Chapter 7

Walleye and Sauger Life History

MICHAEL A. BOZEK, DOMINIC A. BACCANTE, AND NIGEL P. LESTER

7.1 INTRODUCTION

The life history of an organism is the series of chronological events that it experiences in order to survive, grow, mature, reproduce, and recruit to perpetuate the species. The genetic characteristics of each individual and of the population as a whole helps determine whether and how an organism responds to conditions in its environment to maximize its reproductive success (i.e., fitness). More specifically, a combination of the morphological and physiological traits allows organisms to respond to environmental conditions and dictates how it reacts to environmental stochasticity and competition, predation, and prey. These environmental conditions and ecological processes continually influence the genetic composition of a species, and on the other hand, also provide the template with which it can interact with them. In this chapter, life history events are chronicled as life stages, each having its own set of challenges and benefits that walleye and sauger must face to be successful in their respective environments. We first review the life history of walleye in detail and then synthesize our current understanding on how this species demonstrates its ecological and evolutionary success through its life history adaptations and approaches. We then briefly review the life history of sauger and compare and contrast it to the major life history events of walleye.

Walleye and sauger are members of the family Percidae, which includes the darters, freshwater perches, and zander (Sloss et al. 2004; see Chapters 2 and 3). They are found in freshwater rivers systems and lakes throughout North America having their distribution influenced by glacial events and further extended through stocking (see Chapter 4). Walleyes have successfully adapted to habitats in a wide array of aquatic systems across North America (see Chapter 5). They exist in rivers and lakes varying in geography, geology, and land use across a wide latitudinal range, which greatly affects growing season and thus life history strategies. The walleye has been described as a coolwater species but are found along a wide environmental continuum reaching their maximum abundance in cool mesotrophic environments where summer maximum temperatures and oxygen concentrations are optimized for the species (Niemuth et al. 1959; Kitchell et al. 1977). Hokanson (1977) suggested that water temperatures must decline to at least 10°C for successful gonadal maturation in walleye (see Chapter 6), which may impose distributional limits in southern latitudes. Kitchell et al. (1977) believed that walleye optimized environmental conditions along a thermal continuum that falls between warmer centrarchid-dominated systems and colder salmonid-dominated
systems. Initially, walleye may have been a riverine species that colonized lakes through river systems created by glacial meltwaters, but their current distribution indicates that they are equally adapted to both lotic and lentic environments. This generalized habitation has been facilitated by their unique adaptation of scotopic vision, enabling walleyes to forage effectively in a dim-light environment. This scotopic vision allows efficient foraging after dark and in environments that have high turbidity, which can apply to many warmwater riverine environments in particular. Where water clarity is higher, scotopic vision allows efficient nocturnal foraging and, thus, results in a temporal niche that separates the walleye from other top predators.

Across their geographic range, the localized distribution and abundance of walleyes is affected by the fish community. In large lakes, walleyes can coexist with other top predators such as northern pike, muskellunge, lake trout, and smallmouth bass without intense competition (Johnson et al. 1977; Marshall and Ryan 1987; Schupp 1992). In smaller lakes, however, walleyes may not normally coexist at high densities with northern pike, smallmouth bass, and other centrarchids (Johnson et al. 1977; Nate et al. 2003; Fayram et al. 2005). More intense ecological interactions may be the reason for this distribution limitation. Kitchell et al. (1977) believed that lakes smaller than 100 ha reduced the likelihood that walleyes could persist with other top predators although they can persist in lakes as small as 30 ha (Wisconsin Department of Natural Resources, Spillerberg Lake, unpublished data). Fayram et al. (2005) found that in the presence of largemouth bass, walleyes have reduced standing stocks or may be precluded from these systems altogether. In 15 Illinois reservoirs, survival of stocked larval walleyes was negatively related to juvenile centrarchid densities (Hoxmeier et al. 2006), which the authors attributed to predation.

In a geographic sense, walleye is the most successful freshwater top predator in North America; its native distribution spans a latitudinal range that exceeds that of other top predators (e.g., lake trout, northern pike, burbot, muskellunge, smallmouth bass, largemouth bass) and has a climatic gradient of approximately 4,000 annual growing degree-days greater than 5°C (Figure 7.1). The success of walleye is due partly to its preference for cooler water (see Chapters 5 and 6). Across a broad latitudinal range, optimal growth conditions for coolwater species exist at some point during the annual cycle. In contrast, optimal growth conditions for warmwater or coldwater species exist over a smaller latitudinal range. The other factor contributing to the broad success of walleye is the plasticity of its life history. As we demonstrate in this chapter, life history traits such as growth, mortality rate, age and size at maturity, and fecundity may vary widely among walleye populations. Much of this variation can be explained by environmental factors that influence growth.

This chapter has four main goals: (1) describe the events that shape walleye life history; (2) describe the variation that exists in walleye life history; (3) identify the major environmental factors that account for this variation; and (4) apply life history theory to explain this variation. We begin by providing an overview of the walleye life cycle, identifying key stages, and documenting variation in the duration of each stage. Details of each life stage (spawning, egg, young of the year [i.e., age 0], juvenile, adult) are presented in Section 7.2. For each life stage, we summarize empirical findings about environmental factors that contribute to variation in traits. Our presentation of empirical findings builds on previous data syntheses (Colby et al. 1979; Carlander 1997) by incorporating more recent data available in the literature and in government databases (i.e., Ontario and Québec). Specific sources of data are identified in the captions of figures.
Figure 7.1. Growing Degree Days (GDD, °C) in North America and the native distributions of walleye and sauger. Geographic distribution is based on maps in Scott and Crossman (1973). The GDD data are based on New et al. (1999) and available at: www.sage.wisc.edu/atlas/maps.php?datasetid = 31&includerelatedlinks = 1&dataset = 31.
Subsequent sections take a more holistic view of the walleye life history variation and offer an explanation that is based on natural selection. Because selection favors individuals that maximize their fitness, the patterns we observe are expected to be optimal solutions to environmental constraints. We focus on the lifetime growth pattern of walleye and show how this pattern is shaped by reproductive traits and influenced by environmental factors affecting growth potential and mortality rate. In a final section, we provide a brief synopsis of sauger life history, of which much less is known, and contrast its life history with that of walleye.

7.2 THE LIFE CYCLE OF WALLEYE

7.2.1 Overview

The walleye is a relatively successful and plastic species having adapted to a wide array of coolwater habitats in rivers and lakes over a large geographic area of North America (Figure 7.2). Walleyes spawn in spring, just after ice-out in northern latitudes of their range, and require minimum temperatures in winter to allow them to complete gamete maturation, which limits their southern distribution. No parental care is provided and first-year survival is low (generally <1%). Eggs hatch in 10–27 d (inversely related to water temperature; see Chapter 13) and year-classes are inversely correlated to variation in spring water incubation temperatures although causality is not well understood. Larvae quickly become free swimming, and young walleyes go through ontogenetic shifts in diet as they increase in size (see Chapter 8). As adults, they are primarily piscivorous although in some systems and, seasonally, macroinvertebrates may constitute a substantial portion of their diet. Diet is variable and depends upon prey availability in the system where they are located. Growth differs between sexes. Size at maturity is not related to climate whereas age at maturity and longevity are related to climate. Age at maturity ranges from 2 years in the south to 11 years in the north and longevity ranges from 30 years in north to 5 years in south.

7.2.2 Spawning

In northern latitudes, walleyes spawn in the spring and may begin spawning under the ice. In lakes, long-wave radiation warms water along the bottom in shallow areas or warmer water from tributary streams starts to mix with lake water. Increasing temperature acts as a stimulus to initiate spawning movements and migrations and spawning behavior (Eschmeyer 1950; Rawson 1957; Preigel 1970). Timing varies with latitude, from late January in the extreme south to June in the far north, and is influenced by both photoperiod and temperature (Scott and Crossman 1973; Becker 1983; Malison and Held 1996). Photoperiod regulates the annual egg and sperm maturation development cycle, whereas temperature induces actual spawning activity. Water temperature during spawning typically ranges from about 5–7°C in the north to 8–10°C in the south. In Savanne Lake, Ontario (48°N), annual trap netting on spawning grounds from 1972 to 1994 produced the highest catches around 6°C that declined sharply as temperature rose to 10°C (Colby and Baccante 1996). In fact, spawning runs into Oneida Lake, New York, tributaries do not commence in years when tributary stream temperatures are lower than lake temperatures (Forney 1967). And at the southern extreme of their range, walleyes may not spawn if water temperatures do not cool sufficiently (Prentice and Clark 1978). In these
cases, populations can only be sustained through stocking (Colby et al. 1979). While spawning temperatures vary, they may only be plastic within a given time period of seasonal maturation brought about by oogenesis, which is timed to photoperiod. In Lake la Ronge, Saskatchewan, walleye spawning runs begin at higher temperatures (7.2–11.1°C) in years when spawning occurs early (April 30–May 7) whereas they spawned at colder temperatures (3.3–7.2°C) in years when spawning was delayed by cold weather (May 17–21) (Rawson 1957; Hokanson 1977). Similarly, in Lake Winnebago, Wisconsin, walleye spawning runs start sooner in warmer tributary marshes (2.2–15.6°C) than in the larger, colder lake (4–11.1°C) (Preigel 1970; see Chapter 5 for additional details on spawning temperature variation).

Walleye is categorized as a broadcast, simple lithophilous spawner (McElman 1983). In lakes, walleyes typically spawn along shorelines in shallow offshore reefs, on point bars, by islands, and on mid-lake reefs (Eschmeyer 1950; Raabe 2006). In rivers walleyes usually spawn in rapids and riffles where there is adequate flow and oxygen for egg development (Walburg 1972; Stevens 1990). Walleyes may also spawn in less traditional, “unexpected” habitats. For example, walleyes have been known to spawn in marshes on sedges and grasses in the Wolf River, Wisconsin (Preigel 1970) and other systems (Minor 1980). They are generally nocturnal spawners, although they spawn in daytime, particularly near peak spawning periods or when light levels are low (Eschmeyer 1950; Ellis and Giles 1965). Because walleyes

Figure 7.2. Graphical representation of variations in growth, maturation, and longevity of walleye across its geographical range. Once walleye reach maturity, females grow larger than males, as shown by the dotted line trajectory. Egg stage, maturity, and longevity are represented by the letters E, M, and L, respectively.
have highly reflective eyes, they are easily spotted on spawning shoals during the night using a strong beam of light. Typically, males become ripe at cooler temperatures and arrive at the spawning grounds before females and remain there longer after the females have left (Ellis and Giles 1965; Becker 1983). Consequently, the sex ratio on spawning grounds generally favors males. Spawning behavior varies in systems but the pattern is generally representative. According to Ellis and Giles (1965), males approach females, sometimes with alternating erected and flattened dorsal fin, and push females from their side. This behavior, coupled with increasing darting motion, attracts other fish. As the group grows, females release their eggs in bouts, sometimes up to three times per minute. Males then release milt over the area where eggs are deposited.

### 7.2.3 Eggs

Walleyes are highly fecund and their eggs are small, averaging approximately 2 mm (1.3–2.1 mm) in diameter (Smith 1941; Colby et al. 1979). Eggs are fertilized as they are deposited onto spawning substrates and remain adhesive from 1 to 5 h or more. The adhesive properties of the egg chorion may enhance fertilization of the eggs by keeping them closer to sperm that is emitted from the males externally. Distance of the eggs from spawning males affects fertilization; in laboratory studies, increasing depth of initially deposited eggs (i.e., depth of layers of eggs that are clumped) relative to milt decreases egg fertilization. Eggs stacked 10 mm deep had a fertilization rate (i.e., percentage of eggs fertilized) of 65%, whereas eggs stacked 7 mm had fertilization rates of 77% and eggs stacked 4 mm had fertilization rates of 86% (Moore 2003).

Once fertilized, water hardens the external membrane of the eggs, which eventually results in the loss of adhesiveness; the length of time eggs remain adhesive is variable. In Lake Winnebago, eggs were adhesive for 1–2 h, but in hatchery investigations adhesiveness can last up to 5 h while eggs are being stirred and some eggs may adhere to each other for up to 4 d (Krise et al. 1986). Once walleye eggs lose their adhesiveness they can fall into interstitial spaces of coarser substrate matrices or they can be carried from the spawning site by water currents and deposited elsewhere. Fertilized eggs remain hyaline, translucent, and have a fairly firm and robust chorion during incubation. In contrast, unfertilized eggs or dead embryos develop a white speck, eventually turning opaque and often developing a fungus (*Saprolegnia* spp.) initially on the chorion before spreading (Eschmeyer 1950; Johnson 1961; Preigel 1970). *Saprolegnia* kills the eggs by disrupting physiological processes of the developing embryo. As hatching approaches, walleye embryos develop black eyes and the chorion begins to soften and deteriorate. Movement by active embryos eventually breaches the chorion releasing the larval walleye where they initially settle to the bottom or get carried away by currents.

The distribution of eggs within spawning areas is clearly heterogeneous. Raabe (2006) mapped individual spawning locations (i.e., spawning pairs) across a shoreline spawning reef in Big Crooked Lake, Wisconsin. He found individual egg patches (per individual spawning bout) located in nearshore areas (generally <0.5 m depth) and few egg patches were found farther than 5 m from shore despite similar physical habitat conditions other than slight increases in depth. Williamson (2008) found the distribution of walleye eggs was discontinuous laterally both within reefs and among reefs despite sites exhibiting the same habitat conditions. It is likely that these walleye spawning habitats were not saturated, and without territoriality, habitat selection reflects an ideal-free distribution (Fretwell 1972). Egg densities also vary
across systems as a function of availability of suitable spawning habitat and adult population size. Egg densities in lake spawning habitats averaged 1,545 eggs/m² in Lake Winniebigoshish, Minnesota (Johnson 1961) and ranged from 145 to 277 eggs/m² on Sunken Chicken Reef in Lake Erie (Fitzsimons et al. 1995). Egg densities were as high as 6,241 eggs/m² in Ontario streams (Corbett and Powles 1986). In contrast, degraded habitats may have low densities unable to sustain natural recruitment as occurs in Saginaw Bay, Lake Huron, on historical spawning sites (Fielder 2002). Walleye egg densities in these degraded, in-lake reef habitats in Saginaw Bay were as low as 1 egg/m² (Fielder 2002) and artificial reef habitat projects (i.e., “restoration” or “enhancement” projects) often see no egg deposition (Neuswanger and Bozek 2004; Williamson 2008).

The substrate matrix at the spawning site and other proximal substrates may play an important role in successful hatching. In lakes, Johnson (1961), Raabe (2006), and Williamson (2008) found that walleyes used and selected spawning sites very close to shore in shallow water over cobble and gravel substrates. In Lake Winniebigoshish, Johnson (1961) found that hatching success was higher on coarser substrates compared with finer substrates; walleye eggs incubating on muck and detritus substrates had the poorest survival (0.6–4.5%), followed by sand (2.7–13.2%) and gravel–rubble (17.5–34.3%). Similar findings have been corroborated by Eschmeyer (1950), Preigl (1970), and Busch et al. (1975). Nate et al. (2003) found that the relative abundance of sand and silt in littoral zones of Wisconsin lakes was inversely related to walleye standing stocks. In years when water levels recede in lakes and coarser shoreline substrates are exposed, walleyes may spawn on less-favorable, smaller-sized substrates that accumulate offshore. Weak year-classes were observed under these conditions in Lake Winniebigoshish (Johnson 1961) and in Rainy Lake, Ontario–Minnesota (Chevalier 1977). While a majority of walleyes reportedly spawn over coarser substrates, some indeed spawn over smaller substrates such as sand on shallow flats despite widespread availability of coarser substrates as they do in Big Crooked Lake, Wisconsin, although survival was not assessed (Raabe 2006). Walleyes, however, can successfully spawn on other substrates. In the Wolf River, Wisconsin, walleyes spawn on flooded marsh vegetation where water flow continues to oxygenate eggs and they consistently produce large year-classes (Preigl 1970), and Niemuth et al. (1972) found walleyes spawning on root masses along lake shores of Tumas Lake, Wisconsin.

The presumed benefit of larger rock substrates, such as gravel and cobble that have lower embeddedness, is that they provide interstitial spaces for eggs to settle into after they lose their adhesiveness, thus protecting them from siltation, entrainment and transport currents, abrasion, and predation. During transport, eggs can be abraded, which may increase the rate of bacterial and fungal infections that can kill incubating eggs (Oseid 1977). Because walleye eggs are located in shallow lake water where wave energy is highest, they can be transported from spawning sites and then deposited laterally, offshore, or even onshore. In particular, large storms create wave energy that readily transports eggs away from spawning areas. For instance, Raabe (2006) found in lakes that water velocities produced from nearshore wind-wave energy were high enough to move walleye eggs in a spawning area 19% of the time while eggs were incubating there. At that same site, velocities were high enough to entrain and move heavier sand particles 5.5% of the time while eggs were incubating, potentially abrading or burying them. As a result, walleye eggs have been found incubating away from spawning sites in Big Crooked Lake on sand flats adjacent to spawning areas where no spawning actually occurred, but where wave action transported them to that location (Raabe 2006).
Johnson (1961) observed walleye eggs stranded along the shores of Lake Winnebigoshish after spring storms. Roseman et al. (2001) found that the number of walleye eggs removed from spawning sites was dependent on the quality of spawning sites and intensity of wind-wave energy in Lake Erie; sites with greater interstitial spaces retained more eggs during storms. Roseman et al. (2001) observed the loss of 80% of walleye eggs from spawning reefs after a gale-force storm; under those conditions, more eggs were removed from shallow portions of the reef than from deeper portions. In rivers, larger substrates may be even more important. Walleyes spawn at velocities between 0.4 and 1.0 m/s, although caution should be applied to data from faster velocities as measurements may not all be nose (i.e., fish position) velocities (Paragamian 1989; Stevens 1990; Liaw 1991; Ichthyological Associates 1996; VanderKooy and Peterson 1998). Even higher velocities have been reported for walleye spawning (see Kerr et al. 1997). At these consistent higher velocities in lotic environments, interstitial spaces undoubtedly protect eggs by reducing abrasion and preventing their transport to suboptimal incubation locations.

While severe wave action is often detrimental to egg survival, slight water movement across spawning sites is desirable because it oxygenates eggs while preventing sedimentation (Daykin 1965; Oseid and Smith 1976). In assessing embryonic anatomy and physiology of walleye, McElman (1983) observed that the temporary embryonic respiratory system is geared to high levels of dissolved oxygen in water. Kitchell et al. (1977) believed that river- and lake-analogous features of slight water movement allowed walleyes to be successful in reproducing in both environments. In many lakes and rivers, this is achieved by spawning on larger, coarse-grained substrates primarily of gravel and cobble where some water movement occurs within the matrix. Also in lakes, walleyes spawn in shallow water (<1.0 m and primarily <0.5 m deep) very close to shore or on submerged shoals where water movement is common (Eschmeyer 1950; Johnson 1961; Raabe 2006). In rivers, walleyes spawn in riffles where water moves across incubating eggs. In some rivers such as the Wolf River system in Wisconsin, walleyes spawn on submerged cattail beds that create “mats” (Preigel 1970) in which sheet-flow water moves across and through the beds providing oxygen for the developing embryos.

Larger substrates for egg incubation may also reduce access by predators. Predation on walleye eggs in aquatic systems is common, although population-level effects have not yet been substantiated to the point of showing that it negatively affects recruitment thus far, but it is possible. Interstitial spaces in coarser substrates, such as gravel and cobble, afford some protection to walleye eggs from predators. White sucker, a common sympatric species in walleye-inhabited lakes and rivers, are often seen in walleye spawning areas but do not appear to target walleye eggs for predation (Preigel 1970; Wolfert et al. 1975; Corbett and Powles 1986). In many systems, white suckers begin to spawn in proximal areas as walleye spawning ends, so their presence may merely be coincidental. Corbett and Powles (1986) found yellow perch and spottail shiners preyed on walleye eggs but did not assess effects on overall walleye recruitment. Wolfert et al. (1975) found that yellow perch, spottail shiners, stonecat, and white suckers preyed upon walleye eggs in Lake Michigan although yellow perch were the predominant predators. Roseman et al. (1996) found that 86% of white perch contained walleye eggs in their stomachs in Lake Erie. Both Wolfert et al. (1975) and Roseman et al. (1996) felt that predation might only be a problem in years with low temperatures and slow warming rates where eggs would be exposed to predation for extended periods and when white perch spawning would overlap to a greater extent with walleye spawning. In those years, spent white
perch in spawning areas would increase predation rates on walleye eggs as they begin to feed after spawning.

Walleye typically exhibit high egg mortality. Eggs are broadcast over substrates without any site preparation or parental care (e.g., egg fanning, protection from predation) as occurs in centrarchids and other fishes. Egg survival estimates from fertilization through hatching in Lake Goegebic, Michigan, ranged from 25% to 50% (Eschmeyer 1950). Johnson (1961) estimated egg survival ranged from 0.6% to 35.7% among sites in Lake Winnibigoshish, Minnesota, and Engel et al. (2000) reported artificially fertilized egg survival rates in incubation chambers held in situ in Escanaba Lake, Wisconsin, ranged from 19% to 62%. In Oneida Lake, Forney (1976, 1977) estimated 99% mortality occurred before walleye reached 10 mm and believed most mortality occurred during the egg stage. Egg survival rates in Lake Erie have ranged from 7% to 43% (Roseman et al. 1996).

Interannual variation in larval production (Johnston et al. 1995) may be due in part to the quality and quantity of eggs produced in any given year, which are related by the size and size structure of the spawning population (Johnston 1997). Hatching success of eggs is positively related to female age and negatively related to female length adjusted for age (Johnston 1997; Johnston et al. 2007). Some research suggests that most mortality in walleye eggs is evident within the first several days after spawning; eggs at this time are either unfertilized, not viable, or very sensitive to environmental perturbation (Holtze and Hutchinson 1989; Fox 1993; Heidinger et al. 1997). For example, Heidinger et al. (1997) found that 83% of walleye egg mortality occurs within 6 h of fertilization. Latif et al. (1999) found that 80% of the mortality in walleye eggs incubating at 10°C occurred at 50–100 h after fertilization (21–42 thermal units [TU = number of days postfertilization × temperature, °C]).

Environmental effects on eggs during incubation are believed to greatly influence mortality and thus year-class strength in walleyes, although understanding factors directly causing stock–recruitment relations in natural systems needs more research. Survival of walleye eggs in natural systems is initially the result of a combination of suitable incubation temperatures and well-oxygenated water. The influence of temperature and oxygen, as well as other factors, including pH, aluminum ion, and fine sediment, have been studied under laboratory conditions and observed in nature, but effects of temperature and oxygen predominate. Cooler water temperature negatively affects egg development rates, thus increasing the amount of time eggs are subject to other sources of egg mortality such as predation, spread of fungus, wave action and abrasion, and transport to unsuitable substrates. However, while water temperature fluctuations influence year-class strength, there does not appear to be a direct physiological basis for direct mortality on eggs from temperature fluctuations under natural conditions. In fact Koonce et al. (1977) concluded that only under extreme climatic conditions in Lake Erie could lethality be directly attributed to temperature. Engel et al. (2000) found no relation between in situ hatching success and water temperatures in Escanaba Lake from 1985 to 1992. Extended water temperatures below 6°C or above 19°C, however, can be lethal to developing walleye embryos (Smith and Koenst 1975; Schneider et al. 2002). Latif et al. (1999) found that 80% of the mortality in walleye eggs incubated at 10°C occurred at 50–100 h posthatch (21–42 TU) when germinal layers of cells are transformed into various body organs; it is at this time that walleye eggs might be most susceptible to sources of mortality.

The reasons for a lack of temperature fluctuation-associated mortality are twofold. First, walleye eggs are resilient to most water temperature fluctuations they may encounter in nature during spring spawning and incubation periods. Moreover, because walleyes spawn near
ice-out in northern latitudes, the species clearly has evolved to allow eggs to survive at low water temperatures. In the laboratory, Allbaugh and Manz (1964) found development and survival of embryos to the eyed stage was unaffected by temperature fluctuations as high as 21°C. Schneider et al. (2002) found no increase in mortality occurring to the eyed stage when eggs were subjected to either a 20°C temperature fluctuation in 12 h or when eggs were then returned to 10.5°C in 8 h. In the same study, percent hatching success was also not affected by temperature swings of nearly 14°C. Second, the latent heat of water (energy resistance to temperature change) is too high to allow temperatures to fluctuate to the degree they would need to in order to kill incubating eggs in spawning areas. For instance, Raabe (2006) found that variation in temperatures along a depth profile of a walleye spawning area (0–2 m deep) in a northern Wisconsin lake were usually less than 2°C in any 24-h period and in 2 years no temperatures in these shallow spawning areas ever dropped more than 4°C across the entire spawning season; thus, no temperatures at any depth ever approached lethal conditions.

Temperature does influence fertilization and embryonic development rates. Koenst and Smith (1976) found that optimum fertilization rates occurred at 6–12°C in laboratory studies, which correspond to the temperatures often observed at spawning sites in nature (Niemuth et al. 1959; Preigel 1970; Hokanson 1977). On the other hand, optimum incubation temperatures for eggs ranged from 9–15°C with peak hatching occurring at 15°C (Koenst and Smith 1976; Engel et al. 2000). In both laboratory and field studies, egg development rates increase with increasing water temperature (Johnson 1961; Preigel 1970; Koenst and Smith 1976). Colby et al. (1979) reported on work by W. L. Hartman (unpublished data) using data from four different studies to correlate progress to 50% hatching based on average incubation temperature. The resulting equation: \( y = -5.481 + 1.062x \), where \( y \) is 100/d to the mid-hatch time and \( x \) is the average incubation temperature in °C, describes this relationship. In Savanne Lake, Ontario, using Hartman’s equation and measuring water temperatures on the spawning grounds from 1972 to 1991, we estimated the number of days to 50% hatching ranged from 10 to 26 d, with a mean of 18 d (authors’ unpublished results). Incubation to swim-up periods have been reported to range from 10 to 27 d under natural conditions (Niemuth et al. 1959; Johnson 1961; Preigel 1970; Engel et al. 2000) and from 5 to 30 d in laboratory settings (Hurley 1972; Koenst and Smith 1976; McElman and Balon 1979).

Standardized approaches to predict hatching times incorporate thermal units (TU), which are the sum of the mean daily water temperatures above 0°C from fertilization through hatching (see Chapter 13). McElman and Balon (1979) found that at 15°C, walleye embryo eye pigmentation was observed at 76 TU and hatching at 135 TU (approximately 9 d). At lower and more variable water temperatures (7.8–11.1°C), Hurley (1972) observed hatching from 257 to 265 TU. Jones et al. (2003) developed an equation for describing the percent of daily embryonic development as follows: \( y = 0.0479T^2 - 0.2385T + 2.499 \) based on work by Smith and Koenst (1975) where \( y \) is the predicted percent of development per day towards hatching and \( T \) is the mean daily water temperature in °C; values of \( y \) are summed for each day and when \( y \) reaches 100, hatching occurs.

Other characteristics of incubation sites can reduce or inhibit successful hatching of walleyes. Oxygen concentrations above 5–6 mg/L are optimal for walleye egg incubation and survival (Oseid and Smith 1971; see Chapter 6) although Colby and Smith (1967) reported successful, albeit reduced, hatching occurred at levels less than 3 mg/L. Auer and Auer (1990) believed that low dissolved oxygen, along with elevated ammonia nitrogen and hydrogen sulfide at the sediment–water interface in the Fox River, Wisconsin, precluded successful
incubation and hatching. Locations with surficial sediment chemical oxygen demand (COD) greater than 40 mg O_2/g dry weight were not deemed suitable for walleye egg incubation. Ammonia (NH_3) concentrations greater than 29 µg/L are deemed chronically unsuitable for walleye reproduction (USEPA 1976, 1987). Presumably, areas that have gravel–cobble substrates and moving water and that are generally selected for spawning reduce the occurrence of these adverse microhabitat conditions.

Recent studies indicate that hatching success in walleye depends partly on the number of eggs produced (i.e., density-dependent survival) as well as maternal factors affecting the quality of eggs. Evidence of density-dependent survival was provided by Johnston et al. (1995) who showed variation in hatching success was related to annual variation in egg production. Maternal influences on egg and larval survival have been demonstrated in laboratory studies (reviewed by Venturelli et al. 2010b). Both maternal age or size (Johnston 1997; Johnston et al. 2007) and egg quality (e.g., egg size, lipid content; Moodie et al. 1989; Czesny and Dabrowski 1998; Johnston et al. 2007) have positive effects on the survival of eggs and larvae. Egg size has cascading effects because it is positively related to larval size (Moodie et al. 1989; Johnston 1997; Johnston et al. 2007), which, in turn, increases survival through negative effects on cannibalism, deformities, and starvation (Moodie et al. 1989; Johnston and Mathias 1993, 1996). Johnston (1997) found that hatching success in the laboratory was positively related to female age and negatively related to female length adjusted for age. In field studies, Craig et al. (1995) reported higher survival of walleye eggs from females that were older and smaller at age. Pond experiments (Venturelli et al. 2010b) have shown a positive effect of egg size on larval survival after 2 months.

These findings imply that the size and age structure of the spawning population have complex effects on offspring survival. Recent research highlights the value of older fish in contributing differentially to recruitment of fish in general (Kamler 2005; Venturelli et al. 2009) and of walleyes in particular (Johnston 1997; Johnston et al. 2007; Venturelli et al. 2010b). Hansen et al. (1998) found that the abundance of walleyes age 5 and older were the most descriptive in estimating recruitment success in Escanaba Lake. Similarly, Venturelli et al. (2010b) found that the maximum recruitment rate of walleyes in western Lake Erie approximately doubled when the abundance of female walleyes age 5 and older increased from 7% to 21%. These studies underscore the value of older females to recruitment processes. Research by Casselman et al. (2006) also suggests that there is considerable variation in the quality of male walleye sperm. This variation in sperm quality can affect fertilization rates, although its relation to age is not known. In their laboratory studies, male walleyes with the fastest swimming sperm had fertilization rates 40% greater than males with the slowest swimming sperm.

7.2.4 Age 0 (Hatch to Age 1)

7.2.4.1 Habitat Selection and Feeding

At hatching, larvae are 6–9 mm total length (TL) at the caudal fin fold (Preigl 1970; see Chapter 13). Because walleyes hatch without a full complement of fins and fin rays (McElman 1983), they are still technically considered embryos (McElman and Balon 1979; McElman 1983) until they develop further. Fin ray ossification begins at 10 mm TL and is complete by 18 mm (Nelson 1968a). Scale development begins at 24 mm and is complete by 45 mm (Preigl 1964). Adult coloration is developed at about 35 mm (Nelson 1968a).
Age-0 walleyes are ineffective swimmers and can only withstand low water velocities (Walburg 1971). Immediately after hatching, larvae are not free swimming but rather lay on the bottom occasionally moving into the water column. Generally embryos remain sedentary for only a short time (<1 d), making irregular and uncontrolled movements at first but then quickly learning to swim (Becker 1983). Without air in their swim (gas) bladder initially, they are negatively buoyant at first, with their negative buoyancy contributing to their initial sporadic and erratic movements.

Because larvae are not free swimming immediately after hatching, they are subject to water currents caused either by wind–wave interactions in lakes or hydraulic current patterns in streams. The interaction between the strategy of drifting larvae in water currents and their successful transport to suitable nursery areas underlies the successful coupling of two sequential life stage habitat interactions. Raabe (2006) found that water velocities along a shoreline spawning shoal in Big Crooked Lake exceeded levels that could induce transport of eggs up to 19% of the egg incubation period and probably are of a magnitude to influence the movements of free-swimming larvae. Jones et al. (2003) found a decrease in survival of drifting age-0 walleyes with increasing drift distance to nursery habitats. In Lake Erie, water currents carry age-0 walleyes to rearing habitats (Nepszy et al. 1991), and Roseman et al. (2005) found that currents in Lake Erie concentrate zooplankton along with larval walleyes, making these areas good foraging localities. Clearly water currents influence the fate of very young walleyes. High discharge events such as flooding in rivers can also trigger downstream movement of age-0 walleyes (Harvey 1987), although the ecological consequences of these events are not clear.

Walleye embryos hatch with limited yolk and, as a result, need to start feeding soon after hatching; in fact feeding begins before their yolk sacs are completely absorbed (Engel et al. 2000). Initial diet items include small zooplankton such as rotifers, copepods, nauplii, small cladocerans, Chaoborus spp., and chironomids (Mathias and Li 1982; Engel et al. 2000; Galarowicz et al. 2006; Hoxmeier et al. 2006; see Chapter 8). Prey density probably affects growth and survival of age-0 walleyes as food limitations can result in cannibalism and starvation in some systems (Chevalier 1973; Jonas and Wahl 1998). In Lake Erie, pelagic larval walleyes show high spatial overlap with ichthyoplankton density (Roseman et al. 2005). For postswim-up age-0 walleyes, the timing of initial spring phytoplankton blooms and the resulting production of zooplankton that feed on the phytoplankton may be crucial to walleyes at this stage. If phytoplankton growth is delayed, in turn reducing zooplankton density until after larvae emerge, young walleyes may starve. The extent to which that occurs in natural systems is unknown.

Once free swimming, walleyes are believed to move out into open water in some systems to begin openly feeding, primarily on zooplankton (Eschmeyer 1950; Faber 1967; Morsell 1970; Mathias and Li 1982). In Escanaba Lake, age-0 walleyes shifted their habitat use in late June (at 35 mm TL) from pelagic to littoral zone habitats (Engel et al. 2000). Initially in spring, sampling near the water surface with tow nets produced greater catches of age-0 walleyes than did deeper tows; after mid-June, walleyes made night movements near shore where they could be captured by seining at night. In contrast, in Big Clear Lake, Ontario, age-0 walleyes initially used areas of high macrophyte abundance in waters from 2 to 5 m deep (mid-June to mid-July), later shifting to areas of low cover complexity (mid-July to late August) (Pratt and Fox 2001). Those authors believed the shift in habitat choice may have been related to attempts to avoid predation by adult walleyes. However, some studies suggest that
when young walleyes inhabit macrophyte beds, these beds may also be inhabited by largemouth bass where they may get preyed upon; the inverse relations in abundances of walleyes and largemouth bass provide some circumstantial evidence of this possibility (Fayram et al. 2005). Quist and Guy (2004) found that larval walleyes 5–7 d old (initial swim-up) did not respond to simulated predator attacks whereas larval saugeyes (walleye × sauger hybrids) did; but at 12–14 d they both showed avoidance behavioral responses. In rivers, recently hatched walleyes migrate downstream with stream currents and increase their drift rates during periods of low light (i.e., cloudy nights or small moon stages). In northern Ontario, age-0 walleyes appear to orient more to prey items than specific habitat types (Leis and Fox 1996).

Walleye clearly undergo shifts in diet and at each life stage consume the most profitable diet items available (Galarowicz et al. 2006; see Chapter 8). During their first year of life, walleye feeding switches from zooplankton to benthic invertebrates and then to fish (Forney 1966; Colby et al. 1979; Mathias and Li 1982; Fox 1989; Fox et al. 1992; Madon and Culver 1993; Chapter 8). Target prey size increases as walleye grow; gape width limits prey size (Preigle 1970; Hokanson 1977; Serns 1982; Engel et al. 2000). Bremigan and Stein (1994) clearly articulated the necessary link between gape width, available zooplankton size, and recruitment dynamics in fish. The onset of piscivory in walleyes typically occurs between 50 and 80 mm (Smith and Moyle 1945; Smith and Pycha 1960; Walker and Applegate 1976), but has been observed in postlarval walleyes (Li and Mathias 1982) and age-0+ walleyes as small as 30 mm (Maloney and Johnson 1957) and as large as 100 mm (Li and Ayles 1981a, 1981b; Kolar et al. 2003). Smith and Pycha (1960) found walleyes shifting to larger prey than zooplankton at 60 mm TL. In Escanaba Lake, some walleyes consumed prey fish within 2 weeks of hatching, although it was a minor part of their diet (Engel et al. 2000). Similar diet shifts are observed in zander (pikeperch), a close relative of walleye in European waters. For example, Van Densen et al. (1996) reported that zander in a lake in The Netherlands fed exclusively on zooplankton until they reached a length of 40 mm, at which point they began feeding on macroinvertebrates and fish; zanders larger than 70 mm fed exclusively on fish.

Graeb et al. (2005) conducted laboratory experiments to compare the ontogeny of piscivory in walleye (a specialist piscivore) and yellow perch (a dietary generalist). Walleyes of all size-classes (20–80 mm) exhibited piscivorous behavior, whereas yellow perch showed negative to neutral selection for fish prey and slower growth than did walleyes when feeding on fish. Walleyes foraged more efficiently than yellow perch on all prey types, in part because gape widths of walleyes increased more quickly with body size. Galarowicz et al. (2006) examined diet shifts in age-0 walleyes (20–150 mm) through experiments in which zooplankton, benthic invertebrates, and fish were made available at different density combinations. Consumption of each prey type changed with walleye size and prey densities. Small walleyes (20 mm) selected zooplankton and fish, whereas larger walleyes (40–100 mm) selected benthic invertebrates and fish. Walleyes larger than 100 mm selected only fish. This study also revealed that walleye growth can be sustained on benthic invertebrates if they are abundant, but not on zooplankton; walleyes larger than 40 mm actually lose weight when feeding exclusively on zooplankton. (See Chapter 8 for additional discussion of diets and ontogenetic diet shifts.)

Ontogenetic diet shifts in walleye are accompanied by changes in retinal structure that enhance scotopic (dim light) vision and affect habitat selection (Ali and Anctil 1977; Braekevelt et al. 1989; Vandenbyllaardt et al. 1991). The tapetum lucidum, a light-reflecting layer of the retina that increases retinal sensitivity (Craig 1987), is present when fish are 37 mm long and
fully developed when walleyes are 140 mm long. Aggregation of photoreceptor cells to form macroreceptors, which are believed to increase acuity in dim light, begins when walleyes are approximately 60 mm long. Before the development of the tapetum lucidum, walleye are positively phototactic at ambient daytime illumination levels and frequent the limnetic zone, feeding mainly on zooplankton (Houde and Forney 1970). At this stage, walleyes may be attracted to surface waters at night by the use of an artificial light (Regier et al. 1969). Laboratory studies have shown that the phototactic response shifts from positive to negative when walleyes are 32–40 mm long (Bulkowski and Meade 1983). In nature, walleyes 25–30 mm long frequent the littoral zone and are sometimes found in shallow sheltered bays, but walleyes gradually move from littoral shoals into deeper water as summer progresses (Raney and Lachner 1942). This habitat shift, which is correlated with the development of scotopic vision, indicates a continuing adaptation to progressively decreasing light intensities (Ryder and Kerr 1978). Early development of scotopic vision permits young walleyes to exploit dimly lit environments not used by other predators, thereby enabling relatively rapid growth during their first year of life.

7.2.4.2 First-year Growth

The optimum temperature given by Smith and Koenst (1975) for growth of small walleyes (65–87 mm) is 22°C; however, there is some disagreement with respect to a precise value and an optimum range around this value may be more appropriate depending on other environmental conditions (see Chapters 6 and 13). First-year growth of walleyes is highly variable among populations, but much of this variation can be explained by thermal differences (Figure 7.3). This effect was first reported by Colby and Nepszy (1981) who used an agricultural index of thermal energy to explain latitudinal variation in first-year growth of walleye. This index, mean growing degree-days above 5°C (GDD), uses daily measures of maximum air temperature to calculate the cumulative degrees above 5°C during an annual cycle. Colby and Nepszy (1981) showed that mean TL at first annulus increased with GDD, ranging from approximately 100 mm at GDD = 1200°C (northern Ontario) to 240 mm at GDD = 4000°C (southern United States). As illustrated in Figure 7.3, first-year growth is approximately the same for both sexes (Figure 7.3A) and 72% of among-population variation in growth is explained by GDD (Figure 7.3B). Residual variation is expected due to differences in food availability and, thus, consumption rates among populations. Because food consumption combines multiplicatively with temperature in determining growth rate (e.g., Kitchell et al. 1977) residuals are expected to increase with GDD, as illustrated in Figure 7.3B.

7.2.4.3 First-year Survival

Data from a few well-studied walleye populations imply that average survival from egg to age 1 is in the order of 0.01% (Baccante and Colby 1996). The vast majority of eggs deposited each year do not contribute to the age 1+ walleye population because many eggs are not fertilized, fail to hatch, or age-0 fish die as a result of predation, starvation, or disease. Fall surveys of age-0 walleye abundance are often conducted on intensively managed lakes because they provide an index of year-class strength that forecasts harvest potential. For instance Serns (1982, 1983) found that electrofishing catch per unit effort (CPUE) was related to the density of young walleyes in northern Wisconsin lakes. Johnson (1999) was able to signifi-
Figure 7.3. First-year growth of walleyes. Total length at age 1 is mean back-calculated length at first annulus. Points are estimates for 38 populations reported in Colby et al. (1979) or Carlander (1997) for which sex-specific data were available. In panel (A), male estimates are plotted against female estimates to demonstrate that first-year growth does not differ among sexes. In panel (B), mean length at age (i.e., average of male and female estimates) is plotted against GDD, demonstrating that first-year growth increases with GDD: mean length = 25.6 + 0.066 GDD ($r^2 = 0.72$). GDD values for each population were supplied by Yingming Zhao, Ontario Ministry of Natural Resources (see Zhao et al. 2008), based on interpolation of the IPCC 1961–1990 climate normals for North America.
cantly establish that fall age-0 walleye abundances forecasted future years-classes in northern Wisconsin lakes. These studies also indicate high annual variability in fall abundance of age-0 walleyes. Because annual variability in egg production (based on estimates of spawner abundance and fecundity) is low relative to variability in the fall abundance of age-0 walleyes, it is usually assumed that variability in year-class strength is mainly due to variability in survival during the first year.

First-year survival is expected to be highly variable because a large number of abiotic and biotic factors influence young walleye survival. Abiotic factors associated with walleye recruitment include water temperature, wind, and water level characteristics (Eschmeyer 1950; Johnson 1961; Hokanson 1977). Biotic factors include competition, cannibalism, and intraspecific predation. Probably the most important abiotic factor is water temperature. Its importance was first noted by Forney (1976) who found that spring warming influenced year-class strength in Oneida Lake. More recent studies have shown that spring temperatures influence year-class strength in Lake Erie (Madenjian et al. 1996) and in Escanaba Lake (Hansen et al. 1998). Moreover, year-class strength in walleyes appears to be a regional phenomenon (Beard et al. 2003); for lakes within a geographic region, variation in year-class strength was correlated among lakes, suggesting a common environmental determinant such as temperature.

Temperature affects many processes that influence survival during the first year of life. Spring water temperatures alter the timing of spawning and the duration of egg incubation (Busch et al. 1975), which in turn affects the length of time that eggs are exposed to a variety of environmental stressors. Temperature conditions during the spring and summer affect growth and, consequently, vulnerability to predation. It is not surprising, therefore, that first-year growth is sometimes correlated with year-class strength. For zander, Buijse and Houthuijzen (1992) observed that year-class strength in Lake Ijssel, The Netherlands, varied 300-fold over the period 1966–1989 and both mean length and year-class strength in November were highly correlated with mean summer temperature, and thus, with each other. In contrast, Madenjian et al. (1996) observed in Lake Erie that first-year growth was poorly correlated with recruitment. The major determinant of recruitment was abundance of an important prey species (gizzard shad) during the fall before spawning. This result implies that adequate lipid reserves during the winter are needed to support egg production in the following spring. It suggests that recruitment variability is not due solely to variation in first-year survival; variation in egg production may also play a role. More direct evidence was provided by Henderson and Nepszy (1994) who observed variation in year-class strength in Lake Erie was associated with energetic condition of the spawning stock (see also Henderson and Morgan 2002).

A potential side effect of slow growth in age-0 walleyes is size-dependent winter mortality. While common in other species (Shuter et al. 1980; Post and Evans 1989; Bernard and Fox 1997), the effect of body size on winter mortality is somewhat equivocal for walleye. Copeland and Carlile (1998) found no relation between lipid storage and overwinter survival of walleyes in hatchery ponds. Pratt and Fox (2002) did not detect an effect on overwinter survival, but found body weight and lipid concentrations were lower in ponds where predators were present, suggesting that there may be energetic costs associated with avoiding predation. Pratt and Fox (2002) believed that overwinter survival was enhanced in walleyes due to a combination of (1) larger size in the fall relative to other north temperate fishes and (2) continued feeding during winter months (see also Kelso 1972).
Biotic factors also affect age-0 survival and recruitment in walleye. Competition with other species for shared food resources may constrain growth rate, prolonging the period of high vulnerability to predation. While they are small, walleyes are potential prey for many cohabitant fishes including yellow perch, smallmouth bass, rainbow smelt, sauger, bullhead, burbot, northern pike, and others (Colby et al. 1979). In some lakes, cannibalism has also been identified as an important source of predation (e.g., Forney 1980). The importance of biotic factors relative to abiotic factors is hard to quantify, but some recent work has indicated that biotic interactions can have an overriding influence on walleye recruitment (Quist et al. 2003a, 2004). Quist et al. (2003a) proposed a biotic–abiotic confining hypothesis (BACH) to explain the role of abiotic and biotic mechanisms on walleye recruitment. This study examined the impact of white crappies on walleye recruitment in Kansas reservoirs. During years with low white crappie abundance, walleye recruitment was highly variable and probably confined by abiotic factors. However, when white crappie abundance surpassed a threshold, walleye abundance was always low.

These studies suggest that predation can have an overriding influence on first-year survival and, thus, walleye recruitment. Quist et al. (2003a) point out that an important theory regarding the native distribution of percids in North America states that interactions with centrarchids restricted their success in southern latitudes (Collette et al. 1977). Several studies demonstrate that walleye recruitment is generally poor when centrarchids are a dominant member of the fish community (Schiavone 1985; Santucci and Wahl 1993). In Wisconsin lakes, Fayram et al. (2005) found the abundance of largemouth bass was negatively related to the abundance of walleyes in Wisconsin lakes. In the Kawartha Lakes, Ontario, where walleyes were previously dominant, increasing water temperature and clarity in recent years has favored centrarchids and dramatic declines in walleye abundance have occurred (Robillard and Fox 2006). Mechanisms driving the decline in walleyes have not been identified, but it seems likely that centrarchid predation on young walleyes may be an important factor.

**7.2.5 Juvenile (Age 1 to Maturation)**

**7.2.5.1 Habitat Selection and Feeding**

The juvenile life stage in walleye is a period of relatively rapid growth, whose duration varies inversely with growth rate. Minimum size of maturity is approximately 300 mm TL in males and somewhat larger in females. In the south, where growth is more rapid, this size threshold may be attained within 2 years, but in some northern lakes where growth is slow, the juvenile life stage may exceed 10 years (Venturelli et al. 2010a).

Habitat selection of yearling and subadult walleyes appears to match that of adults (Ryder 1977). Preferred water temperature is in the range of 20–24°C (Coutant 1977; Wismer and Christie 1987) and based on other published studies, Christie and Regier (1988) concluded that optimum temperature for walleye growth is 18–22°C. Preferred light intensity was estimated as 8–68 lx by Lester et al. (2004a), based on observations reported by Scherer (1971) and Ryder (1977). Suitable dissolved oxygen concentration has been reported as greater than 3 mg/L although increased opercular venting can occur at 6 mg/L (Petit 1973) (see also Chapters 5 and 6).

The importance of light to walleye behavior was first investigated by Ryder (1977). Diving observations in Ontario lakes indicated that yearling, subadult, and adult walleyes often
swam together in small to medium size schools (i.e., 3–150 fish) and that these three age
categories reacted almost uniformly in movements and feeding behavior under various light
intensities. Because of their high sensitivity to light, walleyes were often observed to be rest-
ing during daytime illumination, partially concealed in the interstices of boulder shoals or in
cover of dense aquatic vegetation, sunken logs, or other debris on lake substrates. Daytime
transects conducted in waters of different transparency indicated that walleyes were less ac-
tive in clear waters. Angling experiments demonstrated that CPUE increased during the eve-
nings as surface illumination levels declined, suggesting that walleyes are more likely to search
for food at twilight or night than on sunny days.

Ryder’s (1977) observations about the importance of light are supported by other stud-
ies. Ultrasonic tracking (Kelso 1976, 1978) verified that walleyes are relatively inactive
during the day and increase their activity at dusk, when they typically initiate feeding. Gillnetting studies (Carlander and Cleary 1949) demonstrated that walleyes are more vul-
nerable to capture at night and that the greatest periods of mobility are dawn and dusk.
The effect of light on walleye behavior is well known to most ardent anglers (Ryder 1977);
walleyes in waters of low transparency are more inclined to be captured throughout day-
light than those in clear lakes. Also, abrupt daytime decreases in subsurface light intensity
(e.g., due to storm clouds and increased wave action) are often associated with increased
catch rates.

The other abiotic factor of key importance to walleye is temperature. Temperature affects
metabolic rate, feeding activity, food conversion efficiency, and consequently, growth of wall-
eyes (Kitchell et al. 1977; see Chapter 6). Maximum growth efficiency of walleye appears to
occur in temperatures of 18–22°C (Hasnain et al. 2010), and when these temperatures occur in
the epilimnion, walleye will reside there even in clear deep lakes, where optimal light condi-
tions during the day exist in deeper water below the thermocline. Under these circumstanc-
es, walleye can be found resting in cover to reduce high light intensity (Ryder 1977).

It is widely acknowledged that walleyes have an affinity for the bottom. Their scotopic
vision provides walleyes with the ability to detect prey in darker conditions than most other
visual predators. This visual advantage is important considering that walleyes do not have
other sensory organs, such as the lateral line, as well developed as in other percids (Disler
and Smirnov 1977). Kerr et al. (1997) reported that preferred substrates are generally thought
to be clean hard materials with abundant cover in the form of boulders, rooted submerged
vegetation, trees, and logs (Holt et al. 1977; Schlagenhaft and Murphy 1985; Johnson et al.
1988; Paragamian 1989). Optimal vegetative cover (percentage of the bottom covered with
aquatic vegetation) is believed to be in the order of 25–45% (McMahon et al. 1984) although
the quantitative basis for this level was unclear.

The combined role of light and temperature in determining suitable walleye habitat in
lakes was explored in a thermal–optical habitat model developed by Lester et al. (2004a).
They showed that suitable habitat, defined as benthic area that offered optimal temperature
and light conditions, was an important determinant of walleye production in Ontario lakes.
Thermal–optical habitat area, combined with a nutrient index (total dissolved solids, TDS),
accounted for 70% of the observed variation in sustained yield of walleyes from angling and
commercial fisheries.

Juvenile walleyes, like adults, are largely piscivorous, opportunistic, and selective, feed-
ing on a large variety of fish species, whereas younger walleyes feed on zooplankton and
benthic invertebrates (Colby et al. 1979; Schneider et al. 1991; Galarowicz et al. 2006; see
Prey availability also plays a role in the diet of juvenile walleyes. Lyons (1987) found that juvenile walleyes selected for darters and against cyprinids in the littoral zone of Sparking Lake, Wisconsin. However, when age-0 yellow perch became abundant, yellow perch became more important in their diet. In contrast, Lyons (1987) also found that juvenile walleyes preferred bluntnose minnow to age-0 yellow perch in laboratory trials suggesting that availability of prey in Sparkling Lake may be a function of both overall abundance and movement (i.e., location) relative to locations of walleyes.

Colby et al. (1979) provided many references that list the diverse prey fish that walleyes feed on. Walleyes have a well-developed set of sharp teeth, which aids them in the capture and retention of prey fish. R. A. Ryder (Ontario Ministry of Natural Resources, personal communication) has observed walleyes to capture a prey fish from the side, and then move it into a position where the head of the prey is pointing into the mouth. Any movements by the prey will then result in forward motion into the walleye’s mouth, and it also ensures that dorsal spines, such as in yellow perch, collapse to facilitate ingestion. Given a choice, it appears that walleyes will select soft-rayed fish instead of rigid-rayed ones. Schneider et al. (1991) report that in Lake Michigan, walleyes were feeding mostly on soft-rayed alewives, white suckers, and rainbow smelt, avoiding common rigid-rayed species, such as yellow perch and brown bullhead. Knight et al. (1984), in a study of walleyes in Lake Erie, found that spiny-rayed fish were the least important prey, contributing from 0% to 40% to the walleye’s diet. Cisco (i.e., lake herring) is an important food item for walleyes in coolwater fish communities (Ryder and Kerr 1978; Kaufman et al. 2006).

7.2.5.2 Sexual Determination

Sexual determination in juvenile walleyes relies on internal examination of gonads. Eschmeyer (1950) provided a detailed description of the development of gonads in the walleye. A distinguishing feature of the ovary is the anterior end, which is broadly rounded or comes to a blunt point. Ovaries in small, 70-mm female walleyes show very little obvious development other than heavy pigmentation throughout their length. As the fish grows to around 130 mm these melanophores are distributed along a narrow band on each side of the ovary. This pigmentation is usually restricted to a few scattered melanophores anterior and dorsal along the ovaries. Testes are distinguishable from ovaries in immature fish by the lack of the blunt anterior end. Testes are more gradually elongated at the anterior end. Testes in small, 70-mm male walleyes are smaller than female ovaries of the same size fish. They are fine threads with virtually no pigmentation (Colby et al. 1979).

7.2.5.3 Juvenile Growth Rate

During the juvenile life stage, male and female walleyes usually grow at the same rate. Differences in growth rate typically do not appear until after maturation, when females sustain higher growth rates. Some studies have reported that females were larger than males by the end of the first year, but this early divergence seems to appear more in the south and in reservoirs where average growth rates tend to be faster (Carlander 1997). Our compilation of the published walleye data indicates that differences in mean length at age do not appear until TL exceeds 350 mm (Figure 7.4), which coincides with the average size of maturity for males (see section 7.2.6.2).
Latitudinal differences exist in seasonal growth patterns and annual growth rate. At northern extremes, water temperature rarely exceeds 22°C and optimum conditions exist for only a short period during the summer. Consequently, most of the annual growth in northern populations occurs from mid-June to August (Forney 1966; Kelso and Ward 1972; Carlander 1997; Swenson 1977). In contrast, summer water temperatures typically exceed 22°C in southern latitudes and most of the annual growth occurs during late summer and autumn (Carlander 1997). For Kansas reservoirs, where temperatures often exceed 26°C throughout the summer, 80% of growth is achieved between August and October (Quist et al. 2002). The latter study also found that mean summer air temperature explained 59–77% of the variation in growth of age-2 and age-3 walleyes, reductions in growth being evident when air temperature exceeded 25°C. Studies have shown that walleye reduce their feeding activity and seek thermal refugia when water temperature exceeds 22°C (Kelso 1972; Ager 1977; Hokanson 1977; Williams 1997; Kocovsky and Carline 2001).

In general, annual growth rate increases from north to south (Carlander 1997). Colby et al. (1979) reported data that indicate fivefold differences in growth between southern and northern populations. Colby and Nepszy (1981) proposed that these differences were largely

![Figure 7.4. Comparison of mean length at age in male and female walleyes. Each point is an age-specific estimate from one population. Dashed line is line of equality; solid curved line is the LOWESS fit. The two lines deviate when TL is greater than 350 mm. Graph includes data from 484 walleye populations (402 in Ontario, 52 in Québec, and 30 in USA). Data sources are Colby et al. (1979), Carlander (1997), Morgan et al. (2003), and Venturelli et al. (2010a).](image-url)
due to variation in annual input of thermal energy, which they measured using GDD. More recent synoptic reviews of walleye growth differences over a broad latitudinal range are provided by Quist et al. (2003b) and Zhao et al. (2008). Both studies confirm the previously reported relationship between walleye growth rates and GDD. Quist et al. (2003b) highlighted the additional importance of food availability in determining growth rates, while Zhao et al. (2008) suggested that life history traits are also linked to ancestral linkages from different glacial refugia.

7.2.6 Adults

7.2.6.1 Determination of Sexual Maturity

Determination of sexual maturity in walleye is usually made by visual inspection of fish. One method is to look for the expression of sexual products (milt, eggs) when fish are captured during the spring spawning season. Alternatively, maturity can be assessed in the fall by internal examination of the ovaries or testes. Duffy et al. (2000) provided a good textual description and photo documentation of the various maturity stages of walleye based on gonad conditions during the fall. However, being mature does not necessarily ensure that an individual will spawn. Henderson and Nepszy (1994) warned that some mature female walleyes with eggs may not spawn if their condition is poor.

7.2.6.2 Age and Size of Maturity

Walleye are iteroparous, reproducing multiple times during their life span. Because onset of sexual maturation varies among individuals within a population, maturation of a population is usually characterized by the age (or size) when 50% of the population is mature. Colby et al. (1979) reported walleyes maturing as early as 2 years in Texas and as late as 8 years in northern Ontario. More recent work has revealed larger variation. In Ontario, walleye maturation ranges from 3 to 11 years in females and 2–9 years in males (Morgan et al. 2003). In some slow-growth populations of northern Québec, walleyes may take as long as 12–15 years to reach maturity (Venturelli et al. 2010a).

A negative correlation between age of maturity and GDD was first noted by Colby and Nepszy (1981). A functional relationship was subsequently described by Baccante and Colby (1996) and has been supported by more recent studies (Gangl and Pereira 2003; Sullivan 2003; Venturelli et al. 2010a). This negative relationship is demonstrated in Figure 7.5A, which is a compilation of published data. Many studies did not distinguish between sexes, but Venturelli et al. (2010a) described sex-specific relationships based on maturity data from Ontario and Québec (shown in Figure 7.5A). These results indicate that males typically mature 1–2 years earlier than do females (Figure 7.5B).

Whereas there is strong support for a relation between GDD and age at maturity, there is no indication that GDD affects size at maturity (Venturelli et al. 2010a). Our data compilation indicates that, on average, males mature at about 350 mm and females at about 450 mm (Figure 7.6A). There is, however, substantial variation among populations in size of maturity (i.e., 262–444 mm in males and 331–562 mm in females for our data set). Male size at maturity is smaller than, but correlated with, female size of maturity (Figure 7.6B). On average, males mature at a total length that is approximately 80% of female length at maturity.
Figure 7.5. In panel (A), age at 50% mature of female and male walleyes (from the same populations) are plotted against GDD. The graph also includes data from studies where sex was not specified. The thin dotted line is the relationship developed by Baccante and Colby (1996) based on combined sex data \(T_m = 3,185/GDD^{0.87}\). Thick lines are sex-specific relationships developed by Venturelli et al. (2010a): females (solid line, \(T_{m,female} = 36,666/GDD^{1.18}\)) and males (dashed line, \(T_{m,male} = 61,846/GDD^{1.31}\)). In panel (B), age at maturity is compared among sexes. Major axis regression (solid line) implies \(T_{m,male} = 1.06\cdot T_{m,female} - 2.6\) \((n = 55, r^2 = 0.82)\). Sex-specific estimates are from Venturelli et al. (2010a) and are based on populations where at least 100 fish of each sex were sampled. Other data (sex not specified) are from Baccante and Colby (1996), Gangl and Pereira (2003), and Sullivan (2003).
Figure 7.6. In panel (A), length at 50% mature of female and male walleyes (from the same populations) are plotted against GDD. The graph also includes data from studies where sex was not specified. Regression analysis indicates that length at maturity is not related to GDD. Horizontal lines are means for each group: 451 mm for females (thick solid), 348 mm for males (thick dashed), and 431 mm for sex not specified (thin dotted). In panel (B), length at maturity is compared among sexes. Major axis regression (solid line) implies $L_{m\text{-male}} = 0.83L_{m\text{-female}} - 23.0$ ($n = 59, r^2 = 0.27$). Data sources are listed in the caption of Figure 7.5.
7.2.6.3 Longevity and Mortality Rate

Some studies have reported sexual differences in longevity suggesting that females live longer than males (Carlander 1997), but large-scale analyses do not indicate consistent differences in longevity. Morgan et al. (2003) estimated mortality rate (a correlate of longevity) in 296 Ontario walleye populations and reported mean annual mortality was almost identical among sexes (28% in females and 30% in males). Rennie et al. (2008) examined maximum age for a subset of these Ontario populations (where sample size was large) and found no significant difference among sexes. Our compilation of walleye data, which spans a broader latitudinal gradient, supports these findings (Figure 7.7).

Walleye longevity, like age at maturity, is inversely related to GDD. Colby and Nepszy (1981) reported that maximum age of walleyes at the northern limit of its range is five times higher (around 20 years) than at the southern extreme (3–4 years). More recent observations indicate that maximum age exceeds 30 years in some northern populations (Venturelli et al. 2010a). Our compilation of data from populations spanning 1000–5000 GDD indicates a range of 4–32 years (Figure 7.8A).

Because longevity is inversely proportional to mortality rate, these results indicate that mortality rate increases with GDD. We applied Hoenig’s (1983) empirical formula to estimate annual instantaneous mortality rate ($Z$) from maximum age ($T_{\text{max}}$) as follows: $Z = 4.22 / T_{\text{max}}^{0.982}$. As illustrated in Figure 7.8B, linear regression implies that, on average, mortality rate increases from approximately 0.15 at 1000 GDD to 0.60 at 3000 GDD. However, for any given value of GDD, mortality estimates are highly variable. This variability is partially due to variation in sample size, because maximum age increases with the number of fish examined, but it may also reflect variation in exploitation rate. To describe the relationship between natural mortality rate and GDD, we assumed that the lowest mortality values at each level of GDD represent lightly exploited populations. This approximation suggests that natural mortality rate increases from approximately 0.13/year at 1000 GDD to 0.39/year at 3000 GDD.

Estimates of natural mortality are rare for walleye populations because walleyes, by virtue of their excellent taste, are a popular target for recreational and commercial harvest. One exception is the Pymatuning Sanctuary in Pennsylvania, a 530-ha impoundment on the Upper Shenango River that has been closed to fishing since it was created in 1933 (Kocovsky and Carline 2001). Estimates of mortality rate in this unexploited population, which ranged from 0.39 to 0.53/year, are slightly higher than our estimate of natural mortality for this climate zone (GDD = 2327, $Z = 0.30$). Nevertheless, because natural mortality rate of this mid-latitude population exceeds total mortality estimates for many populations in colder climates, these results are consistent with the hypothesis that natural mortality increases with GDD.

7.2.6.4 Maximum Body Size

Walleyes exhibit indeterminate growth, implying that they continue to grow after maturation. Most studies that have examined sexual dimorphism report that females grow larger than males. Based on a von Bertalanffy growth model, Quist et al. (2003b) estimated that mean asymptotic length was 496 mm for males and 652 mm for females, implying a ratio of 0.76. We compiled maximum body size data from the published literature. We used mean length of the oldest cohort in each sex. Maximum body size is not related to GDD (Figure 7.9A).
Maximum length of females is usually larger than males (Figures 7.9B). On average, male maximum length is approximately 80% of that of females.

### 7.2.6.5 Frequency of Spawning

The available data suggest that frequency of spawning is annual in most walleye populations. However, there are indications of physiological limitations at northern and southern extremes. Walleyes in some northern populations may not spawn every year, because of short growing seasons (Scott and Crossman 1973). Walleye populations at the southern extreme have failed to reproduce in years when temperatures were high during time of maturation (Colby and Nepszy 1981). Hokanson (1977) reported that a minimum winter temperature of 10°C is near the upper limit for gonadal maturation in walleye, which may limit successful reproduction in southern latitudes, such as Texas (Prentice and Clark 1978; although see Laarman 1978). This constraint may dictate the southern limit of self-sustaining walleye populations.

### 7.2.6.6 Fecundity, Egg Size and Gonadosomatic Index

Walleyes produce large numbers of eggs compared with many other freshwater fish species (Scott and Crossman 1973; Becker 1983). Moreover, fecundity clearly increases as a function of age, but the specific relation varies with geographic location (Figure 7.10), which may be related to differences in productivity across these systems.
Figure 7.8. In panel (A), the observed maximum ages of walleyes from 135 populations are plotted against GDD. In panel (B), estimates of mortality rate based on maximum age (see text for details) are plotted against GDD. The solid line is the least-squares regression: $Z = 0.000201 \cdot \text{GDD} - 0.02493$. The dotted line is a putative minimum estimate of natural mortality (see text for details): $M = 0.13 \cdot \text{GDD}$. Data sources are listed in the caption of Figure 7.7.
Figure 7.9. In panel (A), the maximum length of female and male walleyes (from the same populations) are plotted against GDD. Maximum length was measured as mean length of fish in the oldest cohort. Maximum length does not vary systematically with GDD. Horizontal lines are means for each group: 669 mm for females (solid), 539 mm for males (dashed). In panel (B), maximum length is compared among sexes. Major axis regression (solid line) implies $L_{\text{max,male}} = 0.694 L_{\text{max,female}} + 75.4$ ($n = 107$, $r^2 = 0.21$). Data sources are Colby et al. (1979), Carlander (1997), Kocovsky and Carline (2001), Morgan et al. (2003), and Venturelli et al. (2010a).
Because fecundity increases roughly proportional to body weight, fecundity of a population is usually characterized by its relative fecundity (number of eggs per body weight). Examples shown in Figure 7.11A demonstrate that this relationship may vary widely among populations. Baccante and Colby (1996) showed that relative fecundity increases with GDD, ranging from approximately 40,000 eggs/kg in northern waters (GDD, ~1200) to 80,000 eggs/kg in mid-latitude waters (GDD, ~2500). Insufficient fecundity data were available to examine this trend further south. An enlarged data set, which includes many more observations from Ontario (Lester et al. 2000; Morgan et al. 2003), indicates that fecundity of some northern populations may be as low as 20,000 eggs/kg (Figure 7.11B). The relationship implied by this enlarged data set, however, is virtually identical to that described by Baccante and Colby (1996). The data demonstrate that, while there is a significant positive effect of GDD on relative fecundity, high variability exists within climatic zones. For example, fecundity of populations living at the northern fringe (i.e., GDD = 1100–1300) ranges from 20,000 to 60,000 eggs/kg.

Because egg size may vary, fecundity (i.e., egg number) is not sufficient to describe the reproductive investment of a female fish. A better measure is the gonadosomatic index (GSI), which is the weight of the gonads relative to somatic weight (i.e., body weight excluding the gonads) and which varies considerably during maturation leading up to spawning (see Chapter 6). Eschmeyer (1950) used this index to describe the seasonal development of the reproductive organs in Lake Gogebic, Michigan, and measure the final investment at time of spawning. In this lake, female GSI was 4.7% in October and 16.3% just before spawning.
Figure 7.11. In panel (A), the relationship between fecundity and fish weight is contrasted for two walleye populations in Ontario. Regression through the origin implies relative fecundity is 85,100 eggs/kg on Rice Lake and 20,900 eggs/kg on Wabigoon Lake. In panel (B), estimates of relative fecundity for 100 water bodies are plotted against GDD. The dotted line is the relationship developed by Baccante and Colby (1996) based on a smaller data set: relative fecundity = 24.7·GDD + 14514. The solid line is the least squares fit for the entire data set: relative fecundity = 25·GDD + 11884 \( (n = 100, r^2 = 0.029) \). Data sources are Baccante and Colby (1996), Lester et al. (2000), and Morgan et al. (2003)
Similar values have been reported for Lake Erie (Henderson et al. 1996) and Minnesota lakes (Malison and Held 1996; Figure 6.1 in Chapter 6). Higher GSI values were reported in the Muskegon River, Michigan, (24.1%) and in Saginaw Bay, Lake Huron (27.8%) (Colby et al. 1979). In some cases, reporting of GSI applies a conversion factor to correct for energy density differences between eggs and somatic tissue. For example, Shuter et al. (2005) reported a mean walleye GSI of 24% (range, 9–44%) for 18 inland lakes in Ontario after applying a conversion factor of 1.41 (from Henderson and Nepszy 1994). This expression of GSI more accurately describes the energetic investment. Without this correction factor, these results imply the mean GSI = 17% (range, 6–31%).

Male GSI has also been measured in some populations and is always much less than female GSI (e.g., Eschmeyer 1950; Malison and Held 1996). Male GSI is not a useful index of reproductive investment because the energetic cost of sperm production is very small compared with the female cost of egg production; a small allocation of energy to sperm production is sufficient to produce an abundant supply of sperm.

7.2.6.7 Spawning Migration

Walleyes show fidelity to spawning areas and this homing behavior dictates the movement pattern of adults (Crowe 1962; Olson and Scidmore 1962; Regier et al. 1969; Olson et al. 1978; Colby et al. 1979; Jennings et al. 1996). The distance that walleyes travel to get to their spawning grounds and subsequently disperse to feeding areas varies among populations. Walleyes, although not recognized as strong swimmers compared with other species, such as salmonids, are also capable of moving long distances. Colby et al. (1979) cite various studies that report movements ranging from 50 to nearly 300 km. Colby et al. (1979) also cite studies that report minimal movement between spawning grounds and feeding areas (e.g., <20 km), despite the potential for much larger movement.

Walleye spawning can generally be classified into three life history spawning typologies: (1) lake-resident, (2) river-resident, and (3) lake-resident, river-run spawning although there are many variations of these strategies. In Lake Goegebic, walleyes move inshore to spawn along wind-swept shorelines (Eschmeyer 1950) as they do in many lakes (Niemuth et al. 1959; Johnson 1961; Raabe 2006). In rivers, such as the Wisconsin River, walleyes move into large riffles to spawn (Stevens 1990); river spawning is common (Preigel 1970; Scott and Crossman 1973; Nelson and Walburg 1977; Hartley and Kelso 1991). In the Laurentian Great Lakes, major tributaries play an important role in providing spawning habitat for walleyes (Hayes and Petrusso 1998). In Lake Erie, walleyes consist of different stocks moving either into tributary streams or onto mid-lake reefs to spawn (Stepien 1995; Stepien and Faber 1998; Roseman et al. 2001) as they do in many lakes of all sizes having tributary streams (Geiling et al. 1996). Onshore spawning movement in lake systems is probably guided by thermal conditions that optimize gamete viability and hatching success (Rawson 1957; Forney 1967; Preigel 1970). There is evidence that distinct walleye stocks utilize different spawning areas in larger systems (Preigel 1970; Spangler et al. 1977a; Jennings et al. 1996). Spangler et al. (1977a), reviewing walleyes in Lake Huron, and Jennings et al. (1996), working in a southern U.S. reservoir, both found walleye movements occur among distinct spawning populations in the same waterbody. Spawning migratory behavior is system-specific and further investigations are required to discern under what environmental conditions walleyes will migrate versus being resident. Schupp and Macins (1977) found that walleyes did not migrate far in
Lake of the Woods, Ontario–Minnesota, whereas Ferguson and Derksen (1971) found that walleyes migrate great distances across Lake Huron to spawn. Long migrations may be an important life history component when suitable spawning habitats are distant from foraging areas in larger systems.

Large water bodies, such as the Great Lakes, have diverse habitats, such as relatively shallow and warm bays separated by vast expanses of deep and cold water that can act as ecological barriers to the movements of walleye. However, strong homing instinct can result in remarkable movements. For example, adult walleyes captured and tagged at the mouth of the Current River, near Thunder Bay, Ontario, were released at the north end of Black Bay, a distance of about 150 km. These two locations are separated by large expanses of deep and cold water in Lake Superior; however, within 8 months of their release, 18.2% of the walleyes were recaptured at the source location (Colby and Nepszy 1981).

A study of walleye movements in the Petitot River, British Columbia, furthers our understanding of the scope of seasonal walleye movements (Anderson et al. 2009). The 300-km-long Petitot River flows from Bistcho Lake, Alberta, through northeastern British Columbia into the Liard River. It appears that walleyes in the Petitot River maintain a primarily fluvial life history, using the main stem almost exclusively during spawning and winter periods. However, during the summer, many walleyes migrate as far as 30 km to tributary streams and then return to the main stem in the fall. Individual fish movements were sometimes substantial and rapid. One individual traveled more than 160 km during a 15-d period in late May. Another fish traveled 187 km downstream over a 14-d period in mid-July and then returned to within 2 km of its original location during the following 7 d.

These long migrations are indicative of strong homing behavior in adult walleyes. Olson et al. (1978) suggested that homing is influenced by adult-learned behavior, strengthened through repeated annual movements. Because walleye is a schooling species, the existence of older fish that may guide the spawning migration of younger cohorts is an important consideration in management.

7.3 LIFETIME GROWTH PATTERN

7.3.1 Examples

Examples of lifetime growth patterns in several well-sampled walleye populations are shown in Figure 7.12. Mean length at age of males and females is shown, separated into immature and mature age groups based on estimates of age at 50% maturity. These examples demonstrate some features of walleye growth that seem to have wide applicability: (1) both sexes follow the same growth trajectory before maturation; (2) prematuration growth in length is approximately linear; (3) males usually mature earlier and, thus, at smaller size than females; (4) maturation is usually associated with an abrupt change in growth rate; (5) males usually attain a smaller maximum body size than females.

The von Bertalanffy (VB) growth equation has been widely used to describe and contrast lifetime growth patterns in walleye populations (e.g., Quist et al. 2003b; Sass et al. 2004). Although this model provides a decent approximation of lifetime growth, its value in understanding life history processes has been questioned. On theoretical grounds, it has been argued that a single somatic growth equation cannot cleanly account for the change in energy allocation that
occurs with sexual maturity (Nikolskii 1969; Charnov 1993; Day and Taylor 1997; Charnov et al. 2001). For example, the abrupt changes in walleye growth at maturation cannot be accurately described by the VB growth curve. Furthermore, the structure of the VB model cannot account for sexual differences in lifetime growth pattern; separate fitting of the model to males and females cannot generate results that imply identical growth before maturation.

### 7.3.2 Biphasic Growth Model

An alternative growth model, which accounts for effects of reproduction and has been applied to walleye, is the biphasic growth model (Lester et al. 2004b; Shuter et al. 2005; Quince et al. 2008a, 2008b). The model predicts a rapid, approximately linear, juvenile growth phase,
followed by a gradual reduction in growth rate after sexual maturation. Because the model assumes the annual investment in reproduction by a typical female ($g = \text{gonad weight/somatic weight}$) is constant throughout her reproductive lifetime, it predicts an adult growth pattern that is described by a von Bertalanffy growth function (see Lester et al. 2004b). The parameters of this function ($L_\infty$, $k$, $t_o$) depend on prematuration growth rate ($h$), reproductive investment ($g$), age of maturity ($T$), and a time parameter ($t_1$) that captures the influence of prey size spectrum on early growth. Given a prematuration growth pattern described as:

$$L_t = h(t - t_1)$$

Adult growth is described by the von Bertalanffy function:

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

where $L_\infty = 3h/g$, $k = \log_e(1 + g/3)$ and $t_o = T + \log_e[1 - g(T - t_1)/3]/\log_e(1 + g/3)$.

The model has been labeled as ‘biphasic’ because it implies that accurate description of the lifetime growth pattern requires two functions that separately describe prematuration and postmaturation growth phases. Examples in Figure 7.12 demonstrate that the shapes of walleye growth curves are consistent with this model. Growth is rapid and approximately linear before maturation; changes in growth pattern are associated with age of maturation, and growth is asymptotic during the adult phase. Shuter et al. (2005) showed this model successfully describes growth patterns seen in walleye, as well as other species.

Additional support of this model is revealed by interpretation of its parameters. Prematuration growth rate ($h$) estimates the growth that would occur if all surplus energy was allocated to somatic growth. Departure from this expected trajectory indicates investment in reproduction, which can be estimated from growth curves as $g = 3h/L_\infty$. Because egg production dominates reproductive costs of females, the $g$ value estimated from the female growth curve should reflect the female GSI. For several species, Shuter et al. (2005) found a good match between direct measures of GSI and indirect estimates based on the biphasic model. For walleyes, GSI ranged from 0.09 to 0.44 (mean = 0.24) and indirect estimates ($g$) based on growth curves ranged from 0.14 to 0.35 (mean = 0.22). In this comparison, direct estimates of GSI were corrected for the higher energy content of eggs relative to soma, using a correction factor of 1.41. This correction factor was needed because the GSI parameter ($g$) in the biphasic model measures reproductive investment in energetic units.

### 7.3.3 Optimal Life History Traits

Life history theory attempts to explain variation in life history traits based on the principle of natural selection. Because selection favors individuals that maximize their fitness, the patterns we observe are expected to be optimal solutions to environmental constraints. Under this assumption, the biphasic growth model makes explicit predictions (Lester et al. 2004b) about relationships among mortality rate ($Z$), reproductive investment ($g$), and age at maturity ($T$) according to these relationships:

$$g \approx 1.18(1 - e^{-Z})$$
$$T \approx 1.95/(e^Z - 1) + t_1$$
These equations imply that reproductive investment increases and age at maturity decreases as mortality rate increases. This model also predicts effects of the prey environment on body size. If the scope for growth declines with body size due to a truncated size spectrum of the prey field (i.e., \( t_1 < 0 \)), age of maturity is expected to decrease. Consequently, fish will mature at a smaller size and attain a smaller maximum body size. Support for these model predictions is provided in a study by Shuter et al. (2005) that examined life history variation in Ontario lakes for four species including walleye.

Beverton (1987) applied life history theory to account for the observation by Colby and Nepszy (1981) that reduced walleye longevity in warmer climates is compensated by earlier maturation. This observation is consistent with predictions of the biphasic growth model: mortality rate increases (Figure 7.8) and age of maturity decreases (Figure 7.5) with GDD. In addition, the biphasic model offers an explanation for the observation that relative fecundity increases with GDD (Figure 7.11B); assuming a constant egg size, higher relative fecundity implies higher reproductive investment, which is expected in warmer climates due to the higher mortality rate.

### 7.3.4 Sexual Dimorphism

It is widely recognized that sexual dimorphism exists in walleyes (Eschmeyer 1950; Hile 1954; Carlander and Whitney 1961; Colby et al. 1979; Carlander 1997; Henderson et al. 2003; Quist et al. 2003b; Sass et al. 2004), but it is not entirely clear why. The onset of sexual dimorphism is related to maturation (Figures 7.4 and 7.12). After maturation annual growth increments in males are usually smaller than in females and males attain a smaller maximum body size (Figure 7.9). Given assumptions in the biphasic growth model, slower postmaturation growth in males suggests that reproductive costs are higher than in females. But this explanation seems unlikely because the energetic cost of sperm production is much less than egg production. Henderson et al. (2003) proposed that the lower cost of gamete production in males may be offset by higher activity costs associated with mating. Because males arrive early and stay late on spawning shoals, they forego more feeding opportunities than do females. In addition, males may expend more energy in the spawning act because they must compete with other males to access females. While behavioral costs associated with mating may be higher in males, it seems unlikely that energy expenses during this short period of the year exceed the cost of egg production incurred by females.

An alternative hypothesis is that adult males consume less food than females. Reduced food consumption by adult males has been reported for walleye (Henderson et al. 2003) and yellow perch (Rennie et al. 2008), a close relative of walleye. Assuming that energetic costs of reproduction are higher for females, males would outgrow females if they consumed the same amount of food. Evolutionary benefits of growth-limiting behavior in males exist because male size does not limit the supply of sperm, as opposed to females where body size limits egg production. Male reproductive success is dependent on fertilizing eggs from the greatest number of females that appear briefly on spawning shoals. If small agile males have a greater chance of mating, then high adult growth would not be beneficial; optimal male body size would depend on the size of female spawners. For walleye, the observed body length ratio is approximately 0.78 (Rennie et al. 2008). This ratio describes the average relative length of males to females, when walleyes become mature and also at the end of their lives.
7.4 EFFECT OF CLIMATE ON GROWTH AND DEVELOPMENT

Temperature and food availability are the primary determinants of fish growth and development (Palooheimo and Dickie 1966; Fry 1971; Kitchell et al. 1977). Recently, Neuheimer and Taggart (2007) showed that GDD, an index of ambient thermal energy, can account for much of the variation in growth among species and populations of fish. The value of this index in predicting walleye growth was recognized almost 30 years ago (Colby and Nepszy 1981) and has been confirmed in more recent studies (e.g., Venturelli et al. 2010a).

Lifetime growth patterns of male and female walleyes living in different climatic zones are contrasted in Figure 7.13. These results are based on growth data from 432 walleye populations spanning a GDD range of 1000–4630°C. We divided populations into three climatic zones: (1) northern extreme (<1500°C), (2) mid-latitude (1500–2500°C), and (3) southern extreme (>2500°C). We averaged mean length at age across populations to describe the average growth of males and females in each zone. Growth trajectories demonstrate clearly that walleyes grow more slowly and live longer in colder zones than in warmer ones. For example, in the southern zone (GDD > 2500°C) walleyes reach a total length of 350 mm in approximately 2 years and maximum age is in the order of 10 years. In contrast, walleyes in the north (GDD < 1500°C) need approximately 5 years to reach 350 mm and may live as long as 30 years.

These differences largely disappear when age is expressed in terms of thermal units instead of calendar years (Figure 7.14). Thermal units are measured as cumulative GDD (i.e., age times mean annual GDD of the waterbody). The growth curves for different climatic zones are practically identical when plotted in this manner. On average, walleyes reach a length of 350 mm when they have experienced a cumulative GDD of 6000°C, and longevity is in the order of 30000°C GDD. These results imply that when the temporal unit of rate processes is corrected for temperature differences (using cumulative GDD instead of years), average growth and mortality rates are the same across a broad climatic gradient. This standardization is a powerful tool for exploring the effect of food availability on walleye growth (see Venturelli et al. 2010b). The climate-corrected growth curves also demonstrate that body size and sexual dimorphism are not affected by climate. On average, walleyes attain the same maximum size in different climatic zones and there is a consistent difference between sexes.

7.5 EFFECT OF THE PREY SIZE SPECTRUM ON BODY SIZE

During its lifetime, a walleye undergoes a series of ontogenetic diet shifts, moving successively from smaller to larger prey items as it grows (see Chapter 8). Age-0 walleyes initially feed on zooplankton, switch to benthos, and then become piscivorous. The onset of piscivory occurs in the first year of life when length is between 50 and 80 mm TL (Smith and Moyle 1945; Smith and Pycha 1960; Walker and Applegate 1976). Walleye are capable of consuming fish that are half their length (Campbell 1998). Parsons (1971) observed that the average prey : predator length ratio for Lake Erie declines from 0.44 for 60-mm walleyes to 0.28 for 400-mm walleyes. A similar length ratio trend is evident in Figure 2 of Kaufman et al. (2009) for inland lakes of Ontario. Although walleyes are opportunistic feeders and will feed on small items when they are readily available, the availability of optimally sized prey seems to be an important determinant of growth and maximum body size (e.g., Henderson et al. 2004; Kaufman et al. 2009).
Figure 7.13. Effect of climate on growth and development of walleye. The average mean length at age of males (panel A) and females (panel B) is shown for populations in three climatic zones: GDD < 1500°C, GDD = 1500–2500°C, and GDD > 2500°C. The number of walleye populations in each zone are 101 (GDD < 1500°C), 319 (1500–2500°C), and 11 (GDD > 2500°C). Data sources are Carlander (1997) and walleye survey databases from Ontario and Québec.
Prey size has been shown to be a critical factor affecting growth efficiency in fish (Paloheimo and Dickie 1966; Ryder and Kerr 1978; Pazzia et al. 2002; Sherwood et al. 2002). If a predator lives in a community where a broad range of prey sizes is available, the transition to larger prey species occurs smoothly as the predator grows and potential growth rate remains constant. If the prey field is truncated such that the availability of prey of suitable size does not keep pace with increases in predator size, then potential growth rate will decline owing to the increased foraging costs associated with capturing smaller prey. This decline in growth potential is expected to have implications on size of maturity and maximum body size. Life history theory predicts that optimal size of maturity and maximum size are smaller when the prey field is truncated (e.g., Lester et al. 2004b).

In Ontario, ciscoes provide an important energy-rich large prey item for walleyes (Ryder and Kerr 1978; Colby et al. 1987; Henderson et al. 2004; Kaufman et al. 2006, 2009). In Lac des Milles Lacs, Ontario, an increase in walleye growth rate coincided with a diet switch from yellow perch and sticklebacks to coregonids (primarily cisco) (Colby et al. 1987). Henderson et al. (2004) found that walleyes had higher growth efficiencies, lower ingestion rates, and lower activity levels in lakes where ciscoes were available. Kaufman et al. (2006, 2009) reported similar findings, but also noted that females attained a larger asymptotic size when ciscoes were available as prey. Stomach content analysis revealed that walleyes larger than

Figure 7.14. Effect of climate on growth and development of walleye. Average mean length at thermal age is shown for populations in three climatic zones: GDD < 1500°C, GDD = 1500–2500°C, and GDD > 2500°C, where thermal age is measured as age in years times mean GDD. Mean length at maturity (solid line: females; dashed line: males) is also shown. Number of walleye populations and data sources are as in Figure 7.13.
175 mm TL consumed ciscoes, but ciscoes were more important to larger walleyes. In lakes without ciscoes, where walleyes fed on yellow perch and benthic invertebrates, the frequency of perch in the diet increased with walleye size. In lakes with ciscoes, mean prey size was larger because walleyes switched from smaller perch to larger ciscoes as they grew.

In lakes where forage fish are absent or scarce, walleyes may feed on invertebrates during their whole ontogeny (see references in Colby et al. 1979). Given the importance of prey size in supporting growth, one expects that walleyes in these lakes will be smaller. Growth studies of walleyes that rely primarily on nonfish prey throughout their ontogeny are scarce. Paradis et al. (2006) conducted a field study designed to compare growth of piscivorous and nonpiscivorous walleyes in 10 small (surface area, 25–142 ha) headwater lakes in Québec. Those investigators found that piscivorous males had slightly higher growth than nonpiscivores, but females exhibited no difference. Because assignment of trophic specialization of each fish was based on stomach contents from one midsummer sampling event, it is questionable whether this study correctly separated piscivorous and nonpiscivorous fish. It is possible that all fish fed on a combination of fish and benthic invertebrates and the sampling method merely identified their most recent meal.

The headwater lakes studied by Paradis et al. (2006) are noteworthy because the maximum size of walleyes was relatively small (approximately 450 mm TL for both sexes). In contrast, our growth summary of North American lakes yielded overall means of 701 mm for females and 568 mm for males. These headwater lakes are also remarkable for their high degree of benthivory. Only 16% of walleyes had stomach contents that were exclusively fish and the percentage mass of fish in stomachs was not related to walleye size. Given this high degree of benthivory, we speculate that small body size was due to the lack (or low abundance) of large prey needed to sustain growth of larger walleyes. Ciscoes were not present in any lakes. Yellow perch were present but not abundant, perhaps due to the presence of northern pike, another top predator.

To our knowledge, the only documentation of a walleye population that feeds exclusively on invertebrates throughout their adult life is in Charlie Lake, British Columbia (Figure 7.15) (Baccante and Down 2003). Growth is similar to what Paradis et al. (2006) observed for small headwater lakes in Québec. Female walleyes typically mature at age 5 when they reach a length of 350 mm. Growth is very slow after maturation and, despite living upwards of 15 years, total length never exceeds 450 mm.

Perhaps the most poignant example of the effect of prey size on walleye size comes from U.S. reservoirs where prey fish have been introduced to enhance walleye growth. For example, rainbow smelt were introduced into the Horsetooth Reservoir, Colorado, in 1983 to increase prey availability for walleyes (Johnson and Goettl 1999). Before the introduction, very few large (i.e., > 450 mm) walleye were caught in surveys. The introduction was initially highly successful. Rainbow smelt increased in numbers and walleye diet switched from mostly macroinvertebrates to smelt, resulting in a 50% increase in growth rate and much larger catches of large walleyes. Although this experiment demonstrated that prey size can have a dramatic effect on walleye size, the benefits of the rainbow smelt introduction were short lived because cascading effects subsequently resulted in a walleye recruitment failure (Mercado-Silva et al. 2007).

In summary, theoretical and empirical studies indicate that the prey size spectrum is an important determinant of body size in walleyes. Our understanding of this effect is hampered because many studies that report on walleye growth fail to provide details about the food environment. Nevertheless, it seems safe to conclude that large body size in walleyes is attained only when there is an abundance of large prey items (see Chapter 8 for additional discussion of feeding and bioenergetics).
7.6 DENSITY DEPENDENCE

Our description of walleye life history has focused on population differences and the extent to which traits of a population can be predicted by environmental variables (e.g., climate, size spectrum of the prey). Life history traits, however, are not population constants. Within a population they are expected to vary over time, partly because environmental variables fluctuate, but especially because most life history traits are density dependent. Because growth rate depends on the per capita availability of food, changes in walleye abundance are expected to affect growth rates and have cascading effects on other life history traits.

Processes such as growth, mortality, and reproduction are density dependent if their rates change depending on the number of individuals in a population (see Chapter 9 for additional discussion of relationships between recruitment, growth, and mortality). Density-dependent processes are said to be compensatory when rate changes promote a numerical increase in the population at low densities (Rose et al. 1999). Compensatory density dependence permits populations to persist under conditions of increased mortality and is the basis of concepts such as surplus production and sustainable harvest. Without compensation, any increase in mortality would result in population decline and eventual extinction. Thus, compensatory density dependence must exist for naturally stable populations to persist under harvesting.

Our understanding of density-dependent processes in walleye is limited because within-population variation in abundance is needed to measure this effect. As Carlander (1997) points out, it is not absolute density of the fish that has such a dominant effect on growth, but it
is the population density in relation to carrying capacity. Walleye population density is highly variable among lakes (Baccante and Colby 1996; Nate et al. 2003; Sass et al. 2004). Based on data from 85 lakes, Baccante and Colby (1996) reported a median adult density of 14.8 fish/ha and a maximum density that exceeded 100 fish/ha. Sass et al. (2004) examined growth in 254 Wisconsin walleye populations—where adult density ranged from 1 to 36 fish/ha—and found weak evidence of density-dependent growth among populations. In contrast, there was strong evidence of density-dependent growth within populations. In a subsequent paper, Sass and Kitchell (2005) showed that among-population comparisons revealed stronger evidence of density-dependent growth when abiotic factors, potentially accounting for variation in carrying capacity, were included in the analysis.

Compensatory changes in walleye growth, age of maturation, or fecundity have been reported in case studies where dramatic changes in walleye abundance have occurred. Table 7.1 provides a summary of reported compensatory changes in walleyes. The degree of compensation is expected to depend on the magnitude of change in abundance, but this relationship cannot be determined from these studies because precise measures of walleye density are usually lacking. The potential magnitude of compensation is demonstrated by the results of an extreme removal experiment on Henderson Lake, a small (area = 150 ha) unexploited lake in Ontario (Reid and Momot 1985). Aggressive harvesting reduced adult walleye density approximately 10-fold (from 22 fish/ha to fewer than 2 fish/ha) and resulted in increased prematurity growth, earlier maturity, and increased relative fecundity. Over a 5-year period, size at age 4 increased from 350 to 425 mm, age at maturity decreased from 4.6 to 3.2 years, and fecundity of 500-mm fish increased from 55,000–82,000 eggs per fish. The magnitude of this within-lake variation in life history traits is similar to that observed among populations living in similar climatic zones (Figures 7.3B, 7.5A, and 7.11B). It suggests that when one controls for climate, among-population variation in life history traits may reflect the degree of density-dependent compensation that can exist. It is not recommended, however, that this optimistic view of compensation be adopted for managing fisheries. A precautionary approach could be adopted, for example, by assuming that 50% of variation among populations predicts the potential magnitude of density-dependent compensation.

7.7 PARASITES AND DISEASE

Parasites in walleye and sauger are virtually universal; they are found in most populations and nearly all individuals have some parasites (Colby et al. 1979; see Table 6.4 in Chapter 6). However, very little is known about negative effects that parasites and disease have on walleyes and saugers particularly when it comes to understanding the influence they have on the life history strategies and population dynamics discussed thus far. Undoubtedly, heavier parasite loads or incidences of disease would probably reduce overall fitness affecting growth, age at maturity, and mortality among other life history traits, and this topic warrants further study. Diseases are discussed in more depth in Chapters 6 and 13.

7.8 COMPARATIVE LIFE HISTORY OF WALLEYE AND SAUGER

Like walleye, the sauger is a member of the family Percidae; similarities and differences in their life history traits are summarized in Table 7.2. The distribution of sauger in North
<table>
<thead>
<tr>
<th>Publication</th>
<th>Study site</th>
<th>Methods</th>
<th>Results</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dobie (1956)</td>
<td>Rearing pond</td>
<td>Variation in growth given sixfold in density of fingerlings</td>
<td>• TL at 60 d increased from 40 to 75 mm (+88%) as density declined</td>
</tr>
<tr>
<td>Carlander and Whitney (1961)</td>
<td>Clear Lake</td>
<td>Variation in growth from 1935–1957</td>
<td>• Length at age 3 inversely related to year-class strength</td>
</tr>
<tr>
<td>Anthony and Jorgensen (1977)</td>
<td>Lake Nipissing</td>
<td>Compared growth during periods of high (1967–1976) and low (1936) walleye exploitation</td>
<td>• Length at age 3 increased from 240 to 310 mm (+ 29%)</td>
</tr>
<tr>
<td>Spangler et al. (1977b)</td>
<td>Lake Erie</td>
<td>Compared growth and maturation during periods of high (1927–1933) and low (1964–1966) walleye abundance</td>
<td>• Length at age 2 increased from 180 to 370 mm (+100%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>• Female age at maturity decreased from 4–5 to 3 years (−30%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>• Male age at maturity decreased from 3–4 to 2 years (−42%)</td>
</tr>
<tr>
<td>Muth and Wolfert (1986)</td>
<td>Lake Erie</td>
<td>Examined changes in growth and maturation when abundance increased following closure of the fishery in 1970 (due to mercury contamination)</td>
<td>• Standing stock increased threefold (from 1976 to 1983)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>• Length of age-0 fish in fall decreased from 240 mm in 1961 to 190 mm in 1983 (−21%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>• Percent of age-2 females mature declined from 80% in early 1970s to 7% in 1983</td>
</tr>
<tr>
<td>Shuter and Koonce (1977)</td>
<td>Lake Erie</td>
<td>Examined changes in growth and maturation over a period (1947–1963) when a large decrease in walleye abundance occurred; Index of abundance declined from 120 to 10 fish per trap-net lift</td>
<td>• Length at age 4 increased from 350 to 500 mm as abundance declined; +42%</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>• Decrease in age at maturity</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>• Moderate increase in length at maturity</td>
</tr>
<tr>
<td>Publication</td>
<td>Study site</td>
<td>Methods</td>
<td>Results</td>
</tr>
<tr>
<td>-----------------------------</td>
<td>-----------------------------</td>
<td>--------------------------------------------------------------------------</td>
<td>-----------------------------------------------------------------------------------------------------------------------------------------</td>
</tr>
</tbody>
</table>
| Kempinger and Carline (1977)| Escanaba Lake               | Examined changes in growth over a period (1955–1969) when walleye density fluctuated | • Age-specific length increments were negatively related to walleye biomass (although not significant)  
• Figure 2 in reference suggests annual length increment at age 4 increased from 25 to 60 mm as biomass declined from 30 to 5 kg/ha (+140%) |
| Reid and Momot (1985)       | Henderson Lake              | Experimental harvesting reduced adult walleye abundance approximately 10-fold (22 to 2 fish/ha) | • Length at age 4 increased from 350 to 425 mm (+21%)  
• Age at maturity decreased from 4.6 to 3.2 years  
• Fecundity at 500 mm TL increased from 55,000 to 82,000 eggs per fish (+50%) |
| Baccante and Reid (1998)    | Savanne Lake                | Experimental harvesting reduced walleye abundance 25%; compared fecundity before and after reduction | • Fecundity at 500 mm TL increased from 47,800 to 59,900 eggs per fish (+25%) |
| Fox and Flowers (1990)      | Rearing ponds               | Examined growth during 6 weeks after stocking larval walleye; threefold variation in larval density | • Length at 6 weeks increased from 41.3 to 48.9 mm (+18%); weight increased from 470 to 788 g (+68%) |
| Muth and Ickes (1993)       | Lake Erie                   | Fecundity compared in periods of low (1966) and high (1990–1991) abundance | • Mean egg production of the dominant spawner age group (4 to 8 years) was 25% lower when abundance was high |
| Doire et al. (2002, cited in Simoneau et al. 2005) | Five small lakes of mid-northern Québec | Compared growth before and after intensive experimental fishing | • Growth rate increased 30% in some lakes |
Table 7.1. Continued.

<table>
<thead>
<tr>
<th>Publication</th>
<th>Study site</th>
<th>Methods</th>
<th>Results</th>
</tr>
</thead>
</table>
| Schueller et al. (2005) | Big Crooked Lake    | Examined growth, maturation and fecundity over a period (1997–2003) of declining walleye abundance; Adult abundance declined from 17 to 7 fish/ha | • Length at age 3 increased from 305 to 370 mm (+21%)  
• Female age at maturity declined from 4.9 to 3.9 years (~20%)  
• Variation in fecundity was not related to density |
| Venturelli et al. (2009) | Eight lakes in Ontario | Compared prematuration growth rate during periods of high and low abundance                                                                 | • Prematuration growth rate was, on average, 1.3-fold higher when abundance was low  
• For a population where GDD = 2200, this change implies length at age 3 increases from 330 to 419 mm (+26%) |
Table 7.2. Comparison of life history characteristics between walleye and sauger.

<table>
<thead>
<tr>
<th>Life history characteristic</th>
<th>Walleye</th>
<th>Sauger</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Season</td>
<td>March to June, depending on latitude. In the north, immediately after ice-out.</td>
<td>Starts at the tail end of walleye spawning.</td>
<td>Derback (1947); Eschmeyer (1950); Preigel (1970); Scott and Crossman (1973)</td>
</tr>
<tr>
<td>Temperature</td>
<td>Normally 6.7 to 8.9°C Documented from 5.6 to 11.1°C. Optimal = 10.3°C</td>
<td>Begins at temperatures 3.9–14.4°C. Optimal 7.7°C Follows walleye spawning.</td>
<td>Carufel (1963); Scott and Crossman (1973); Colby et al. (1979); Hasnain et al. (2010)</td>
</tr>
<tr>
<td>Habitat</td>
<td>Shorelines and shallow offshore reefs in lakes. Spawning in rivers Primary substrates are gravel and cobble, but may be mixed with sand and boulders. Site fidelity for return spawners.</td>
<td>Same as walleye.</td>
<td>Cobb (1923); Eschmeyer (1950); Crowe (1962); Preigel (1964, 1969); Walburg (1972); Colby et al. (1979); Stevens (1990); Jeffrey and Edds (1999); Jaeger et al. (2005); Raabe (2006); Bellgraph et al. (2008)</td>
</tr>
<tr>
<td>Mating</td>
<td>Nocturnal Polygamous Broadcast eggs No parental care</td>
<td>Same as walleye.</td>
<td>Ellis and Giles (1965); McElman (1983)</td>
</tr>
<tr>
<td>Egg diameter</td>
<td>1.3–2.1 mm</td>
<td>1.0–1.9 mm Smaller than walleye.</td>
<td>Smith (1941); Carufel (1963); Nelson (1968a); Colby et al. (1979); Graeb et al. (2007)</td>
</tr>
<tr>
<td>Eggs</td>
<td>Fertilization success</td>
<td>3–100%</td>
<td>Colby et al. (1979)</td>
</tr>
</tbody>
</table>
## Table 7.2. Continued.

<table>
<thead>
<tr>
<th>Life history characteristic</th>
<th>Walleye</th>
<th>Sauger</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Incubation</strong></td>
<td>Decreases with increasing temperature 14 d at 12.8°C</td>
<td>Decreases with increasing temperature 9 d at 12.8°C, 21 d at 8.7°C</td>
<td>Nelson (1968a,1968b); Walburg (1972)</td>
</tr>
<tr>
<td><strong>Eggs</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature allowing greatest hatching success</td>
<td>9–15°C</td>
<td>4.5–12.8°C</td>
<td>Scott and Crossman (1973); Colby et al. (1979)</td>
</tr>
<tr>
<td><strong>Optimal development temperature</strong></td>
<td>13.5°C</td>
<td>12.2°C</td>
<td>Hasnain et al. 2010</td>
</tr>
<tr>
<td><strong>Length at hatch</strong></td>
<td>6.0–8.6 mm</td>
<td>4.5–6.2 mm</td>
<td>Scott and Crossman (1973); Colby et al. (1979)</td>
</tr>
<tr>
<td><strong>Length at yolk sac absorption</strong></td>
<td>10 mm</td>
<td></td>
<td>Nelson (1968a)</td>
</tr>
<tr>
<td><strong>Scale development</strong></td>
<td>24–45 mm TL</td>
<td></td>
<td>Becker (1983)</td>
</tr>
<tr>
<td><strong>Development of tapetum lucidum</strong></td>
<td>37–140 mm TL Developed only in the ventral region of the retina.</td>
<td>More uniformly distributed in the retina. Adapted for dimmer light than walleye.</td>
<td>Ali and Anticil (1977); Collette et al. (1977); Bulkowski and Meade (1983); Braekevelt et al. (1989); Vandenbyslaardt et al. (1991)</td>
</tr>
<tr>
<td><strong>Age 0</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Response to light</strong></td>
<td>Shifts from positive to negative when 32–40 mm TL Coincides with development of the tapetum lucidum.</td>
<td>Similar to walleye but sauger have higher negative phototropism than walleye.</td>
<td>Scott and Crossman (1973); Ali and Anticil (1977); Hackney and Holbrook (1978); Bulkowski and Meade (1983); Amadio et al. (2005)</td>
</tr>
<tr>
<td>Life history characteristic</td>
<td>Walleye</td>
<td>Sauger</td>
<td>References</td>
</tr>
<tr>
<td>----------------------------------</td>
<td>------------------------------------------------------------------------</td>
<td>----------------------------------------------------------------------</td>
<td>---------------------------------------------------------------------------</td>
</tr>
<tr>
<td><strong>Ontogenetic diet shifts (onset of piscivory)</strong></td>
<td>Initially feeds on zooplankton, then benthos and then fish. Onset of piscivory is typically at 50–80 mm TL.</td>
<td>Diet similar to walleye. Piscivorous when 70–110 mm TL.</td>
<td>Smith and Moyle (1945); Smith and Pycha (1960); Nelson (1968b); Walker and Appelgate (1976); Mathias and Li (1982); Frey (2003); Galarowicz et al. (2006)</td>
</tr>
<tr>
<td><strong>Length at age 1</strong></td>
<td>76–375 mm</td>
<td>74–244 mm</td>
<td>Colby et al. (1979); Carlander (1997, Table 8-6)</td>
</tr>
<tr>
<td><strong>Diurnal feeding pattern</strong></td>
<td>Primarily nocturnal, but more daytime foraging when turbidity is high.</td>
<td>Same as walleye. When sympatric with walleye, sauger forage more demersally.</td>
<td>Rawson and Scholl (1978); Wahl and Nielsen (1985); Lyons (1987); Graeb et al. (2007)</td>
</tr>
<tr>
<td><strong>Prey–predator length ratio</strong></td>
<td>Average 44% when 60 mm TL. Average 28% when 400 mm TL. “Walleye larger than 40 mm actually lose weight when forced to feed exclusively on plankton” (Galarowicz et al. 2006).</td>
<td></td>
<td>Parsons (1971); Swenson (1977); Galarowicz et al. (2006)</td>
</tr>
<tr>
<td><strong>Juvenile (age 1 to maturation)</strong></td>
<td>Diet System-specific. Consumes a wide array of fish species. Also consume larger invertebrates when they are readily available.</td>
<td>Same as walleye.</td>
<td>Mathias and Li (1982); Wahl and Nielsen (1985); Lyons (1987); Frey (2003); Galarowicz et al. (2006); Kaufman et al. (2009)</td>
</tr>
</tbody>
</table>
### Table 7.2. Continued.

<table>
<thead>
<tr>
<th>Life history characteristic</th>
<th>Walleye</th>
<th>Sauger</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Final temperature preferenda</strong></td>
<td>19.6°C</td>
<td>22.5°C</td>
<td>Hasnain et al. (2010)</td>
</tr>
<tr>
<td><strong>Optimal growth temperature</strong></td>
<td>22.0°C</td>
<td>22.1°C</td>
<td>Hasnain et al. (2010)</td>
</tr>
</tbody>
</table>
| **Length at 50% maturity** | Female: 330–560 mm  
Male: 250–450 mm | Female: 284 mm  
Male: 249 mm | Preigel (1969, sauger); this chapter (walleye) |
| **Age at 50% maturity** | Female: 4–14 years  
Male: 2–13 years  
Increases south to north. | Combined sex: 2–8 years  
Increases south to north. | Carufel (1963, sauger); Vasey (1967); Walburg (1972); Carlander (1997); this chapter (walleye) |
| **Adult** | | | |
| **Longevity** | 3–30 years  
Increases south to north. | 2–13 years  
Increases south to north. | Carlander (1997, Table 8-6, sauger); this chapter (walleye) |
| **Sexual dimorphism** | Begins at maturity.  
Females larger than males at maturity.  
Females attain a larger maximum length. | Mature females may be slightly larger than males. | Hassler (1957); Carlander (1997); Quist et al. (2003) |
| **Mean TL at maximum age** | Female: 440–830 mm  
(mean = 670 mm)  
Male: 383–700 mm  
(mean = 540 mm) | Combined sex: 296–635 mm | Carlander (1997, sauger); this chapter (walleye) |
### Table 7.2. Continued.

<table>
<thead>
<tr>
<th>Life history characteristic</th>
<th>Walleye</th>
<th>Sauger</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Von Bertalanffy growth parameter ($L_\infty$)</td>
<td>Combined sex: 443–1,020 mm (mean = 733 mm)</td>
<td></td>
<td>Quist et al. (2003, walleye); Sass et al. (2004, walleye)</td>
</tr>
<tr>
<td>Von Bertalanffy growth parameter ($k$, per year)</td>
<td>Combined sex: 0.07–0.59 (mean = 0.20)</td>
<td>Combined sex: 0.11–0.55 (for latitudes 42° to 48° N) Increases with growing degree-days.</td>
<td>Braaten and Guy (2002, sauger); Quist et al. (2003, walleye); Sass et al. 2004, walleye</td>
</tr>
<tr>
<td>Absolute fecundity (no. eggs/female)</td>
<td>10,000–400,000 Increases with body size.</td>
<td>10,000–209,000 Increases with body size.</td>
<td>Carlander (1997, sauger); this chapter (walleye)</td>
</tr>
<tr>
<td>Relative fecundity (no. eggs/kg)</td>
<td>18,000–85,000</td>
<td>33,000–106,000</td>
<td>Carlander (1997, sauger); this chapter (walleye)</td>
</tr>
</tbody>
</table>
America, like walleye, is widespread primarily in northern latitudes. While both species co-occur across much of their ranges, saugers are more limited in distribution, both geographically and environmentally. They are found primarily in larger, more turbid or stained rivers or large shallow lakes (Davidoff 1978; Rawson and Scholl 1978; Hesse 1994; Vallazza et al. 1994; Pegg et al. 1997); rivers are believed to be their evolutionary origin (Balon et al. 1977). Saugers range across Canada from southern and mid-latitudes of Alberta, Saskatchewan, Manitoba, through Ontario to nearly James Bay, and east across Québec to the St. Lawrence River. Their range extends south into the United States through New England along the west side of the Appalachian Mountains south to the Ohio River systems, west to Arkansas and Tennessee, and northwest to Montana and Wyoming in the Missouri River system (Scott and Crossman 1973; see Chapter 4). Although both species are extensively managed, the distribution of sauger has not been artificially expanded nearly to the degree that has occurred with walleye, although stocking can be common locally (Lynch et al. 1982; Flamming and Willis 1993; Summers et al. 1994; White and Schell 1995), and their abundance across their native range appears to be in decline (Pegg et al. 1997; Bellgraph et al. 2008). Recent declines of sauger distribution and abundance have raised concerns. Jaeger et al. (2005) felt that the highly migratory nature of saugers, high site fidelity, and a wide array of habitats and turbidities needed for successful execution of its complete life cycle make it sensitive to habitat fragmentation by dams. Sauger populations are believed to be in decline in some portions of their range, but particularly in large rivers where impoundments have altered access to traditional spawning areas and have reduced suspended sediment loads (Bellgraph et al. 2008). In Norris Reservoir, Tennessee, saugers do not spawn in the impoundment proper, but rather in tributary streams (Fitz and Holbrook 1978).

Where walleyes and saugers exist sympatrically, hybridization and backcrossing occur, and hybrid progeny are referred to as saugeyes (see Chapter 3 for additional details). Hybrids and their backcrosses are fertile and are difficult to discriminate from either parental species morphologically (Clayton et al. 1973; Billington et al. 1997; Fiss et al. 1997). Saugeyes occur both naturally (Billington et al. 1997) or are produced purposefully in hatcheries and stocked (Heidinger and Brooks 1998) (see Chapters 12 and 13). Natural hybridization occurs as saugers spawn at the tail end of walleye spawning in similar habitats; alteration of native habitats may increase hybridization rates (Billington et al. 1997). In the Illinois River, Illinois, spawning by walleyes and saugers overlap considerably and hybridization may be facilitated by high turbidity levels (140 Jackson Turbidity Units), which may reduce visual recognition of potential conspecific mates (Mills et al. 1966; Heidinger and Brooks 1998). Saugeyes exhibit hybrid vigor, growing faster than either parental species, and they are more tolerant than walleyes of warm, eutrophic reservoir conditions (Lynch et al. 1982; Malison et al. 1990; Fiss et al. 1997). However, stocking saugeyes into systems where walleyes and saugers are native or already established can be a problem. In systems where saugeyes become established, viable walleye populations may become difficult to maintain or establish although causality for walleye declines is unclear (Fiss et al. 1997), and where stocked, saugeyes can backcross with either parental stock and produce viable offspring (White and Schell 1995; Fiss et al. 1997).

Environmental features associated with sauger populations help explain distributional patterns. In general, saugers prefer warm deep pools and runs with low water current velocities and high turbidity (Crance 1988; Vallazza et al. 1994; Gangl et al. 2000). In the Wind River, Wyoming, saugers were most abundant in river reaches where pools and runs were more than 1 m deep, daily summer water temperatures exceeded 20°C, and alkalinity ex-
ceeded 130 mg/L (Amadio et al. 2006). Summer thermal preferences of adult saugers are 20–28°C (Dendy 1948; see Chapter 6) and thermal bioenergetic constraints may limit their northern distribution (Braaten and Guy 2002). Ryder et al. (1964) identified that the northern distribution of sauger appears to correspond to the 15.6°C isotherm. Walleyes and saugers have a somewhat similar physiological thermal optima (mean of tolerance, preference, metabolic rate, performance, circulation, and growth) of approximately 22°C (e.g., see Chapter 6), although saugers favor lower temperatures for spawning (optimal spawning temperature: walleye = 10.3°C, sauger = 7.7°C; Hokanson 1977; Hasnain et al. 2010). Interestingly, optimum egg development temperatures are more similar than spawning temperatures with eggs developing optimally at 13.5°C for walleye and 12.2°C for sauger (Hasnain et al. 2010). Dendy (1948) found saugers occurred at deeper depths and therefore cooler water than did walleyes (18.6–19.2°C for saugers versus 20.6–23.2°C for walleyes) in Tennessee reservoirs. Swenson and Smith (1976) found similar thermal trends in Lake of the Woods, Minnesota. Amadio et al. (2005) determined that the upstream distributional boundaries of saugers in four western rivers corresponded to low summer temperatures, higher channel slopes, and water diversion dams that limited upstream distribution. The highest sauger biomass was associated with river reaches where pool and run depths were greater than 1.0 m, the mean daily summer water temperatures were over 20°C, and alkalinity was greater than 130 mg/L. In the southeastern United States, important sauger fisheries were developed when reservoirs impounded their formerly riverine habitats; sauger fisheries primarily occur in low-gradient main-stem reservoirs (e.g., Cumberland and Tennessee river reservoirs) whereas walleyes more commonly typify upland tributary reservoirs (Hackney and Holbrook 1978). In Tennessee River impoundments, saugers are relatively abundant at elevations below 250 m above sea level (asl) while walleyes are sporadic below 300 m asl but are more common at higher elevations (Hackney and Holbrook 1978). This trend appears to correspond to lower elevation main-stem reservoirs being warm, shallow, and turbid and having large inflowing rivers in them where saugers are more common, versus cooler, deeper, clearer, higher-elevation systems that lack large tributary streams where walleyes are more common.

In natural systems, saugers and walleyes appear to partition habitat relative to turbidity and temperature, but in altered systems they may overlap more, at least temporarily as populations adjust (Bellgraph et al. 2008). Saugers exhibit less environmental plasticity than do walleyes, but can be sympatric over a wide geographic distribution where environmental conditions are suitable for both species. Saugers also have scotopic vision similar to walleyes because of the presence of the tapetum lucidum, and they prefer habitats with low light conditions (Moore 1944; Ali and Anctil 1968, 1977). However, saugers are even more negatively phototaxic than walleyes; walleyes have more retinal epithelial pigment and less reflecting material than saugers from similar localities, which correlate to differences in habitat selection and behavior. As a result, saugers prefer darker, more turbid water than do walleyes (Ali and Anctil 1968, 1977). In fact saugers not only have more reflecting material in their eyes, they have it more evenly distributed within the retina making them adapted to more turbid systems, particularly where clay minerals may remain in suspension. As a result, saugers prefer large turbid lakes, such as Lake Winnebago, Wisconsin, and Lakes Manitoba and Winnipeg, Manitoba, and larger turbid rivers, such as the Yellowstone and Missouri rivers and lower sections of their respective tributaries (Hesse 1994).

Saugers are the most migratory of all percids and will migrate hundreds of kilometers to spawn (Scott and Crossman 1973; Collette et al. 1977; Bellgraph et al. 2008; Kuhn et al. 2008).
In spring, mature adults usually move upstream and spawn in main river channels, tributary streams, or along lake shorelines, although in the Yellowstone River, there is a downstream spawning migration (Jaeger et al. 2005). In the middle Missouri River, saugers migrate up to 260 km with similar length migrations occurring in the lower Yellowstone River (<300 km) (Jaeger et al. 2005; Bellgraph et al. 2008). In Watts Bar Reservoir, Tennessee, saugers migrate 160 km from the lower reaches of the reservoir upriver to the upstream dam for spawning (Minton and McLean 1982). Graeb et al. (2009) found that saugers shifted habitat selection from historical remnant river reaches that had been altered by Fort Randall Dam in the Missouri River to occupy new lower river delta habitats where physical conditions were more like the historical predam state. These new habitats were warmer, more turbid, and actively meandering, thereby providing suitable habitat. Impoundments not only limit the migratory nature of saugers, but the reduction in sediment load and the concomitant reduction in turbidity has reduced the length of suitable habitat for saugers throughout western river systems.

Growth of saugers is highly variable across their range, and depends on temperature and food diversity and abundance. Saugers do not grow as large as walleyes, but can have faster seasonal growth rates, and maximum growth and food consumption can occur later in the season than in walleyes. In a study of feeding ecology of saugers in the Ohio River, Wahl and Nielsen (1985) found fastest growth for saugers occurred during October and November, compared with August and September for walleyes in Lake of the Woods, Minnesota (Swenson and Smith 1973). Higher growth and food consumption of saugers in the Ohio River continued into winter. This is thought to be due to different temperature patterns and increased availability of gizzard shad. This same seasonal growth pattern was observed by Minton and McLean (1982) for saugers in Watts Bar Reservoir. However, Minton and McLean (1982) also pointed out that this increased winter growth pattern observed in some sauger populations, does not occur in all populations, and is highly dependent on prey abundance and composition. In Norris Reservoir, Tennessee, Fitz and Holbrook (1978) found that sauger growth rates were faster than in northern populations.

Saugers vary among systems in their degree of sexual dimorphism. Female saugers are either similar in size to males or can be larger than males, although in these systems the differences are not as large as is seen in walleyes (Carlander 1950; Hassler 1957; Quist et al. 2003b). Length at age between male and female saugers in Garrison Reservoir, North Dakota, is nearly equal for ages 1 and 2, and by age 5, there is less than 3 cm difference (Carufel 1963). In Lake of the Woods, age-5 and age-6 male and female saugers differ less than 2 cm (standard length, SL) (Carlander 1950). Age at maturity ranges from 2 to 8 years depending upon latitude (i.e., climate) and prey; in Lewis and Clark Lake, South Dakota, saugers mature in 3–4 years (Walburg 1972).

Fecundity of saugers in Garrison Reservoir, North Dakota, increased with size and age, ranging from 6,500 to 17,000 eggs/kg (Carufel 1963). In that study, age-3 saugers produced 13,000 eggs whereas age-7 fish produced 101,000 eggs. Simon (1946) reported 50,000 eggs for a 1.4-kg sauger from Wyoming. Fecundity of age-2 Lake Erie saugers ranged from 58,000 to 77,400 eggs (Rawson and Scholl 1978). Gamete maturation in walleye and sauger occurs at temperatures below 12°C, which may limit their southern distribution, although the presence of centrachids may also play a role as well (Collette et al. 1977). A summer gonadal refractory period ensures an annual reproductive cycle in walleye and sauger (Collette et al. 1977). Saugers spawn at approximately the same temperature as do walleyes: e.g., 3.9–11.7°C in North Dakota (Carufel 1963), 14.4°C in Tennessee (see Hokanson 1977), 7.2–8.3°C in a...

Like walleyes, saugers are broadcast spawners and provide no parental care to eggs or young. Similarly, eggs are only adhesive briefly although accounts vary as to the degree of adhesion and duration of adhesiveness. Spawning by saugers generally occurs over coarse substrates (i.e., gravel and larger-sized substrates) in main-stem and tributary river channels and tailwaters below reservoirs (Bellgraph et al. 2008). In rivers, saugers spawn in habitats that create optimal combinations of water velocities and rock substrates. In Lake Winnebago, Wisconsin, saugers spawn along rocky shorelines (Preigel 1969). In western rivers, saugers use meanders along natural bedrock outcrops during the spawning season (Nelson 1968b; St. John 1990; Hesse 1994; Jeffrey and Edds 1999). Staging or spawning of saugers in bluff pools (i.e., pools hydraulically constrained by bedrock outcrops) and artificially created rip-rap pools may occur because they combine suitable substrates and velocities for spawning, but also have secondary currents that may offer velocity refuge for staging fish (Bellgraph et al. 2008). In Lake Erie, saugers spawn along shale bedrock ridges and sand–gravel substrates in the Sandusky River and cobble–boulder riffles in the Maumee River (Rawson and Scholl 1978). In the Yellowstone River, saugers show site fidelity with respect to spawning areas (Jaeger et al. 2005).

Sauger eggs are similar in size to walleye eggs. Diameter of sauger eggs from Garrison Reservoir, North Dakota, ranged from 1.0 to 1.8 mm (Carufel 1963). Eggs from saugers in Missouri River reservoirs ranged in diameter from 1.3 to 1.5 mm with their caloric density (cal/g dry weight) varying from 2,600 to 3,400; caloric content increased with increasing TL of females (Graeb et al. 2007). Sauger eggs have been collected in drift samples below spawning sites on the Missouri River (Nelson 1968b); 68% of eggs collected with suction pumps at depths between 0.6 and 4.0 m in the Missouri River were viable immediately after spawning (Nelson 1968b). Female saugers of intermediate age (age 4–6) and large sizes (460–520 mm TL) in Missouri River reservoirs had the highest quality eggs based on size and caloric content (Graeb et al. 2007). Eschmeyer and Smith (1943) reported saugers did not spawn at temperatures below 10°C and eggs were deformed when low temperatures persisted.

Sauger hatching occurred in 21 d at 8.7°C in Lewis and Clark Lake, South Dakota (Walburg 1972). Nelson (1968b) also found hatching occurred in 21 d at 8.3°C and 9–14 d at 12.8°C (Nelson 1968a). At hatching, larvae range in size from 4.5 to 6.2 mm TL and remain sedentary on the bottom for approximately 7–9 d until their yolk is absorbed. Hatchery-reared saugers ranged from 4.62 to 5.09 mm TL at hatching (Nelson et al. 1965). Colder water temperatures increase mortality as larval development is reduced, thus subjecting larvae to planktonic drifting for longer periods of time (Walburg 1972). Larvae (4.8–7.46 mm TL) in the Missouri River drifted downstream after hatching (Nelson 1968b) and arrived downstream in the reservoir approximately 1 week after initiating drifting. Considerable numbers of larval saugers are lost through dams on the Missouri River while they are drifting downstream. Shorter water-residence times in the reservoir increase water velocities sufficiently high enough to carry drifting larvae through the lake proper and to the dams (Walburg 1972).

Sauger year-classes fluctuate widely in southern U.S. reservoirs and appear to be a relatively synchronous, region-wide phenomenon (i.e., years of high and low abundance occur across systems) although specific factors responsible for year-class strength are not well studied (Hackney and Holbrook 1978). Adult year-class strength was inversely related to water level fluctuations over the spawning grounds during egg incubation in Missouri River res-
ervos (Nelson 1968b). Fluctuating water levels eliminated viable eggs presumably due to
stranding (Nelson 1968b). Benson (1973) found 10-fold increases in young sauger abundance
in years after high diel water fluctuations from hydropower operations were reduced. Pitlo
(2002) found that year-classes of both saugers and walleyes (fall age 0) were correlated with
spring water temperatures (April 15–May 5) in Pool 13 of the upper Mississippi River. Wal-
burg (1972) found 80% of the variation in sauger year-class strength in Lewis and Clark Lake
was explained by water level fluctuation, reservoir exchange rate, and water temperature.

As with walleye, the diet of sauger is a function of ontogeny and prey availability (see
Chapter 8). Larvae begin feeding on zooplankton (e.g., *Cyclops* spp.) before the yolk sac is
completely absorbed and then shift to larger zooplankton with increasing size (e.g., *Diap-
tomus* spp., *Daphnia* spp.); distinct selectivity of zooplankton occurs (Nelson 1968b). As
saugers grow, they become piscivorous. Adult saugers in the Ohio River consumed gizzard
shad, emerald shiner, and other fishes, with prey consumption averaging 1.1% of their body
weight per day (Wahl and Nielsen 1985). They fed on smaller fish at warmer temperatures and
larger fish at cooler temperatures seasonally. Depending on the system, saugers may feed on
the same prey items as walleyes suggesting potential diet overlap and resource competition,
but saugers and walleyes may partition space (with saugers occurring at deeper depths and in
some systems foraging on different prey species) thus reducing competition. In lakes where
saugers are sympatric with walleyes and yellow perch, the proportion of the community con-
sisting of walleyes and yellow perch is reduced (Clady 1978). In the middle Missouri River,
diet overlap between walleyes and saugers was substantial during spring and summer (Bell-
graph et al. 2008); both preyed upon emerald shiners and stonecats in spring, and stonecats,
with lesser amounts of emerald shiners, macroinvertebrates, and mottled sculpins in summer.
In Lake of the Woods, saugers selected primarily benthic trout-perch throughout summer but
increased yellow perch in their diet in July and August; their consumption rates increased
with increasing wave activity (Swenson 1977). Walleyes in the same system foraged more on
yellow perch, rainbow smelt, and *Notropis* spp. over the same time period. This diet differ-
ence suggests that resource partitioning can and does occur at times between these species,
although the phenomenon is not universal across systems.

### 7.9 SUMMARY

Walleye and sauger have successfully colonized a wide array of habitats across northern
latitudes of North America. These species occur sympatrically and allopatrically; where sym-
patric, they may hybridize and backcross, particularly in altered environments. Walleyes ex-
hibit a variety of life history strategies across a wide geographic and climatic region of North
America, exhibiting considerable plasticity in habitat use, growth patterns, survival, and re-
cruitment rates. Their success in a variety of different environmental conditions in lakes and
rivers underscores a complex, yet flexibly adaptive organism suited to colonize and persist
in these habitats. While closely related, saugers exhibit a somewhat less flexible life history
strategy, and even hybridize and backcross with walleye under certain conditions. Life history
strategies within a system vary with abiotic and biotic factors that influence growth, matura-
tion, reproduction, recruitment, and survival. These factors vary across the geographic distri-
bution of both species, which is strongly influenced by climate (i.e., growing degree-days).
Management of these species that recognizes the differences in life history variation that have
been successful locally will most likely have the most successful long-term outcomes.
7.10 ACKNOWLEDGMENTS

Dominic Baccante acknowledges his friends Peter Colby and Kevin Roberts for the many good memories, fun, and productive times at the Walleye Research Unit in Thunder Bay, Ontario. Also appreciated is the help of Jessica Baccante, Heather Hopkins, and Roxanne Smith, all with the British Columbia Ministry of Environment, for helping with all aspects of literature search, maintaining a reprint library, and proof-reading. Serena Baccante drew the walleye sketches used in Figure 7.2. We thank R. Ryder, J. Deacon, L Paulson, and W. Wawrzyn for their contributions to fisheries and aquatic resources and the incredible professional mentorship they provided throughout their lives to so many. C. Jacobson provided support and inspiration. We gratefully acknowledge the Ontario Ministry of Natural Resources and the Ministère des Ressources Naturelles du Québec for providing access to walleye survey databases and Trevor Middel for producing the map in Figure 7.1. We thank R. Klumb, P. Brown, B. Sloss, B. Jackson, and A. Musch who all reviewed earlier drafts of the chapter. M. Bozek thanks R. Bozek, Sr. for always giving so much and always expecting our best effort.

7.11 REFERENCES

University of Wisconsin, Madison, Wisconsin, USA, July 20–24, 2003. University of Wisconsin Sea Grant Institute, Madison.


Carlander, K. D. 1950. Growth rate studies of saugers, Stizostedion canadense canadense (Smith) and yellow perch, Perca flavescens (Mitchell) from Lake of the Woods, Minnesota. Transactions of the American Fisheries Society 79:30–42.


Gangl, R. S., D. L. Pereira, and R. J. Walsh. 2000. Seasonal movements, habitat use, and spawning areas of walleye (Stizostedion vitreum) and sauger (S. canadense) in Pool 2 of the upper Mississippi River, Minnesota. Minnesota Department of Natural Resources, Investigational Report 482, St. Paul.


Kaufman, S. D., J. M. Gunn, G. E. Morgan, and P. Couture. 2006. Muscle enzymes reveal walleye (Sander vitreus) are less active when larger prey (cisco, Coregonus artedi) are present. Canadian Journal of Fisheries and Aquatic Sciences 63:970–979.


