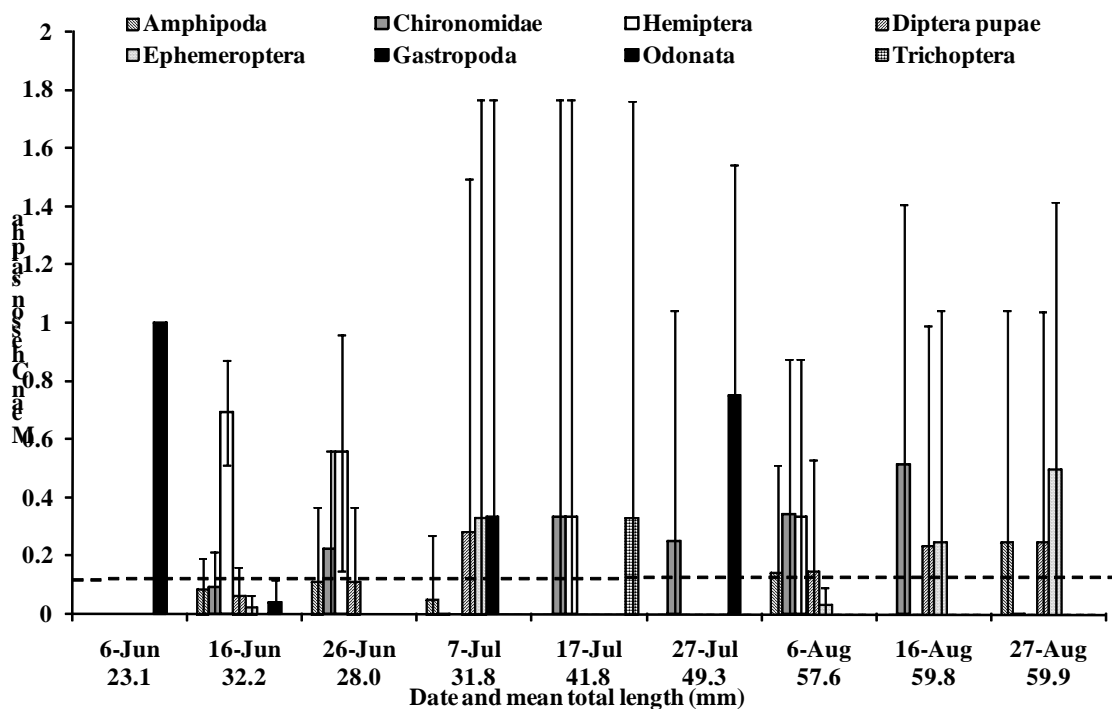


Figure 3-4. Mean (95% confidence intervals) prey selection (Chesson's α) by yellow perch in Pelican Lake, Nebraska, 2004 by prey category of benthic invertebrates. Confidence intervals above the random feeding (dashed) line indicate positive selection, values below the line indicate negative selection, and values overlapping the line indicate neutral selection.

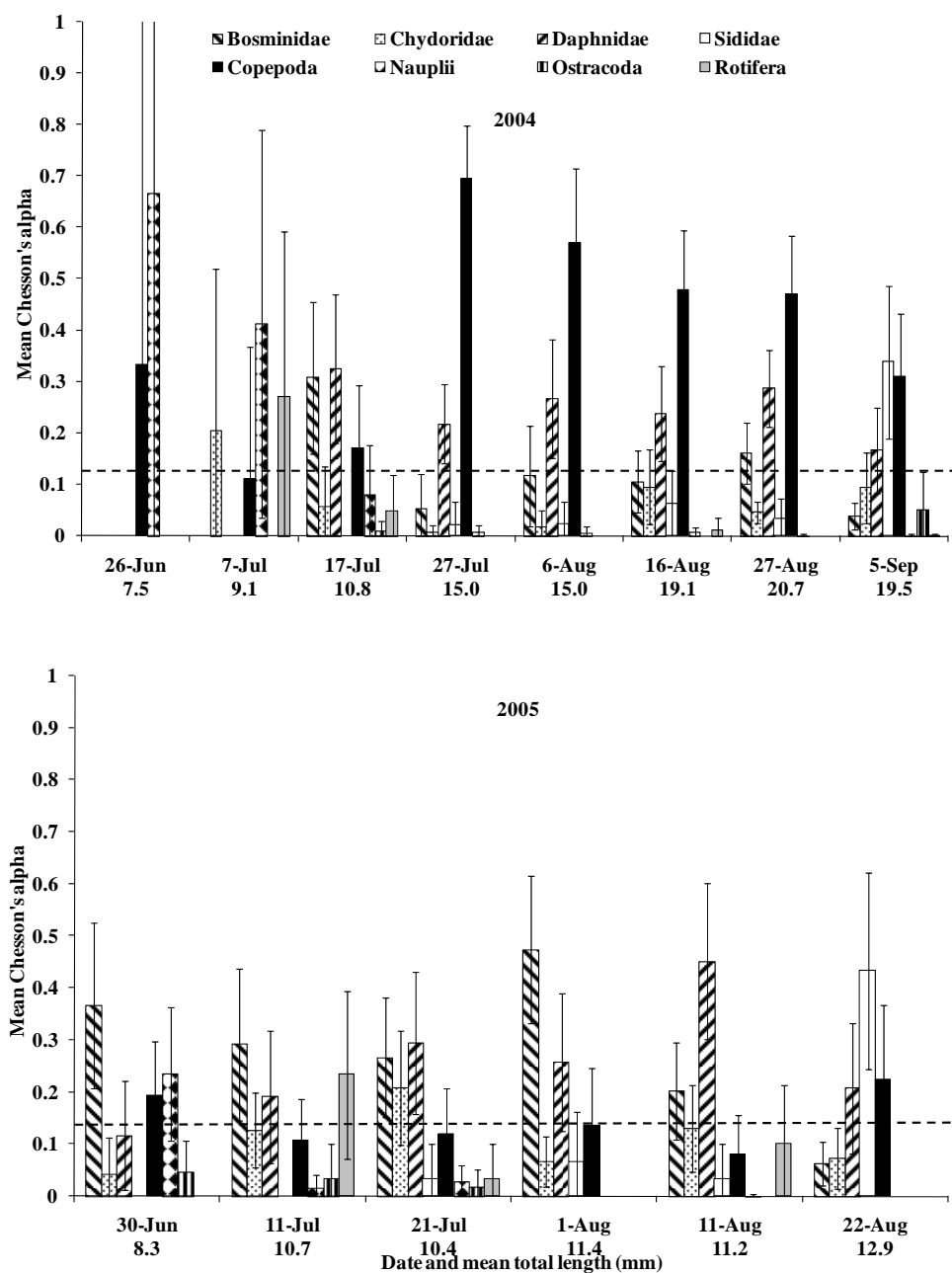


Figure 3-5. Mean (95% confidence intervals) prey selection (Chesson's α) by bluegill in Pelican Lake, Nebraska, 2004 and 2005 by prey category of zooplankton. Confidence intervals above the random feeding (dashed) line indicate positive selection, values below the line indicate negative selection, and values overlapping the line indicate neutral selection.

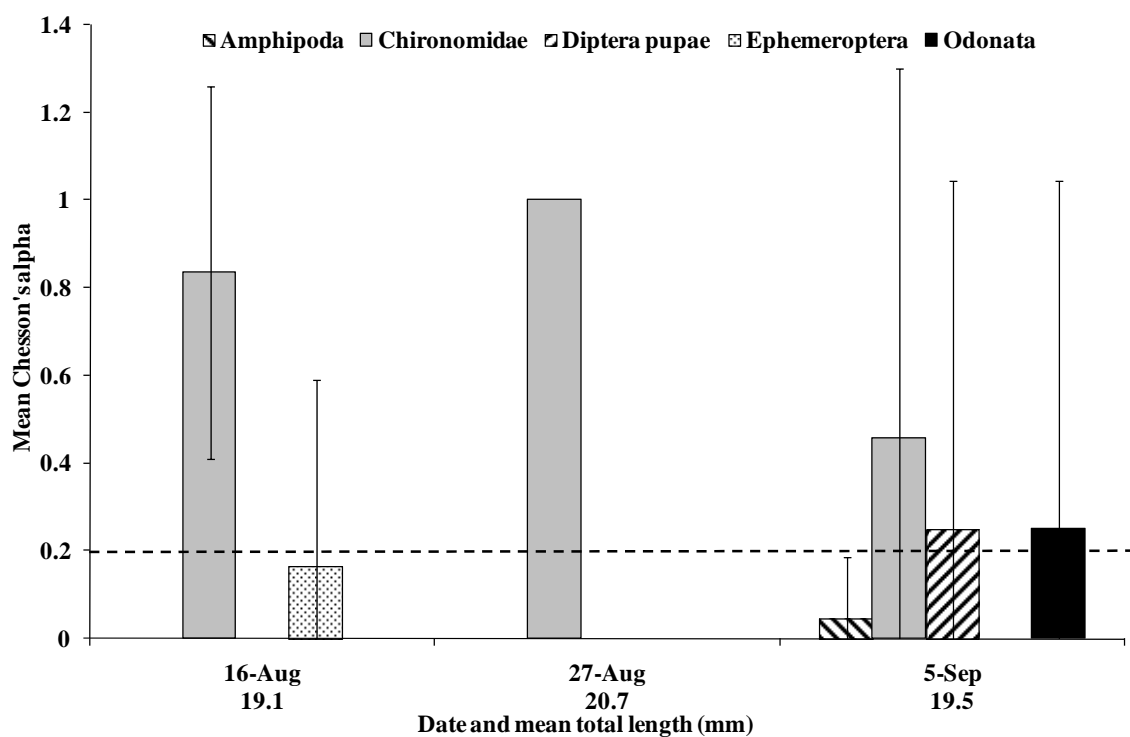


Figure 3-6. Mean (95% confidence intervals) prey selection (Chesson's α) by bluegill in Pelican Lake, Nebraska, 2004 by prey category of benthic invertebrates. Confidence intervals above the random feeding (dashed) line indicate positive selection, values below the line indicate negative selection, and values overlapping the line indicate neutral selection.

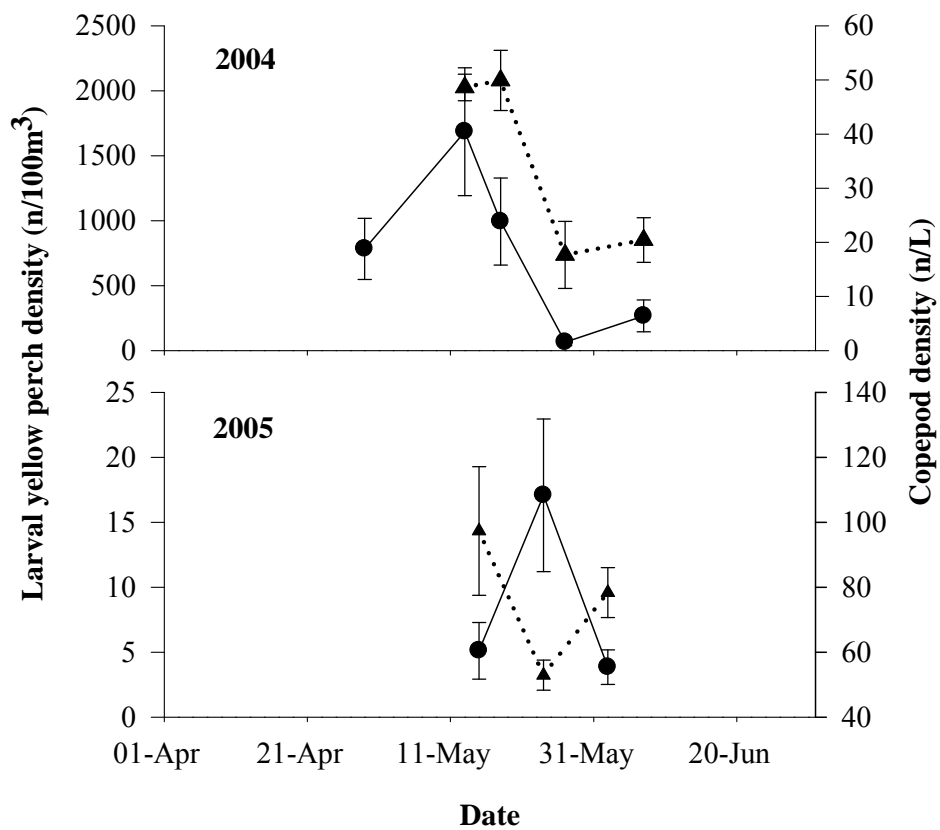


Figure 3-7. Larval yellow perch density (solid line) and copepod density (broken line) in Cameron Lake, Nebraska in 2004 and 2005 (n = number).

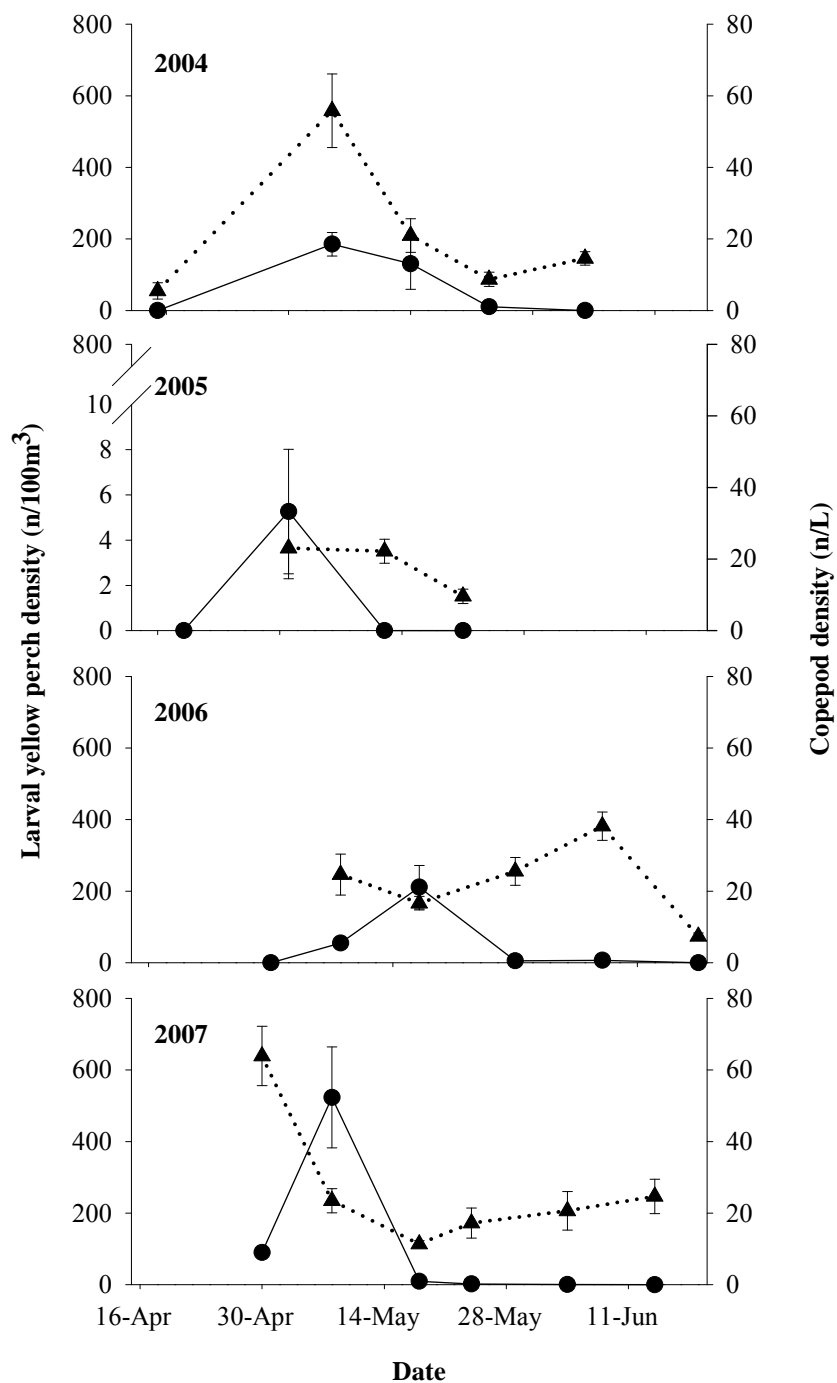


Figure 3-8. Larval yellow perch density (solid line) and copepod density (broken line) in Pelican Lake, Nebraska 2004-2007 (n = number).

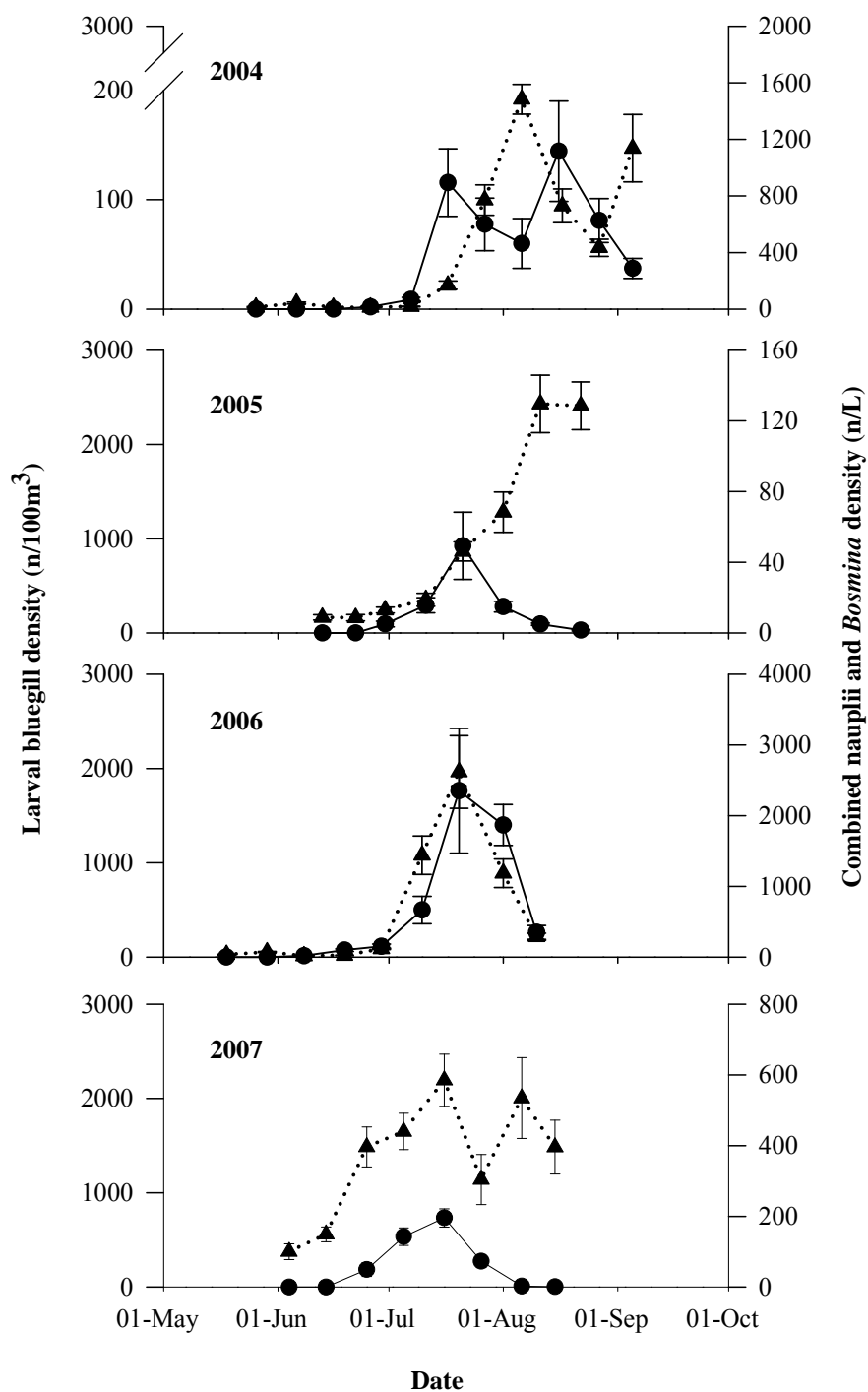


Figure 3-9. Larval bluegill density (solid line) and combined nauplii and *Bosmina* density (broken line) in Pelican Lake, Nebraska 2004-2007 (n = number).

Chapter 4.

Assessing recruitment of bluegill and yellow perch in Nebraska Sandhills lakes through examination of multiple life stages

Recruitment dynamics of fish populations ultimately structure fish communities (Diana 1995). Fish recruitment may be regulated by direct and indirect factors. Abiotic factors such as physical habitat, temperature, and weather (Beard 1982; Pope et al. 1996; Jackson and Noble 2000; Casselman et al. 2002), and biotic factors such as food availability and competition (Prout et al. 1990; Welker et al. 1994; Ludsin and DeVries 1997; Bunnell et al. 2003), and predation (Forney 1971; Houde 1987; Rice et al. 1987b; Santucci and Wahl 2003) can affect recruitment.

Overwinter mortality of age-0 fish may depress survival and the effect is often size-specific (Oliver et al. 1979; Post and Evans 1989; Johnson and Evans 1991; Thompson et al. 1991), with smaller individuals experiencing higher mortality rates than larger ones. Starvation due to inadequate lipid reserves has been cited as the direct cause of overwinter mortality (Oliver et al. 1979; Adams et al. 1982; Miranda and Hubbard 1994). Starvation can also influence mortality indirectly by increasing predation risk (Miller et al. 1988; Jonas and Wahl 1998) via reduced swimming capabilities (Rice et al. 1987a) and/or lowering growth rates (Werner and Gilliam 1984; Post and Prankevicus 1987). Large individual age-0 sizes may increase the probability of winter survival (Post and Evans 1989; Miranda and Hubbard 1994; Garvey et al. 1998). In addition, factors

determining growth rates such as hatch timing, food availability, and competition may have important implications for recruitment of temperate-latitude fishes.

The bluegill is typically considered a colonial, multiple-spawning fish (Werner 1969; Gross and MacMillan 1981) with a small percentage displaying solitary nesting activities (Gross and MacMillan 1981; Neff et al. 2004). In addition, the bluegill spawning season is protracted, often extending over several summer months (Beard 1982; Cargnelli and Gross 1996; Garvey et al. 2002). Protracted spawning in bluegill may be considered a form of bet-hedging whereby reproductive output is distributed over several reproductive bouts because larval and juvenile survival is highly variable (Winemiller 2005) depending on variable, albeit broadly predictable, environmental conditions. Finally, nest guarding is regarded as a major behavioral adaptation associated with elevated predation levels on larvae (Balon 1975) and is well developed in bluegills (Avila 1976; Dominey 1981). Garvey et al. (2002) reported that inshore densities of larval bluegills were bimodal, peaking once in late May and again in early July in Lake Opinicon, Ontario. Chvala (2000) found that bluegill larvae were first collected in two Nebraska Sandhills lakes during June, but the spawning season was comparatively extended in one lake compared with the other. Temporal variability in hatching date may have consequences for growth, and ultimately recruitment, of age-0 bluegill to age 1.

Differences in the timing of hatching may affect the growth of gape-limited fish, thereby affecting their ability to consume larger-sized prey, increasing their energy intake, and ultimately reaching a large size before onset of winter (Goodgame and Miranda 1993; Phillips et al. 1995; Post 2003). Although early hatching is commonly

assumed to lead to a large size and decreased mortality before the onset of the first winter, some studies have identified factors that can result in higher mortality for early-hatched fish compared with late-hatched fish. Garvey et al. (2002) found that age-0 bluegill hatched earlier in the year in an Ontario lake commonly did not survive to the juvenile stage due to high larval mortality. Santucci and Wahl (2003) reported that early-hatched bluegill were subject to higher mortality through predation by largemouth bass in Illinois.

Like bluegill, variable recruitment commonly occurs in percid populations (Koonce et al. 1977; Willemsen 1977; Hackney and Holbrook 1978; Newsome and Aalto 1987) and numerous studies have documented such patterns in yellow perch (e.g., Forney 1971; Koonce et al. 1977; Mills et al. 1989). Critical time periods, or bottlenecks, of high mortality may exist for some species (Hjort 1914; May 1974) and researchers commonly incorporate this factor when describing recruitment processes (Marr 1956). This critical period is thought to occur early in age-0 yellow perch cohort development (Forney 1971; Clady 1976; Anderson et al. 1998). Alternatively, several studies reported that year-class strengths of walleye (another percid) in Oneida Lake (Forney 1976) and largemouth bass (a centrarchid) in southern reservoirs (Novinger 1988; Sammons and Bettoli 1998) are determined later in development, although larval mortality events may still be important as they can substantially affect cohort size. In addition, Houde (1989) reported that subtle shifts in daily mortality and growth may be ultimately responsible for influencing recruitment. Describing the type and relative importance of mortality factors during this

critical period is difficult (Marr 1956; Braum 1978) because mechanisms influencing recruitment may differ both spatially and temporally, and may be species specific.

Although yellow perch recruitment has been correlated to environmental factors (Craig et al. 1979; Kallemeyn 1987; Treasurer 1989; Pope et al. 1996; Ward et al. 2004), agreement regarding the relative importance of these factors is low (Koonce et al. 1977), suggesting that recruitment regulation is variable among systems or is regulated by more complex factors. Size-selective overwinter mortality has been documented for yellow perch (Post and Prankevicius 1987; Post and Evans 1989; Johnson and Evans 1991), but the effect of overwinter mortality on perch recruitment has not been well analyzed. However, Post and Evans (1989) predicted that overwinter starvation mortality of yellow perch, based on simulation modeling, could greatly influence year-class strength in Southern Ontario.

I investigated recruitment dynamics of bluegill and yellow perch and potential relationships with abiotic and biotic variables in two Sandhills lakes. Bluegill and yellow perch were studied in Pelican Lake, Nebraska over four years and yellow perch were also studied in Cameron Lake, Nebraska over two years. My objectives were to describe and compare several life-stages of bluegill and yellow perch. I indexed the larval, juvenile, spring age 1, and adult populations each year and concurrently assessed abiotic and biotic variables that may affect each life stage. I used otoliths to determine hatch date and daily growth rates for age-0 bluegill and yellow perch. Exploratory analyses were performed to identify potential abiotic and biotic variables that may be related to recruitment.

Methods

Study areas

Cameron Lake is a 39-ha, shallow (mean depth = 1.8 m) natural lake in Rock County of the Sandhills region of north central Nebraska (McCarragher 1977). Submergent and emergent vegetation coverage was low (< 17% total coverage) in 2004 and 2005. The fish community was simple, primarily composed of yellow perch, green sunfish, black bullhead, common carp, fathead minnow, and golden shiner. The lake was closed to angling for over 12 months preceding my study, with little fishing effort for the previous three years (personal communication, R. Lackaff, property owner). The lake is used for commercial harvest of yellow perch (TL > ~ 76 mm). The lake watershed is mostly mid and tall-grass prairie and primarily used for livestock grazing (personal communication, R. Lackaff, property owner).

Pelican Lake is a 332-ha, shallow (mean depth = 1.3 m) natural lake in Cherry County of the Sandhills region of north central Nebraska within the Valentine National Wildlife Refuge (McCarragher 1977). Total vegetation coverage (emergent and submergent) ranged from 40 to 57% from 2004 to 2007. The fish community was relatively simple and similar to Cameron Lake; comprised primarily of bluegill, largemouth bass, yellow perch, northern pike, black bullhead, common carp, and fathead minnow. The lake watershed is mostly mid and tall-grass prairie and limited livestock grazing is allowed. A detailed description of the study lakes is given in Table 2-1.

Larval fish

Larval trawling was conducted at Pelican Lake from 2004 to 2008 and at Cameron Lake from 2004 to 2005. Larval yellow perch were obtained from Pelican and Cameron lakes and larval bluegill were obtained from Pelican Lake using a surface trawl with a 0.76-m diameter and 1,000- μm mesh (bar measure) towed in large, oblong circles. Isermann et al. (2002) found no difference in yellow perch density estimates by comparing a 500 and 1,000- μm mesh trawl, although the 1,000- μm size was less likely to become fouled with algae and zooplankton. Trawl duration was 3-5 min at an estimated speed of 1.75 m/sec. Larval sampling occurred approximately every 10 d from late April to early September in Pelican Lake and from late April to mid-June in Cameron Lake. In Pelican Lake, five randomly chosen locations within the lake were trawled on each occasion. Each random location was paired as a nearshore (<100 m from emergent, littoral vegetation) and an offshore (>100 m from emergent, littoral vegetation) site to account for potential migrational patterns (Post and McQueen 1988) for a total of 10 trawling locations per occasion. In Cameron Lake, four randomly chosen locations within the lake were trawled on each occasion and paired as described above for a total of eight trawling locations per occasion. The number of recently hatched (e.g., TL \leq 13 mm) bluegill and yellow perch larvae in the lakes was indexed using a flowmeter (Ocean Test Equipment, Inc.) in the mouth of the trawl, which allowed determination of water volume towed. All larval samples were preserved in 70% ethanol and returned to laboratory for identification and further analysis.

Larval fishes were identified to genus using identification keys (Auer 1982; Holland-Bartels et al. 1990). All larvae were counted and up to 200 fish per sample were

measured (mm TL) from each site. Larvae of TL ≤ 13 mm were used to calculate larval abundances; fish of TL > 13 mm were considered juvenile fish. Based on our observations, trawl catches generally declined for fish > 13 mm indicating a likely migration to littoral habitats as well as gear avoidance. Garvey et al. (2002) characterized bluegill larvae < 15 mm TL. Bluegills generally begin a migration to littoral habitats between 12 and 20 mm TL (Werner and Hall 1988; Garvey et al. 1998; Santucci and Wahl 2003) and yellow perch begin migrating between 8 and 40 mm TL (summarized by Urho 1996).

Larval fish density of each species was analyzed with a Wilcoxon sum of ranks test to determine if differences in density between inshore and offshore sites existed within a lake on a given date (NPAR1WAY procedure; SAS 9.1 [2002]). If no difference between strata was detected then density was reported for the entire lake on each sampling date. Peak density of larval bluegill and yellow perch was examined for differences within lakes, among years using one-way analysis of variance (ANOVA; SAS 9.1 2002). Post-hoc comparisons were performed using the Student-Newman Keuls multiple range test.

Sagittal otoliths were removed from 30 fish of each species per sampling date when adequate numbers were collected from each lake to obtain estimates of hatching date and daily growth (Taubert and Coble 1977). Otoliths were wiped clean and mounted on microscope slides with cyanoacrylic cement. Prepared otoliths were viewed under a 400X magnification microscope that projected images to a monitor to aid in the enumeration of daily growth increments. Daily growth increment counts were conducted

by two independent readers; if counts were within 5 d the counts were averaged. When disparity was greater than 5 d, a third experienced reader was consulted and the otolith was read in concert until consensus was reached. When all readers did not come to a consensus the otolith was removed from the data set. Taubert and Coble (1977) reported that the first growth increment occurred at swim-up for bluegill; Garvey et al. (2002) confirmed this and reported that swim-up occurred approximately 3 d post hatching. Therefore, hatching date for individual bluegill in my study was calculated by adding 3 d to the growth increment count. Length at time of hatching for yellow perch varies among studies, but can be as short as 4–5 mm (Heidinger and Kayes 1986; Fisher et al. 1998); length at time of swim-up varies from 6 to 10 mm (Whiteside et al. 1985; Powles and Warlen 1988). Powles and Warlen (1988) reported that the first increment formation in yellow perch larvae occurred 1–3 d posthatch; therefore, hatch date for yellow perch was corrected by adding 2 d to the estimates. The corrected age (days) estimate was then subtracted from the collection date to determine hatching date. To estimate the number of fish hatched throughout the spawning season, the abundance estimate (number/100 m³) was multiplied by the hatch date estimates, similar to an age-length key (DeVries and Frie 1996). Finally, average daily growth was calculated by dividing the total length at capture by the number of days since hatch and expressed as mm/d. Mean daily growth of larval bluegill and yellow perch was examined for differences within lakes, among years using one-way analysis of variance (ANOVA; SAS 9.1 [2002]). For bluegill, mean larval daily growth rates were examined for differences between hatching period and among years with two-way ANOVA. Hatching period was categorized as early (i.e., June) and

late (i.e., July and August). Post-hoc comparisons were performed using the Student-Newman Keuls multiple range test. Significant interaction terms were further assessed using one-way ANOVA with a Bonferroni correction applied.

Juvenile fish

Juvenile bluegill and yellow perch were collected from Pelican Lake in August or September 2004-2008 and juvenile yellow perch were collected from Cameron Lake in August using cloverleaf traps in the same years as trawling collections were made. The same cohorts were sampled the following April or May as age-1 fish. Each three-lobed cloverleaf trap was constructed of galvanized 6.4-mm bar mesh, with three 12.7-mm wide openings between lobes to accommodate entrance of small yellow perch (Brown and St. Sauver 2002). Each lobe was 50-cm in diameter with 41-cm height. Juvenile fish were preserved in 90% ethanol and enumerated in the laboratory. All fish were identified and measured (TL in mm), mean total length was calculated for each sampling period, and length-frequency histograms were constructed. Size-selective overwinter mortality was investigated by comparing length-frequency histograms between fall and spring samples. Size-selective overwinter mortality will increase the mean total length and decrease the variance in size of the survivors (in the absence of growth, Ricker 1969; Post and Evans 1989). I used these criteria to investigate the occurrence of size-selective overwinter mortality. Mean total length and coefficient of variation was compared between samples to test the significance of changes in mean size and variation through winter. In addition, the occurrence of size-selective mortality may be difficult to detect if

a threshold exists above which mortality rates are constant and a subset of fish in the population in a given year are larger than that size. To this end, I truncated the length-frequency histograms by removing bluegill greater than 60 mm and yellow perch greater than 90 mm TL, representing the upper tail of the length-frequency distributions but not removing a significant portion of the distribution. Finally, to separate size-selective mortality from potential growth between samples I employed empirical quantile-quantile (QQ) plots (Chambers et al. 1983). Total length at quantiles 1, 5, 10, 25, 50, 75, 90, 95, and 99 were determined for fall and spring samples. The difference between fall and spring total lengths at each quantile was determined and plotted. A plot with a negative slope would be evidence for size-selective overwinter mortality. A larger magnitude of difference between the smallest quantiles would indicate that the smallest fish are underrepresented.

Adult fish

Adult bluegill (i.e., age 2) and yellow perch (i.e., age 1) were collected and aged using otoliths (described in Chapter 2) to track and compare the age-0 abundances and examine if these year classes recruited to the adult population. Age-frequency histograms were constructed and examined for relative year-class strength. Finally, peak larval density was related to fall catches of age-0 fish, spring catches of age-1 fish, and adult collections of age-2 bluegill and age-1 yellow perch using correlation analysis.

Zooplankton

Zooplankton was collected at the time of each trawling sample. Zooplankton was collected during the daytime as two replicates at each site using a 2-m long tube sampler (Rabeni 1996). Samples were filtered through a 65- μm mesh net and stored in 90% ethanol. Benthic macroinvertebrates were sampled at the same time and sites using a 231-cm² Ekman grab sampler.

Zooplankton were enumerated and identified to family for cladocerans (i.e. Bosminidae, Chydoridae, and Daphnidae), and as cyclopoid or calanoid copepods, copepod nauplii, ostracods, and rotifers. Other uncommon taxa were also noted. Each sample was diluted with water to a measured volume of 30 mL. Three subsamples were then taken with a 5-mL Hensen-Stempel pipette and placed in a Ward counting wheel. Up to 20 individuals of each category were measured (mm TL) and all individuals were counted. The total number of zooplankton of each taxon in a sample was calculated by dividing the number of organisms counted by the proportion of the sample volume processed. Density was then calculated by dividing the number of zooplankters of each taxon by the volume of the water filtered with the tube sampler. I then used taxon-specific, length-dry weight equations (Dumont et al. 1975; Mason 1977; McCauley and Kalff 1984; Culver et al. 1985; Lynch et al. 1986) to convert length to biomass. Potential differences in mean density within months, among years were assessed with a one-way ANOVA. Post-hoc comparisons were performed using the Student-Newman Keuls multiple range test. Alpha levels were adjusted using the Bonferonni correction to account for year*month interactions.

Benthic macroinvertebrates

Benthic macroinvertebrates were collected at the time of each trawling sample. Two replicate benthic macroinvertebrate samples were collected at each site, strained through a 583- μm mesh sieve in the field, and stored in 90% ethanol. Replicate samples were collected and processed separately. Macroinvertebrates were identified to order and enumerated using a dissecting microscope in the laboratory. The most common macroinvertebrate taxa were reported and less common taxa were pooled into an “other” category. Up to 20 individuals of each taxon were measured (mm TL) and all individuals were counted. Density was then calculated by dividing the number of benthic invertebrates of each taxon by the area sampled with the Ekman grab (i.e. 231-cm²). I then used taxon-specific, length-dry weight equations (Eckblad 1971; Dumont and Balvay 1979; Smock 1980; Benke et al. 1999) to convert length to biomass. Biomass was not estimated for oligochaetes due to a lack of reliable length-weight conversions. Potential differences in mean density within months, among years were assessed with a one-way ANOVA. Post-hoc comparisons were performed using the Student-Newman Keuls multiple range test. Alpha levels were adjusted using the Bonferroni correction to account for year*month interactions.

Phytoplankton

Phytoplankton biomass was indexed using chlorophyll-*a* estimated from replicate water samples at each site using a 2-m long tube sampler. Water (100 mL) was filtered through filters (Whatman glass fiber filters, 0.45 μm) in the field and extracted in the

laboratory following the methods described by Lind (1985). Two samples of unfiltered lake water were collected at each site and frozen for later determination of total phosphorous following the methods of Wetzel and Likens (1991). From the same sampling locations, total alkalinity and pH were measured using a water chemistry analysis kit (Hach Company, Loveland, CO), and total dissolved solids (TDS) were recorded 0.5 m below the surface using an electronic meter (Hach Company, Loveland, CO). Secchi disk transparency was measured at each site during daytime and dissolved oxygen (DO) was measured 0.5 m below the surface using an electronic DO meter (Fisher Scientific, Pittsburgh, PA). Water temperature was measured hourly with an *in situ* automatic temperature logger (Onset Computer Corporation, Pocasset, MA) and expressed as the mean temperature/24-h period.

Vegetation

Submergent and emergent vegetation coverage was quantified annually during July. Sampling was conducted following the methods outlined by Paukert et al. (2002a) and values were expressed as percent coverage of different vegetation types (i.e., emergent or submergent). Total percent vegetation coverage was examined for differences within lakes, among years using a Chi-square multiple comparison technique (PROC GENMOD and MULTTEST procedures, SAS 9.1 2002; Zar 1984).

Exploratory analyses

Exploratory analyses of variables related to different indices of fish abundance and fish growth were performed for bluegill and yellow perch in Pelican Lake. The abundance indices that were examined were peak larval abundance, fall age-0 abundance, spring age-1 abundance, age-2 bluegill abundance, and age-1 yellow perch abundance. The growth indices that were examined were mean daily growth rate of early- and late-hatched bluegill, mean daily growth rate of yellow perch, and mean TL of juvenile fish captured in the fall. Relationships were investigated for these indices with various measures of biotic and abiotic variables (described above). Factor analysis (principal components analyses [PCA] with varimax rotation) was employed to reduce the dimensionality of the data sets because of the large number of independent variables that were measured. The PCA was used to identify meaningful combined (i.e., created) variables. The PCA was completed using SAS software (SAS 2002). Independent variables and the subsequent principal component (PC) groupings were placed into five categories: benthic macroinvertebrate variables, zooplankton variables, climate variables, habitat variables, and physicochemical variables. Benthic macroinvertebrate and zooplankton variables included measures of mean monthly density of the most dominant taxa. Climate variables included various measures of air temperature, precipitation, wind, and winter severity (see Chapter 2). Habitat variables included measures of DO, water temperature, and vegetation coverage. Physicochemical variables included measures of Secchi depth, conductivity, total dissolved solids, alkalinity, and pH. Principal components were retained based on a combination of the eigenvalue-one criteria (Kaiser 1960) and the proportion of variance method. Principal components with

eigenvalues > 1.0 were retained until the cumulative proportion of variance accounted for by the principal components was greater than or equal to 0.70 (Stevens 2002). Variables that loaded (greater than 40%) on more than one factor were omitted in interpretation (Stevens 2002) because it is unclear which dimension these complex variables describe. The PC scores were then related to the described fish indices using correlation analysis. I accepted an α of 0.10 as a useful target for this exploratory analysis. Because my unit of observation is one year, this analysis was hampered by a low number of observations (i.e., 4 years). Therefore plots of significant correlations were examined for the potential undue influence of data pairs.

Results

Trawl collections of bluegill larvae in Pelican Lake indicated protracted spawning in all years (Figure 4-1). Larvae appeared in the trawls in mid- to late June in all years. The spawning season was generally 2 months long. Larvae appeared the earliest in 2006; they were first captured on June 8 in Pelican Lake (Appendix 1). Larval bluegills were collected into August in all years.

Larval fish densities did not differ between inshore and offshore strata for bluegill on any date (Wilcoxon two-sample test, $P > 0.05$, Appendix 1). Peak bluegill larval density was highly variable among years and was primarily unimodal, with peaks consistently occurring in mid-July (Figure 4-1). Mean peak larval density ranged from 116 to 1,760 larvae/100 m³. In 2004 there were two peaks in larval bluegill density; the second peak in density occurred in mid-August. The highest density was 1,760

larvae/100 m³ in 2006 and lowest density was 116 larvae/100 m³ in 2004 (Figure 4-1). Results of the one-way ANOVA indicated that density varied by year ($P < 0.05$, $F = 3.21$, $df = 3$). Larval density was highest in 2006, moderate in 2005 and 2007, and lowest in 2004 (Figure 4-1).

Trawl collections of yellow perch larvae in Cameron and Pelican lakes indicated a truncated spawning period in all years (Figure 4-2). Larvae appeared in the trawls in late April or early May in all years and lakes. The spawning season was generally 2.5 weeks long. Larvae appeared earliest in Cameron Lake in 2004 (30 April) and latest in Pelican Lake in 2006 (9 May). Larval yellow perch densities did not differ between inshore and offshore strata for either species on any date (Wilcoxon two-sample test, $P > 0.05$, Appendix 2). Peak larval density of yellow perch was highly variable between lakes and among years, and was unimodal; peaks occurred in mid-May but peak date varied by several weeks among years (Figure 4-2). Mean peak larval density ranged from 5 to 1,685 larvae/100 m³. The highest density was 1,685 larvae/100 m³ in Cameron Lake in 2004 and lowest density was 5 larvae/100 m³ in Pelican Lake in 2005 (Figure 4-2), a potential year-class failure or at least a weak year class. Water temperatures in Pelican and Cameron lakes in 2005 rose to nearly 15 C but then dropped to nearly 5 C over a period of 2 weeks in late April (Figure 4-2) which coincided with the yellow perch hatching period (Figure 4-4).

Results of the one-way ANOVA indicated that density varied by year in Cameron Lake ($P < 0.01$, $F = 10.14$, $df = 1$) and in Pelican Lake ($P < 0.01$, $F = 7.68$, $df = 3$). In

Cameron Lake, density was higher in 2004 than 2005. In Pelican Lake, density was higher in 2007 than in 2004, 2005, or 2006 (Figure 4-2).

Hatching Dates

Bluegill hatching generally began in early to mid-June (Figure 4-3) coinciding with sustained water temperatures of 20 C or greater. Hatching duration was the longest in Pelican Lake in 2004 (56 d); water temperatures were cooler in early summer and did not rise and remain over 20 C until early July (Figure 4-2). In addition, there were two peaks in larval abundance in 2004 accompanied by a comparatively extended hatching duration (Figure 4-3). Water temperatures dropped by approximately 8 C in late July for an extended time period before rising again, which corresponds with the time period between the two peaks in larval abundance (Figure 4-1). Bluegill began hatching earliest in 2006 when early summer water temperatures were comparatively warmer than the other years.

Yellow perch hatching began in April in all years typically when water temperatures rose consistently above 7 C (Figure 4-4). Yellow perch began hatching in early April in Pelican Lake in 2007, the year with the comparatively warmer spring (Figure 4-1). Yellow perch began hatching in late April/early May in Pelican and Cameron lakes in 2005. Finally, the hatching period was somewhat extended in Cameron Lake in 2004, lasting for 47 d (Figure 4-4). Water temperature data were not available for Cameron Lake in 2004.

Mean average daily growth rate of larval bluegill ranged from 0.16 to 0.50 mm/day over the four years of study. Results of the two-way ANOVA of average daily growth rate indicated that growth varied by year ($P < 0.01$, $F = 21.78$, $df = 3$) and by hatching period ($P < 0.01$, $F = 24.99$, $df = 1$). In addition, the year*hatching period interaction was significant ($P < 0.01$, $F = 19.44$, $df = 3$). The later hatched bluegill (mean = 0.34 mm/d) grew faster than earlier hatched bluegill (mean = 0.27 mm/d) with the exception of 2004 (Figure 4-5). For early hatched bluegill, differences were detected in growth rates among years (Bonferonni correction, $\alpha = 0.025$, $P < 0.01$, $F = 60.33$, $df = 3$, Appendix 3). Specifically, larvae in 2005 grew fastest followed by 2006 larvae, and 2004 and 2007 larvae which did not differ from each other (Figure 4-5). Differences in mean daily growth rates for late hatched larvae were also detected among years (Bonferonni correction, $\alpha = 0.025$, $P < 0.01$, $F = 5.18$, $df = 3$). Specifically, larvae in 2006 grew faster than those in 2007. Larval bluegill growth in 2004 and 2005 was similar to all other years (Figure 4-5).

Mean average daily growth rate of larval yellow perch ranged from 0.27 to 0.35 mm/d in Cameron Lake and from 0.23 to 0.37 in Pelican Lake. Results of the one-way ANOVA of average daily growth rate indicated that growth varied by year in Cameron Lake ($P < 0.01$, $F = 7.50$, $df = 1$) and in Pelican Lake ($P < 0.01$, $F = 41.71$, $df = 3$, Appendix 3). In Cameron Lake, larval growth was faster in 2005 than 2004 (Figure 4-5). In Pelican Lake, growth was fastest in 2004, moderate in 2005 and 2006, and slowest in 2007 (Bonferonni correction; $\alpha = 0.0125$; Figure 4-5).

Juvenile fish

Collections of juvenile bluegill and yellow perch in cloverleaf traps in Pelican Lake were variable among years in spring and fall (Table 4-1). Insufficient sample sizes precluded comparison of overwinter mortality for some pairs of years. For bluegill and yellow perch in Pelican Lake, I compared fall and spring length-frequency histograms in 2004-2005, 2006-2007, and 2007-2008. Yellow perch samples in Cameron Lake were inadequate in 2005 to examine potential size-selective overwinter mortality.

Mean total length of juvenile bluegill ranged from 29 to 35 mm in fall and ranged from 36 to 38 mm in spring (Table 4-2). All *t*-tests indicated significant differences in total length from fall to spring while variability (i.e., coefficient of variation [CV]) in total length was similar or increased from fall to spring. Visual inspection of length-frequency histograms indicate that growth likely occurred between sampling occasions (Figure 4-6). Quantile-quantile (QQ) plots revealed size differential growth overwinter but no size-selective mortality occurred (Figure 4-7). In the 2004/2005 and 2006/2007 winters, the incremental change in length was greater for larger individuals than for smaller individuals and the slopes of the QQ regression plots were significantly different from the 1:1 line ($P < 0.01$). This explains the length-frequency distributions spanning a greater length range in spring compared to the previous fall (Figure 4-6). The slope of the QQ regression plot for the 2007/2008 winter was not different than the 1:1 line ($P = 0.23$) indicating that growth occurred between sampling occasions but the incremental change in length was the same for all sizes and no size-selective overwinter mortality occurred (Figure 4-7).

Mean total length of juvenile yellow perch ranged from 45 to 62 mm in fall and from 63 to 73 mm in spring (Table 4-2). All *t*-tests indicated significant differences in total length from fall to spring while variability in total length decreased from fall to spring. Visual inspection of length-frequency histograms indicated that growth likely occurred between sampling occasions in 2004/2005 and 2007/2008 (Figure 4-8). Quantile-quantile (QQ) plots revealed that growth occurred overwinter but no size-selective overwinter mortality occurred in 2004/2005 and 2006/2007 (Figure 4-9). The slope of the QQ regression plots were not different than the 1:1 line for 2004/2005 ($P = 0.13$) and 2006/2007 ($P = 0.16$) indicating that growth occurred between sampling occasions but the incremental change in length was the same for all sizes and no size-selective overwinter mortality occurred. The slope of the QQ regression plot for the 2007/2008 winter was different than the 1:1 line ($P < 0.05$) indicating that growth and some size-selective overwinter mortality occurred between sampling occasions (Figure 4-9). The proportion of smaller fish decreased from fall 2007 to spring 2008 even though growth occurred (Figure 4-8).

Adult fish

Age-frequency histograms of adult bluegill were qualitatively examined revealing relatively consistent recruitment (i.e., no missing year classes) within my study period (Figure 4-10). Histograms were examined for 2006, 2007, and 2008; histograms were not examined in 2005 due to inadequate sample size. Catch of age-1 bluegill was not examined because these fish are likely not of a size to fully recruit to the modified-fyke

nets. Thus, I was able to examine potential recruitment of the 2004, 2005, and 2006 year class. The 2004 year class appears to have recruited in relatively higher numbers and was evident in the population over the three years of collection. The 2005 year class was evident in 2007 and 2008 but the numbers were relatively lower in the 2008 sample. From the 2008 sample it appears that the 2006 year class has also recruited, at least to age 2.

Age-frequency histograms for adult yellow perch revealed recruitment of the 2006, 2005, and 2004 year classes by presence of fish from those years (Figure 4-11). Catches of adult yellow perch were low in all years making interpretation of the age structure challenging. In fact, no yellow perch were collected in 2006 and collections in the other years were <30 fish. Age-1 fish are likely recruited to the modified-fyke nets and it appears that the 2006 year class was relatively strong as these fish were collected in greater numbers in 2007 and 2008. At least some of the bluegill and yellow perch survived to recruit to the adult population in each year studied.

Finally, none of my indices of life stage abundance were related, within or among species (Appendix 4). Peak density of larval bluegill was not correlated to juvenile fall catches ($r = 0.55$, $P = 0.45$, $N = 4$), juvenile spring catches ($r = 0.67$, $P = 0.33$, $N = 4$), or adult catches of age-2 bluegill ($r = 0.41$, $P = 0.73$, $N = 3$). Peak density of larval yellow perch was not correlated to juvenile fall catches ($r = -0.12$, $P = 0.82$, $N = 6$), juvenile spring catches ($r = -0.04$, $P = 0.95$, $N = 6$) or adult catches of age-1 yellow perch ($r = -0.22$, $P = 0.78$, $N = 4$).

Invertebrates

The zooplankton community of Pelican Lake displayed varying biomass dynamics from 2004 to 2007 (Figure 4-12). Generally, larger daphnids dominated the community early in the season and declined by early to mid-June in all years with the exception of 2005 when they remained abundant throughout the season. Copepods were generally most abundant in mid-summer. *Bosmina* populations were most abundant later in the season, typically coinciding with a decreased daphnid population. Other taxa (i.e., chydorids and copepod nauplii) were less abundant in most years (Figure 4-12). Results of the two-way ANOVAs of density (Table 4-3) for the different zooplankton categories by year and month (i.e., May-August) indicated varying densities in every instance as well as significant year*month interactions ($P < 0.0001$). *Post-hoc* one-way analyses of variance were performed for each zooplankton category within each month to examine yearly differences (Bonferroni correction, $\alpha = 0.0125$). Of 24 different statistical examinations, 21 of those had significant differences in density within months, among years (Table 4-3). Individual-year, among-month differences were not examined due to the expected dynamic nature of zooplankton populations. Notably, July *Bosmina* density was over five-fold higher in 2006 than the other years and July and August cladoceran density was over five-fold higher in 2007 than the other years.

The zooplankton community of Cameron Lake was largely dominated by daphnids, *Chydorus*, copepods, and copepod nauplii in 2004 and 2005 (Figure 4-13). Daphnid abundance declined in early June 2004 but remained abundant throughout my 2005 sampling dates. Results of the two-way ANOVAs of density for the different

zooplankton categories by year and month (i.e., May-June) indicated varying densities in many instances as well as significant year*month interactions ($P < 0.05$). Rotifer density did not vary among months or years in Cameron Lake ($P > 0.05$, $df=1$). *Post-hoc* one-way analyses of variance were performed for each zooplankton category within each month to examine yearly differences (Bonferroni correction, $\alpha = 0.025$). Of 12 different statistical examinations, eight exhibited significant differences in density within months, among years (Table 4-4). Individual-year, among-month differences were not examined due to the expected dynamic nature of zooplankton populations. Notably, May *Bosmina* density was over 30-fold higher in 2004 than in 2005.

For Pelican Lake, results of the two-way ANOVAs for density (n/m^2) of the different macroinvertebrate categories by year and month (i.e., May-August) indicated varying densities of oligochaetes, chironomids, other taxa, and total macroinvertebrates as well as significant year*month interactions ($P < 0.05$). *Post-hoc* one-way analyses of variance were performed for these macroinvertebrate categories within each month to examine yearly differences (Bonferroni correction, $\alpha = 0.0125$). Density of ephemeropterans, odonates, amphipods, and gastropods were similar among seasons and years ($P > 0.05$). Of 16 different statistical examinations, 12 of those had significant differences in density within months, among years (Table 4-5). Notably, chironomids were over twice as abundant in June of 2004 than in any other year. Biomass of the major invertebrate taxa in Pelican Lake and Cameron Lake are summarized in Appendix 5.

For Cameron Lake, results of the two-way analyses of variance of density (number/m²) of the different macroinvertebrate categories by year and month (i.e.; May-June) indicated varying densities of oligochaetes, chironomids, other taxa, and total macroinvertebrates as well as significant year*month interactions ($P < 0.05$). *Post-hoc* one-way analyses of variance were performed for these macroinvertebrate categories within each month to examine yearly differences (Bonferroni correction, $\alpha = 0.025$). Density of ephemeropterans, amphipods, and hirudineans were similar among seasons and years ($P > 0.05$). Of eight different statistical examinations, six of those had significant differences in density within months, among years (Table 4-6). Notably, chironomids and oligochaetes were over twice as abundant in 2004 compared to 2005.

Phytoplankton (as indexed by chlorophyll-*a*) was lower in spring and increased in concentration throughout the season in Pelican Lake, ranging from 1.3 to 253.7 $\mu\text{g/L}$ (Figure 4-14). Results of the two-way ANOVAs for chlorophyll-*a* concentration ($\mu\text{g/L}$) by year and month (i.e.; May-June) indicated varying phytoplankton concentrations as well as significant year*month interactions ($P < 0.05$). *Post-hoc* one-way analyses of variance were performed within each month to examine yearly differences (Bonferroni correction, $\alpha = 0.0125$). Among-year differences were detected within all months. In general, 2006 and 2007 had higher phytoplankton concentrations than 2004 and 2005 (Figure 4-14). Chlorophyll-*a* in Cameron Lake ranged from 5.3 to 184.4 $\mu\text{g/L}$ in May and June in 2004 and 2005. An increasing trend over time was again observed (Figure 4-15). Results of the two-way analyses of variance of chlorophyll-*a* concentration ($\mu\text{g/L}$) by year and month (i.e.; May-June) indicated varying phytoplankton concentrations as

well as significant year*month interactions ($P<0.05$). *Post-hoc* one-way analyses of variance were performed within each month to examine yearly differences (Bonferroni correction, $\alpha = 0.025$). Yearly differences were detected within both months. Phytoplankton concentration in May was higher in 2005 while the concentration was lower in June in 2005 (Figure 4-13).

Total phosphorous concentrations in Pelican Lake ranged from 18.4 to 24.4 $\mu\text{g/L}$ in May through August from 2004 to 2007 (Figure 4-16). Results of the two-way analyses of variance of total phosphorous concentration ($\mu\text{g/L}$) by year and month (i.e.; May-August) indicated no differences in concentration as well as no year*month interactions ($P>0.05$). Total phosphorous concentrations in Cameron Lake ranged from 18.4 to 28.3 $\mu\text{g/L}$ in May and June in 2004 and 2005 (Figure 4-17). Results of the two-way analyses of variance of total phosphorous concentration ($\mu\text{g/L}$) by year and month (i.e.; May-June) indicated varying phosphorous concentrations as well as a significant year*month interaction ($P<0.05$). *Post-hoc* one-way analyses of variance were performed within each month to examine yearly differences (Bonferroni correction, $\alpha = 0.025$). Total phosphorous concentrations were higher in May and June of 2005 than in 2004 ($P<0.025$).

Other mean physical and chemical measurements for Pelican Lake and Cameron Lake are summarized in Appendix 6. Secchi depth was variable and ranged from 12.9 to 171.0 cm in Pelican Lake and from 6.4 to 12.5 cm in Cameron Lake. Secchi depth generally decreased throughout each season. Dissolved oxygen ranged from 4.8 to 9.5 mg/L in Pelican Lake and from 7.0 to 11.0 mg/L in Cameron Lake. Conductivity ranged

from 342 to 880 $\mu\text{S}/\text{cm}$ in Pelican Lake and from 210 to 600 $\mu\text{S}/\text{cm}$ in Cameron Lake. Alkalinity ranged from 119.7 to 324.9 mg/L in Pelican Lake and from 85.5 to 171.0 mg/L in Cameron Lake. Finally, pH ranged from 7.5 to 10.0 in Pelican Lake and from 7.5 to 8.5 in Cameron Lake.

Total vegetation coverage ranged from 40 to 57 % in Pelican Lake and from 15.0 to 16.7% in Cameron Lake (Table 4-7). Percent coverage was lower in Pelican Lake in 2004 compared with 2005 through 2007 ($\chi^2= 17.92, P < 0.01$) and similar in 2004 and 2005 in Cameron Lake ($\chi^2= 0.52, P > 0.05$).

Principal Components Groupings

For the invertebrate variables, my PCA indicated that the first two principal components explained 82% of the variability (Table 4-8). Invertebrate PC 1 was interpreted primarily as an index of overall invertebrate density in May and June (Table 4-9). Principal component 2 was primarily an index of chironomid and hirudinean density in July and August.

For the zooplankton variables, PCA indicated that the first two principal components explained 85% of the variability (Table 4-8). Zooplankton PC 1 was interpreted primarily as an index of *Bosmina*, copepod, and nauplii density in August (Table 4-9). Principal component 2 was primarily an index of cladoceran density throughout the summer months.

For the climate variables, PCA indicated that the first two principal components explained 78% of the variability (Table 4-8). Climate PC 1 was primarily an index of

wind speed from March to August (Table 4-9). Principal component 2 was negatively loaded by April air temperature and positively loaded by August air temperature suggesting that these variables are inversely related to an underlying dimension.

For the habitat variables, PCA indicated that the first two principal components explained 85% of the variability (Table 4-8). Habitat PC 1 was an index of total vegetation coverage while PC 2 was solely loaded by May water temperature (Table 4-9).

For the physicochemical variables, PCA indicated that the first two principal components explained 97% of the variability (Table 4-8). Physicochemical PC 1 was primarily an index of Secchi depth and pH throughout the summer months. Principal component 2 was an index of a mixture of alkalinity, conductivity, and total dissolved solids measures (Table 4-9). All bivariate correlations are summarized in Appendix 7.

Correlations with bluegill life-stage and growth indices

Mean CPUE of juvenile bluegill in the fall was negatively correlated with climate PC 2 ($r = -0.99$, $P < 0.01$, Figure 4-18) which was loaded by April and August air temperature in an inverse fashion. Mean CPUE of juvenile bluegill in the spring was negatively correlated with habitat PC 2 from the previous year ($r = -0.91$, $P = 0.09$, Figure 4-18). In this instance, May water temperatures were negatively related to CPUE of juvenile bluegill, although a high CPUE in 2006 appeared to place undue influence on this relationship. Mean CPUE of age 2 bluegill was negatively correlated with physicochemical PC 1 in the hatching year ($r = -0.99$, $P = 0.03$, Figure 4-18). The correlation is based on three data pairs because age 2 fish from the 2007 year class will

not be collected until 2009. Peak larval density of bluegill was not significantly correlated to any of the principal components ($P > 0.10$).

Mean daily growth of early-hatched bluegill was negatively correlated with mean CPUE of juvenile yellow perch in the fall ($r = -0.96$, $P = 0.04$; Figure 4-19). Growth of late-hatched bluegills was positively correlated to both fall CPUE of age 0 ($r = 0.97$, $P = 0.03$) and spring CPUE of age-1 bluegill ($r = 0.96$, $P = 0.04$), and negatively correlated to climate PC 2 ($r = -0.93$, $P = 0.07$, Figure 4-19). Finally, mean TL of bluegill in fall was positively correlated with mean peak abundance of bluegill larvae ($r = 0.96$, $P = 0.04$; Figure 4-18).

Correlations with yellow perch life-stage and growth indices

Peak larval density of yellow perch was negatively correlated with invertebrate PC 2 ($r = -0.97$, $P = 0.03$, Figure 4-18). High larval densities were therefore related to low densities of chironomids and hirudineans in July and August. No other indices of yellow perch abundance were correlated to any of the principal components ($P > 0.10$).

Mean daily growth of yellow perch was negatively correlated with spring CPUE of age-1 yellow perch ($r = -0.78$, $P = 0.07$, Figure 4-19). No other yellow perch growth indices were correlated to indices of abundance or any of the principal components ($P > 0.10$, Appendix 7).

Discussion

A single peak of larval bluegill abundance was observed in all years with one exception. Two peaks in larval abundance were observed in 2004, but overall abundance was low that year. Bluegills are typically assumed to be synchronous colonial spawners that exhibit a protracted spawning season, although a small percentage (4.5 – 7.0%) will nest solitarily (Gross and MacMillan 1981; Neff et al. 2004). A mid-summer temperature drop may have interrupted the bluegill spawn in 2004 and thus resulted in an apparent bimodal appearance when overall synchrony may not be occurring. Beard (1982) indicated that fluctuations in water temperature provided stimuli for repeated spawning and were thus related to the overall length of the spawning season. Although there are many examples of multiple peaks in larval bluegill abundance or direct observations of multiple spawning bouts, examples of years with a single peak in larval density are well-documented. The frequency of sampling in my study (i.e., 7-10 d) was likely adequate to identify multiple peaks in abundance and the use of a 1,000- μ m mesh trawl is likely effective at capturing newly hatched bluegill (Isermann et al. 2002). Elevated turbidity precluded direct observation of bluegill spawning or nesting activity in my study. Beard (1982) reported a range of four to eleven spawning bouts in three Wisconsin lakes. Dominey (1981) reported that bluegill breeding synchrony was greater within colonies than among colonies. He noted that even neighboring colonies may cycle out of phase. Consequently, the ability to detect distinct spawning events may be limited as a result of potential asynchronous colony spawning events in a water body as large as Pelican Lake. In addition, daily age estimates have a margin of error of approximately 7 d. A loss of resolution in the identification of specific hatching days may have occurred.

Notwithstanding, I contend that potential multiple peaks in hatching were identifiable with our sampling method.

Larval bluegill densities in my study lake differed among years and were relatively low when compared to those reported in other studies. Thus, a plausible hypothesis is that a longer spawning season at lower latitudes may lead to increased larval densities. Beard (1982) reported that longer spawning seasons (mediated by appropriate water temperatures) resulted in a greater number of individual spawning periods in Wisconsin. I found several instances of larval densities from lower latitudes up to 20-fold higher than our observations (Partridge and DeVries 1999; Kim and DeVries 2000; Santucci and Wahl 2003), but most observations were within two to three times of my estimates (Mayhew 1976; Sammons and Bettoli 2002). In addition, several studies at higher latitudes reported similar or lower densities than we encountered (Bryan 1989; Garvey et al. 2002; Jolley et al. 2009). Generally, bluegill populations at lower latitudes may have the potential to reach relatively high larval densities in some years but may also exhibit lower densities more comparable to our study (Kolar et al. 2003). A suite of factors may interact in complex ways, leading to variable larval densities and subsequent recruitment. As a result, direct comparisons to previous research are challenging. Interacting factors may include abiotic factors such as physical habitat, temperature, and weather (Beard 1982; Pope et al. 1996; Jackson and Noble 2000; Casselman et al. 2002) and biotic factors such as food availability and competition (Partridge and DeVries 1999; Rettig and Mittelbach 2002), predation (Houde 1987; Gray et al. 1998; Santucci and Wahl 2003), and lake productivity (Latta and Merna 1977).

The larval bluegill duration (as a surrogate of spawning season) in my study ranged from 1 to 2 months in Pelican Lake. Jolley et al. (2009) found that latitude and larval bluegill duration were generally negatively correlated. The expected, extended spawning season was observed in Crane Lake, Indiana, where larval bluegills were collected from early June to early September (Werner 1969). Beard (1982) reported bluegill spawning durations from 31 d to 112 d in three Wisconsin lakes. Chvala (2000), who evaluated the reproductive biology of bluegill in two Nebraska Sandhills lakes, found that while larvae were initially collected in both lakes during June, the spawning season was relatively extended in one lake compared with the other. Newly hatched (i.e., 4–6 mm) larvae were collected at Cozad Lake between June 5 and July 24, while newly hatched larvae were only collected from Pelican Lake between June 25 and July 9. Egg-diameter distributions from bluegill ovaries in both lakes had multiple modes, indicating multiple-spawning (i.e., fractional spawning) capabilities.

An inverse relation between latitude and frequency of bluegill spawning bouts is often assumed but was not observed by Jolley et al. (2009). While three or more spawning bouts are common in more southerly waters, such occurrences are rarer at northern latitudes, although Jolley et al. (2009) reported evidence of three spawning bouts in one South Dakota impoundment. However, even at this more northerly latitude, the influence of latitude could not be discerned as substantial inter-annual variation in the number of spawning bouts within a water body was found. Thus, geographic location alone certainly does not explain the frequency of bluegill spawning and this topic certainly warrants further investigation.

Growth rates of larval bluegill were variable in my study with later-hatched bluegill growing faster than early-hatched fish in most years. Garvey et al. (2002) reported that later-hatched bluegill grew more rapidly than earlier-hatched fish through September but that growth rates were similar by October. Growth rates of fish typically increase with temperature, given adequate prey, to some optimum (Jones 2002). Increased growth rates of later-hatched fish in my study may simply have been influenced by warmer summer temperatures. Breck (1993) suggested that warmer temperatures may have led to a relatively larger size of age-0 bluegill in Michigan ponds. Although my estimated mean daily growth rates were variable they fell within the range reported by other researchers (i.e., 0.14-0.70 mm/d; Werner 1969; Beard 1982; Breck 1993; Welker et al. 1994; Cargnelli and Gross 1996; Partridge and DeVries 1999; Santucci and Wahl 2003). In addition, mean total length of juvenile bluegill by fall in Pelican Lake (range 29-35 mm) was within the reported range (23-70 mm TL) for populations in Clear Lake, Iowa (Ridenhour 1960), Michigan ponds (Latta and Merna 1977) and northern Wisconsin lakes (Beard 1982). In addition, mean TL of bluegill captured in the fall of 2008 in five nearby Sandhills lakes ranged from 31 to 38 mm (J.C. Jolley, unpublished data), slightly higher than those observed in Pelican Lake. Reported mean TL of juvenile bluegill in the fall from Lake Opinicon, Ontario (Garvey et al. 2002) and several lakes in Central Wisconsin (Toneys and Coble 1979) were higher than those observed in my study.

My exploratory correlation analysis indicated that growth of early-hatched bluegills was negatively related to abundance of juvenile yellow perch in the fall. Yellow

perch typically hatch 2 months prior to bluegill and thus likely have a competitive size-advantage over bluegill larvae. Early-hatched bluegills often have higher survival (Beard 1982; Cargnelli and Gross 1996) likely due to the ability to attain larger sizes by fall thereby increasing overwinter survival. In contrast, early-hatched bluegills may be subject to variable environmental factors (e.g., temperature) and elevated predation mortality, thereby reducing survival to the fall (Garvey et al. 2002; Santucci and Wahl 2003). Later-hatched fish may compensate for a shorter growing season with increased growth rates owing to more conducive water temperatures. This may be the situation in Pelican Lake as growth of late-hatched bluegill was related to mean CPUE of juvenile bluegill in the fall and following spring. Faster-growing, late-hatched bluegills may contribute more to year-class strength than their earlier-hatched counterparts. Hatch date estimates of juvenile bluegill collected in the fall are necessary to confirm this contention, and otoliths are difficult to age (i.e., daily increment counts) by this time of year.

Although densities of yellow perch larvae varied considerably (>300%) among years it appears that recruitment of yellow perch was relatively consistent in Pelican and Cameron Lake over the years examined. Most other Sandhills lakes studied exhibited relatively consistent recruitment with the exception of Marsh Lake (see Chapter 2). Large annual variation in yellow perch year-class strength is common (Hamley et al. 1983; Henderson 1985) although recruitment patterns may vary among water bodies within a localized region (Lott 1991; Lucchesi 1991; Isermann et al. 2007). The early life stages are commonly reported as the time when year-class strength is formed (Clady 1976; Forney 1971; Mills and Forney 1981). My observed densities of larval yellow

perch were generally higher than reported values of density in six South Dakota glacial lakes monitored for over eight years (Jansen 2008). Densities were similar in two years to Long Lake, Michigan (Hoffman et al. 2001) and generally similar to or higher than reported densities from southern Lake Michigan (Dettmers et al. 2005). My observed densities were lower than those reported in two embayments of Lake Ontario (Mason and Brandt 1996) and also lower than estimates of larval Eurasian perch in Scotland (Treasurer 1989).

The hatching period of yellow perch was relatively truncated in all years with the exception of 2004 in Cameron Lake (47 d). This is consistent with previous findings of a narrow spawning period and hatching window for yellow perch (Clady 1976; Weber and Les 1982; Powles and Warlen 1988; Fisher 1996; Isermann and Willis 2008). Yellow perch may also protract their spawning under suitable environmental conditions. Fitzgerald et al. (2001) inferred a spawning period >9 weeks in Lake St. Clair, Michigan and Lake Opinicon, Ontario mediated by a strong El Niño climatic phenomenon and Sandström et al. (1997) documented protracted spawning of Eurasian perch mediated by a heated effluent plume, although these examples appear to be the exception. Isermann and Willis (2008) suggested that factors prior to, during, or immediately following hatching may play a critical role in the recruitment of yellow perch under the constraint of a narrow spawning window. In 2005, yellow perch hatched over a very narrow time frame in Pelican Lake (4 d) and larvae were only collected in low numbers on one day, likely indicating a relatively weak initial year class. Concurrently, Pelican Lake experienced a drop in water temperature from nearly 17 C to nearly 6 C over a period of 2

weeks in late April. This corresponded to the time period when yellow perch eggs would have been incubating and hatching. It is unclear whether the eggs or newly hatched larvae were negatively affected by this cold front. Jansen (2008) simulated the effect of a cold front on yellow perch eggs and found no decrease in egg survival suggesting that the newly hatched larval stage may be more susceptible than eggs to these extreme weather events. Longhenry (2006) attributed the lack of larval yellow perch abundance in semi-permanent wetlands in South Dakota to a cold-front that decreased the water temperature from 12 C to 8 C in 24 h. In general, a higher abundance of yellow perch swim-up larvae, with fewer abnormalities, are produced during a shorter hatching period when water temperatures gradually increase (Hokanson and Kleiner 1974). Treasurer (1989) reported that newly hatched Eurasian perch larvae were more susceptible to sudden temperature changes than were embryos. Sandhills lakes are shallow and windswept; they thus are susceptible to erratic temperature changes and can warm and cool quickly. I am uncertain why the yellow perch hatching period was more protracted in Cameron Lake in 2004.

The abundance indices of yellow perch life stages were not correlated to the abiotic and biotic variables (i.e., principal components) with the exception of peak larval density and invertebrate PC 2. This PC was loaded by July and August densities of chironomids and hirudineans. If the correlation is not spurious, it is possible that elevated densities of larval yellow perch may consequently depress later season abundance of these invertebrates through predation. Alternatively, larval abundance and invertebrate PC 2 may be related to another, unmeasured variable. For example, due to the voltinism

in chironomid populations, density alone is insufficient to fully characterize the population dynamics of this taxa. There are typically multiple overlapping generations of chironomids present in an ecosystem and identification of specific instar stage is necessary to describe these dynamics (Tokeshi 1995), but beyond the scope of my study. No other correlations were significant, although these analyses were based on a low number of observations ($N \leq 6$).

I did not detect differences in larval bluegill or yellow perch densities between inshore and offshore strata as has been reported by others (Werner 1969; Post and McQueen 1998). Pelican Lake is almost entirely littoral with patchily distributed submergent and emergent vegetation throughout the lake (Paukert 2001). This feature of Sandhills lakes likely precludes larvae from becoming spatially stratified within the lake.

Growth rates of larval yellow perch were variable in my study. First-year growth seems to be quite variable both spatially and temporally (e.g., Post and McQueen 1994). Although previously reported data on daily growth rates of yellow perch are scarce, Whiteside et al. (1985) reported rates of approximately 0.57 – 0.66 mm/d in Lake Itasca, Minnesota and Fisher and Willis (1997) reported daily growth rates of 0.45 – 0.65 mm/d in two eastern South Dakota lakes. Mean total lengths of juvenile yellow perch in my fall samples (range 45-62 mm) may have been slightly smaller than those reported elsewhere. Some other ranges reported were 71-89 mm in Clear Lake, Iowa (Ridenhour 1960), 78-90 mm in Lake Winnebago, Wisconsin (Weber and Les 1982), 61-70 mm in Ontario (Post and Evans 1989), and 60-90 mm in Lake Oneida, New York (Irwin et al. 2009). In addition, mean total length of yellow perch captured in the fall in four nearby Sandhills

lakes ranged from 60 to 83 mm J.C. Jolley, unpublished data). Growth of poikilothermic animals is largely mediated by temperature, but other factors may override or mask the effects of temperature on growth. Some researchers did not find thermal effects on age-0 yellow perch growth and recruitment (Weber and Les 1982; Henderson 1985; Post and McQueen 1994) while others have found the converse (Kallemeyn 1987; Ward et al. 2004). Various measures of the thermal regime may correlate to year-class strength only in certain instances (Koonce et al. 1977; Henderson and Nepszy 1988). Post and McQueen (1994) attributed the majority of the variation in growth of age-0 yellow perch to the availability of benthic and planktonic prey. Some of my observations suggest that temperature may be important to the early life-stages of yellow perch although correlational evidence was not found. Thermal effects may only become evident under extreme conditions in localized areas (Eshenroder 1977; Henderson 1985; Newsome and Aalto 1987). Other factors such as predation rates and availability of prey may override temperature effects (Forney 1971; Crowder 1980; Mason and Brandt 1996). In addition, small changes in a single factor affecting mortality may consequently affect recruitment (Houde 1987).

My estimates of larval density for both species were a poor predictor of later season catches or recruitment to the adult population. Abundance of larval bluegill may not be related to juvenile survival (and resulting recruitment) in lakes that contain piscivore populations (Cargnelli and Gross 1996; Partridge and DeVries 1999) suggesting that events occurring after the larval life-stage may determine year-class strength. Previous researchers have found indices of larval abundance useful in predicting later life

stage abundance. Anderson et al. (1998) reported that larval yellow perch abundance was positively correlated with fall juvenile abundance and Fisher and Willis (1997) reported that August juvenile abundance was positively correlated with larval abundance in south Dakota lakes, although continued research indicated a weaker relation (Isermann 2003; Jansen 2008). Forney (1971) reported that high trawl catches of age-0 yellow perch corresponded to subsequent dominant year classes in Lake Oneida. Sammons and Bettoli (1998) also reported that larval abundances of crappie and white bass *Morone chrysops* were accurate predictors of later year-class strength. The lack of correlation between larval abundance and later life-stage abundance in my study should be interpreted cautiously as analyses were based on a low number of observations. Significant events may be occurring after the larval stage in my study lakes that directly contribute to year-class formation.

I found little evidence of size-selective overwinter mortality for bluegill or yellow perch in Pelican Lake. Differences in mean total length of bluegill and yellow perch from fall to spring indicate that some growth likely occurred between sampling occasions, which has also been reported by Santucci and Wahl (2003) for bluegill. In one year in Pelican Lake, larger bluegill may have grown more than smaller bluegill over the winter time period. Toney and Coble (1979) only documented size-selective overwinter mortality of bluegill in one out of three lakes and several hatchery ponds. Santucci and Wahl (2003) found little evidence for size-selective overwinter mortality of bluegill although they documented high overall mortality through the first winter. Size-selective mortality of yellow perch may have occurred in the winter of 2007/2008. Overwinter

size-selective mortality has been documented experimentally for yellow perch (Johnson and Evans 1989) and in two lakes in Ontario (Post and Prankevicius 1987; Post and Evans 1989). Size-selective overwinter mortality may not be ubiquitous to bluegill and yellow perch in Nebraska Sandhills lakes. Relatively severe winters did not occur over the course of my study.

Vegetation coverage in Pelican Lake was higher (range 40-57%) than that previously reported (i.e., 36%, Paukert and Willis 2000). Although higher vegetation coverage in lakes may lead to higher panfish abundance (Lucchesi 1991; Hinch and Collins 1993) and relatively lower numbers of larger fish (Colle et al. 1987), Paukert et al. (2002b) reported that vegetation coverage was not linked to panfish quality in Nebraska Sandhills lakes. Schneider (1999) also suggested that increased submergent vegetation may not be detrimental to Michigan bluegill populations when harvest is low (1-3% exploitation) and there is an adequate food supply, which may be the situation in Nebraska Sandhills lakes (Paukert 2001).

My study provides some of the first system-wide information on the dynamics of age-0 bluegill and yellow perch. The baseline environmental dataset paired with the abundance and growth indices of the different life stages will continue to be assembled (n = 10 years). As more data are available, the effects of specific abiotic and biotic variables on recruitment may be identified. My exploratory analyses indicated that temperature, winter severity, and growth rates may affect survival and ultimate recruitment to the adult population.

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Table 4-1. Mean catch per unit effort (CPUE; number per trap night) and associated standard errors, N for bluegill and yellow perch sampled with cloverleaf traps in Pelican and Cameron Lakes, 2004-2008.

Lake	Species	Year	Season	Mean CPUE
Pelican	Bluegill	2004	Fall	52 (21, 6)
		2005	Spring	11 (1, 60)
			Fall	44 (11, 16)
		2006	Spring	0 (0, 65)
			Fall	83 (16, 26)
		2007	Spring	35 (7, 26)
			Fall	9 (2, 26)
	2008	Spring	0.5 (0.1, 99)	
	Yellow perch	2004	Fall	26 (5, 23)
		2005	Spring	1 (0.2, 60)
			Fall	3 (1, 16)
		2006	Spring	0 (0, 65)
			Fall	17 (3, 26)
		2007	Spring	17 (3, 26)
Fall			25 (5, 26)	
2008	Spring	39 (15, 99)		
Cameron	Yellow perch	2004	Fall	4 (1, 14)
		2005	Spring	0 (0, 12)
			Fall	0 (0, 16)
		2006	Spring	3 (0.5, 36)

Table 4-2. Mean total length and associated standard errors, N of bluegill and yellow perch sampled with cloverleaf traps in Pelican and Cameron Lakes, 2004-2008. Results of fall to spring comparisons of mean TL are given by *t* statistic, degrees of freedom (*df*), and *P* value.

Lake	Species	Year	Season	Mean TL	CV	<i>t</i>	<i>df</i>	<i>P</i>	
Pelican	Bluegill	2004	Fall	29 (0.1, 508)	11	-32.6	1,159	<0.0001	
		2005	Spring	36 (0.2, 668)	13				
			Fall	31 (0.1, 705)	11	-	-	-	
		2006	Spring	-	-	-	-	-	
			Fall	35 (0.1, 1983)	15	-16.7	1,509	<0.0001	
		2007	Spring	38 (0.2, 857)	15				
		Fall	32 (0.3, 184)	12	-4.4	206	<0.0001		
	2008	Spring	36 (0.9, 24)	13					
		Yellow perch	2004	Fall	45 (0.2, 564)	11	-43.6	134	<0.0001
	2005		Spring	73 (0.6, 108)	9				
			Fall	49 (0.2, 51)	3	-	-	-	
	2006		Spring	-	-	-	-	-	
	Fall		62 (0.4, 433)	12	-2.1	862	0.04		
2007	Spring		63 (0.3, 431)	11					
	Fall	61 (0.2, 555)	9	-24.6	1,999	<0.0001			
2008	Spring	67 (0.1, 1446)	8						
Cameron	Yellow perch	2004	Fall	54 (0.4, 104)	8	-	-	-	
		2005	Spring	-	-	-	-	-	
			Fall	-	-	-	-	-	
		2006	Spring	86 (1, 12)	4	-	-	-	

Table 4-3. Mean density (number/L) and associated standard errors of zooplankton taxa by month in Pelican Lake, Nebraska, 2004-2007. Mean density in columns followed by different letters were significantly different (within months, among years; $P < 0.05$); those without letters were not different.

Year	Month	<i>Bosmina</i>	Copepoda	Cladocera	Copepod nauplii	Rotifera	Total
2004	May	1.2 ^c	22.1 ^b	64.1	6.5 ^c	12.9	116.1 ^c
		(0.1)	(4.7)	(11.7)	(1.7)	(10.5)	(16.6)
2005		60.4 ^b	16.3 ^a	256.8	24.4 ^{ab}	12.8	384.4 ^a
		(10.0)	(3.2)	(28.3)	(5.1)	(3.9)	(44.3)
2006		1.1 ^c	20.1 ^b	42.2	37 ^a	2.9	109.6 ^c
		(0.1)	(2.4)	(4.8)	(5.4)	(0.5)	(9.2)
2007		107.3 ^a	15.7 ^b	88.5	17.1 ^{bc}	2.2	240.6 ^b
		(14.1)	(2.0)	(7.6)	(2.4)	(0.3)	(21.6)
2004	June	1.1 ^b	21.8	4.7 ^b	19.7 ^a	235.0 ^a	306.0 ^a
		(0.1)	(4.6)	(0.8)	(3.8)	(64.7)	(64.9)
2005		3.3 ^b	14.1	57.4 ^b	8.4 ^b	4.2 ^b	97.7 ^b
		(0.6)	(1.3)	(6.9)	(1.1)	(0.8)	(7.8)
2006		26 ^b	24.7	9.6 ^b	21.8 ^a	184.7 ^a	288.6 ^a
		(6.3)	(4.1)	(1.4)	(3.0)	(27.4)	(31.6)
2007		181.5 ^a	22.9	157.8 ^a	26.7 ^{ba}	19.0 ^b	423.9 ^a
		(31.2)	(2.7)	(25.1)	(3.3)	(5.5)	(61.4)
2004	July	278.9 ^b	43.8 ^a	60.1 ^b	28.8 ^b	150.6 ^a	593.4 ^b
		(65.9)	(5.7)	(11.5)	(4.2)	(19.5)	(87.9)
2005		18.1 ^b	13.9 ^b	94.6 ^b	10.8 ^b	1.3 ^b	140.0 ^b
		(2.6)	(1.8)	(7.0)	(2.6)	(0.1)	(9.2)
2006		1,907.5 ^a	46.8 ^a	255.9 ^b	83.9 ^a	204.7 ^a	2,548.4 ^a
		(316.4)	(7.5)	(50.2)	(10.1)	(45.3)	(365.8)
2007		353.2 ^b	50.7 ^a	1,363.1 ^a	67.8 ^a	43.6 ^b	1,901.1 ^a
		(37.7)	(6.5)	(274.3)	(7.3)	(10.2)	(294.0)
2004	August	753.0 ^a	48.6 ^a	175.7 ^b	56.8 ^a	44.0 ^b	1,101.3 ^b
		(100.2)	(3.5)	(14.1)	(4.0)	(8.7)	(102.2)
2005		92.6 ^b	11.7 ^b	180.4 ^b	7.6 ^c	1.0 ^b	292.2 ^c
		(8.4)	(1.2)	(16.8)	(1.2)	(0.0)	(20.4)
2006		687.4 ^a	33.5 ^a	165.7 ^b	25.9 ^b	4.5 ^b	942.8 ^b
		(140.8)	(5.0)	(16.3)	(5.3)	(1.3)	(143.4)
2007		404 ^{ab}	39.6 ^a	1,015.1 ^a	38.9 ^b	144.5 ^a	1,658.0 ^a
		(64.6)	(7.4)	(70.0)	(5.2)	(38.6)	(113.0)

Table 4-4. Mean density (number/L) and associated standard errors of zooplankton taxa by month in Cameron Lake, Nebraska, 2004-2005. Mean density in columns followed by the same letter were significantly different (within months, among years; $P < 0.05$); those without letters were not different.

Year	Month	<i>Bosmina</i>	Copepoda	Cladocera	Copepod nauplii	Rotifera	Total
2004	May	151.7 ^a (13.0)	37.3 ^b (4.6)	1,155.5 ^a (114.3)	22.9 ^b (4.7)	69.4 (18.0)	1,440.3 ^a (139.3)
2005		4.9 ^b (1.2)	75.1 ^a (11.4)	550.8 ^b (58.9)	57.6 ^a (6.3)	61.1 (12.3)	758.8 ^b (78.5)
2004	June	14.1 (2.6)	20.4 ^b (4.1)	233.0 ^b (35.3)	16.3 (1.8)	45.7 (5.6)	330.9 ^b (40.2)
2005		19.2 (3.0)	78.3 ^a (7.7)	497.9 ^a (51.1)	16.7 (3.0)	51.1 (10.2)	666.1 ^a (71.5)

Table 4-5. Mean density (number/m²) and associated standard errors of macroinvertebrate taxa by month in Pelican Lake, Nebraska, 2004-2007. Mean density in columns followed by the same letter were significantly different (within months, among years; $P < 0.05$); those without letters were not different.

Year	Month	Order Ephemeroptera	Order Odonata	Order Amphipoda	Class Hirudinea	Class Gastropoda	Class Oligochaeta	Family Chironomidae	Other	Total
2004	May	8.3	2.1	26.9	28.0	0.0	1,012.5a	671.9	228.8a	1963.9
		(4.4)	(1.4)	(22.8)	(14.9)	(0.0)	(188.2)	(72.6)	(61.5)	(265.0)
2005		3.6	2.2	60.1	72.5	31.9	134.8b	949.9	27.5b	1274.0
		(2.4)	(1.6)	(20.0)	(24.4)	(20.8)	(30.9)	(149.5)	(9.7)	(152.3)
2006		8.0	2.2	47.8	39.1	2.2	515.2b	1107.3	23.2b	1742.8
		(4.6)	(1.6)	(23.8)	(9.5)	(1.2)	(114.6)	(149.1)	(7.7)	(223.3)
2007		2.2	0.0	5.1	32.6	2.9	258b	910.2	68.1b	1271.1
		(1.2)	(0.0)	(2.3)	(12.3)	(2.7)	(64.8)	(148.3)	(18.2)	(184.4)
2004	June	5.0	0.8	92.9	77.5	3.9	750.2a	1,582.6a	256.4a	2,710.5a
		(2.8)	(0.8)	(62.7)	(14.9)	(2.0)	(171.9)	(308.8)	(68.9)	(339.3)
2005		4.0	3.4	44.6	87.5	4.0	97.3b	513.8b	6.9b	759.8b
		(2.5)	(2.1)	(13.8)	(25.5)	(2.4)	(22.7)	(111.2)	(2.3)	(118.4)
2006		2.9	2.2	135.5	76.8	3.6	79.0b	701.5b	46.4b	1,043.5b
		(1.4)	(1.2)	(37.8)	(20.5)	(2.1)	(20.3)	(132.7)	(9.8)	(174.1)
2007		10.1	0.0	45.7	120.3	1.4	166.7b	697.9b	63.0b	1,092.8b
		(6.7)	(0.0)	(30.0)	(28.6)	(1.0)	(60.2)	(141.0)	(12.4)	(171.4)
2004	July	13.0	0.0	368.1	166.7	3.6	226.1	1,191.4a	52.2ab	2,012.4a
		(11.0)	(0.0)	(284.5)	(44.4)	(1.8)	(62.1)	(195.5)	(20.8)	(417.8)
2005		4.3	0.0	54.4	46.7	0.0	141.3	1,410.9a	2.2b	1,659.9ab
		(3.0)	(0.0)	(32.6)	(16.0)	(0.0)	(28.5)	(235.5)	(2.2)	(261.2)
2006		0.0	1.1	30.4	109.8	3.3	81.5	280.5b	21.7ab	529.4b
		(0.0)	(1.1)	(24.2)	(41.6)	(1.8)	(21.0)	(56.1)	(8.3)	(90.5)
2007		0.7	2.9	5.8	34.1	0.7	210.2	360.9b	73.2a	680.5b
		(0.7)	(2.9)	(5.1)	(9.2)	(0.7)	(61.4)	(52.4)	(14.2)	(104.9)

Table 4-5 continued.

Year	Month	Order Ephemeroptera	Order Odonata	Order Amphipoda	Class Hirudinea	Class Gastropoda	Class Oligochaeta	Family Chironomidae	Other	Total
2004	August	23.3 (22.5)	6.2 (4.0)	15.5 (9.7)	82.3 (28.9)	6.2 (4.2)	168.5 (22.2)	485.3b (75.8)	70.7b (25.6)	844.8ab (134.5)
2005		1.4 (1.0)	5.1 (5.1)	165.2 (151.1)	113.8 (25.8)	1.4 (1.0)	108.0 (20.9)	953.7a (163.2)	29.7b (7.8)	1,365.3a (227.4)
2006		1.1 (1.1)	0.0 (0.0)	10.9 (10.9)	46.7 (12.0)	1.1 (1.1)	80.4 (19.7)	331.5b (76.2)	18.5b (6.6)	490.2b (85.1)
2007		0.0 (0.0)	8.7 (7.6)	0.0 (0.0)	30.4 (17.5)	0.0 (0.0)	130.4 (27.4)	168.5b (72.3)	282.6a (123.7)	600.0b (161.3)

Table 4-6. Mean density (number/m²) and associated standard errors of macroinvertebrate taxa by month in Cameron Lake, Nebraska, 2004-2005. Mean density in columns followed by the same letter were significantly different (within months, among years; $P < 0.05$); those without letters were not different.

Year	Month	Order Ephemeroptera	Order Odonata	Order Amphipoda	Class Hirudinea	Class Oligochaeta	Family Chironomidae	Other	Total
2004	May	1.0	0.0	1.0	1.0	2,152.3 ^a	898.6 ^a	369.6 ^a	3,299.3 ^a
		(1.0)	(0.0)	(1.0)	(1.0)	(259.9)	(135.0)	(80.4)	(351.3)
2005		0.0	0.0	6.8	0.0	818.0 ^b	388.6 ^b	111.4 ^b	1,270.4 ^b
		(0.0)	(0.0)	(6.8)	(0.0)	(110.2)	(58.2)	(35.2)	(137.0)
2004	June	0.0	2.7	2.7	2.7	1,728.3 ^a	394.0	347.8 ^a	2,320.8
		(0.0)	(2.7)	(2.7)	(2.7)	(337.1)	(140.7)	(74.7)	(442.0)
2005		0.0	0.0	0.0	0.0	584.3 ^b	652.2	54.5 ^b	1,263.6
		(0.0)	(0.0)	(0.0)	(0.0)	(106.9)	(117.2)	(48.4)	(164.4)

Table 4-7. Percent vegetation coverage by type, and mean and maximum water depths in Pelican Lake and Cameron Lake, Nebraska, 2004-2007.

Lake	Year	N	Total vegetation	Sparse emergent	Moderate emergent	Dense emergent	Sparse submergent	Moderate submergent	Dense submergent	Mean depth (cm)	Maximum depth (cm)
Pelican	2004	132	40.2	2.3	0.8	4.5	0.0	21.2	11.4	117.1	221.0
	2005	85	51.8	5.9	9.4	8.2	8.2	8.2	11.8	143.7	210.0
	2006	89	53.9	14.6	9.0	10.1	5.6	7.9	6.7	120.1	245.0
	2007	79	57.0	5.1	10.1	31.6	1.3	0.0	8.9	123.3	236.0
Cameron	2004	20	15.0	0.0	0.0	15.0	0.0	0.0	0.0	83.2	110.0
	2005	30	16.7	0.0	0.0	16.7	0.0	0.0	0.0	84.4	124.0

Table 4-8. Eigenvalues, proportion of variance explained, and cumulative variance explained by principal components (PC) analyses for independent variables measured in Pelican Lake, Nebraska from 2004 to 2007. Components were separated into benthic macroinvertebrate, zooplankton, climate, habitat, and physicochemical categories.

Component	PC	Eigenvalue	Difference	Variance	
				Proportion explained	Cumulative
Benthic macroinvertebrates	1	10.203	3.827	0.510	0.510
	2	6.376	2.955	0.319	0.820
Zooplankton	1	11.752	3.225	0.490	0.490
	2	8.527	4.806	0.355	0.845
Climate	1	10.240	4.051	0.488	0.488
	2	6.189	1.617	0.295	0.782
Habitat	1	5.653	3.660	0.628	0.628
	2	1.993	0.638	0.221	0.850
Physicochemical	1	11.565	3.772	0.578	0.578
	2	7.793	7.150	0.390	0.968

Table 4-9. Results of factor analysis (i.e., principal components analysis [PCA] with varimax rotation) of independent variables measured in Pelican Lake, Nebraska from 2004 to 2007. Factor scores with a “*” were those selected for the factor (loadings greater than 40). Variables that loaded (greater than 40) on more than one factor were omitted in interpretation.

Component	Variable	PC 1	PC 2
Benthic macroinvertebrates	May chironomid density	-96*	-23
	June chironomid density	95*	-11
	July chironomid density	37	93*
	August chironomid density	-13	97*
	August hirudinean density	11	96*
	June oligochaete density	98*	4
	August oligochaete density	96*	10
	May other density	99*	-1
	June other density	96*	-13
	June total density	96*	-9
Zooplankton	August total density	-1	99*
	June <i>Bosmina</i> density	12	97*
	August <i>Bosmina</i> density	92*	-30
	August copepod density	99*	16
	June cladoceran density	-21	98*
	July cladoceran density	11	97*
	August cladoceran density	10	99*
	August nauplii density	95*	13
	August rotifer density	34	93*
	May total density	-90*	27
Climate	April air temperature	11	-98*
	July air temperature	98*	21
	August air temperature	-21	92*
	March wind	100*	4
	April wind	99*	8
	May wind	99*	12
	June wind	100*	5
	July wind	99*	7
August wind	100*	0	
	Total annual precipitation	16	92*

Table 4-9 continued

Component	Variable	PC 1	PC 2
Habitat	May water temperature	12	99*
	Total vegetation coverage	93*	34
Physicochemical	June Secchi depth	98*	-18
	July Secchi depth	98*	11
	August Secchi depth	96*	-27
	May conductivity	23	97*
	August conductivity	99*	-12
	May total dissolved solids	19	98*
	August total dissolved solids	96*	-27
	May alkalinity	12	99*
	June alkalinity	2	94*
	May pH	-95*	-30
	June pH	-95*	24
	July pH	-98*	-11
	August pH	-96*	6

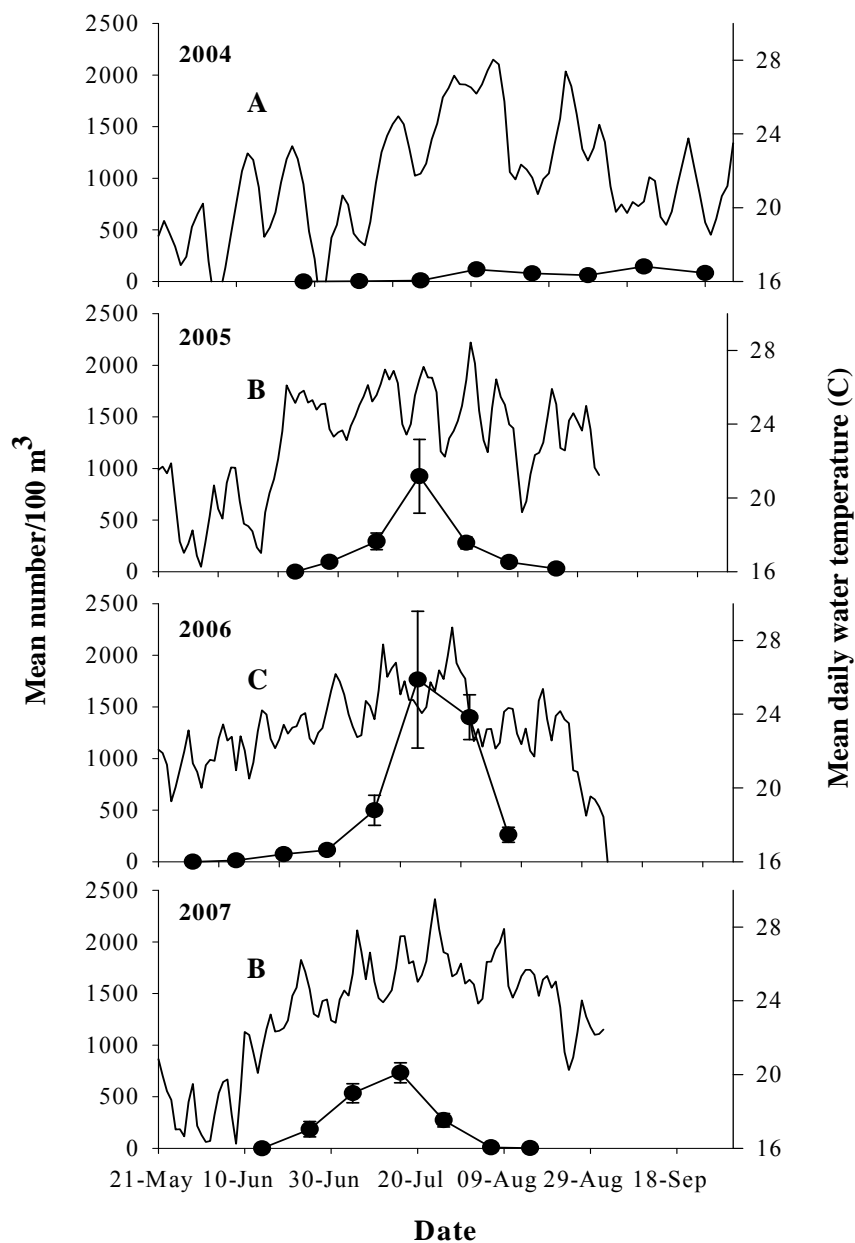


Figure 4-1. Mean larval bluegill density (\pm SE) and mean daily water temperature (C) in Pelican Lake, Nebraska from 2004 to 2007. Panels with different letters had significantly different peak densities ($\alpha = 0.05$).

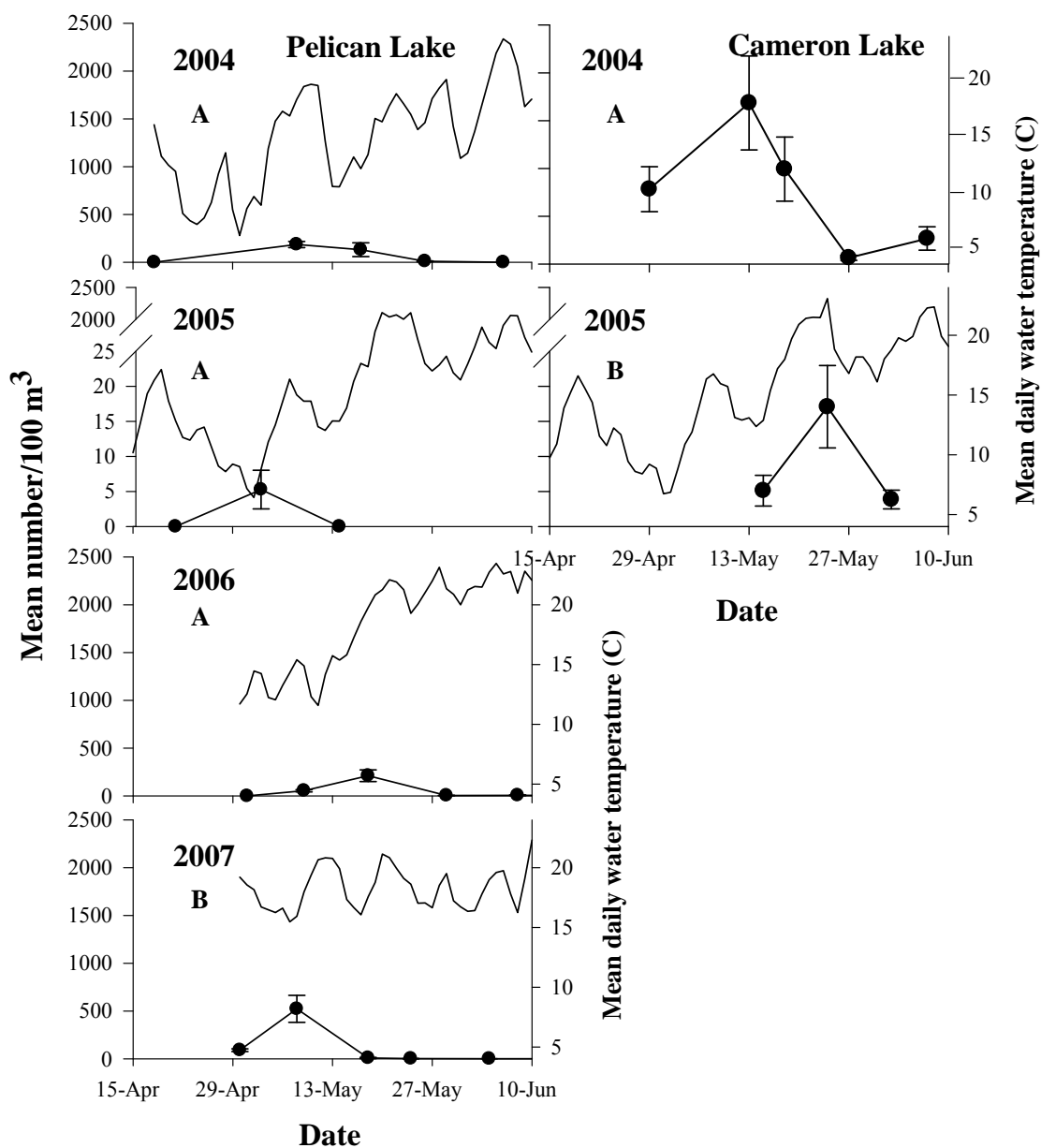


Figure 4-2. Mean larval yellow perch density (\pm SE) and mean daily water temperature (C) in Pelican Lake and Cameron Lake, Nebraska from 2004 to 2007. Panels with different letters within lakes had significantly different peak densities ($\alpha = 0.05$). The temperature logger was not recovered in Cameron Lake in 2004.

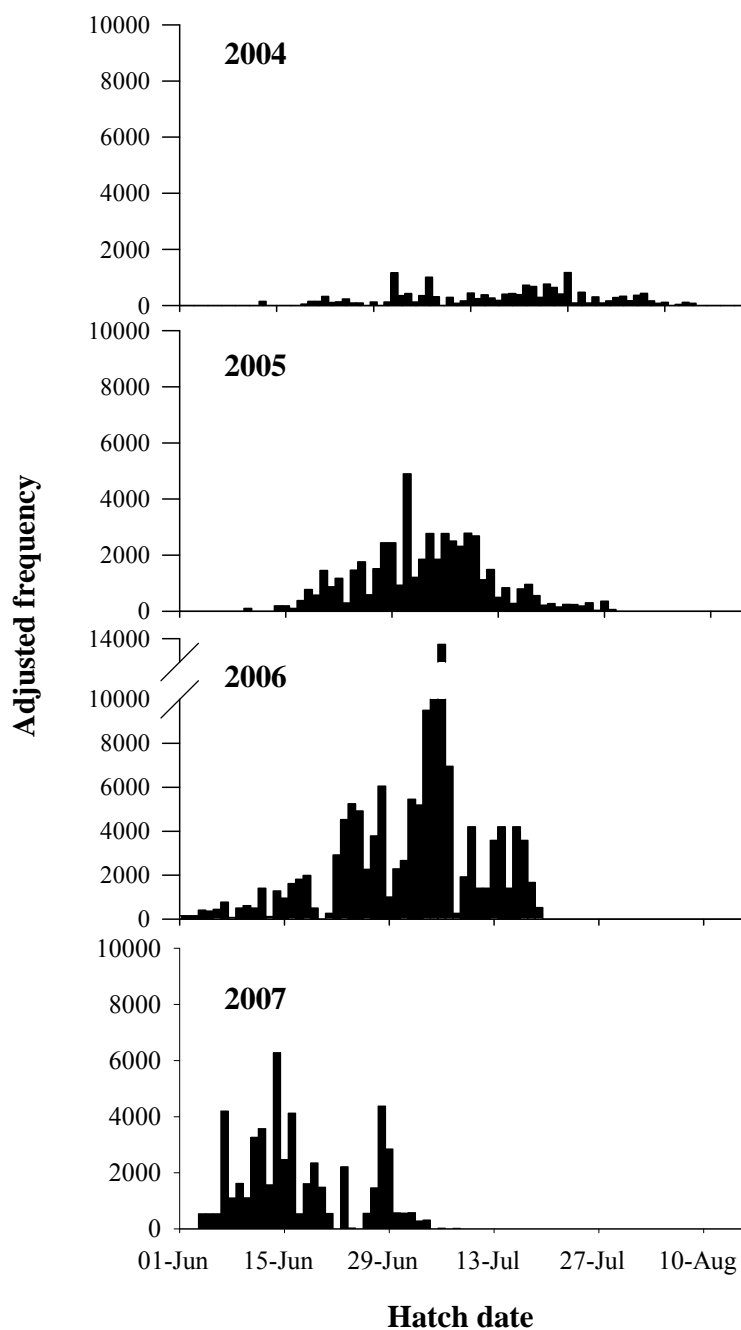


Figure 4-3. Bluegill hatch date frequency in Pelican Lake, Nebraska from 2004 to 2007. Bluegill hatch dates were weighted by corresponding larval abundances.

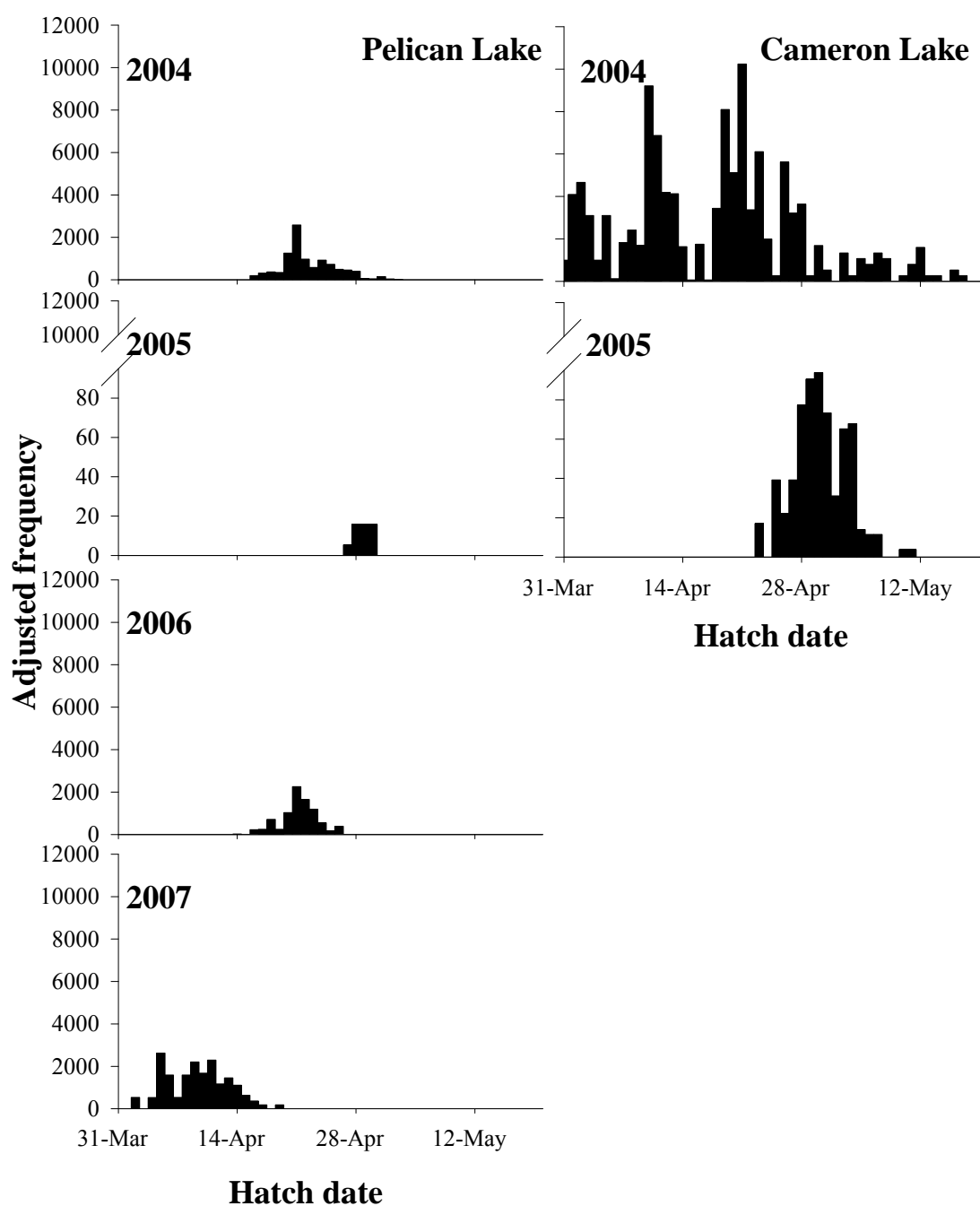


Figure 4-4. Yellow perch hatch date frequency in Pelican Lake and Cameron Lake, Nebraska from 2004 to 2007. Yellow perch hatch dates were weighted by corresponding larval abundances.

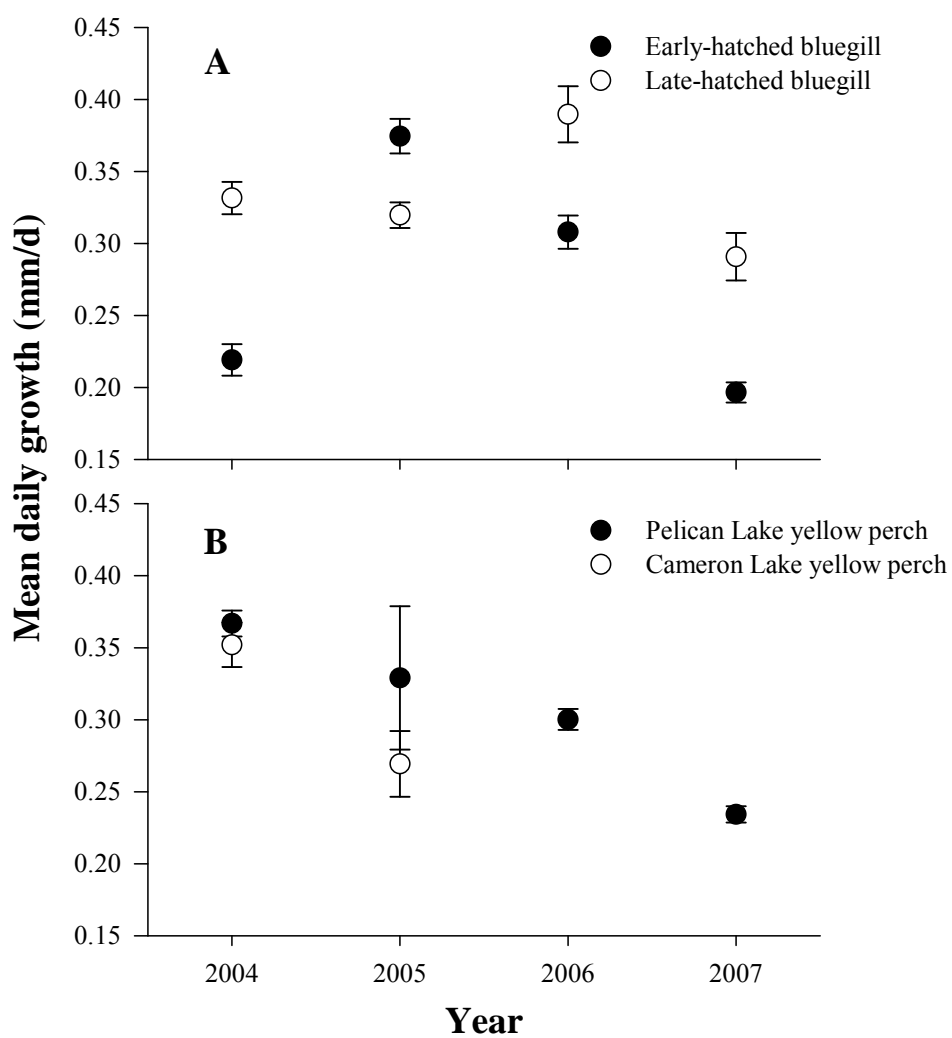


Figure 4-5. Mean daily growth rates mm/d of early- and late-hatched bluegill in Pelican Lake (A) and yellow perch in Pelican Lake and Cameron Lake, Nebraska (B) 2004-2007.

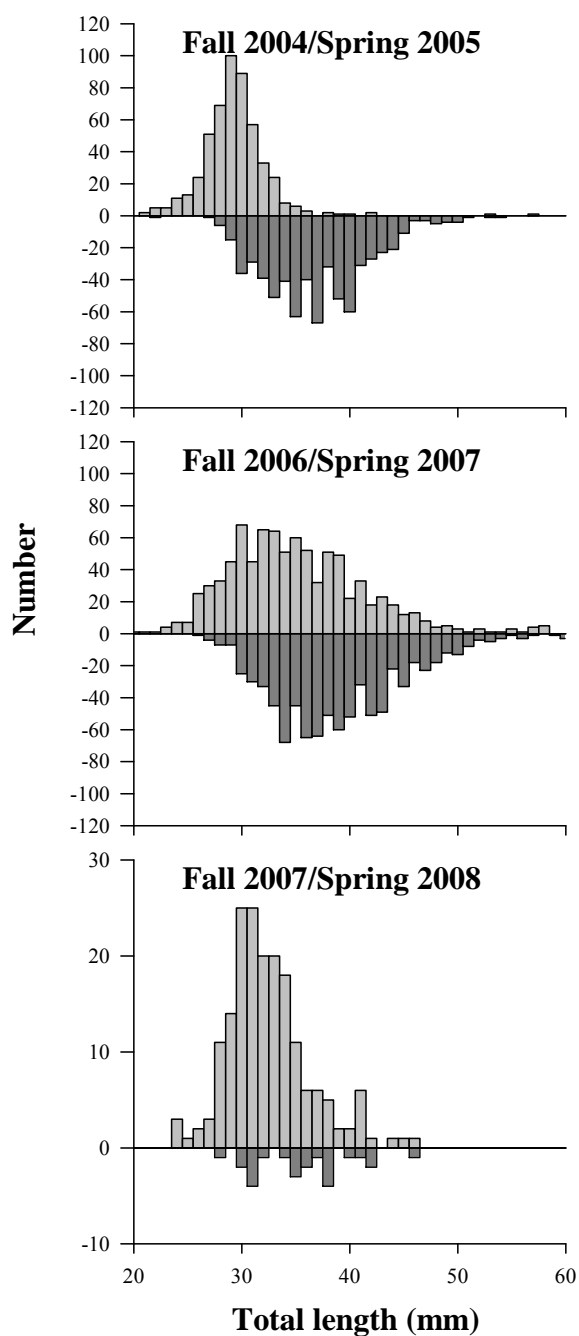


Figure 4-6. Fall and spring size distributions of bluegill from the 2004, 2006, and 2007 year classes captured in cloverleaf traps at Pelican Lake, Nebraska. Values above the x-axis are from the fall and values below the x-axis are from the following spring.

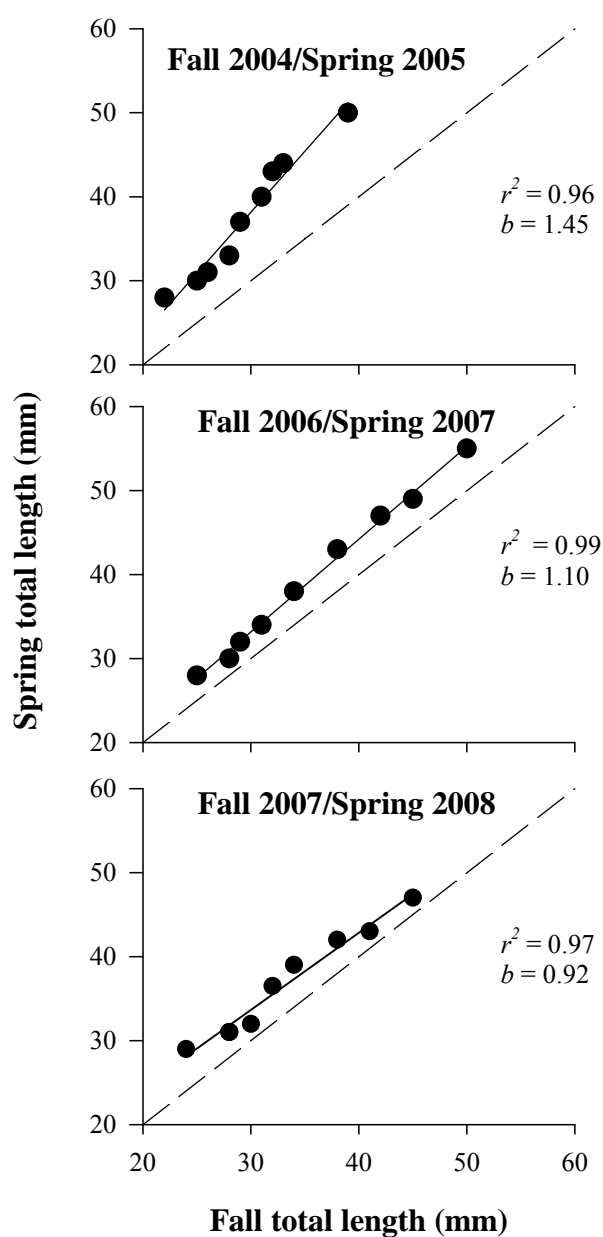


Figure 4-7. Empirical quantile-quantile plots of the length-frequency data for the 2004, 2006, and 2007 bluegill cohorts in Pelican Lake, Nebraska. The broken line is the 1:1 relationship and solid line is the least squares regression for each cohort. Coefficients of determination (r^2) and regression slopes (b) are indicated.

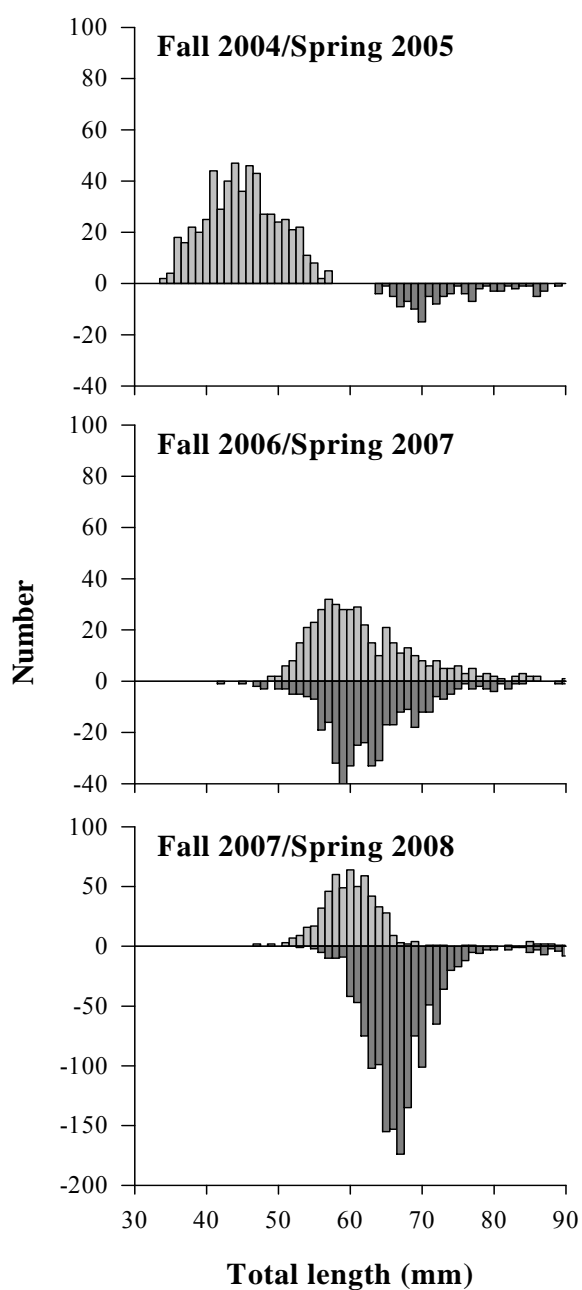


Figure 4-8. Fall and spring size distributions of yellow perch from the 2004, 2006, and 2007 year classes captured in cloverleaf traps from Pelican Lake, Nebraska. Values above the x-axis are from the fall and values below the x-axis are from the following spring.

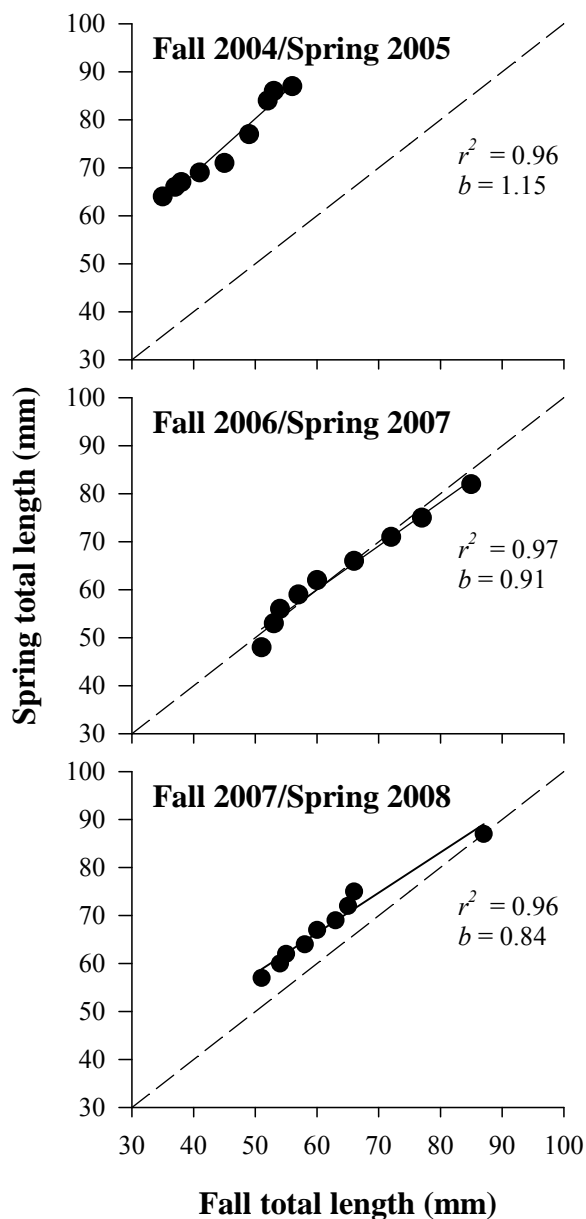


Figure 4-9. Empirical quantile-quantile plots of the length-frequency data for the 2004, 2006, and 2007 yellow perch cohorts in Pelican Lake, Nebraska. The broken line is the 1:1 relationship and solid line is the least squares regression for each cohort. Coefficients of determination (r^2) and regression slopes (b) are indicated.

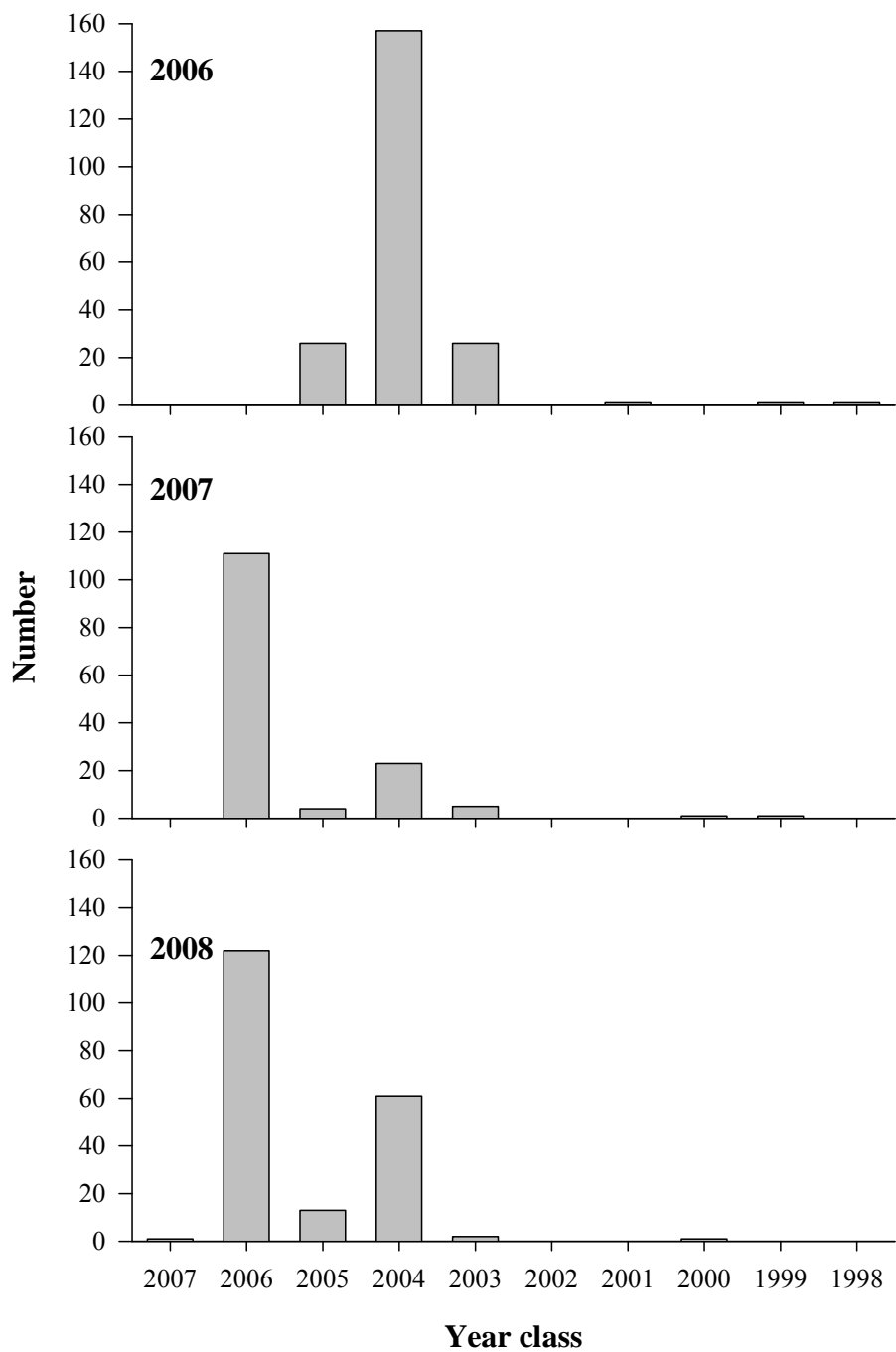


Figure 4-10. Age-frequency histograms of adult bluegill collected with modified-fyke nets from Pelican Lake, Nebraska collected in 2005-2008.

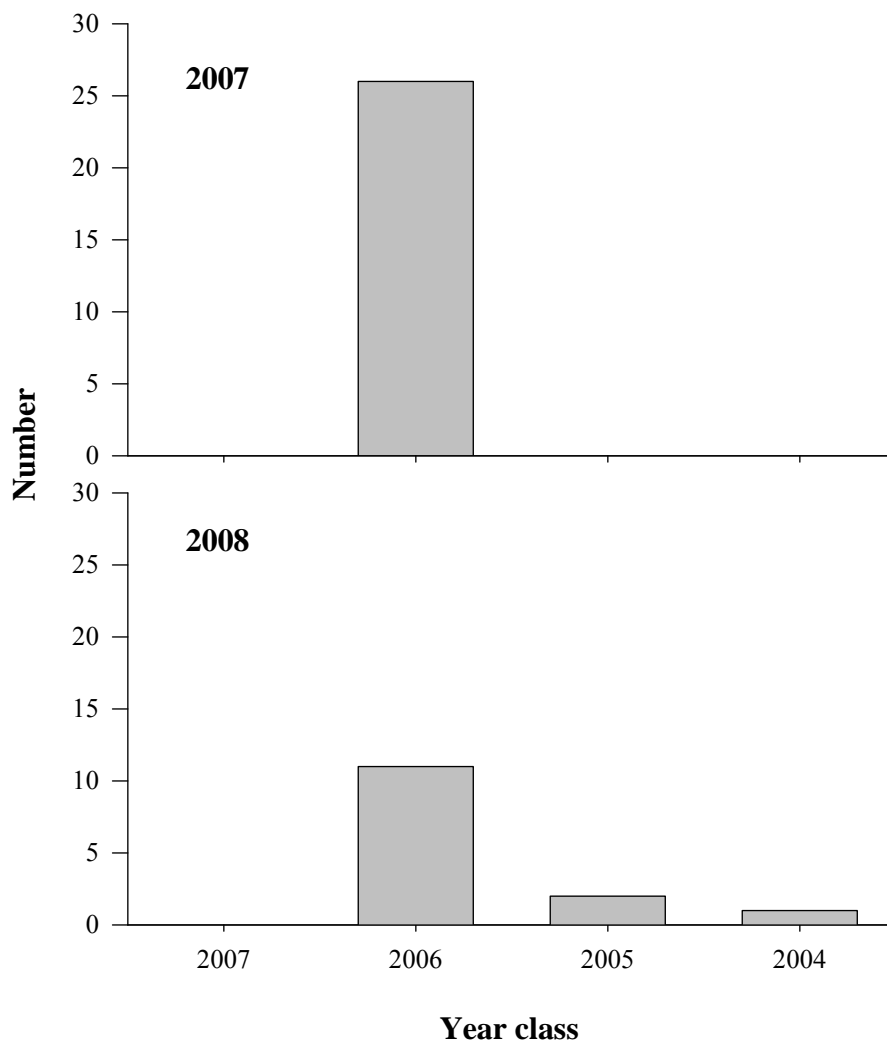


Figure 4-11. Age-frequency histograms of adult yellow perch collected with modified-fyke nets from Pelican Lake, Nebraska collected in 2005-2008.

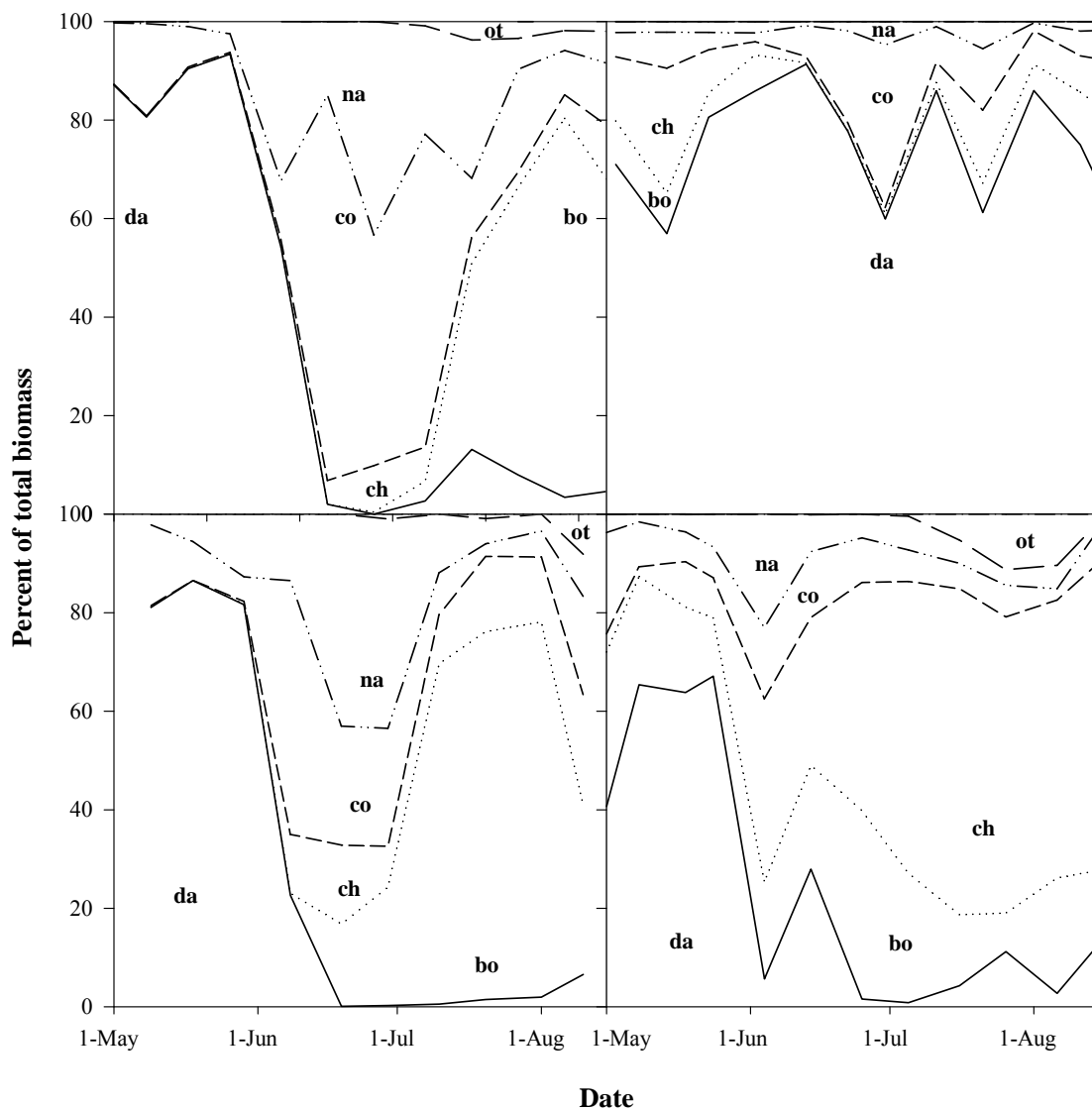


Figure 4-12. Percent of biomass for the zooplankton taxa in Pelican Lake, Nebraska, 2004-2007. Taxa are: da = daphnid (*Daphnia* and *Ceriodaphnia*), bo = *Bosmina*, ch = *Chydorus*, co = calanoid and cylopoid copepod, na = copepod nauplii, and ot = other zooplankton.

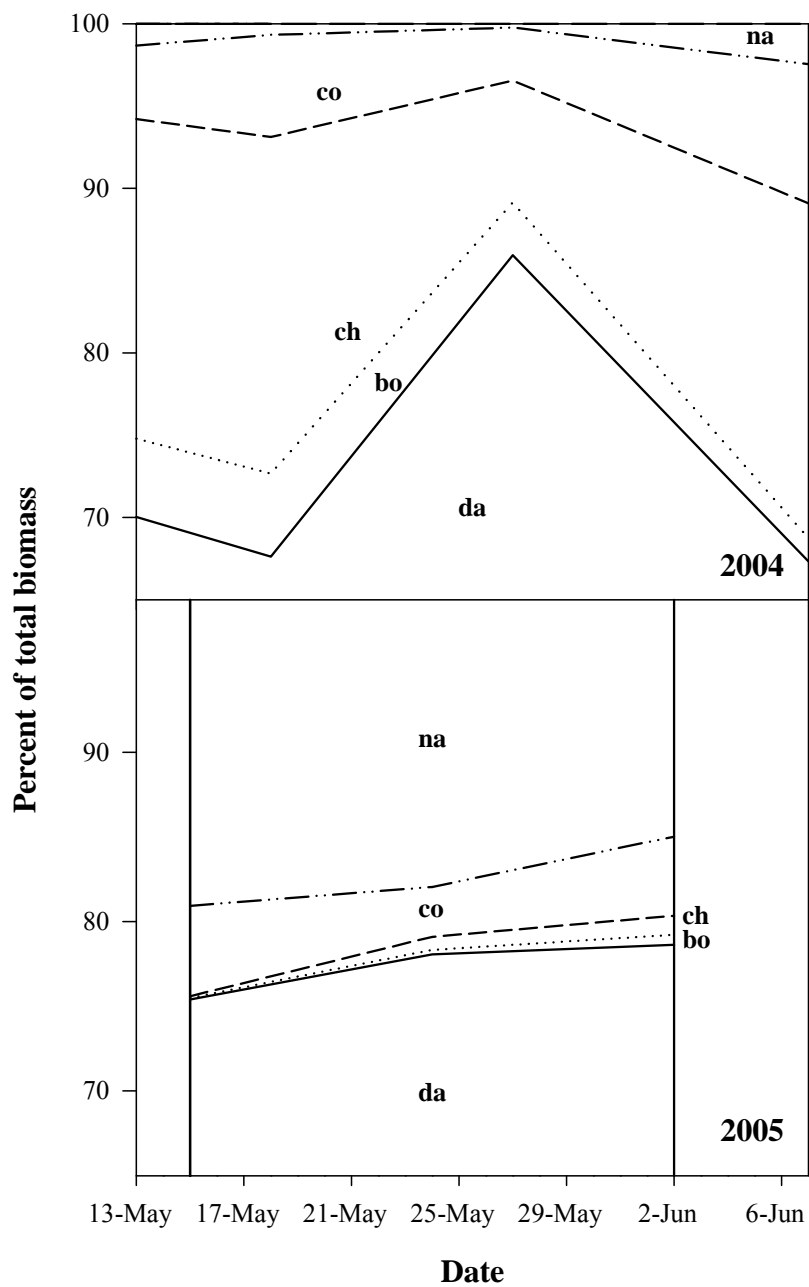


Figure 4-13. Percent of biomass for the zooplankton taxa in Cameron Lake, Nebraska, 2004-2005. Taxa are: da = daphnid (*Daphnia* and *Ceriodaphnia*), bo = *Bosmina*, ch = *Chydorus*, co = calanoid and cylopoid copepod, and na = copepod nauplii.

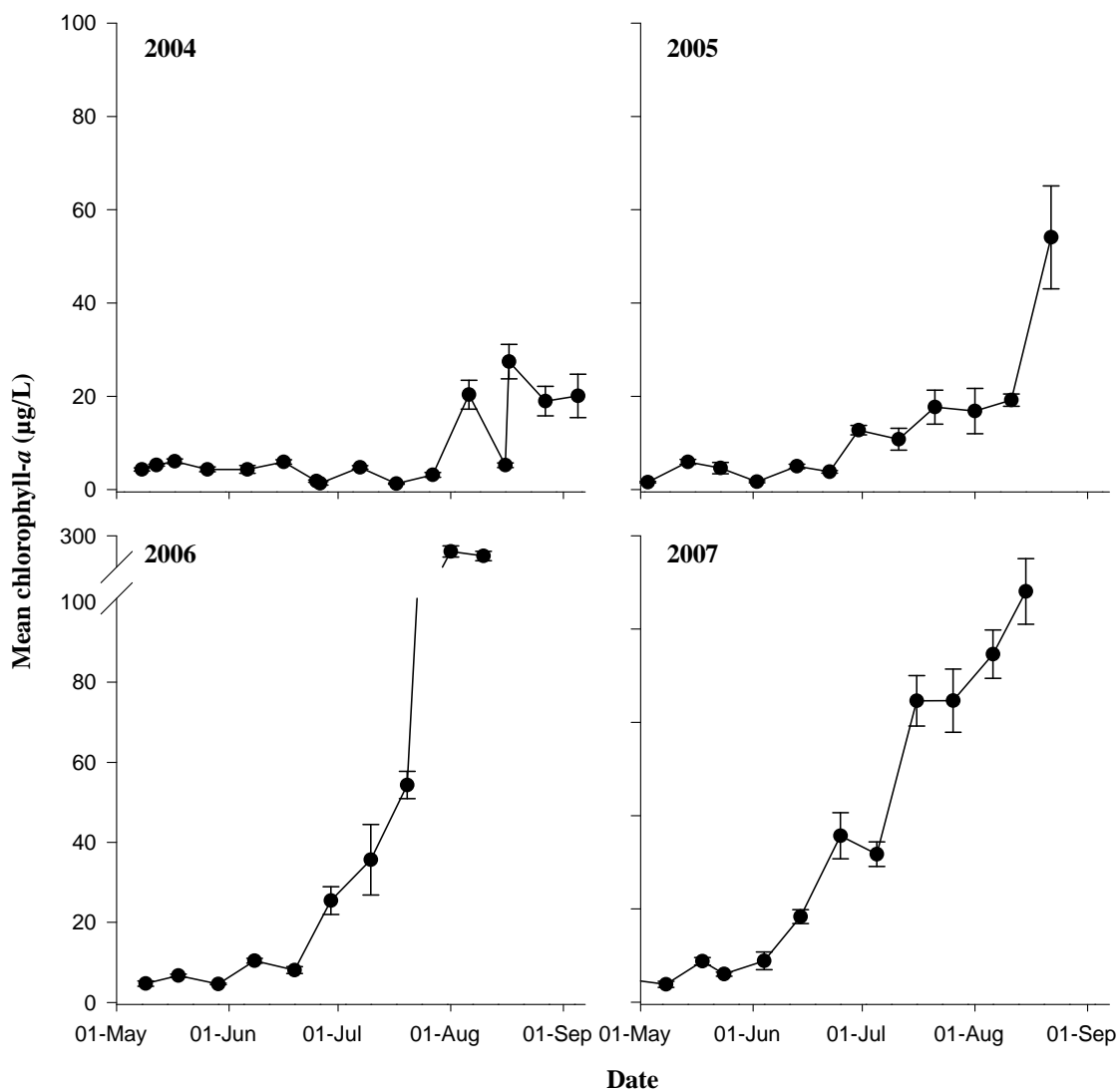


Figure 4-14. Mean (\pm SE) chlorophyll-*a* concentration ($\mu\text{g/L}$) from phytoplankton samples collected from Pelican Lake, Nebraska, 2004-2007.

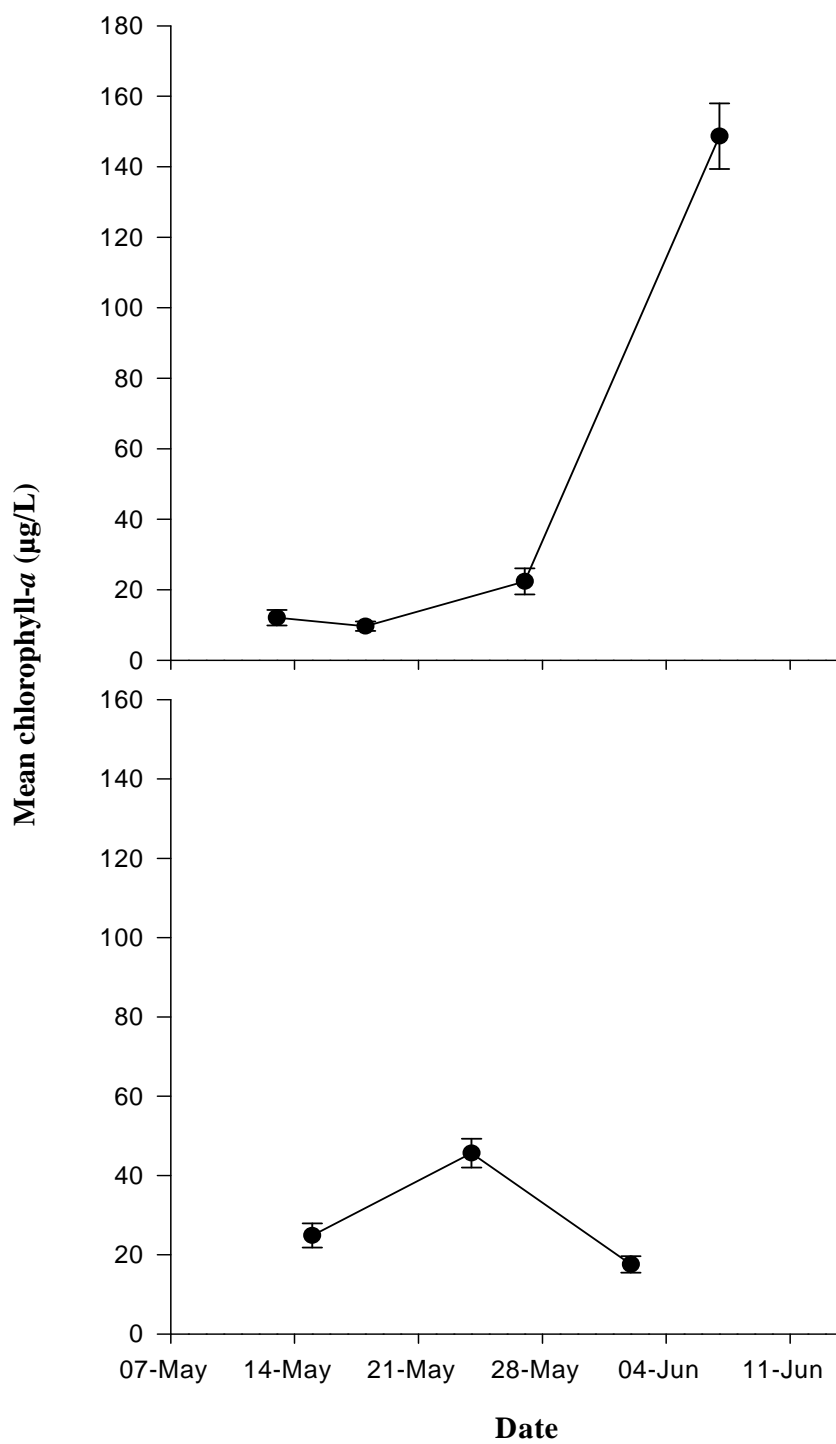


Figure 4-15. Mean (\pm SE) chlorophyll-*a* concentration ($\mu\text{g/L}$) from phytoplankton samples collected from Cameron Lake, Nebraska, 2004-2005.

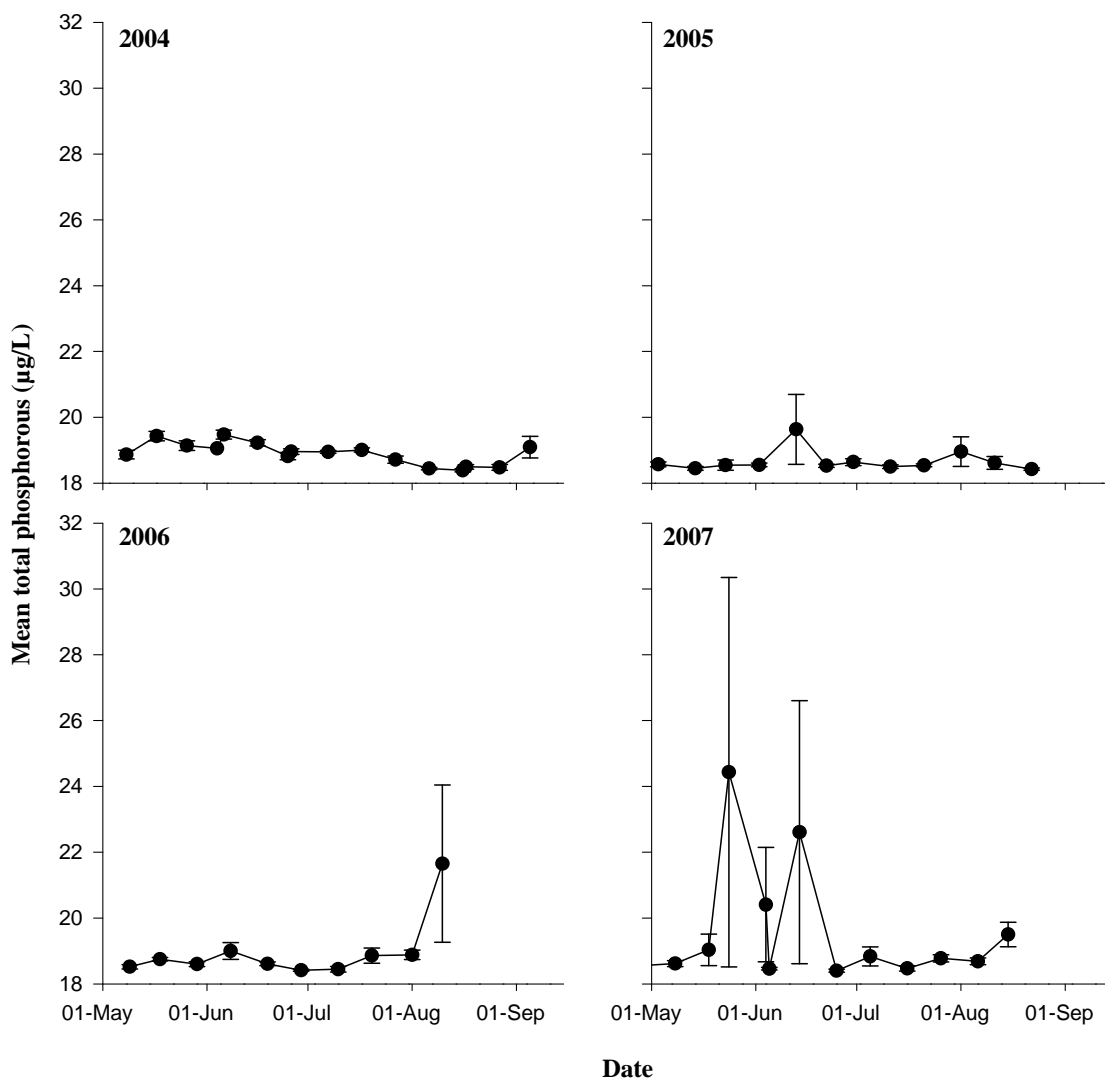


Figure 4-16. Mean (\pm SE) total phosphorous ($\mu\text{g/L}$) concentration for water samples collected from Pelican Lake, Nebraska, 2004-2007.

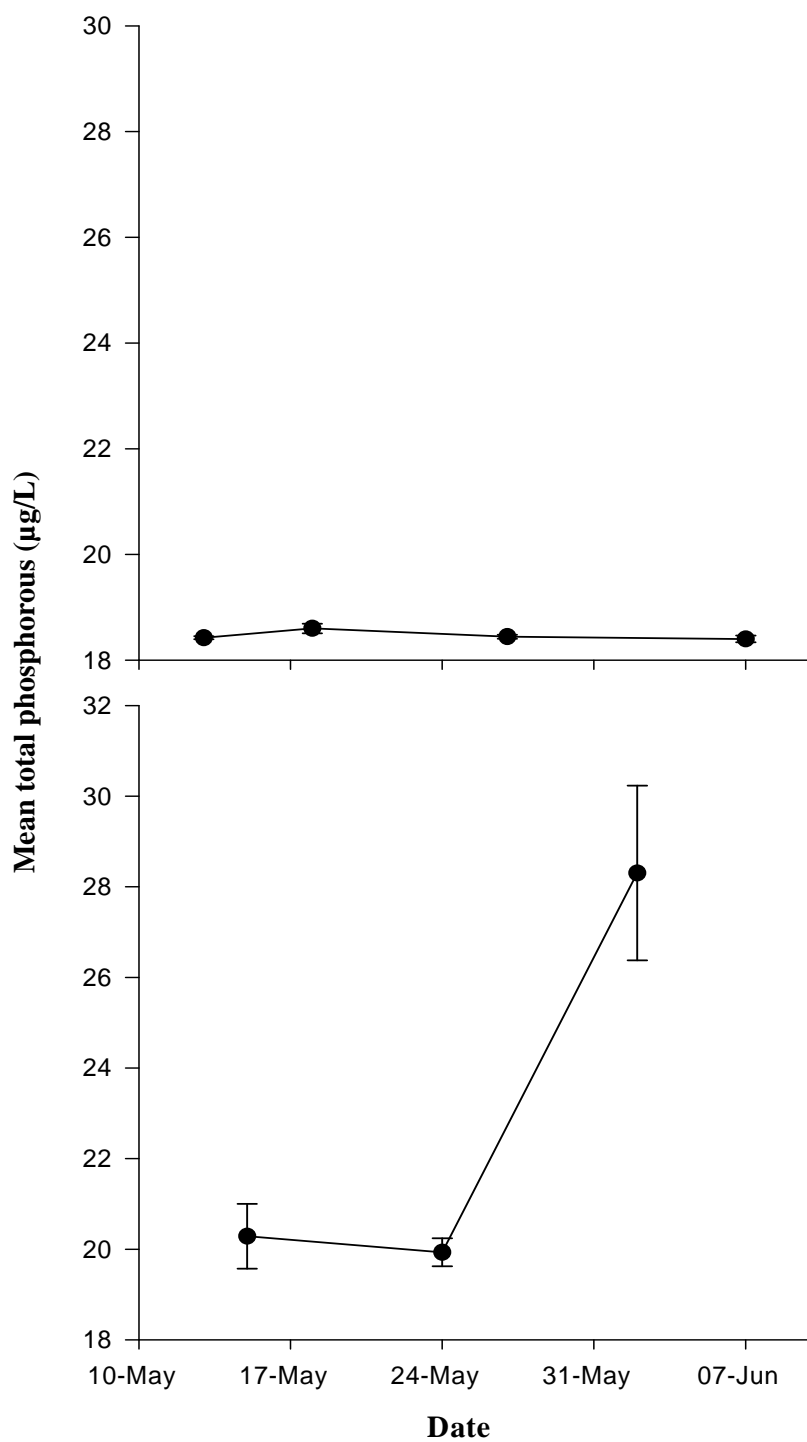


Figure 4-17. Mean (\pm SE) total phosphorous ($\mu\text{g/L}$) concentration for water samples collected from Cameron Lake, Nebraska, 2004-2005.

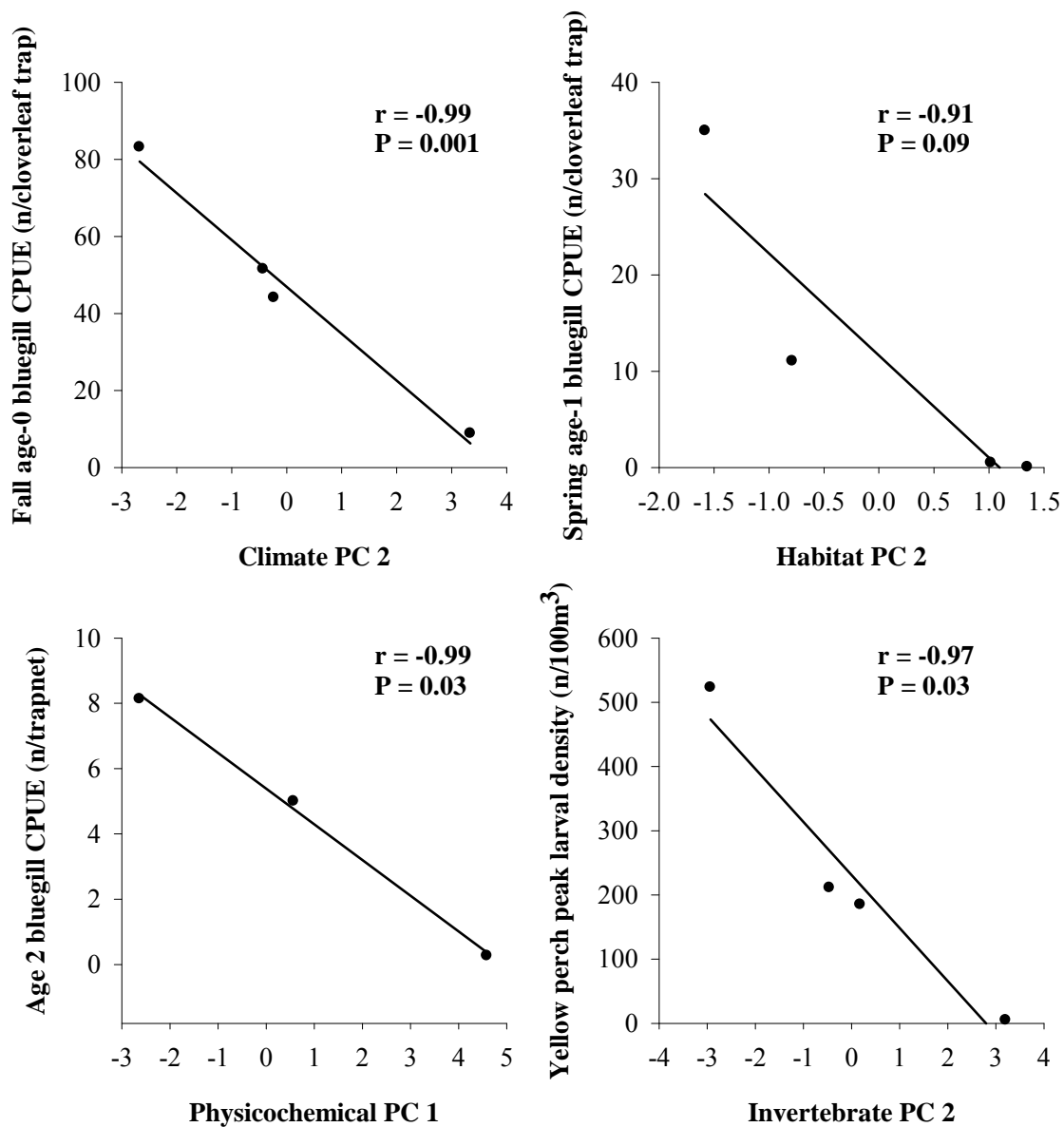


Figure 4-18. Correlations between selected bluegill and yellow perch abundance indices (mean catch per unit effort [CPUE]) and principal components (PC).

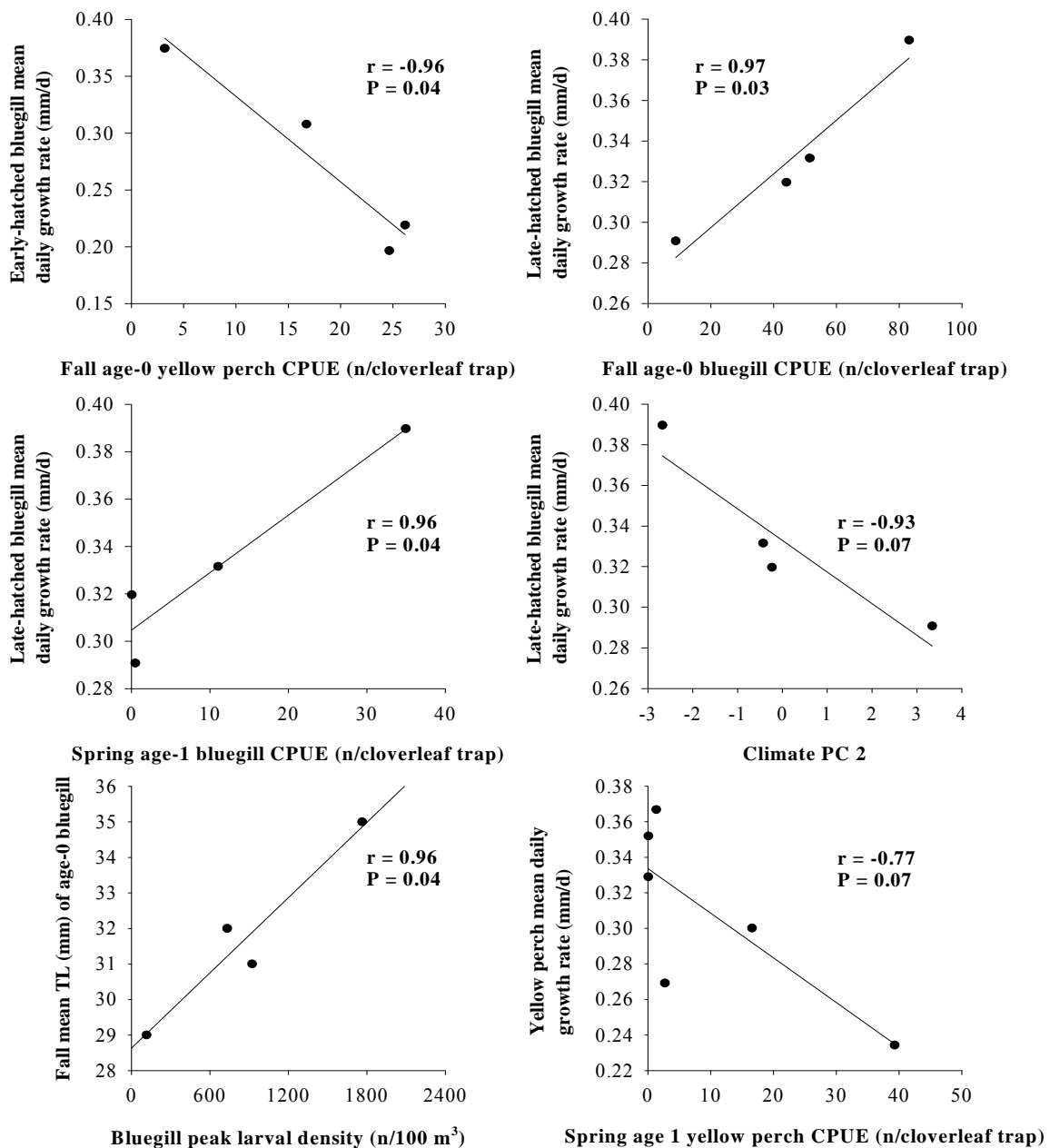


Figure 4-19. Correlations between selected bluegill and yellow perch growth indices, abundance indices, and principal components (PC). Hatch periods for bluegill are early (i.e., June) and late (i.e., July and August). Total length = TL.

Chapter 5.

Yellow perch food habits and extent of piscivory in West Long Lake, Nebraska

Yellow perch food habits and prey selection have been well-documented throughout its geographical range (Moffett and Hunt 1945; Keast 1977; Lott et al. 1996; Reed and Parsons 1996; Fullhart et al. 2002; Wilkens et al. 2002). Yellow perch undergo a size-mediated ontogenetic diet shift in their first year (Whiteside et al. 1985) from small-bodied zooplankters for first-feeding larvae, to comparatively larger zooplankters (Mills et al. 1989; Graeb et al. 2004), to benthic macroinvertebrates (Pycha and Smith 1955; Ney and Smith 1975), and eventually shifting to limited piscivory as they reach larger sizes (Keast 1985; Fullhart et al. 2002; Graeb et al. 2006). Yellow perch also engage in cannibalism (Clady 1974; Tarby 1974). Conversely, larger yellow perch are not obligate piscivores and may have high-quality populations with adequate availability of macroinvertebrates (Lott et al. 1996). Food habits vary temporally following the dynamics in availability of different prey taxa (Knight et al. 1994). Intense piscivory in a short time-period may influence recruitment of age-0 fishes. The effect of yellow perch predation on bluegill populations has been a topic of interest (Moffett and Hunt 1945; Anderson and Schupp 1986; Reed and Parsons 1996; Schneider and Breck 1997; Fullhart et al. 2002).

The food habits of intermediate sized yellow perch (TL 80-200 mm), have been examined infrequently, especially during the winter. Although Wilkens et al. (2002) documented the food habits of yellow perch in West Long Lake, Nebraska they did so

over the three open-water seasons and excluded the winter period. Predation on age-0 bluegill by yellow perch typically occurs during the winter (Moffett and Hunt 1943; Schneider and Breck 1997; Fullhart et al. 2002). Thus, the objective of my study was to describe the food habits of large (i.e., TL \geq 200 mm) and small (i.e., TL < 200 mm) yellow perch in West Long Lake, Nebraska.

Methods

West Long Lake is a 25-ha, shallow (mean depth = 1.3 m) natural lake in Cherry County of the Sandhills region of north central Nebraska (McCarragher 1977). Peak coverage of submergent and emergent vegetation combined was 92% in 2005 and 2006. The fish community was simple, composed primarily of yellow perch, bluegill, northern pike, largemouth bass, black bullhead, fathead minnow, and golden shiner. A detailed description of West Long Lake is provided in Table 2-1.

Yellow perch \geq 80 mm TL were collected quarterly (i.e., October, February, May, July) from West Long Lake from October 2005 to July 2006 to determine the food habits in that population. Fish were collected with experimental gill nets (six 7.6-m long panels of 13, 19, 25, 32, 38, and 51 mm bar meshes) with 2-3 h soak time. I placed nets randomly in the lake when possible but had to avoid areas of dense submergent vegetation coverage in summer and fall as the nets would not fish properly. In winter the vegetation had senesced and density was still low in the spring sample. Captured fish were immediately placed on ice and returned to the laboratory. Fish were measured (TL in mm) and weighed (wet weight in g). Yellow perch were separated into small (TL 80-

199 mm) and large (TL \geq 200 mm) length groups for diet analysis. Stomachs were removed and placed in 10% formalin within 6 h of capture. After 1 week, stomachs were placed in water for 3-5 d and then placed in 95% ethyl alcohol and stored until diet items were identified.

Food items were identified using a fiber optic illuminator and dissecting microscope. Macroinvertebrates were typically identified to order and fishes were identified to species when possible. Wet weight of each prey taxon was recorded to the nearest 0.01 g after blotting to remove excess water (Hyslop 1980). Prey digested beyond identification was placed into an “unidentified” category. Percent frequency of occurrence, percent composition by number, and percent composition by weight were calculated for diet items by individual fish.

Results

In October 2005, 39 yellow perch (\geq 200 mm TL) were collected and 18% had empty stomachs (Table 5-1). Forty-seven yellow perch (\geq 200 mm TL) were collected in February 2006, of which 30% had empty stomachs. In May and July of 2006, two different length groups of yellow perch were collected. In May, 37 larger (i.e., TL \geq 200 mm) and 16 smaller (TL 80-199 mm) yellow perch were examined. Empty stomachs occurred in 8% and 6% of those fish, respectively. In July, 14 larger and 35 smaller yellow perch were examined. Empty stomachs occurred in 7% and 0% of those fish, respectively. Smaller yellow perch were not collected in the fall and winter sampling efforts.

Large yellow perch (i.e., TL \geq 200 mm) had a wide diet breadth, with 18 different prey categories identified (Table 5-2). Benthic macroinvertebrates were prevalent in all seasons as diet items for large yellow perch (Figure 5-1). Chironomids, amphipods, and odonates consistently had the highest percent occurrence, percent by biomass, and percent by number and were therefore important prey items in most seasons. Lepomid sunfishes became a common prey item in the fall and winter sample (Table 5-2), and dominated percent biomass in the winter (Figure 5-1). Zooplankton were rarely consumed and made up a minor portion of the diet (Figure 5-1).

Small yellow perch (i.e., TL <200 mm) preyed upon fewer taxa than large fish, with nine different prey types identified (Table 5-3). Benthic macroinvertebrates composed the majority of the diets examined. Chironomids, diptera pupae, amphipods, and ephemeropterans had consistently high values of percent of occurrence, percent by biomass, and percent by number in spring and summer samples. Fish were not consumed during May and July samples and zooplankton made up a minor portion of the diet in the two seasons examined (Table 5-3).

Discussion

My results during the open-water season mirror those of Wilkens et al. (2002) who reported that yellow perch in West Long Lake largely fed on benthic macroinvertebrates. Those researchers did not examine diets of yellow perch in the winter. I found increased consumption of fish in the diets of yellow perch in the winter. The majority of these were lepidomid sunfishes, likely bluegill. Bluegill is the most

abundant sunfish in West Long Lake and other sunfishes were rarely documented (Paukert and Willis 2000).

West Long Lake has an abundant macroinvertebrate population (Paukert and Willis 2000) likely mediated by the dense submergent vegetation present (Paukert and Willis 2003a). Yellow perch may feed almost exclusively on benthic macroinvertebrates when they are readily available (Keast and Fox 1992). Lott et al. (1996) reported that fast-growing yellow perch populations in eastern South Dakota lakes were associated with diet high in macroinvertebrates. Fish prey was rarely consumed in that study.

Abundance of yellow perch in West Long Lake in 2006 was moderate with a high-quality size structure (Jolley et al. 2008). The larger relative proportion of 200-mm and longer yellow perch may be more likely to prey on age-0 bluegill. However, Fullhart et al. (2002) found that yellow perch ≥ 130 mm TL regularly consumed fish and perch as small as 65 mm consumed lepomids in several Minnesota lakes.

I suspect that the population of yellow perch in West Long Lake may have the potential to affect bluegill year-class strength. Bioenergetics modeling might be used to determine if my speculation is correct. However, population estimates for yellow perch and bluegill have not been conducted in West Long Lake since 2001 (Paukert et al. 2003), and such data would be necessary to understand fish community dynamics. The 2001 biomass estimates at West Long Lake indicated only 15 kg/ha for bluegill, but 127 kg/ha for yellow perch. Elevated predation on bluegill has been reported to affect recruitment (Garvey et al. 2002; Santucci and Wahl 2003). In addition, age-0 yellow perch have a size advantage over age-0 bluegill given their earlier spawning times.

Yellow perch typically hatch two months prior to bluegill (see Chapter 4) and may attain a size adequate to prey on larval bluegill in the first year, although this was not observed in nearby Pelican Lake (see Chapter 3). Food habits of juvenile yellow perch may be lesser known and future research that targets these fish, especially in the winter, could reveal additional insights. In addition to yellow perch, West Long Lake also had a population of largemouth bass that was dominated by 300-mm and larger individuals and a moderate density of smaller northern pike (Jolley et al. 2008), both known predators of bluegill (Margenau et al. 1998; Paukert and Willis 2003b; Santucci and Wahl 2003). Predation on bluegill populations can have the positive effect of reducing density, decreasing intraspecific competition, and increasing size structure; yellow perch piscivory may be important.

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Table 5-1. Number of small (total length [TL] = 80-199 mm) and large (TL \geq 200 mm) yellow perch examined for prey items, percent with empty stomachs, and mean total lengths (mm, standard errors [SE] are in parentheses) from West Long Lake, Nebraska 2005-2006.

Size	Season	Number examined	Number with prey	% Empty	Mean TL
<200 mm	Spring	16	15	6.3	101 (1)
	Summer	35	35	0.0	149 (2)
	Fall	0	-	-	-
	Winter	0	-	-	-
\geq 200 mm	Spring	37	34	8.1	269 (4)
	Summer	14	13	7.1	261 (5)
	Fall	39	32	17.9	268 (4)
	Winter	47	33	29.8	265 (4)

Table 5-2. Stomach contents of yellow perch (TL \geq 200 mm) from West Long Lake, Nebraska 2005-2006.

Taxon	Percent occurrence	Percent by biomass	Percent by number
October 2005			
Chironomidae	56.4	22.3	55.7
Amphipoda	53.8	3.7	15.1
Ephemeroptera	2.6	0.2	0.1
Odonata	53.8	48.7	26.9
Hirudinea	2.6	0.2	0.1
Trichoptera	5.1	1.4	0.2
Diptera pupae	5.1	0.3	1.2
Oligochaeta	2.6	0.0	0.1
Gastropoda	2.6	0.2	0.1
Unidentified insect	2.6	0.8	0.1
<i>Lepomis</i> spp.	2.6	1.4	0.1
<i>Micropterus salmoides</i>	2.6	18.6	0.1
Unidentified fish	7.7	2.2	0.3
February 2006			
Chironomidae	38.3	20.4	70.3
Amphipoda	31.9	4.7	19.6
Ephemeroptera	8.5	0.5	0.8
Odonata	17.0	14.6	5.7
Hirudinea	2.1	2.4	0.2
Trichoptera	2.1	0.3	0.3
Lepidoptera	2.1	2.1	0.2
<i>Lepomis</i> spp.	14.9	54.0	1.8
Unidentified fish	2.1	0.9	0.2
Cladocera	8.5	0.0	0.8
Copepoda	2.1	0.0	0.2
May 2006			
Chironomidae	73.0	29.8	40.8
Amphipoda	40.5	4.9	13.8
Ephemeroptera	13.5	1.3	0.9
Odonata	35.1	10.4	2.6
Trichoptera	8.1	1.1	0.4
Diptera pupae	83.8	47.0	40.6
Hemiptera	2.7	0.1	0.1
Unidentified insect	2.7	0.1	0.1
Unidentified fish	5.4	5.4	0.3
Cladocera	5.4	0.0	0.4
July 2006			
Chironomidae	78.6	13.4	67.5
Amphipoda	71.4	83.9	22.8
Odonata	21.4	0.6	1.0
Hirudinea	7.1	0.4	1.0
Diptera pupae	42.9	1.5	6.2
Oligochaeta	7.1	0.1	0.7
Hydracarina	7.1	0.1	0.3
Unidentified insect	7.1	0.1	0.3

Table 5-3. Stomach contents of yellow perch (TL 80-199 mm) from West Long Lake, Nebraska 2005-2006.

Taxon	Percent occurrence	Percent by biomass	Percent by number
May 2006			
Chironomidae	68.8	22.1	43.0
Amphipoda	6.3	1.0	0.7
Ephemeroptera	43.8	18.3	10.6
Odonata	31.3	16.3	5.6
Diptera pupae	56.3	40.4	35.9
Hemiptera	6.3	1.0	0.7
Unidentified insect	6.3	1.0	0.7
Cladocera	18.8	0.0	2.8
July 2006			
Chironomidae	100.0	34.7	26.9
Amphipoda	100.0	57.5	61.8
Odonata	6.1	0.3	0.1
Diptera pupae	60.6	5.7	2.5
Oligochaeta	6.1	0.3	0.1
Unidentified insect	6.1	1.5	0.1
Cladocera	24.2	0.0	8.4

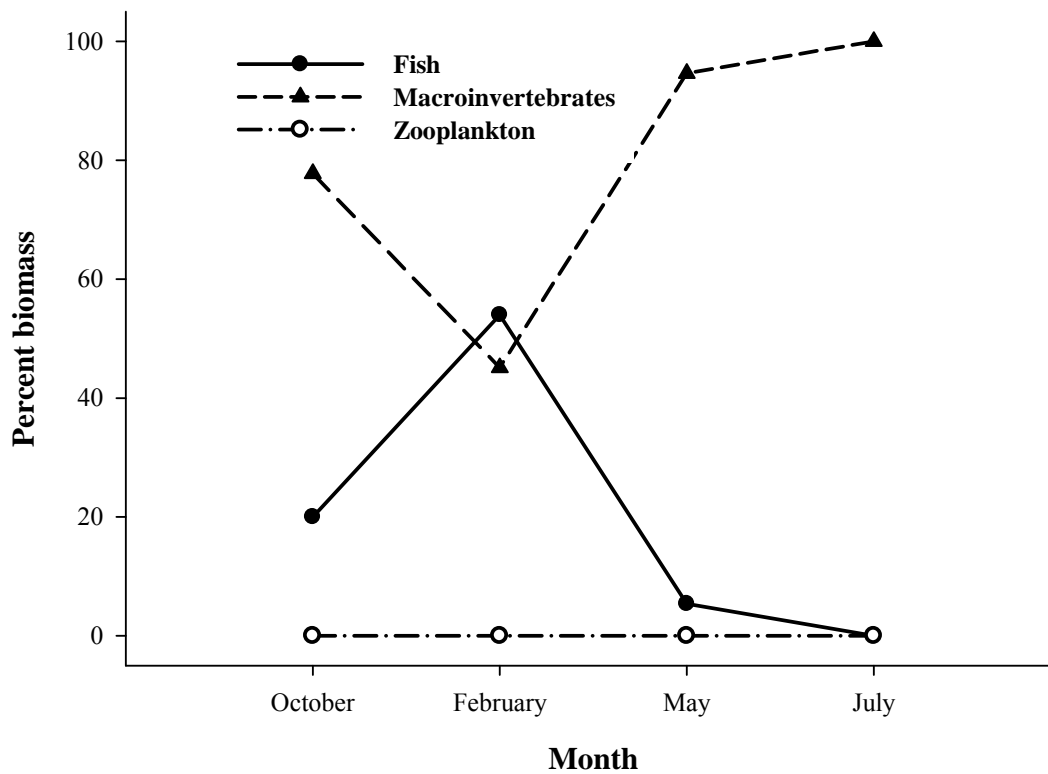


Figure 5-1. Food habits by season for large yellow perch ($TL \geq 200$ mm) in West Long Lake, Nebraska, 2005-2006.

Chapter 6

Summary and Research Needs

My research addressed several aspects of the recruitment dynamics of bluegill and yellow perch that were needed to understand and manage these valuable sport fishes in Nebraska Sandhills lakes. My study provides some of the first ecosystem-wide information on the dynamics of age-0 bluegill and yellow perch. I found, over the years examined, that no single factor appears to affect bluegill and yellow perch recruitment. Instead, a suite of factors, are likely interacting in complex ways to ultimately govern the recruitment of these species. Bluegill and yellow perch exhibited relatively consistent recruitment (no missing year classes detected). Climate did not act similarly on bluegill or yellow perch populations (based on analyses of year-strength of multiple adult populations) broadly across a series of Nebraska Sandhills lakes as year-class strength was found to be asynchronous among populations. Based solely on the analysis of climate variables I found some support for the concept of climatic influence on bluegill and yellow perch recruitment. Environmental factors related to recruitment of bluegill and yellow perch showed the common positive effect of spring warming and precipitation. The exploratory nature of my analysis may have identified environmental variables related to recruitment that may be indirect and challenging to fully elucidate without further, in-depth examination of potential mechanisms. Lake-specific factors may be more important in determining recruitment; therefore, management actions may need to be determined on a lake-by-lake basis.

Larval bluegill and yellow perch had an abundant food source of zooplankton in Pelican Lake and Cameron Lake. Bluegill selected copepod nauplii and *Bosmina* spp. while yellow perch selected copepods, findings consistent with previous research. Matches in larval abundance and prey production were common; exact matches were often observed. No mismatches in predator production and prey production were ever detected. In addition, it is unknown if mismatches may lead to decreased survival and recruitment of these species. Although a potential weak year class or year-class failure of yellow perch may have occurred in Pelican Lake in 2005, larvae were matched to their prey even though all larvae examined had empty stomachs. Yellow perch hatched two months prior to bluegill, establishing the potential for predation by yellow perch on newly hatched bluegill. However, no bluegill larvae were found in yellow perch stomachs as yellow perch were likely not large enough to consume bluegill larvae. Given that zooplankton were abundant and well-timed to larval fish abundance over the initial years of this study, the match-mismatch hypothesis alone may not be able to fully account for observed recruitment variability in the populations that I studied. My results are contrary to previous experimental research indicating zooplankton biomass affects the survival of larval fishes.

Larval bluegill density was variable across years throughout my study. In addition, a single peak in abundance was observed in most years, contrary to the long-held assumption of multiple spawning bouts throughout a spawning season, although the spawning season was protracted, which is consistent with previous research. Timing of hatch for bluegill was remarkably consistent throughout my study. Late-hatched bluegill

typically grew faster than those hatched earlier in the season. Faster-growing, late-hatched bluegills may contribute more to year-class strength than their earlier-hatched counterparts as growth of these fish was correlated with fall catch per unit effort (CPUE) of juvenile bluegill in the fall. No evidence of size-selective overwinter mortality of bluegill was detected in my study and bluegill commonly continued to grow over the winter time period.

Yellow perch larval density was also variable in my study although it appears that recruitment to the adult population was relatively consistent over the time period studied. The yellow perch spawning season was truncated, which is consistent with previous findings. Little evidence for size-selective overwinter mortality of yellow perch was detected although it may have occurred in one year. In addition, yellow perch appeared to grow throughout the first winter. My estimates of larval density for both species were a poor predictor of later season catches or recruitment to the adult population. My exploratory analyses indicated that temperature, winter severity, and growth rates may be important determinants of survival and ultimate recruitment to the adult population for both species.

Seasonal food habits of adult yellow perch indicated that benthic invertebrates, an abundant resource, were a large component of the diet during the primary growing season (i.e., open water). Increased predation on age-0 bluegills was observed in the fall and even more so over the winter time period suggesting the potential to affect recruitment of bluegill.

My study was the first segment of an ongoing research project. The investigation of recruitment dynamics of bluegill and yellow perch in Pelican Lake will be continued for a total of 10 years. My results should be interpreted with caution as they are based on four years of data collection. The addition of more years to the dataset may increase our power to determine potential factors related to recruitment. Below I describe several specific research questions generated from my work.

Research needs

- 1) Continued research into the recruitment dynamics of bluegill and yellow perch in Pelican Lake is warranted. My analyses were often hampered by the low number of years of observation ($n=4$), which make relations challenging to detect and increase the likelihood of spurious relations. More years of data may increase our ability to detect specific mechanisms related to survival of bluegill and yellow perch. Increasing our environmental dataset with continued research may also open up more advanced analytical opportunities. A promising technique involves the Ecopath model (Christensen and Pauly 1992; Pauly et al. 2000), which creates a mass-balanced overview of ecosystem resources. Linked trophic groups within an ecosystem and their interactions can then be investigated. The groups can be defined as individual species or groups of species and then divided into ontogenetic groups. Information required by the model should be available at the conclusion of this study (e.g., biomass estimates, mortality rates, diet composition, and consumption estimates). The primary goal of the model is to describe all mortality by partitioning

- different mortality factors. This technique coupled with bioenergetic modeling may be valuable.
- 2) Exact determination of the contribution of specific ‘cohorts’ of larval fishes to recruitment could be extremely valuable. Knowledge of hatching estimates of juvenile fishes collected in the fall could specifically help us determine which groups of larvae are directly contributing to year-class strength. Alternatively, cohort specific mortality rates may also shed light on this question. In addition, factors leading to increased mortality of selected cohorts could be more easily understood.
 - 3) Larval fish losses to predation have commonly been an alternative explanation for variable recruitment. Investigations of the predation rates on age-0 bluegill and yellow perch may be valuable to determine the extent of ‘biotic’ versus ‘abiotic’ control of recruitment. Examination of yearly abundance indices of predatory fish (i.e., largemouth bass and northern pike) may be valuable.
 - 4) Overwinter mortality that is not size-specific may affect recruitment. Knowledge of overall mortality rates over the winter time period could increase our understanding of this life stage. Information such as dissolved oxygen levels throughout the winter may assist in determination of mechanisms related to potentially elevated mortality during this time period.

References

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Appendix 1. Mean density of larval bluegill (number/100 m³) and number of trawls (N) from Pelican Lake, 2004-2007. Standard errors are in parentheses. Inshore locations are <100 m from emergent vegetation and offshore locations are ≥100 m from emergent vegetation.

Year	Date	Inshore		Offshore		Overall	
		Mean density (number/100 m ³)	N	Mean density (number/100 m ³)	N	Mean density (number/100 m ³)	N
2004	6-Jun	0 (0)	5	0 (0)	5	0 (0)	10
	16-Jun	0 (0)	5	0 (0)	5	0 (0)	10
	26-Jun	1 (1)	6	3 (2)	4	2 (1)	10
	7-Jul	9 (3)	5	9 (2)	5	9 (2)	10
	17-Jul	140 (59)	5	91 (21)	5	116 (31)	10
	27-Jul	52 (33)	4	94 (34)	6	77 (24)	10
	6-Aug	27 (15)	4	93 (38)	4	60 (23)	8
	16-Aug	120 (53)	5	169 (80)	5	144 (46)	10
	27-Aug	36 (9)	5	126 (26)	5	81 (20)	10
2005	5-Sep	23 (13)	4	52 (9)	4	37 (9)	8
	2-Jun	0 (0)	5	0 (0)	5	0 (0)	10
	13-Jun	0 (0)	5	0 (0)	4	0 (0)	9
	22-Jun	0 (0)	4	0 (0)	5	0 (0)	9
	30-Jun	122 (58)	5	67 (21)	5	95 (30)	10
	11-Jul	413 (135)	5	173 (60)	5	293 (80)	10
	21-Jul	551 (263)	5	1,297 (661)	5	924 (358)	10
	1-Aug	219 (65)	5	338 (92)	5	278 (57)	10
	11-Aug	95 (23)	5	89 (11)	5	92 (12)	10
2006	22-Aug	36 (14)	5	21 (8)	5	28 (8)	10
	29-May	0 (0)	4	0 (0)	5	0 (0)	9
	8-Jun	24 (12)	5	0 (0)	5	12 (7)	10
	19-Jun	60 (17)	4	81 (19)	6	72 (13)	10
	29-Jun	111 (32)	5	114 (40)	5	113 (24)	10
	10-Jul	643 (273)	5	353 (104)	5	498 (146)	10
	20-Jul	1,894 (1,224)	5	1,633 (684)	5	1,764 (662)	10
	1-Aug	1,113 (157)	5	1,687 (384)	5	1,400 (218)	10
	10-Aug	202 (69)	5	320 (133)	5	261 (73)	10
2007	4-Jun	0 (0)	5	0 (0)	5	0 (0)	10
	14-Jun	0 (0)	5	0 (0)	5	0 (0)	10
	25-Jun	113 (40)	5	256 (143)	5	185 (74)	10
	5-Jul	425 (48)	5	642 (176)	5	533 (93)	10
	16-Jul	600 (147)	5	864 (110)	5	732 (97)	10
	26-Jul	163 (40)	5	382 (108)	5	273 (65)	10
	6-Aug	11 (2)	5	7 (2)	5	9 (2)	10
	15-Aug	3 (2)	5	3 (2)	5	3 (1)	10

Appendix 2. Mean density of larval yellow perch (number/100 m³) and number of trawls (N) from Cameron Lake, 2004-2005, and Pelican Lake, 2004-2007. Standard errors are in parentheses. Inshore locations are <100 m from emergent vegetation and offshore locations are ≥100 m from emergent vegetation.

Lake	Year	Date	Inshore		Offshore		Overall	
			Mean density (number/100 m ³)	N	Mean density (number/100 m ³)	N	Mean density (number/100 m ³)	N
Cameron	2004	29-Apr	-	-	-	-	782 (235)	11
		13-May	1,929 (899)	5	1,379 (220)	4	1,685 (492)	9
		18-May	985 (488)	4	999 (535)	4	992 (335)	8
		27-May	33 (22)	4	94 (48)	4	64 (27)	8
		7-Jun	308 (179)	4	225 (192)	4	267 (122)	8
		15-May	7 (4)	4	3 (1)	4	5 (2)	8
	2005	24-May	10 (5)	4	24 (10)	4	17 (6)	8
		2-Jun	2 (2)	4	5 (2)	4	4 (1)	8
		18-Apr	-	-	-	-	0 (-)	1
Pelican	2004	8-May	166 (23)	6	208 (66)	5	185 (31)	11
		17-May	168 (98)	5	36 (28)	2	131 (72)	7
		26-May	16 (11)	3	7 (2)	5	11 (4)	8
		6-Jun	0 (0)	5	0 (0)	5	0 (0)	10
		21-Apr	-	-	0 (-)	1	0 (-)	1
		3-May	9 (5)	5	2 (1)	5	5 (3)	10
	2005	14-May	0 (0)	5	0 (0)	5	0 (0)	10
		9-May	33 (10)	5	77 (16)	5	55 (12)	10
		18-May	266 (102)	5	156 (68)	5	211 (61)	10
		29-May	7 (3)	5	2 (1)	5	5 (2)	10
		8-Jun	4 (4)	5	8 (8)	5	6 (4)	10
		19-Jun	0 (0)	4	0 (0)	6	0 (0)	10
	2006	30-Apr	77 (3)	5	103 (28)	5	90 (14)	10
		8-May	513 (213)	5	533 (210)	5	523 (141)	10
		18-May	5 (4)	5	14 (12)	5	9 (6)	10
		24-May	2 (1)	5	2 (1)	5	2 (1)	10
		4-Jun	0.45 (0.45)	5	0 (0)	5	0.22 (0.22)	10
		14-Jun	0 (0)	5	0 (0)	5	0 (0)	10

Appendix 3. Mean daily growth (mm/d), standard error (SE), and sample size (N) of larval yellow perch in Cameron Lake, 2004-2005, and Pelican Lake, 2004-2007 and for larval bluegill by hatch period in Pelican Lake, 2004-2007. Hatch periods for bluegill are early (i.e., June) and late (i.e., July and August).

Lake	Species	Year	Hatch period	Mean daily growth (mm/d)	SE	N
Cameron	Yellow perch	2004	Overall	0.35	0.02	75
		2005		0.27	0.02	24
Pelican	Yellow perch	2004		0.37	0.01	50
		2005		0.33	0.05	10
		2006		0.30	0.01	59
		2007		0.23	0.01	65
		2007		0.23	0.01	65
Pelican	Bluegill	2004	Early	0.22	0.01	43
		2005		0.37	0.01	60
		2006		0.31	0.01	82
		2007		0.20	0.01	85
		2007		0.20	0.01	85
		2004	Late	0.33	0.01	106
		2005		0.32	0.01	88
		2006		0.39	0.02	49
		2006		0.39	0.02	49
		2007		0.29	0.02	8

Appendix 4. Bivariate Pearson correlation matrix between bluegill and yellow perch life stage indices. Contrasts correspond to the same year class of fish. Correlation coefficients (r) are followed in parentheses by number of data pairs and P value. Catch per unit effort is denoted CPUE.

	Bluegill peak larval abundance	Bluegill fall CPUE	Bluegill spring (age 1) CPUE	Bluegill age 2 CPUE	Yellow perch peak larval abundance	Yellow perch fall CPUE	Yellow perch spring (age 1) CPUE	Yellow perch age 1 CPUE
Bluegill peak larval abundance		0.55 (4, 0.45)	0.67 (4, 0.33)	0.41 (3, 0.73)	-0.08 (4, 0.92)	-0.42 (4, 0.58)	0.20 (4, 0.80)	0.92 (4, 0.08)
Bluegill fall CPUE	0.55 (4, 0.45)		0.87 (4, 0.13)	0.90 (3, 0.29)	-0.58 (4, 0.42)	-0.23 (4, 0.77)	-0.53 (4, 0.47)	0.82 (4, 0.18)
Bluegill spring (age 1) CPUE	0.67 (4, 0.33)	0.87 (4, 0.13)		0.95 (3, 0.21)	-0.10 (4, 0.90)	0.12 (4, 0.88)	-0.06 (4, 0.94)	0.90 (4, 0.11)
Bluegill age 2 CPUE	0.41 (3, 0.74)	0.90 (3, 0.29)	0.95 (3, 0.21)		0.96 (3, 0.18)	0.68 (3, 0.53)	0.84 (3, 0.36)	0.66 (3, 0.54)
Yellow perch peak larval abundance	-0.08 (4, 0.92)	-0.58 (4, 0.42)	-0.10 (4, 0.90)	0.96 (3, 0.18)		-0.12 (6, 0.82)	-0.04 (6, 0.95)	-0.22 (4, 0.78)
Yellow perch fall CPUE	-0.42 (4, 0.58)	-0.23 (4, 0.77)	0.12 (4, 0.88)	0.68 (3, 0.53)	-0.12 (6, 0.82)		0.59 (6, 0.22)	-0.27 (4, 0.73)
Yellow perch spring (age 1) CPUE	0.20 (4, 0.80)	-0.53 (4, 0.47)	-0.06 (4, 0.95)	0.84 (3, 0.36)	-0.04 (6, 0.95)	0.59 (6, 0.22)		-0.03 (4, 0.97)
Yellow perch age 1 CPUE	0.92 (4, 0.08)	0.82 (4, 0.18)	0.89 (4, 0.11)	0.66 (3, 0.54)	-0.22 (4, 0.78)	-0.27 (4, 0.73)	-0.03 (4, 0.97)	

Appendix 5. Mean biomass (g/m^2) of major invertebrate taxa in Pelican Lake and Cameron Lake, Nebraska 2004-2007. Standard errors are in parentheses.

Lake	Year	Date	Order Ephemeroptera	Order Odonata	Order Trichoptera	Order Amphipoda	Class Hirudinea	Class Gastropoda	Family Chironomidae	
Pelican	2004	18-Apr	-	0.44 (0.44)	0.08 (0.08)	0.18 (0.18)	0.03 (0.03)	-	1.01 (0.31)	
		8-May	0.01 (0.01)	-	-	-	-	-	2.01 (0.37)	
		17-May	0.01 (0.01)	-	-	0.08 (0.08)	0.01 (0.01)	-	1.92 (0.40)	
		26-May	0.01 (0.01)	0.03 (0.02)	-	-	0.02 (0.01)	-	2.87 (0.51)	
		6-Jun	-	-	-	0.01 (0.01)	0.06 (0.02)	-	3.60 (1.13)	
		16-Jun	0.01 (0.01)	0.04 (0.04)	-	0.04 (0.03)	0.16 (0.04)	35 (15)	2.34 (0.75)	
		26-Jun	-	-	-	-	0.05 (0.02)	-	9.37 (2.25)	
		7-Jul	-	-	-	-	0.09 (0.02)	-	10.37 (2.54)	
		17-Jul	-	-	-	0.03 (0.03)	0.32 (0.10)	13 (13)	3.95 (0.85)	
		27-Jul	0.02 (0.01)	-	0.01 (0.01)	0.10 (0.10)	0.23 (0.12)	10 (5)	1.56 (0.47)	
		6-Aug	0.02 (0.01)	-	-	-	0.08 (0.06)	28 (28)	4.61 (1.01)	
		16-Aug	-	-	-	-	0.08 (0.03)	-	0.80 (0.24)	
		27-Aug	-	0.01 (0.01)	-	-	0.08 (0.04)	20 (20)	0.02 (0.01)	
		5-Sep	-	0.80 (0.43)	-	-	0.29 (0.19)	0.60 (0.39)	98 (78)	1.10 (0.53)
	2005	3-May	-	-	-	0.02 (0.01)	0.05 (0.02)	29 (29)	1.37 (0.23)	
		14-May	-	-	0.01 (0.01)	0.03 (0.02)	0.02 (0.01)	4 (4)	0.55 (0.15)	
		23-May	-	0.04 (0.03)	-	0.06 (0.03)	0.13 (0.06)	291 (251)	0.50 (0.11)	
		2-Jun	-	-	-	-	0.03 (0.01)	11 (7)	0.18 (0.05)	
		13-Jun	0.03 (0.03)	0.15 (0.08)	-	0.03 (0.02)	0.18 (0.07)	11 (11)	0.59 (0.29)	
		22-Jun	-	-	-	-	0.03 (0.01)	8 (8)	1.21 (0.40)	
		30-Jun	0.01 (0.01)	-	-	-	0.04 (0.02)	-	2.02 (0.83)	
		11-Jul	-	-	-	0.02 (0.01)	0.10 (0.03)	-	5.42 (0.86)	
		21-Jul	-	-	-	-	0.01 (0.01)	-	7.16 (2.31)	
		1-Aug	-	-	-	-	0.15 (0.07)	19 (19)	9.54 (1.47)	
		11-Aug	-	0.02 (0.02)	-	0.11 (0.10)	0.19 (0.07)	10 (10)	1.13 (0.30)	
		22-Aug	-	-	-	-	0.11 (0.04)	-	2.18 (0.87)	
		2006	9-May	-	0.02 (0.02)	-	0.01 (0.01)	1.60 (0.66)	-	2.37 (0.46)
			18-May	-	-	-	-	0.85 (0.20)	-	2.12 (0.48)
29-May	-		0.07 (0.07)	0.02 (0.01)	0.04 (0.03)	0.64 (0.24)	25 (17)	0.93 (0.28)		
8-Jun	0.01 (0.01)		0.05 (0.03)	-	0.03 (0.01)	2.34 (1.07)	-	1.36 (0.41)		
19-Jun	-		-	0.01 (0.01)	0.01 (0.01)	0.78 (0.51)	30 (16)	1.33 (0.67)		
2006	29-Jun	-	-	0.01 (0.01)	0.01 (0.01)	3.00 (1.14)	-	0.63 (0.12)		
	10-Jul	-	-	-	0.01 (0.01)	3.89 (1.18)	22 (14)	0.51 (0.12)		
	20-Jul	-	0.01 (0.01)	-	-	2.74 (2.05)	2 (2)	0.33 (0.10)		
	1-Aug	-	-	-	-	1.26 (0.41)	53 (53)	0.46 (0.17)		
	10-Aug	-	-	-	0.02 (0.02)	0.86 (0.36)	-	0.80 (0.24)		
2007	30-Apr	0.01 (0.01)	-	-	0.02 (0.01)	0.01 (0.01)	-	1.97 (0.47)		
	8-May	-	-	-	0.01 (0.01)	0.02 (0.01)	24 (18)	1.25 (0.26)		
	18-May	-	-	-	-	0.01 (0.01)	-	0.39 (0.11)		
	24-May	0.01 (0.01)	-	0.01 (0.01)	-	0.04 (0.02)	-	0.51 (0.18)		
	4-Jun	0.02 (0.01)	-	0.01 (0.01)	0.02 (0.02)	0.20 (0.05)	2 (2)	0.94 (0.30)		
	14-Jun	-	-	-	-	0.14 (0.06)	-	0.88 (0.30)		
	25-Jun	0.03 (0.03)	-	-	0.03 (0.03)	0.11 (0.07)	0.85 (0.85)	0.88 (0.31)		
	5-Jul	-	-	-	-	0.02 (0.01)	-	0.49 (0.13)		
	16-Jul	-	-	-	-	0.02 (0.01)	-	0.62 (0.16)		
	26-Jul	-	-	-	-	0.05 (0.02)	-	0.32 (0.05)		
	6-Aug	-	-	-	-	0.01 (0.01)	-	0.65 (0.35)		
	15-Aug	-	-	-	-	0.01 (0.01)	-	0.19 (0.03)		

Appendix 5 continued

Lake	Year	Date	Order Ephem- eroptera	Order Odonata	Order Trichoptera	Order Amphipoda	Class Hirudinea	Class Gastropoda	Family Chiron- omidae
Cameron	2004	13-May	-	-	-	-	-	-	4.19 (0.72)
		18-May	-	-	0.01 (0.01)	-	-	-	2.48 (0.43)
		27-May	-	-	-	-	-	-	0.82 (0.20)
	2005	2-Jun	-	0.02	-	-	-	-	-
		7-Jun	-	-	-	-	-	-	0.47 (0.17)
		15-May	-	-	-	-	-	-	0.35 (0.07)
		24-May	-	-	-	0.01 (0.01)	-	-	0.18 (0.04)
		2-Jun	-	-	-	-	-	-	0.90 (0.16)

Appendix 6. Physical and chemical characteristics of Pelican Lake and Cameron Lake, 2004-2007.

Lake	Year	Date	Mean Secchi depth (cm)	Mean dissolved oxygen (mg/L)	Mean conductivity ($\mu\text{S}/\text{cm}$)	Mean TDS (g/L) ¹	Mean alkalinity (mg/L)	Mean pH
Pelican	2004	8-May	-	8.4 (0.1)	417 (3)	-	239.40 (3.12)	8.0 (-)
		17-May	-	9.0 (0.1)	888 (57)	1356.7 (113.4)	245.10 (3.60)	8.2 (0.1)
		26-May	86 (11)	7.1 (0.0)	849 (247)	604.4 (60.9)	254.60 (4.46)	8.1 (0.1)
		6-Jun	-	8.7 (0.0)	384 (5)	392.0 (5.33)	239.40 (-)	8.5 (-)
		16-Jun	93 (4)	8.9 (0.2)	392 (4)	396.0 (2.67)	235.98 (2.28)	8.0 (-)
		26-Jun	94 (4)	7.8 (0.2)	390 (2)	400.0 (-)	210.33 (2.61)	8.1 (0.1)
		7-Jul	106 (3)	8.5 (0.1)	372 (6)	384.0 (6.53)	218.88 (2.28)	8.2 (0.1)
		16-Jul	102 (4)	7.1 (0.0)	372 (2)	380.0 (-)	230.85 (3.82)	8.1 (0.1)
		27-Jul	75 (6)	8.4 (0.1)	394 (3)	404.0 (2.67)	210.33 (5.13)	8.3 (0.1)
		6-Aug	53 (2)	8.8 (0.4)	388 (3)	400.0 (5.35)	226.58 (4.27)	8.5 (-)
	16-Aug	55 (3)	6.7 (0.2)	426 (16)	472.0 (30.58)	222.30 (-)	8.5 (-)	
	27-Aug	40 (2)	8.3 (0.1)	658 (18)	864.0 (31.52)	213.75 (2.85)	8.9 (0.1)	
	5-Sep	43 (3)	9.5 (0.0)	690 (80)	1035.0 (168.13)	190.24 (2.14)	9.1 (0.1)	
	2005	3-May	130 (6)	8.8 (0.1)	343 (4)	358.0 (2.00)	165.87 (2.61)	8.0 (-)
		14-May	54 (6)	7.1 (0.2)	-	-	159.03 (2.61)	8.1 (0.1)
		23-May	80 (16)	7.0 (0.1)	-	532.0 (16.11)	147.49 (3.13)	8.3 (0.1)
		2-Jun	-	5.1 (0.6)	-	-	169.29 (1.71)	8.1 (0.1)
		13-Jun	111 (18)	6.9 (0.4)	-	-	147.49 (3.13)	8.0 (-)
		22-Jun	152 (-)	6.2 (0.4)	-	-	167.58 (3.42)	8.0 (0.1)
		30-Jun	109 (3)	7.7 (0.1)	-	-	169.29 (3.07)	7.9 (0.1)
11-Jul		124 (11)	8.1 (0.1)	-	-	182.97 (2.61)	8.1 (0.1)	
21-Jul		78 (2)	4.8 (0.7)	566 (71)	728.0 (137.44)	230.85 (3.82)	8.3 (0.1)	
1-Aug		94 (8)	7.0 (0.1)	446 (24)	524.0 (48.52)	215.46 (3.78)	8.7 (0.1)	
11-Aug	70 (2)	8.4 (0.1)	702 (29)	1028.0 (55.87)	254.79 (3.99)	8.2 (0.1)		
22-Aug	55 (4)	7.0 (0.0)	494 (75)	632.0 (142.46)	159.03 (3.65)	8.8 (0.1)		
2006	9-May	47 (34)	5.3 (0.3)	506 (18)	620.0 (32.11)	199.50 (2.85)	8.2 (0.1)	
	18-May	-	6.0 (0.6)	866 (190)	1324.0 (369.52)	253.08 (4.27)	8.4 (0.1)	
	29-May	100 (5)	7.4 (0.0)	415 (8)	438.0 (17.24)	242.82 (3.42)	8.4 (0.1)	
	8-Jun	52 (3)	7.2 (0.1)	506 (6)	628.0 (13.40)	266.76 (4.56)	8.2 (0.1)	
	19-Jun	87 (4)	7.6 (0.1)	471 (16)	586.0 (33.21)	251.37 (3.65)	8.6 (0.1)	

Appendix 6 continued.

Lake	Year	Date	Mean Secchi depth (cm)	Mean dissolved oxygen (mg/L)	Mean conductivity (μ S/cm)	Mean TDS (g/L) ¹	Mean alkalinity (mg/L)	Mean pH
Pelican	2006	29-Jun	54 (2)	6.8 (0.3)	402 (24)	470.0 (46.88)	225.72 (4.27)	9.0 (0.1)
		10-Jul	52 (3)	7.4 (0.0)	421 (19)	528.0 (37.97)	213.75 (2.85)	8.8 (0.1)
		20-Jul	30 (1)	4.5 (0.2)	364 (3)	408.0 (6.80)	217.17 (3.65)	9.0 (-)
		2-Aug	21 (1)	7.2 (0.2)	342 (2)	352.0 (3.27)	222.30 (2.55)	9.3 (0.1)
		10-Aug	23 (1)	7.5 (0.1)	462 (22)	602.0 (41.79)	191.52 (4.27)	9.5 (-)
	2007	30-Apr	102 (5)	7.9 (0.2)	376 (2)	384.0 (2.67)	133.38 (4.27)	8.0 (-)
		8-May	152 (4)	7.0 (0.0)	372 (1)	380.0 (-)	159.03 (2.61)	8.3 (0.1)
		18-May	59 (5)	7.5 (0.1)	414 (17)	428.0 (19.82)	160.74 (2.80)	8.7 (0.1)
		24-May	82 (6)	6.9 (0.1)	371 (3)	394.0 (6.00)	147.06 (3.78)	8.9 (0.1)
		4-Jun	70 (6)	7.5 (0.0)	625 (104)	898.0 (201.36)	155.61 (3.99)	8.8 (0.1)
		14-Jun	66 (3)	7.7 (0.3)	746 (48)	1106.0 (92.43)	162.45 (3.82)	8.3 (0.1)
		25-Jun	38 (2)	7.6 (0.1)	651 (66)	886.0 (114.66)	150.48 (3.42)	8.6 (0.1)
		5-Jul	37 (1)	7.5 (0.0)	764 (41)	1204.0 (88.98)	275.31 (7.84)	9.0 (0.1)
		16-Jul	23 (1)	7.8 (0.3)	639 (137)	944.0 (269.75)	128.25 (2.85)	9.0 (0.1)
		26-Jul	23 (1)	6.0 (0.3)	368 (6)	414.0 (14.92)	160.74 (3.78)	9.3 (0.1)
6-Aug	22 (1)	7.3 (0.1)	412 (55)	504.0 (109.33)	159.03 (3.65)	9.5 (0.1)		
15-Aug	17 (1)	6.8 (0.3)	342 (2)	368.0 (6.80)	167.58 (2.28)	9.3 (0.1)		
Cameron	2004	13-May	21 (2)	7.9 (0.4)	600 (144)	844.0 (196.1)	129.96 (4.19)	8.5 (-)
		18-May	39 (2)	9.1 (0.0)	410 (29)	600.0 (45.7)	136.80 (-)	8.4 (0.1)
		27-May	52 (2)	7.8 (0.1)	260 (9)	290.0 (19.6)	162.45 (3.23)	7.9 (0.1)
		7-Jun	24 (1)	7.7 (0.1)	225 (2)	230.0 (3.8)	153.90 (-)	8.1 (0.1)
	2005	15-May	56 (3)	7.0 (0.1)	210 (-)	220.0 (-)	104.74 (3.87)	8.0 (-)
		24-May	54 (2)	7.9 (0.2)	223 (2)	230.0 (3.8)	111.15 (3.23)	8.4 (0.1)
		2-Jun	57 (2)	7.1 (0.1)	493 (35)	750.0 (56.2)	119.70 (-)	7.7 (0.1)

¹ Total dissolved solids

Appendix 7. Bivariate Pearson correlation matrix between bluegill and yellow perch abundance and growth indices and principal components (PC). Correlation coefficients (r) are followed in parentheses by number of data pairs and P value. Mean catch per unit effort is denoted CPUE and total length is denoted TL.

	Invertebrate		Physicochemical		Habitat		Zooplankton		Climate	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Bluegill peak larval abundance	-0.78 (4, 0.22)	0.01 (4, 0.99)	-0.32 (4, 0.68)	-0.18 (4, 0.82)	0.79 (4, 0.21)	-0.31 (4, 0.69)	0.07 (4, 0.93)	-0.10 (4, 0.90)	-0.56 (4, 0.44)	-0.50 (4, 0.50)
Bluegill fall CPUE	0.04 (4, 0.96)	0.34 (4, 0.62)	-0.03 (4, 0.97)	0.70 (4, 0.30)	-0.02 (4, 0.98)	-0.80 (4, 0.20)	0.01 (4, 0.99)	-0.89 (4, 0.11)	-0.13 (4, 0.87)	-0.99 (4, 0.01)
Bluegill spring (age 1) CPUE	-0.06 (4, 0.94)	-0.12 (4, 0.88)	-0.52 (4, 0.48)	0.56 (4, 0.44)	0.33 (4, 0.67)	-0.91 (4, 0.09)	0.46 (4, 0.54)	-0.68 (4, 0.32)	-0.60 (4, 0.40)	-0.79 (4, 0.21)
Bluegill age 2 CPUE	0.11 (3, 0.93)	-0.97 (3, 0.15)	-0.99 (3, 0.03)	0.65 (3, 0.55)	0.43 (3, 0.71)	-0.99 (3, 0.09)	0.96 (3, 0.17)	-0.88 (3, 0.31)	-0.94 (3, 0.23)	-0.84 (3, 0.36)
Yellow perch peak larval abundance	-0.08 (4, 0.92)	-0.97 (4, 0.03)	-0.80 (4, 0.20)	-0.42 (4, 0.58)	0.49 (4, 0.51)	0.07 (4, 0.93)	0.78 (4, 0.22)	0.62 (4, 0.38)	-0.70 (4, 0.30)	0.69 (4, 0.31)
Yellow perch fall CPUE	0.58 (4, 0.42)	-0.82 (4, 0.18)	-0.72 (4, 0.28)	0.29 (4, 0.71)	-0.08 (4, 0.92)	-0.40 (4, 0.60)	0.88 (4, 0.12)	0.02 (4, 0.98)	-0.50 (4, 0.51)	0.33 (4, 0.67)
Yellow perch spring (age 1) CPUE	-0.42 (4, 0.58)	-0.88 (4, 0.12)	-0.76 (4, 0.24)	-0.63 (4, 0.37)	0.75 (4, 0.25)	0.17 (4, 0.83)	0.64 (4, 0.36)	0.73 (4, 0.27)	-0.76 (4, 0.24)	0.63 (4, 0.37)
Yellow perch age 1 CPUE	-0.47 (4, 0.53)	0.07 (4, 0.93)	-0.34 (4, 0.66)	0.23 (4, 0.77)	0.56 (4, 0.44)	-0.64 (4, 0.36)	0.17 (4, 0.83)	-0.47 (4, 0.53)	-0.53 (4, 0.47)	-0.77 (4, 0.23)

Appendix 7 continued.

	Invertebrate		Physicochemical		Habitat		Zooplankton		Climate	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Overall										
bluegill daily growth	-0.04 (4, 0.96)	0.82 (4, 0.18)	0.51 (4, 0.49)	0.52 (4, 0.48)	-0.24 (4, 0.76)	-0.37 (4, 0.63)	-0.54 (4, 0.46)	-0.77 (4, 0.23)	0.37 (4, 0.63)	-0.90 (4, 0.10)
Early-hatched										
bluegill daily growth	-0.50 (4, 0.50)	0.84 (4, 0.16)	0.64 (4, 0.36)	-0.06 (4, 0.94)	0.06 (4, 0.94)	0.13 (4, 0.87)	-0.79 (4, 0.21)	-0.27 (4, 0.73)	0.42 (4, 0.58)	-0.57 (4, 0.43)
Late-hatched										
bluegill daily growth	-0.08 (4, 0.92)	0.17 (4, 0.83)	-0.25 (4, 0.75)	0.61 (4, 0.39)	0.19 (4, 0.81)	-0.85 (4, 0.15)	0.19 (4, 0.81)	-0.79 (4, 0.21)	-0.36 (4, 0.64)	-0.93 (4, 0.07)
Yellow perch daily growth	0.66 (4, 0.34)	0.70 (4, 0.30)	0.59 (4, 0.41)	0.81 (4, 0.19)	-0.85 (4, 0.15)	-0.34 (4, 0.66)	-0.41 (4, 0.59)	-0.82 (4, 0.18)	0.66 (4, 0.34)	-0.61 (4, 0.39)
Fall bluegill mean TL	-0.75 (4, 0.25)	-0.27 (4, 0.73)	-0.56 (4, 0.44)	-0.23 (4, 0.77)	0.90 (4, 0.10)	-0.35 (4, 0.65)	0.32 (4, 0.68)	0.01 (4, 0.99)	-0.76 (4, 0.24)	-0.35 (4, 0.65)
Fall yellow perch mean TL	-0.71 (4, 0.29)	-0.65 (4, 0.35)	-0.77 (4, 0.23)	-0.48 (4, 0.52)	0.97 (4, 0.03)	-0.14 (4, 0.86)	0.55 (4, 0.45)	0.39 (4, 0.61)	-0.90 (4, 0.10)	0.11 (4, 0.89)