Chapter 9
Winter biology of centrarchid fishes

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9.1   Introduction

Temperate latitudes experience a predictable annual cycle of alternating warm and cold periods that can result in below freezing conditions, ice cover, and alterations to aquatic habitats that persist for a substantial portion of a year. Winter represents a very interesting and challenging time of the year that exerts a strong selective pressure on individual survival, community structure, and year class strength for centrarchid fishes. Despite the impact of this time on both individuals and populations, we are only beginning to comprehend how this period of the year can influence centrarchid fishes.

   The purpose of this chapter is to summarize the current literature that defines the ecological, behavioral, and physiological alterations experienced by centrarchid fishes both prior to and during winter. Because of the paucity of information on winter biology of centrarchid fishes, this chapter has been written in a general format whereby studies of different centrarchid fishes have been pooled to identify trends that exist across the entire family. Where appropriate, exceptions to these general trends have been noted. A general over-arching question does emerge from work to date despite the lack of broad research coverage in many areas of centrarchid winter biology: What physiological and ecological changes occur to ensure survival prior to and during a period of reduced energy intake?

9.2   Definition of "winter"

We define "winter" as the period of the year between the autumnal equinox and prior to the onset of spawning in centrarchid fishes. This definition encompasses the suite of physical, biochemical, and structural changes to both water and fish that result from reduced water temperature and day length, and allows for the onset and termination of the "winter" period that varies with latitude.

   Centrarchids can experience a broad range of climatic conditions during winter across their range. Pronounced latitudinal gradients in winter conditions exist with growing degree days and summer temperatures both declining with latitude, whereas both winter severity (i.e. lower daily temperatures) and winter length increase with latitude. Centrarchids residing in Alabama farm ponds, for example, may briefly experience winter water temperatures that range from 4 to 13°C (Swingle 1952), whereas water temperatures for centrarchids at the northern edge of their range may be near freezing for several consecutive months. This latitudinal variation in winter severity has several pronounced implications for many of the ecological, physiological, and geographic characteristics observed within this family.

9.3   Current research

One trend that emerged while writing this chapter was the paucity of research that has been conducted on the winter ecology and physiology of centrarchid fishes. To illustrate this, we used three common academic search engines (Fish and Fisheries Abstracts, Web of Science, and CISTI Source) to perform literature searches and collect reference materials. The search terms used were truncations designed to maximize the number of potential hits associated with winter conditions.

Table 9.1 Results of literature searches using three academic search engines to locate reference materials.

Search string	Fish and fisheries worldwide	Web of science	CISTI source
Fish* and (ice or snow or winter)	4178	4918	2074
Centrarch* and (ice or snow or winter)	132	22	7
Micropt* and (ice or snow or winter)	94	63	39
Lepom* and (ice or snow or winter)	63	42	14
Pomox* and (ice or snow or winter)	33	10	7
Ambloplit* and (ice or snow or winter)	9	3	2
Enneacan* and (ice or snow or winter)	2	1	0
Archoplit* and (ice or snow or winter)	0	0	0
Centrarch* and habitat*	1019	102	28
Centrarch* and reprod*	515	69	16

*Truncated search strings are shown here, and searches were set up to scan entire articles for the truncated search strings.

Searches scanned entire articles for keywords, and the keywords used included all of the different genera in the centrarchid family (See Chapter 1 in this volume) as well as the terms ice, snow, and winter. Results from these searches are shown in Table 9.1 and highlight the lack of studies focusing on centrarchids in winter. When a general search string such as [Fish* and (ice or snow or winter)] was queried, several thousand hits were generated for each of the three search engines used (Table 9.1). Similar research focusing on centrarchid fishes, however, is proportionally scarce with only 161 total references generated for all three search engines combined when the search string [centrarch* and (ice or snow or winter)] was run (Table 9.1). In contrast, for topics such as centrarchid habitat, there were approximately five times more citations listed than for winter ecology (Table 9.1). This lack of information can likely be attributed to the numerous inherent challenges associated with studying fish in winter, including: difficulty in fish collections through ice, safety issues concerning ice and cold water, as well as the obvious discomfort of outdoor work during cold temperatures. Despite these challenges, however, sufficient studies have been performed to provide a general understanding of the impact of winter on centrarchid fishes.

9.4   Temperature

One of the most significant impacts of winter conditions on centrarchid fishes is a reduction in ambient water temperature brought about by changes in solar radiation. Temperature affects almost all levels of biological organization including molecular diffusion rates, membrane structure, organ function, and respiration rates. Both calendar date and latitude have a significant impact on the amount of solar radiation (Gates 1962; Figure 9.1). Both the amount of radiation and the angle at which it strikes the Earth decrease as months advance from the summer solstice and as latitudes increase (Gates 1962). Less solar radiation is transferred to water and more radiation is reflected by the water surface during winter periods in temperate regions.

9.4.1   Ice

Ice formation on lakes results from a predictable pattern based on latitude, volume, and fetch (Shuter *et al*. 1983). Ice can be intermittent throughout the winter or it can accumulate to thicknesses approaching 1 m or more in certain northern
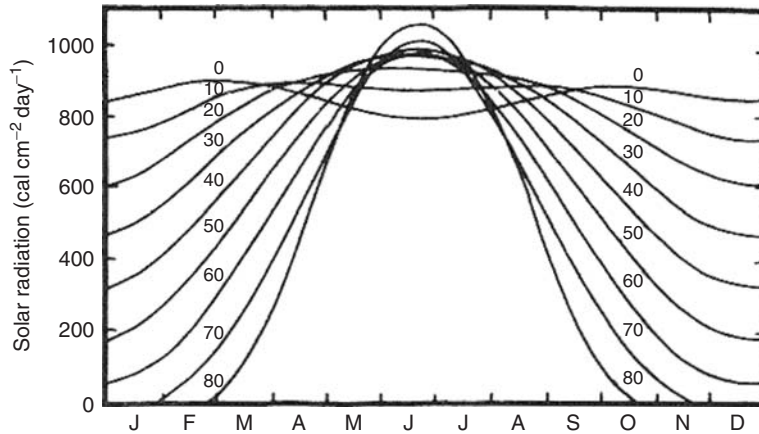
Figure 9.1 Amount of solar radiation (cal·cm^{-2}·day^{-1}) received on a horizontal surface for different latitudes at various times of the year. Latitude is presented in 10° intervals and abbreviated calendar month is shown on the *x*- axis beginning on the left with January (J, January; F, February; M, March, etc.). Figure from Wetzel (1983), Elsevier [(Harcourt Publishers) http://www.thomsonrights.com/permissions/action/start].

locations and persist for several months. As snow is added on top of ice or if ice is not transparent, both albedo (Grenfell and Maykut 1977) and light attenuation increase and light levels can fall to near zero <1 m below the surface (Welch *et al*. 1987). This can have important implications for photosynthetic and aerobic organisms throughout a waterbody.

   In streams and rivers, the energy of flowing water may be sufficient to prevent formation of surface ice despite cold temperatures. Despite this lack of ice cover, flowing water at high latitudes only warms a few hundredths of a degree above freezing during winter except in locations of groundwater inflow, input from tributaries, or at gaps in ice formation (Belatos *et al*. 1993). Super-cooled water in turbulent areas can form frazil ice crystals that can remain suspended in the water or possibly coat objects in the river (Belatos *et al*. 1993; Prowse 1994). Frazil ice can accumulate on virtually any underwater surface with significant accumulations being termed anchor ice (Benson 1955; Belatos *et al*. 1993; Prowse 1994). Although anchor ice may float downstream without any consequences to fishes, it can contain sand, gravel, organic materials, and benthic invertebrates (Benson 1955), and accumulations on the substrate can create a false bottom causing the river to rise above its normal depth (Belatos *et al*. 1993). Anchor ice, coupled with the growth of surface ice in slower river reaches, can extend the entire depth of the water column effectively removing large portions of backwater lotic habitats (Prowse 1994; Gent *et al*. 1995). The full extent of ice on stream erosion, stream flow, dissolved oxygen levels, and lotic fishes is not fully understood (Prowse 1994). The extent to which most of these processes can affect lotic centrarchids in rivers and streams has not been well studied.

9.4.2   *Photosynthesis*

Primary productivity in temperate latitudes follows the annual cycle of solar radiation discussed earlier. During winter, the amount of emergent macrophytes (Miranda and Pugh 1997), submergent macrophytes, phytoplankton (Wetzel 2001), and epilithic algae (Harrison and Hildrew 1998) all decline in abundance, with more pronounced decreases occurring at high latitudes. This seasonal decline in primary producers is largely due to a reduction in water temperature (Rooney and Kalff 2000), but also appears to be associated with reduced light levels (Welch and Kalff 1974). Phytoplankton adapted to low temperature and reduced light conditions can survive under ice (Philips and Fawley 2002) and may continue to photosynthesize, with this activity typically occurring in the upper portions of a waterbody (Wetzel 2001). In general, however, aquatic dissolved oxygen concentrations decrease in winter as a result of reductions in photosynthetic macrophytes and phytoplankton, elimination of atmospheric oxygen exchange because of ice, decomposition in the benthos, and inputs

of oxygen-poor groundwater (Schreier *et al*. 1980; Prowse 1994). This reduction in dissolved oxygen may be responsible for several behavioral modifications for centrarchid fishes during winter and can result in mortality.

9.5   Dissolved oxygen and winterkill

A reduction in dissolved oxygen under ice during winter is a common occurrence and has been reported for many different waterbodies at high latitudes. Extensive fish mortality can result if hypoxic conditions persist for extended periods and escalate to the depletion of oxygen within the water (Greenbank 1945; Fox and Keast 1990). Depletion of oxygen can occur for many reasons such as a lack of photosynthesizing vegetation, oxygen consumption through benthic decomposition, and ice cover preventing the exchange of oxygen with the environment (Danylchuk and Tonn 2003). The potential to develop hypoxic conditions in northern waterbodies can be predicted (Jackson and Lasenby 1982) and is influenced by factors such as waterbody depth, trophic status, basin morphometry, degree of water mixing, macrophyte abundance, percent littoral area, and total phosphorous (Mathias and Barica 1980; Meding and Jackson 2003). Shallow, eutrophic waters rich in phosphorous and littoral macrophytes at northern latitudes appear to be the most prone to winter hypoxia (Mathias and Barica 1980; Meding and Jackson 2003), and the quantity of dissolved oxygen within a waterbody can vary across winters (Greenbank 1945; Danylchuk and Tonn 2003). Winterkill can occur on a local scale such as in an isolated lake or pond, and studies have shown that such events can result in the loss of 85% of pumpkinseed from the population (Fox and Keast 1990). Winterkill can also occur at a landscape scale as a result of severe winters, such as described in Greenbank (1945) who documented "a considerable number of lakes in Southern Michigan" that experienced winterkill in the winter of 1935–1936 resulting in the deaths of hundreds of thousands of fish, with centrarchids likely included. Declines in large numbers of fish as a result of winterkill can have repercussions that cascade throughout an ecosystem. Changes as a result of winterkill influence the relative abundance of individuals or species (composition), and can affect age of first maturity, species richness, ecosystem biomass, or food web dynamics (Shuter and Koonce 1977; Micheli *et al*. 1999).

Laboratory investigations examining the oxygen tolerances of centrarchid fishes have focused on only a few species with results consistently showing a profound resilience to hypoxic conditions. Laboratory studies with bluegill showed that, at 25°C, fish could survive for 24 h in dissolved oxygen concentrations that had been reduced to 0.7 mg/l (Moss and Scott 1961). Laboratory studies have also shown that largemouth bass held at 23.7°C will avoid waters with dissolved oxygen concentrations below 2.4 mg/l and show preference for water at or above 4 mg/l (Burleson *et al*. 2001), but can survive dissolved oxygen concentrations below 1.0 mg/l (Moss and Scott 1961). Field studies during winter tend to corroborate these lab investigations and suggest that many centrarchid fishes are quite tolerant to hypoxic conditions. Lethal dissolved oxygen concentrations have been reported as ranging between 0.4 and 2.0 mg/l for pumpkinseed, bluegill, and black crappie during winter conditions (Moore 1942; Cooper and Washburn 1949). Cooper and Washburn (1949) and Johnson (1965) reported that significant winterkill of centrarchid fishes was unlikely provided dissolved oxygen concentrations remained above 1.0 mg/l, while Knights *et al*. (1995) recommended 2–3 mg/l dissolved oxygen for overwintering bluegill and black crappie. Cooper and Washburn (1949) also observed live bluegill and pumpkinseed congregating at holes cut in the ice of a Michigan lake despite the fact that dissolved oxygen in the lake had been below 1.0 mg/l for over a week, and was 0.4 mg/l when fish were observed. Prolonged exposure to dissolved oxygen concentrations below 2.6 mg/l in a winter simulation experiment did not influence spawning activity in black crappie (Carlson and Herman 1978). Finally, Moore (1942) noted that smaller centrarchid fishes were more likely to die during periods of oxygen depletion, likely because of elevated metabolic rates relative to larger fish. It is believed that the reduced metabolic rate (Section 9.6) and activity levels (Section 9.9) of overwintering fish allow survival at low-oxygen tensions.

Laboratory and field studies suggest that, with the onset of hypoxia under ice, fish exhibit several predictable behavioral responses in an attempt to survive low-oxygen conditions. First, laboratory studies with bluegill documented that dissolved oxygen levels below 2.0 mg/l resulted in increased ventilation rates as fish attempt to increase the flow of water over their gills and maximize oxygen uptake (Petrosky and Magnuson 1973). Hypoxic conditions have also been shown to increase activity levels in bluegill, likely as fish attempted to search for more oxygenated waters (Petrosky and Maguson 1973). Next, many species such as yellow perch (*Perca flavescens*), northern pike (*Esox lucius*), and several small-bodied minnows all showed an increased association with the ice/water interface during hypoxia because dissolved oxygen levels in this depth zone are often elevated relative to other areas of a waterbody (Magnuson and Karlen 1970; Magnuson *et al*. 1985;

Petrosky and Magnuson 1973). Bluegill do not appear to associate with the ice/water interface during hypoxia, and, as a result, died from hypoxic exposure prior to other fishes in experimental conditions (Petrosky and Magnuson 1973).

Finally, studies with small-bodied minnows showed that declining oxygen levels motivate fish to migrate to more oxygen-rich waters thereby avoiding hypoxic conditions (Magnuson *et al.* 1985); similar studies involving centrarchid fish are somewhat conflicting. Some studies report the movements of centrarchids in response to low dissolved oxygen, whereas others note either a reluctance or inability to move despite near hypoxic waters. Greenbank (1945), for example, noted dead and dying fish crowded in an area with dissolved oxygen concentrations of only 0.4 mg/l, while only 13 m away, dissolved oxygen concentrations were 2.8 mg/l—unfortunately, fish species were not named in that study. More specifically, Knights *et al.* (1995) showed that dissolved oxygen concentrations influenced habitat decisions by overwintering bluegill and black crappie, and a drop in oxygen concentrations below 2 mg/l caused fish to seek higher dissolved oxygen concentrations even though this subjected them to temperatures below 1°C and increased current velocities. Both Raibley *et al.* (1997) and Gent *et al.* (1995) documented that overwintering largemouth bass were active and roamed throughout backwater habitats despite dissolved oxygen concentrations of 1–2 and 3–6 mg/l, respectively, but avoided more oxygenated main channel areas. While main channel areas may contain increased levels of dissolved oxygen relative to hypoxic backwater areas, main channel waters are also colder than back water areas and have increased current velocity. Thus, fish inhabiting main channel areas would experience increased activity levels, a reduction in swimming ability (Section 9.7), and a concomitant increase in energy consumption. All of these factors would increase the rate of energy consumption, and possibly mortality.

In addition to the immediate population-level impacts of mortality from winterkill, repeated bouts of winterkill are suspected to have altered the life history and species composition of resident fishes and populations. Pumpkinseed that reside in ponds with frequent winterkill were shown to display a more "r-selected" life history with smaller body sizes, smaller length at maturity, higher gonadal investment, and higher fecundity relative to conspecifics from stable lake environments (Fox and Keast 1990; Fox and Keast 1991).

9.6   Physical and physiological changes

The internal temperature of a fish seldom deviates from that of its surroundings because of the relatively large surface area of gills and the close contact between blood and water (Reynolds *et al.* 1976; Hazel 1993). Reductions in water temperature that accompany winter are experienced throughout an entire fish and are accompanied by a suite of physiological changes that can be seen at the cellular, tissue, and individual levels. In general, decreases in temperature of 10°C result in reductions in the rate of reactions by a factor of 2 or 3. Consequently, both the standard metabolic rate and the active metabolic rate of fishes decline at low temperatures such that oxygen consumption and scope for activity are lowest with reduced water temperature (Beamish 1970; Cech *et al.* 1979; Robinson *et al.* 1983; Clarke and Fraser 2004). This relationship has been established for several centrarchid species including largemouth bass (Johnson and Charlton 1960; Lemons and Crawshaw 1985) and bluegill (Wohlschlag and Juliano 1959). The term "metabolic rate," however, encompasses the sum of a suite of physical and chemical processes involved in anabolism, catabolism, and cell energetics, all of which are influenced by temperature (Randall *et al.* 1997). Cold temperatures, for example, slow the activity of enzymes, ion pumps, and ion channels (Somero 1995; Hochachka 1988) and will alter the phase state, rate of motion, and packing arrangement of cellular membranes (Hazel 1993). Cold temperatures also produce changes in neural function in poikilothermic vertebrates, and virtually all neural processes (synaptic gain, conduction velocity, refractory period) are slowed with cooler temperatures (Montgomery and MacDonald 1990). The degree to which this cooling affects the performance of individuals and populations, however, will depend on the species in question and the actual temperatures involved (Montgomery and MacDonald 1990). The extent to which cold temperatures affect the nervous system of centrarchid fishes is unknown as two reviews on this subject (Prosser and Nelson 1981; Montgomery and MacDonald 1990) did not mention any centrarchid species. Low temperatures slow the digestion rates of many fish species including largemouth bass (Markus 1932; Molnár and Tölg 1962; Fänge and Grove 1979), and also lowers the cardiac performance of fish (Driedzic 1992).

Many eurythermal fish species experience modifications in internal physiology in an attempt to combat the reductions in reaction rates and physiological processes that accompany cold water temperatures. Studies of this nature have been conducted using centrarchid fishes, but the paucity of data and disparity between studies preclude clear identification

of trends or strategies both within and among species. For example, winter-acclimated fish often increase metabolism-related enzyme levels to improve their ability to utilize metabolic pathways despite reduced temperatures (Hazel and Prosser 1974; Driedzic *et al.* 1996). This trend was documented by Kolok (1991a) who showed significant increases in the activity of heart citrate synthase from cold-acclimated smallmouth bass suggesting an increased ability to maintain performance despite cold temperatures. In contrast, studies by Sephton and Driedzic (1991) documented that acclimation to 5°C did not alter the activity rate of citrate synthase in smallmouth bass hearts suggesting a decrease in performance for cardiac tissue during winter. Shaklee *et al.* (1977) noted similar within-species discrepancies for winter acclimation strategies for green sunfish (*Lepomis cyanellus*). These authors showed that enzymes from different metabolic pathways (aerobic, anaerobic, etc.) often exhibited different up- or down-regulation both across and within tissues (Shaklee *et al.* 1977) and called for additional studies to elucidate tissue-specific responses to cold acclimation. Furthermore, Tschantz *et al.* (2002) documented significant differences in the activity levels of several different aerobic and anaerobic enzymes for five different centrarchid species during winter acclimation (largemouth bass, green sunfish, bluegill, black crappie, and white crappie) both across species and tissues. No clear trend related to phylogeny could be determined by these authors, further emphasizing that the metabolic strategies employed by centrarchid fishes in dealing with winter conditions vary significantly across species, tissues, and enzymes.

Similarly, acclimation to winter conditions often results in an increase in heart (ventricle) mass relative to body mass (often called the heart somatic index), and it is believed that this occurs to maintain swimming capacity in cold conditions (Driedzic *et al.* 1996). Across several centrarchid species, an increase in ventricular mass during winter was reported for black crappie, white crappie, and smallmouth bass, but not for green sunfish, bluegill, or largemouth bass suggesting species-specific differences in winter performance following acclimation (Kolok 1991a; Sephton and Driedzic 1991; Tschantz *et al.* 2002). Discrepancies across studies may result from the sizes/ages of fish used, latitude (severity of winter), or photoperiod (Section 9.15), and further work in this area is required to elucidate trends.

9.7   Swimming abilities

For all fish, swimming speeds can be categorized as sustained, prolonged, and burst (Hoar and Randall 1978). While sustained and prolonged swimming represent slow-speed aerobic activity that can typically be maintained for extended time periods, burst swimming represents high-intensity, anaerobic activity that can only be maintained for short durations such as during prey capture or predator avoidance (Hoar and Randall 1978). As a result of reductions in water temperature that accompany winter, fish experience several biochemical and physiological changes within their muscle tissue that reduce their capacity to maintain swimming performance relative to summer levels. Low temperature reduces the force generated by muscle, the rate of force development, and maximum power output for the muscle of poikilothermic organisms, although few studies have examined these trends specifically in fishes (Rall and Woledge 1990). Across a range of fish species, however, studies have shown that low water temperatures increase the amount of time required for muscle to contract, while reducing maximum tail beat frequency, therefore lowering maximum swimming speed (Wardle 1980). In addition, reduced temperature impairs the locomotory capacity of fishes by reducing the shortening velocity and power output of muscle (Rome 1990; Hazel 1993). In addition to limitations in swimming performance driven by muscle, reductions in the scope for activity may be driven by a reduced scope for cardiac output at low temperatures (Kolok *et al.* 1983) or a decline in the ability of organisms to uptake and transport oxygen (Pörtner 2002).

These physiological limitations in muscle are reflected in studies of winter swimming performance, including several involving centrarchid fishes; reductions in water temperature result in a decline in the prolonged swimming speed of several centrarchid species including largemouth bass, smallmouth bass (Beamish 1978; Hanson *et al.* 2007; Figure 9.2), and white crappie (Parsons and Smiley 2003). Additionally, the swimming performance of largemouth bass acclimated to 20°C was significantly higher than the fish acclimated to 5°C (Kolok 1992), and Larimore and Duever (1968) noted a significant decline in the swimming ability of smallmouth bass fry (21–23 TL in mm) below 10°C.

To compensate for impairments in muscle capacity associated with low temperatures, many studies have reported alterations to fish muscle properties that attempt to maintain performance. For example, studies involving rainbow trout (*Oncorhynchus mykiss*) report that mitochondrial density, membrane structure, and aerobic capacity in red muscle all show cold-induced alterations intended to enhance the ability of muscle to respire aerobically despite low water temperatures
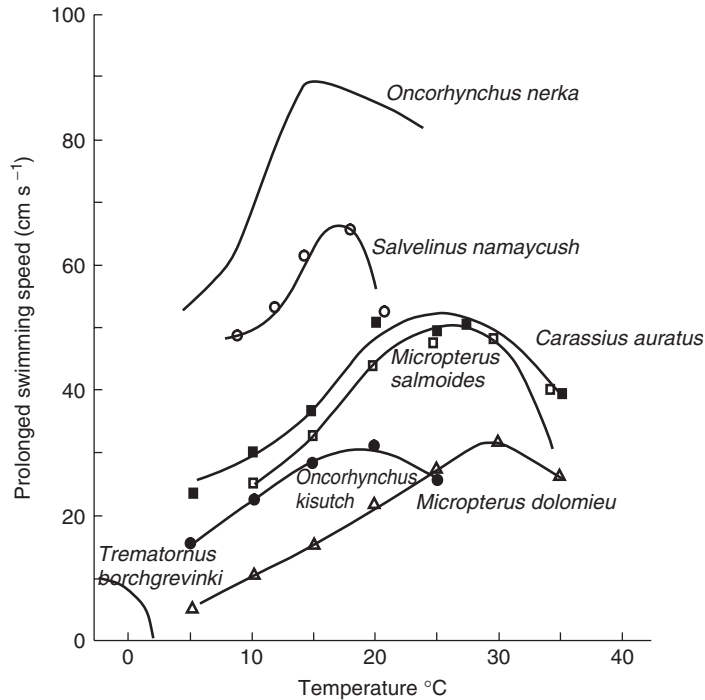
Figure 9.2 Prolonged swimming speed of various fish species across a range of temperatures. Figure from Beamish (1978) [Elsevier (Academic Press, New York) http://www.elsevier.com/wps/find/obtainpermissionform.cws_home/obtainpermissionform].

(Pörtner 2002; Guderly 2004). Evidence also exists to suggest that many of the contractile properties of fish muscle can acclimate to cold temperatures potentially permitting a return to near-normal swimming performance (Johnston *et al*. 1990). A study by Kolok (1991a) documented that the cross-sectional area of red muscle in the caudle peduncle of smallmouth bass and green sunfish increased with cold acclimation, suggesting the potential for increased swimming performance in winter for these species. To date, a few studies have examined the influence of temperature on burst swimming, but results suggest that burst speed is independent of temperature effects (Beamish 1978), although low temperatures will prolong the time to recovery from such activity (Cooke *et al*. 2003).

9.8   Species ranges and life history traits

Magnuson *et al*. (1979) proposed that temperature was an ecological resource similar to food or habitat, and that fish compete for access to appropriate thermal resources to maximize their performance and fitness. Along with Magnuson *et al*. (1979), several additional authors have described lethal (Fry 1971), tolerance (Brett 1970), and performance (Fry 1971) factors associated with temperature gradients that interact to define the thermal niche of fishes, with the geographical limits of the thermal conditions within this niche defining a fish's range and distribution. This theory of temperature-defined species distributions has proved correct for many fishes. Studies by Brandt *et al*. (1980) revealed that fishes in Lake Michigan partitioned habitat according to thermal boundaries, while both Meisner *et al*. (1987) and Shuter and Post (1990) showed that the geographical limits of many Ontario fishes could be delineated by climatic contours associated with temperature and growing season (Figure 9.3). Furthermore, many fish species are confined to southerly regions despite the absence of physical barriers, possibly because of restrictions in thermal niches and reduced performance at higher
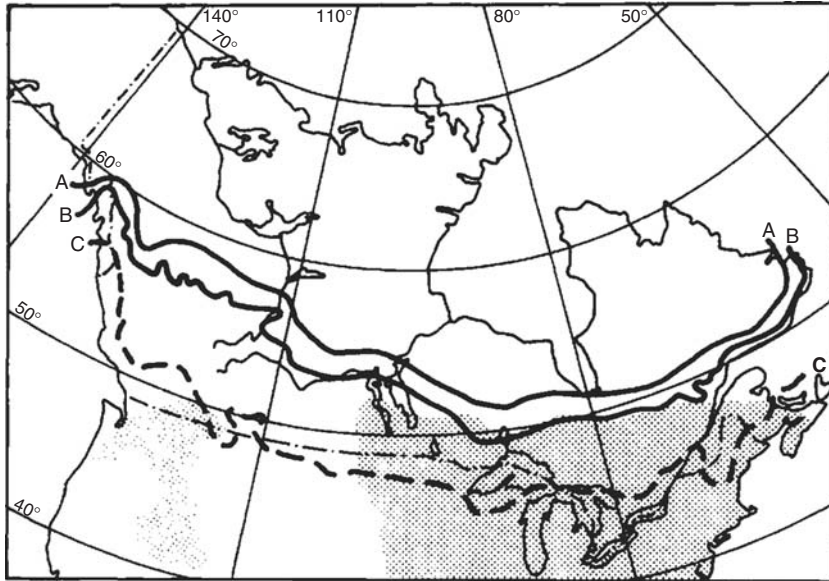
Figure 9.3 Distribution of smallmouth bass in North America (shaded area) and northern limit predicted by computer modeling based on mortality with high food availability (Line A) and low food availability (Line B). Dashed line (C) represents the latitude at which winter starvation likely begins to influence population behavior. Figure from Shuter and Post (1990) [The American Fisheries Society (1990)119:314–336].

latitudes (Meisner *et al*. 1987; Shuter and Post 1990; Pörtner 2002), in part explaining the reduction in species diversity observed at high latitudes (McAllister *et al*. 1986; Allen *et al*. 2002).

Latitude and climate clines (i.e. the extent and duration of winter conditions) can also impact life history characteristics of centrarchid fishes. Latitude has been shown to influence the growth rates of largemouth bass (Carlander 1979; Modde and Scalet 1985) and bluegill (Modde and Scalet 1985) and other fish species [e.g., brown trout *Salmo trutta* (Jensen *et al*. 2000)]. Record adult size for largemouth bass declines with increasing latitude (Modde and Scalet 1985). In a review of age and growth patterns for largemouth bass and smallmouth bass in North America, Beamsderfer and North (1995) found clear evidence for the effect of growing season on life history parameters (Figure 9.4). Increasing latitude results in older ages at 30.0 and 28.0 cm TL for largemouth and smallmouth bass, respectively. Similarly, increasing average air temperature results in faster growth to young adult size for both species. For largemouth bass, Beamsderfer and North (1995) found a significant negative correlation between natural mortality and latitude as well as degree days above $10°C$, a measure of growing season duration for bass (Figure 9.4). Mean air temperature was positively correlated with natural mortality in largemouth bass. Taken together, the latitudinal clines in life history for largemouth and smallmouth bass found in Beamsderfer and North's (1995) survey certainly reflect growing season, and its corollary, winter duration. Trade-offs between allocation of energy to growth or reproduction lie at the heart of life history variation in fish (Danylchuk and Fox 1994; Lester *et al*. 2004), so factors influencing this allocation process, such as winter duration, appear to be essential in understanding life history variation in centrarchid fishes. The ecological and physiological alterations to individuals and ecosystems associated with the onset of winter interact to influence the abundance, range, distribution, and life history characteristics of centrarchids.

9.9   General activity level

Consistent with the impairments to physiological performance listed in Section 9.6, laboratory studies all document a reduction in the activity level of centrarchid fishes during winter conditions relative to summer, but species-specific
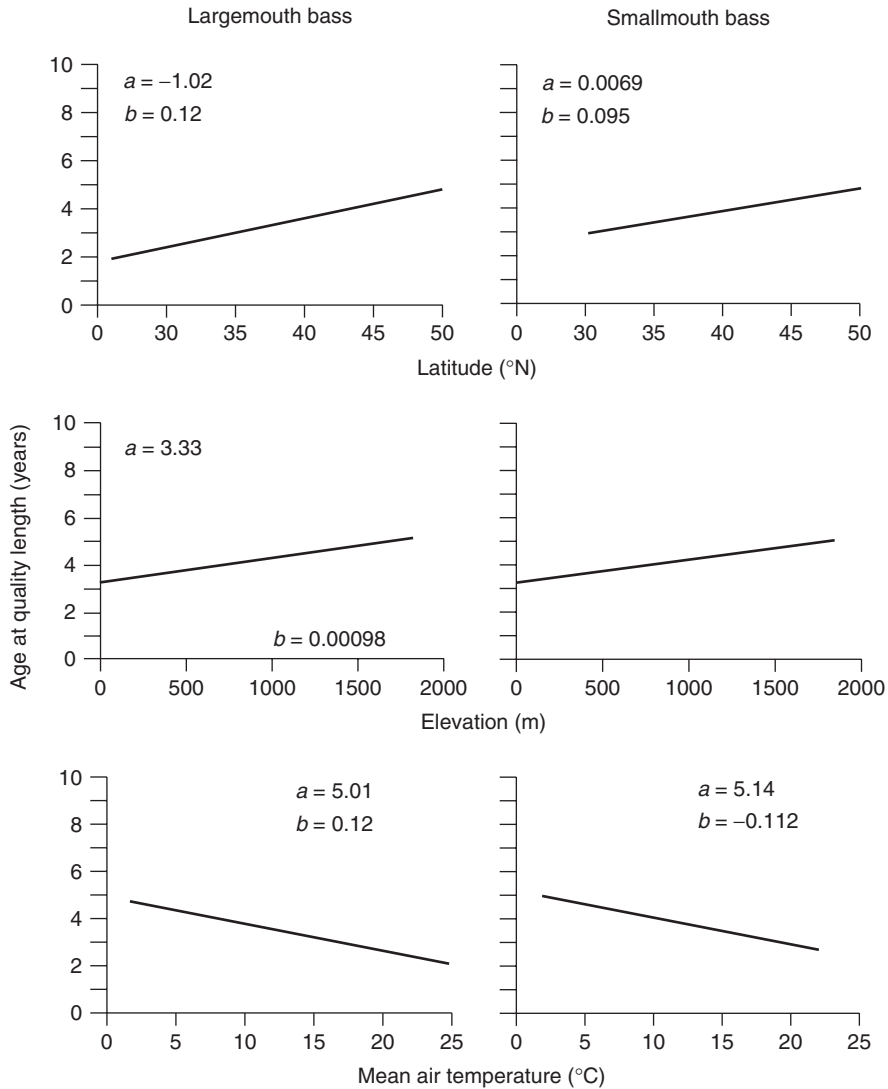
Figure 9.4 Relationship between age at quality length and latitude, elevation, and mean air temperature for 698 populations of largemouth bass and 409 populations of smallmouth bass. Figure redrawn from Beamsderfer and North (1995)—data points have been removed to emphasize trend lines in each panel [North American Journal of Fisheries Management (1995)15:688–704].

differences do exist. For example, activity levels of largemouth bass in laboratory experiments remained constant despite reductions in water temperature until approximately 7°C, at which point activity levels diminished (Crawshaw 1984; Lemons and Crawshaw 1985; Figure 9.5). Similarly, laboratory studies by Tschantz *et al*. (2002) documented a reduction in swimming activity of largemouth bass, green sunfish, bluegill, and black crappie to near dormant at cold temperatures, while the swimming activity of white crappie was not affected by cold.

Existing evidence indicates that the activity levels and movement rates of centrarchid fishes are reduced considerably in winter, but are not completely eliminated. It is not clear if this reduced activity is necessitated through reduced food intake,
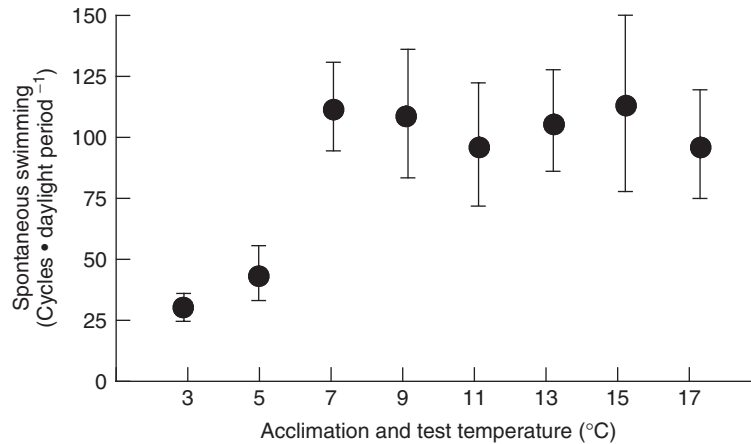
Figure 9.5 Spontaneous swimming activity around a circular tank during daylight for largemouth bass held at different temperatures. Sample sizes in each acclimation group from 3–17° are 6, 7, 9, 7, 5, and 8, respectively, and error bars show ±1 SEM. Figure from Lemons and Crawshaw (1985) [Physiological Zoology, University Of Chicago Press (1985)58:175–180].

a temperature-induced reduction in metabolism and performance, or a combination of these factors. Conversely, it has been proposed that the reductions in activity levels exhibited by centrarchid fishes are facultative rather than obligate (Kolok 1991a). This hypothesis has resulted from several lines of evidence listed earlier including the observation that several centrarchid species appear to continue feeding during winter (Moffett and Hunt 1943; Gent *et al*. 1995). Centrarchids have the capability of substantial swimming bouts despite near freezing temperatures (Lyons and Kanehl 2002; Karchesky and Bennett 2004). Multiple compensatory physiological changes have been noted to cardiac tissue, muscle tissue, and metabolic enzymes that would suggest an ability to maintain performance during winter conditions (Kolok 1991a; Tschantz 2002). Furthermore, these compensatory alterations were similar for a reportedly "winter quiescent" species (smallmouth bass) and a "winter active" species (green sunfish) (Kolok 1991a). Thus, evidence exists to suggest that winter quiescence in some species of centrarchids may be facultative rather than obligate, and this reduction in activity level may function to minimize maintenance costs at times of reduced food availability.

9.10   Winter movements

Although the results of laboratory studies generally agree in classifying many overwintering centrarchids as dormant, results from several field investigations would suggest otherwise. Field studies investigating the movements of centrarchid fishes during winter all document reductions relative to summer (Warden and Lorio 1975; Hubert and Lackey 1980; Todd and Rabeni 1989; Horton and Guy 2002) and researchers have labeled some radio-tagged centrarchids as "inactive" during winter periods (Munther 1970; Warden and Lorio 1975). Also, studies involving a whole-lake telemetry array revealed that the distribution of fish within the lake was constricted considerably during winter periods relative to summer (Caleb Hasler, unpublished data, Figure 9.6; Hasler *et al*. 2007). However, for many studies, movements by centrarchid fishes during winter are quite common. Karchesky and Bennett (2004), for example, documented travel of some largemouth bass between two overwintering areas despite water temperatures of 3°C, while Greenbank (1956) noted considerable winter movements of several fish species, especially black crappie, to and from an ice-covered backwater area of the Mississippi River. Despite water temperatures of 4°C, Todd and Rabeni (1989) documented movements of stream-dwelling smallmouth bass in Missouri of 120 m/day, while Lyons and Kanehl (2002) reported that overwintering smallmouth bass in Wisconsin exhibited regular movements of 100–200 m/week in water temperatures less than 1°C. Thus, while laboratory studies would suggest that centrarchids are dormant during winter, several field investigations document movement and activity levels in centrarchids during this period.
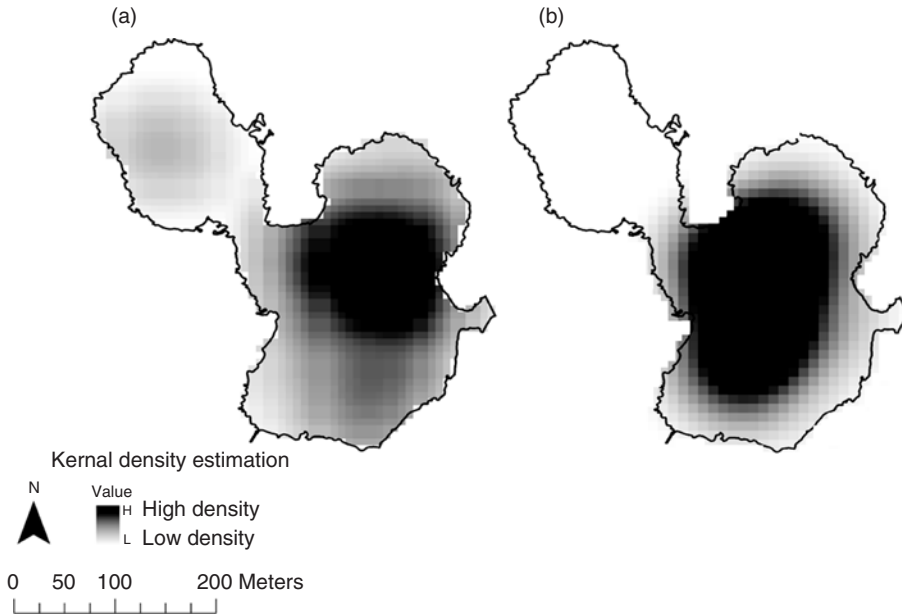
Figure 9.6 Distributions (kernel densities) of largemouth bass within a lake in summer (a) and in winter (b). Darker shading refers to a higher density of fish, and lighter shading refers to a lower density of fish. Locations were determined using a fixed telemetry array capable of detecting fish locations within the entire lake at fine temporal and spatial scales, and for each season, the locations of fish for 10 consecutive days were anaylzed (Caleb Hasler, unpublished data).

A recent synthesis by Lyons and Kanehl (2002) suggested that the magnitude of downstream movements by smallmouth bass to larger water bodies may be correlated with winter severity. Studies of smallmouth bass movements prior to winter in Idaho (Munther 1970) and Missouri (Todd and Rabeni 1989), where winters were mild, documented winter downstream migration of fish <1 km. In Wisconsin, where winters are more severe, smallmouth bass migrated between 6.5 and 69 km to downstream wintering areas during late fall (Langhurst and Schoenike 1990; Lyons and Kanehl 2002), highlighting the influence of river conditions during winter on this behavior.

Despite an apparent general reduction in activity during winter, further research is needed to assess winter activity among centrarchid species. Sorting through proximate causes (e.g., impaired neuronal transmission capabilities, reduced muscle performance) and ultimate causes (e.g., lowered metabolic rates, lowered food availability, reduced need for movements) behind reduced activity during winter is an important area for future research. Activity levels during winter are believed to be influenced by prey assemblages, water temperature, energy stores, and the presence of predators, but a clear influence of these variables on activity level has not yet been established (Micucci *et al*. 2003; Garvey *et al*. 2004).

9.11 Feeding

A common assumption is that feeding ceases during winter for centrarchid fishes. This idea stems from several laboratory studies suggesting inactivity during winter (Crawshaw 1984; Lemons and Crawshaw 1985), and several studies listed below showing a little or no winter feeding. In contrast, current theory for coolwater fishes suggests that winter feeding occurs, but only to permit individuals to maintain minimal activity rates and routine metabolism rather than to fuel growth or gonadal development, and that feeding only occurs when energy stores decline to a critical level (McCauley and Kilgour 1990; Conover 1992; Metcalfe and Thorpe 1992; although see Post and Parkinson 2001). This theory was highlighted in winter simulation experiments by Metcalfe and Thorpe (1992) who showed that juvenile Atlantic salmon
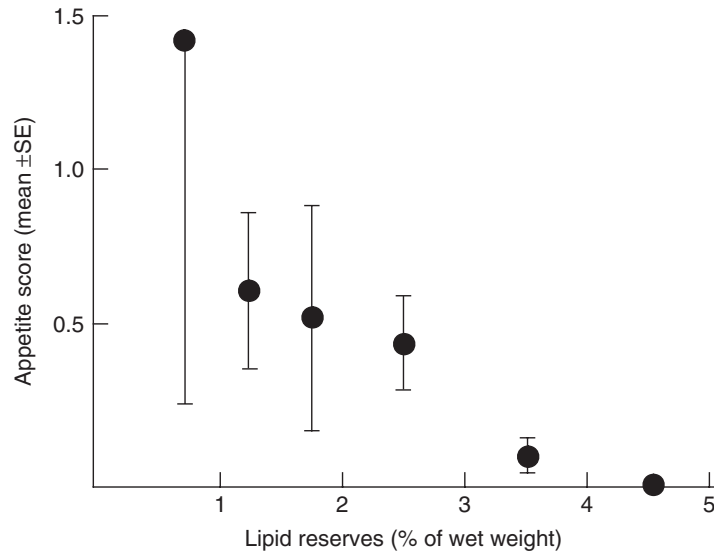
Figure 9.7 Relationship between the estimated energy stores of Atlantic salmon (lipid reserves as a percentage wet weight) and their appetite score (scale of 0–6 for presentation of pelleted food) after 3 weeks of food deprivation. Figure from Metcalfe and Thorpe (1992) [Journal of Animal Ecology Blackwell Publishing (1992)61:175–181 JournalsRights@oxon. blackwellpublishing.com]

(*Salmo salar*) above a certain nutritional threshold would refuse all food presented to them. If food was withheld and the nutritional status of the fish fell, feeding would resume until the nutritional status was re-established (Figure 9.7). This theory of periodic feeding to defend energy levels has not been tested explicitly with centrarchid fishes, but both modeling simulations (Garvey *et al*. 2004) and laboratory/field studies listed below indirectly support this hypothesis.

9.11.1 Laboratory studies

Laboratory feeding studies involving overwintering fish typically present individuals with prey items *ad libitum,* reducing the need for energetically expensive foraging bouts or prey searching. Across all studies, results show that, under simulated winter conditions, the feeding rates of centrarchid fishes are reduced relative to warmer water temperatures (Hathaway 1927; Markus 1932; Coble 1975; Oliver *et al*. 1979; Johnson and Charlton 1960). For species such as largemouth bass and smallmouth bass, cessation of feeding was documented when water temperatures fell below 3–10°C (Markus 1932; Coble 1975; Johnson and Charlton 1960; Lemons and Crawshaw 1985) and 7.1°C (Oliver *et al*. 1979), respectively. In contrast, however, Hathaway (1927) showed a decrease in food consumption rates of bluegill, pumpkinseed, and largemouth bass when water temperatures were cooled to 10°C, but all three species continued to consume food as winter simulations continued. Although results from laboratory studies show that feeding by centrarchid fishes is reduced at low temperatures, the cessation of feeding does not appear to be universal suggesting that feeding in winter can occur in the field for some or all species.

9.11.2 Feeding in the wild

Feeding by centrachids can be greatly reduced, but does not appear to cease completely during winter—even at high latitudes. Snyder and Peterson (1999) documented that bluespotted sunfish (*Enneacanthus gloriosus*) in Mississippi fed

Figure 9.8   Largemouth bass collected by angling thorough ice in Ontario, Canada.

during winter, and VanderKooy *et al*. (2000) noted that bluegill (*Lepomis macrochirus*), redspotted sunfish (*Lepomis miniatus*), and redear sunfish (*Lepomis microlophus*) across a range of sizes sampled from a Mississippi estuary all continued feeding during winter, primarily on invertebrate prey. Collections of fish through the ice in Ontario by Keast (1968) noted that rock bass (*Ambloplites rupestris*), bluegill, smallmouth bass, and largemouth bass collected at water temperatures between 6.5 and 8.5°C appeared to have not eaten for several weeks. In contrast to these field studies, however, collections of bluegill by hook-and-line angling through the ice in Michigan revealed that 83% of individuals caught had food in their stomachs consisting mainly of invertebrates such as Cladocera and Ostracods, although feeding rates were reduced relative to summer food intake (Moffett and Hunt 1943). Similarly, Bulow *et al*. (1981) reported that the stomach fullness of bluegill sampled in the winter was reduced relative to summer levels, but the fish still had food in their stomachs. Food consumption during winter is certainly implied when anglers are able to catch fish. Studies by Rach and Meyer (1982) estimated that anglers fishing through the ice in Wisconsin harvested 2.41 bluegill per hour over a 17-week winter fishery. Gent *et al*. (1995) documented the winter harvest of largemouth bass outfitted with radio transmitters suggesting that this species also feeds during winter (Figure 9.8), and Knights *et al*. (1995) noted that anglers caught black crappies when fishing through the ice. Experiments by Garvey *et al*. (2004) showed that if predatory largemouth bass were absent, energy reserves for overwintering small (<94 mm) largemouth bass could increase because of foraging. Thus, both laboratory and field investigations agree that winter feeding in centrarchid fishes is reduced relative to summer levels. Even at high latitudes, however, some centrarchid fishes continue to feed during winter, and fish are therefore not completely dormant at this time.

9.12   Growth

Winter growth appears to virtually stop for fishes at high latitudes, and is decreased substantially for lower-latitude centrarchids (Hoxmeier *et al*. 2001). Pessah and Powles (1974), for example, documented no growth in Ontario pumpkinseed held at 5°C, slow growth in fish at 10°C, and substantial growth for fish held at higher temperatures. Bluegill ceased to grow during winter weather in several Indiana lakes (Gerking 1966) and Alabama ponds (Smith and Swingle 1940), and within a population of largemouth bass, smaller individuals appear to cease growing before larger individuals (Miranda and Hubbard 1994a). Ratios of the quantity of RNA/DNA can be used to indicate recent growth rates in fish (Bulow 1970), and studies of bluegill in Tennessee showed a reduction in RNA/DNA ratios in the winter indicating a reduction in growth.

A more heuristic approach to considerations of centrarchid growth during winter is to regard growth as an energy allocation strategy during a time period of reduced energy intake. Modeling experiments by Garvey and Marschall (2003)

and Garvey *et al*. (2004) revealed that, during winter when food availability and fat reserves are low, small individuals invested in growth more than larger individuals in an effort to increase fat stores and reduce energetic demands, whereas larger individuals prioritized energy investment into gonadal tissue rather than growth.

9.12.1   *Energy allocation*

Latitudinal clines in age, growth, and life history reflect differing energy allocation patterns between somatic growth and reproduction as a function of growing season and winter duration. This is clearly present in largemouth bass and smallmouth bass (Beamsderfer and North 1995; Figure 9.4; Section 9.8). Because feeding stops or is greatly reduced during winter (Section 9.11), the energy allocation strategy ought to reflect the seasonal shifts in feeding behaviors. The period of highest energy storage for adult male smallmouth bass is in the fall prior to the winter period (Mackereth *et al*. 1999). During winter, approximately two-thirds of this stored energy is utilized prior to the open water (ice-out) spring period (Mackereth *et al*. 1999). We believe the pattern of large energy stores established in the fall to meet energy demands during reduced energy intake in winter is a common centrarchid energy allocation strategy. Energy storage for winter survival versus allocating energy to somatic growth will be a function of winter duration and the selective pressures facing individuals. Selective pressures on individuals could, in turn, affect growth in the juvenile stage, maximum attained size, and the age of maturation (Lester *et al*. 2004).

9.13   Aggregations

One of the most curious and understudied aspects of centrarchid ecology is the formation and maintenance of aggregations of individuals during winter. The formation of aggregations during winter conditions has been reported for some, but not for all centrarchid fishes, although studies involving numerous species have yet to be undertaken. Breder and Nigrelli (1935) held 10 centrarchid species under identical laboratory condition, and noted that true "aggregations" formed only in smallmouth bass and redbreast sunfish (*Lepomis auritus*), while black crappie formed loose clusters of multiple individuals. The other six centrarchid species examined [bluegill, green sunfish, pumpkinseed, warmouth (*Lepomis gulosus*), rock bass, and bluespotted sunfish] preferred to remain solitary during winter simulations, and often migrated to nonflowing water (Breder and Nigrelli 1935). Webster (1954) documented the formation of winter aggregations of smallmouth bass in Cayuga Lake and noted both the propensity of aggregations to repeatedly and predictably form in the same location in the lake and that smaller fish arrive at wintering areas prior to larger individuals. Karchesky and Bennett (2004) documented two aggregations of overwintering largemouth bass in an Idaho river that contained 95% of 19 tagged individuals, while Carlson (1992) reported that 59% of the largemouth bass fishery ≥ 305 mm estimated to be in the Hudson River overwintered at five different sites. Langlois (1936) documented the formation of winter aggregations of spotted bass in Ohio ponds. Langhurst and Schoenike (1990) showed that smallmouth bass migrated 69–87 km downstream in the Embarrass River system to reach their overwinter site.

The stimulus for the formation of winter aggregations for wild centrarchids has been attributed to water temperatures below 16–10°C, reductions in day length, and die off aquatic macrophytes (Langlois 1936; Webster 1954; Savitz *et al*. 1993; Karchesky and Bennett 2004). In laboratory studies of the redbreast sunfish, Breder and Nigrelli (1935) noted that fish swam independently at 9°C, formed feeble aggregations at 7°C, and formed a quiescent resting school at 5°C. Furthermore, Breder and Nigrelli (1935) noted that such aggregations were only present during conditions of daylight; when lights in the laboratory were turned off or if the flow of water to the tank was stopped, the fish dispersed. The aggregation was re-formed, however, when lights were turned on and current was re-established indicating the importance of visual cues for aggregation formation and maintenance. A similar propensity for aggregations to occur only during daylight hours was observed in largemouth bass by Hasler *et al*. (2007). Finally, Breder and Nigrelli (1935) noted that redbreast sunfish re-formed aggregations to remain facing into the current if the location of the current was changed, and a variety of aggregation shapes and dimensions could be formed by varying the velocity of water entering the tank.

The formation of winter aggregations or loose associations of individual fish is an intriguing component of the life history of many centrarchid species. Winter aggregations are especially interesting when one considers the extent of research

on habitat selection by centrarchid fishes and the trade-off between foraging profitability and minimizing mortality risk that drives habitat selection (Mittelbach 2002). Habitat selection in centrarchids during the growing season is fairly well understood in the context of this trade-off (Stein 1979; Mittelbach 2002). How this trade-off drives habitat selection during winter is an important research question. Foraging is reduced or ceases, aggregations or loose associations of individuals develop at long distances from summer home ranges, and minimizing energetic costs appears to be paramount. Indeed, macrophyte areas that are important structural components of habitat selection for many centrarchid fishes in the growing season (Stein 1979; Savino and Stein 1982; Tonn and Magnuson 1982; Eadie and Keast 1984; Persson and Eklöv 1995) die back during the winter and therefore cannot provide refuge. What trade-offs in habitat selection are present that promote the formation of aggregations in some of the largest species of centrarchid fishes, smallmouth and largemouth bass? Day/night changes in the grouping behavior, where individuals are aggregated at night and only loosely associated during the day, adds additional complexity to questions of habitat selection. In the case of *Micropterus* species, aggregations may simply represent habitat selection by individuals seeking to minimize physiological maintenance costs while maximizing oxygen uptake or limited foraging opportunities. Formation of aggregations in *Micropterus* spp., however, points to added benefits from forming social groupings of top predators.

9.14   Winter habitat

Both Chapman (1966) and Cunjak (1996) proposed that habitat is the main factor regulating fish populations during winter because low water temperatures reduce metabolic costs and minimize the need to feed and defend territories. Cunjak (1996) also proposed minimizing energy expenditure by fish during winter (e.g., obtaining sufficient oxygen, protection from winter freshet, and access to refugia) was more important than was protection from predators and access to food resources. Despite this importance of refugia during winter, little is currently known about the winter habitat requirements of the majority of centrarchid fishes.

Centrarchid fishes prefer to overwinter in water that is deeper and slower-moving relative to their summer habitat, although the deepest portions of a waterbody are not necessarily occupied (Lyons and Kanehl 2002). This may simply mean moving offshore into deeper regions of the lake or reservoir where they currently reside (Lewis and Flickinger 1967; Kraai *et al*. 1991; Savitz *et al*. 1993; Curry *et al*. 2005). In large lakes, movements to wintering areas can involve large-scale movements of many individuals to relatively few traditional overwintering locations (Webster 1954). In stream and river ecosystems, movements to overwintering areas involve fish seeking out larger, deeper sections of a river/stream or the confluence of streams. This phenomenon has been documented for smallmouth bass (Munther 1970; Langhurst and Schoenike 1990; Bunt *et al*. 2002), largemouth bass (Carlson 1992), redeye bass (*Micropterus coosae*) (Parsons 1953), and spotted bass (Trautman 1981). Lateral movements to slow-moving or backwater areas of large rivers have also been documented for bluegill (Knights *et al*. 1995), black crappie (Knights *et al*. 1995), and largemouth bass (Raibley *et al*. 1997; Karchesky and Bennett 2004). These winter migrations appear to begin when water temperatures fall below approximately 8–16°C (Munther 1970; Paragamian 1981; Langhurst and Schoenike 1990; Karchesky and Bennett 2004) or with reductions in daylight (Webster 1954). Habitats with deep, slow-moving waters are likely desirable to centrarchids as they provide cover and shelter from excessive flow thereby minimizing energy expenditure. Access to warm water relative to cooler main channel areas may also be important (Bodensteiner and Lewis 1994). Deep pools may also allow fish to avoid capture from potential mammalian (Alexander 1979; Carss *et al*. 1990) and avian predators (Sayler and Lagler 1940). Two notable exceptions to this trend include a stream-dwelling population of smallmouth bass in Missouri that showed no seasonal change in depth from summer to winter (Todd and Rabeni 1989) and a portion of a stream-dwelling population of smallmouth bass in Ontario that overwintered in a riverine environment rather than migrate downstream to a common overwinter site in a lake (Barthel 2004). Winter habitat selection by overwintering centrarchids may also be influenced by dissolved oxygen concentrations, and this is discussed in Sections 9.4.2 and 9.5.

Surprisingly little work has been done to quantify the habitat requirements of overwintering centrarchids at small spatial scales. Furthermore, the paucity of studies and the occasional conflict in results precludes identification of species-wide trends. For example, Paragamian (1981) showed a preference of river-dwelling smallmouth bass for gravel and cobble substrate (≤256 mm) rather than boulders during winter. In contrast, Todd and Rabeni (1989) reported that stream-dwelling smallmouth bass associated with boulders almost exclusively during winter. Furthermore, Hubert and Lackey (1980) found

no difference in seasonal habitat use for smallmouth bass in a Tennessee reservoir with fish using structures such as overbanks, river channels and dropoffs consistently throughout the year. Even within a single waterbody, Webster (1954) noted that overwintering smallmouth bass could be associated with boulders, crevices, or no structure at all. Although these differences may simply represent site- or population-specific preferences, they also suggest that the stimulus for aggregation formation at a site is based more on location than on the microhabitat features that have been quantified to date. Other studies have shown overwintering largemouth bass associated with vegetation, boulders, and rock ridges (Carlson 1992; Karchesky and Bennett 2004), overwintering bluegill associated with submerged vegetation (Cunjak 1996), whereas overwintering pumpkinseed preferred woody debris, cobble-boulders, as well as vegetation Cunjak (1996). The lack of any clear, detectable pattern of preferred habitat at small scales points to a stronger watershed perspective for understanding habitat selection at larger scales. The relatively few studies of wintering habitat selection in rivers (e.g., Langhurst and Schoenike 1990; Carlson 1992) reinforce the need to consider larger watershed scales when examining winter habitat for centrarchid fishes.

Winter habitat studies employing telemetry focus on centrarchid adults because of the lower size limits imposed by the technology. Winter habitat selection by juvenile centrarchids is therefore an area of research that is largely unexplored. Given the importance of first year survival in centrarchid populations, habitat selection during the critical winter months is an important area for investigation.

9.15   Photoperiod

While many of the changes in behavior and physiology described earlier can likely be attributed to reductions in water temperature during winter, some studies have suggested that numerous changes arise independent of ambient water temperatures and are linked to photoperiod. For example, studies have shown that temperature preference (Otto *et al*. 1976) and swimming activity (Sandström 1983) can both fluctuate seasonally in fish as a result of photoperiod variation. Additionally, Beamish (1964) showed that the metabolic rate of brook trout (*Salvelinus fontinalis*) and white suckers (*Catastoumus commersoni*) declined within 3 days as a result of starvation, even though water temperature remained constant. In centrarchid fishes, Mischke and Morris (1997) reported that spawning in captive bluegill could be initiated by reducing photoperiod without exposing fish to prolonged winter water temperatures. Laboratory experiments with green sunfish documented that food consumption, food conversion efficiency, and growth all declined with reduced photoperiod when fish were held at constant temperatures (Gross *et al*. 1965), and work by Petit *et al*. (2003) revealed that food consumption in largemouth bass was also influenced by photoperiod. Kolok (1991b) showed that the swimming performance of largemouth bass at cold water temperatures was reduced with seasonally inappropriate photoperiod regimes relative to fish experiencing similar temperatures but natural photoperiod regimes. Finally, Evans (1984) showed that pumpkinseed exhibited a temperature-independent drop in metabolic rate associated with reductions in photoperiod, and studies of rainbow trout (Dickson 1971), threespined stickleback (*Gasterosteus aculeatus*) (Meakins 1975), brook trout (Beamish 1964), and brown trout (Beamish 1964) have all documented a similar seasonal fluctuation in metabolic rate that is not dependant on temperature. Evans (1984) hypothesized that temperature-independent variation in metabolism may be related to predictable winter conditions and designed to reduce maintenance costs when food resources are scarce, thereby increasing the likelihood of overwinter survival. Thus, it is not clear if the observed changes in behavior and physiology exhibited by centrarchid fishes in the winter can be attributed exclusively to water temperature, or if factors associated with variation in photoperiod are also responsible. Kaya and Hasler (1972), for example, suggest that a combination of elevated water temperatures and increased day length is necessary to stimulate gonadal development in green sunfish following exposure to winter conditions.

9.16   Overwinter survival

Numerous studies have concluded that survival during the first winter of life represents a "critical period" for many centrarchid fishes often exerting a strong influence on year class strength (Shuter *et al*. 1980; Parkos and Wahl 2002). Curry *et al*. (2005) showed that winter mortality for age-0 smallmouth bass in New Brunswick can exceed 78% of the population

highlighting how large winter-induced mortality can occur at the population level. Currently it is believed that overwinter survival is primarily governed by two processes that are not mutually exclusive: starvation and predation.

9.16.1 Starvation

The "classic" theory of overwinter survival for young-of-the-year centrarchids suggests that fish rely on lipid reserves accumulated in summer and fall for overwinter fuel, and mortality results when these lipid stores have been depleted. This reliance on energy stores occurs because winter feeding rates at cold temperatures appear to be significantly reduced (Section 9.11) and many prey items, especially for smaller fishes, are no longer present. As latitude and the degree of winter severity increase, it is hypothesized that this accumulation of lipids for overwinter survival increases in magnitude and importance relative to lower latitudes (Shuter *et al*. 1980; Schultz and Conover 1997). Lipids represent an efficient, easily deposited, and stable method of energy storage containing 8.0 kcal/g of energy compared with 1.6 kcal/g for carbohydrates and 3.9 kcal/g for protein (Phillips 1969). Currently it is believed that decreasing water temperature stimulates lipid accumulation (Hazel and Prosser 1974; Shul'man 1974), lipid deposits in aerobic muscle (Egginton and Sidell 1989), and increased lipid metabolism (Hazel and Prosser 1974), all to facilitate overwinter survival. Consequently, prior to the onset of winter, lipid levels in wild adult smallmouth bass (Mackereth *et al*. 1999) and age-0 largemouth bass (Miranda and Hubbard 1994a; Ludsin and DeVries 1997) were at their highest, and were lower during spring sampling—a result corroborated by laboratory studies simulating winter conditions for juvenile largemouth bass (Toneys and Coble 1979) and juvenile smallmouth bass (Oliver *et al*. 1979). Niimi (1972) noted that largemouth bass starved for 40 days at 25°C consumed protein and lipid in a ratio of 60:40, while Savitz (1971) noted that bluegill catabolized both fat and protein to obtain energy during a 29-day starvation experiment at 23.9°C.

9.16.2 Allometry

Size appears to play an important role in determining lipid stores and energy utilization (and therefore overwinter survival) based on three relationships. First, larger fish store a greater mass-specific quantity of lipids than do the smaller individuals (Shul'man 1974; Shuter *et al*. 1980; Adams *et al*. 1982; Shuter and Post 1990; Schultz and Conover 1999; Curry *et al*. 2005). An allometric accumulation of fat reserves has been shown for several centrarchid species including smallmouth bass (Shuter *et al*. 1980; Mackereth *et al*. 1999; Curry *et al*. 2005), largemouth bass (Adams *et al*. 1982), and bluegill (Cargnelli and Gross 1997). Two rare exceptions to this trend, however, include Miranda and Hubbard (1994a) and Bernard and Fox (1997) who did not document an allometric relationship for the accumulation of lipids for largemouth bass and pumpkinseed, respectively, potentially as a result of interannual variation in lipid accumulation within a population. Second, the mass-specific metabolic rate of larger fish is lower than smaller individuals (Brett 1965; Brett and Groves 1979). Third, smaller individuals have a greater energetic cost of swimming than do larger fish (Schmidt-Nielsen 1972). Larger fish therefore accumulate more energy stores than do smaller fish, use the accumulated energy at a slower rate, and spend less energy when swimming, thereby increasing their probability of surviving conditions of reduced food intake during winter (Shuter *et al*. 1980; Schultz and Conover 1999).

Most models therefore propose that smaller centrarchid fishes experience increased overwinter mortality relative to larger individuals because of starvation resulting from reduced food intake and elevated energy consumption. This size-selective mortality hypothesis has been corroborated by both laboratory and field collection studies that pair fall and spring fish collections (Johnson 1965; Oliver *et al*. 1979; Shuter *et al*. 1980; Adams *et al*. 1982; Miranda and Hubbard 1994b; Bernard and Fox 1997; Post *et al*. 1998; Curry *et al*. 2005), and in the case of smallmouth bass, this mechanism can account for its northern limit in the biogeographic range of the species (Shuter *et al*. 1980; Shuter and Post 1990). Experiments that increase ration availability to overwintering largemouth bass permit individuals to maintain energy stores resulting in increased survival (Garvey *et al*. 1998; Fullerton *et al*. 2000).

Recently, studies have suggested that size-selective starvation may not be the only factor governing overwinter survival in centrarchid fishes. Several studies (Shirley and Andrews 1977; Toneys and Coble 1979; Kohler *et al*. 1993) report little evidence for size-dependent overwinter mortality among overwintering centrarchids. Additionally, both Adams *et al*.

(1982) and Miranda and Hubbard (1994b) reported size-selective overwinter mortality of largemouth bass in Tennessee and Mississippi, respectively, with Kohler *et al*. (1993) reporting no size-selective overwinter mortality for largemouth bass in Illinois. If the sole factor governing overwinter survival of centrarchid fishes was the interaction between energy stores, temperature, and body size, then one would expect an inverse linear relationship to exist between overwinter survival of small centrarchid fishes and latitude as a result of more severe and prolonged winter conditions at high latitudes (Garvey *et al*. 1998). In fact, in a literature review by Garvey *et al*. (1998) examining overwinter survival of largemouth bass, higher survival of large individuals at high latitudes was not consistent among studies (Table 9.2). Additionally, using hatchery ponds in Wisconsin, Toneys and Coble (1979) did not report size-selective overwinter mortality for green sunfish, but noted size-selective mortality for one-third of the bluegill populations and one-half of largemouth bass populations sampled. While this lack of size-dependant mortality may have been observed because the populations examined did not include the extreme northern edge species ranges (Shuter and Post 1990), they do suggest that factors in addition to starvation may be involved in controlling overwinter survival, increasing the complexity associated with overwinter mortality of centrarchid fishes.

9.16.3   Predation

Predation is believed to be a second factor that can influence overwinter survival for centrarchids, especially at lower latitudes. As with starvation, predation is more likely to increase winter mortality for smaller fish, as smaller fish may be forced

Table 9.2   Summary of studies examining the effect of size on overwinter survival of largemouth bass.

Source	Latitude (°)	Did large age-0 largemouth bass have greater overwinter survival relative to smaller largemouth bass?
Ludsin and DeVries 1997	33	Yes[a]
Miranda and Hubbard 1994a	34	Yes[a]
Miranda and Hubbard 1994b	34	Sometimes[b]
Adams *et al*. 1982	36	Yes[a]
Boxrucker 1982	36	Yes[a]
Shirley and Andrews 1977	36	No
Aggus and Elliott 1975	37	Yes[a]
Chang 1971	38	No
Isley 1981	38	No
Kohler *et al*. 1993	40	No
Garvey *et al*. 1998	40	Sometimes[b]
Green 1982	43	Yes[b]
Toneys and Coble 1979	43	Sometimes[c]
Kolander 1992	45	No
Wright 1993	46	No

Studies are arranged in the order of increasing latitude.
Table from Garvey *et al*. (1998) [NRC Research Press (rp.business@nrc-cnrc.gc.ca) (CJFAS)].
[a] In these studies, differential mortality likely resulted from energy reserve depletion during winter.
[b] Mortality of smaller largemouth bass was attributed to predation.
[c] Size-selective mortality occurred in lake studies where predators were present, and did not occur in hatchery pond experiments without predators.

to forage before larger individuals, because of the increased energetic costs described earlier. Both Micucci *et al*. (2003) and Miranda and Hubbard (1994b) demonstrated that predation was the proximate source of size-dependant overwinter mortality in midlatitude and southern largemouth bass populations, respectively. Predation during winter conditions may either create or mask size-dependant mortality described earlier based on predator abundance and prey availability (Garvey *et al*. 2004). For example, if prey abundance is low and predators are present, smaller fish may need to forage thereby exposing themselves to predators. Conversely, if prey availability is increased, fish of all sizes can reduce the frequency of foraging bouts, possibly eliminating size-selective mortality despite low water temperatures (Garvey *et al*. 2004). Finally, the impacts of both starvation and predation on winter mortality appear to be exacerbated at colder temperatures and/or higher latitudes (Garvey *et al*. 1998; Table 9.2).

9.16.4   Other potential mechanisms for overwinter mortality

While starvation and predation are two prominent causes of mortality for overwintering centrarchids, additional reasons for mortality have been suggested. Specifically, during winter conditions, centrarchid fishes may be more susceptible to sub-lethal stressors than at other times of the year, possibly because of reduced energy stores. For example, studies have shown that young-of-the-year largemouth bass are vulnerable to low pH levels during winter leading to mortality because of gill damage (Leino and McCormick 1993; Parkos and Wahl 2002) or osmoregulatory dysfunction in smallmouth bass (Cunningham and Shuter 1986). Peles *et al*. (2000) showed that radiocesium (^{137}Cs) levels in largemouth bass peaked in winter/spring months possibly increasing the likelihood of mortality, while Lemly (1993) suggested that winter stress syndrome (WSS) results in greater overwinter mortality for warmwater fishes. Mortality from WSS results from lipid depletion that occurs when external stressors (such as parasites, selenium, or wastewater) increase the energetic demands of fish, but the combination of reduced photoperiod and low water temperatures inhibit feeding to replenish energy stores, thus accelerating death by starvation (Lemly 1993; Lemly 1996). Additionally, Raibley *et al*. (1997) noted that, when river levels fall during winter, fish are often forced to abandon their preferred still, backwater overwinter habitats for main channel areas. While main channel areas may contain increased levels of dissolved oxygen relative to hypoxic backwater areas, main channel waters are also colder than back water areas and have increased current velocity. Thus, fish inhabiting main channel areas would experience increased activity levels, a reduction in swimming ability (Section 9.7), and a concomitant increase in energy consumption.

9.17   Conclusions and future directions

Over 70 years ago Hubbs and Trautman (1935) recognized the importance of winter conditions for the survival of fish and called for an end to the annual indoor migration of fisheries scientists during winter. In particular, Hubbs and Trautman (1935) highlighted investigations of winter habitat requirements and the impacts of winter water levels and ice damage on fish populations as important areas for future research. Little work has been done to quantify winter habitat requirements of most centrarchid species, regardless of age, sex, size distribution, or latitudinal variation. Indeed, ecological research during winter has generally received little attention relative to warmer seasons (Campbell *et al*. 2005).

   In general, the strategy for winter survival for centrarchid fishes appears to center around the conservation of lipid stores accumulated during the summer and fall. This can occur through reductions in metabolic rates and reductions in activity levels as fish seek shelter from current and energetically expensive environmental conditions. The physiological strategies employed by centrarchid fishes for overwinter survival currently appear to vary by species, tissue, and enzyme examined, and further study is required before clear trends in this area can be identified. These generalizations, however, are based primarily on the studies of largemouth bass and bluegill, with few studies occurring at the true northern extreme of the species ranges. Ultimately, the ability of a species to tolerate prolonged winter conditions appears to dictate their distribution and range, emphasizing the control of winter conditions on centrarchids. Understanding the physiological, behavioral and ecological responses of centrarchid fishes of all life stages to winter conditions is important.

The debate concerning the prevalence of size-selective mortality (e.g., Table 9.2) is in part a debate about ecological processes across a latitudinal gradient ranging from the northern limits of centrarchid distribution to its southern limits. Life history variation detected at latitudinal scales reflects changes in selective process on physiological rates and tolerances across the geographic range of any centrarchid species. Winter (or its corollary, summer growing season) is a very important period in the life history of centrarchid fish. A comparative, latitudinal approach to understanding life history trade-offs (growth versus reproduction) and physiological characteristics of different populations subjected to different winter severities is an important research area for the future.

In addition, it is important to examine the winter habitat selection of centrarchid fishes at various life stages. The formation of wintering aggregations, possibly with fish from widely dispersed locations, is an important element of this effort. Entire populations of some species may be located in small areas for extended periods of each year. The impact of land use and habitat destruction on the summer survival and reproduction of many fishes has been documented resulting in management plans and recommended conservation strategies (i.e. maintenance of riparian habitats for lotic fishes). To date, we know very little about the overwintering habitat requirements of the majority of centrarchid fishes (preferred flow rates, dissolved oxygen requirements, water depths, etc.) making successful management decisions challenging. For example, land use activities such as dams or water draw down that reduce winter stream flow will reduce available habitat and access to certain areas for centrarchid fishes and the extent to which these practices affect survival and recruitment has not been adequately quantified (Maceina 2003). Backwater habitats important to the overwinter survival of centrarchids are being lost due to sedimentation and athropogenic disturbances, but the impact of this habitat loss on overwinter survival and recruitment of centrarchids needs to be quantified (Karr *et al*. 1985; Gent *et al*. 1995; Knights *et al*. 1995). Although dredging of backwater areas has shown potential to provide suitable overwinter habitat for largemouth bass, if dissolved oxygen levels are not maintained and flow rates are not optimized, fish will leave the backwater areas for the main channel where flows are greater resulting in an increased probability of mortality (Gent *et al*. 1995).

Recent climate models suggest that global warming will increase North American air temperatures resulting in a corresponding increase in aquatic temperatures (Meisner *et al*. 1987; Eaton and Scheller 1996; DeStasio *et al*. 1996; Fang and Stefan 1998). This is expected to be more pronounced for higher latitudes relative to lower latitudes (DeAngelis and Cushman 1990; Fang and Stefan 1998). Accurate predictions regarding the potential cascade of responses by aquatic communities to climate changes are difficult because of unpredictable responses by variables such as dissolved oxygen, wind patterns, macrophyte abundance, watershed connectivity, precipitation patterns, and zooplankton abundance (Chen and Folt 1996; Magnuson and DeStasio 1996; DeStasio *et al*. 1996). In general, however, it is believed that the predicted increases in ambient temperatures will reduce the severity of winters at high latitudes possibly leading to a northward range expansion of more southerly centrarchid species (Meisner *et al*. 1987; Regier *et al*. 1989; Shuter and Post 1990). The relative abundance of various fish species will also likely be affected by temperature change as a result of alterations in thermal niches, prey availability, and oxygen conditions (Meisner *et al*. 1987). To date, little attention has been paid to the responses of small centrarchid fishes to increased water temperatures (Regier *et al*. 1989) and relatively little work has focused on the response of southern centrarchids to elevated temperatures. Because of the pronounced impact of winter conditions on the distribution and abundance of centrarchid fishes, the effect of global warming on this family cannot be accurately predicted without a solid understanding of winter ecology.

Finally, we must obtain greater understanding of winter ecology of centrarchids to better inform bioenergetics modeling. Currently, many bioenergetics models for overwintering centrarchid fishes assume that individuals stop feeding during winter and often fail to acknowledge the role of predation in influencing overwinter survival (Shuter *et al*. 1980; Lyons 1997). Studies by Wright *et al*. (1999) showed that existing bioenergetics models fare poorly in predicting the responses of largemouth bass to winter conditions (possibly because models to date have underestimated the role of predation and feeding in overwinter survival), emphasizing the need to improve our understanding of this period of the year.

Winter conditions, and the changes that they bring, represent an interesting, challenging, and important time of the year for centrarchid fishes. Continued research and study should reveal the role of winter on population structure, individual survival, life history variation, and year class strength. Winter field work is accompanied by several inherent challenges, but further study will aid in the management and conservation of this valuable family of fishes.

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