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BIOLOGICAL SYNOPSIS OF FIVE SELECTED FLORIDA CENTRARCHID FISHES WITH AN EMPHASIS ON THE EFFECTS OF WATER LEVEL FLUCTUATIONS

ST. JOHNS RIVER WATER MANAGEMENT DISTRICT

Biological Synopsis of Five Selected Florida Centrarchid Fishes with an Emphasis on the Effects of Water Level Fluctuations

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Executive Summary

Withdrawals of ground or surface waters can alter historic hydrological cycles and negatively affect fish populations. Florida's Water Management Districts are charged with setting Minimum Flows and Levels (MFLs) for individual water bodies to prevent significant ecological harm. Fishes in Florida are economically and ecologically valuable. For example, freshwater recreational fishing in Florida had an economic output of US$1.9 billion in 2001. The sunfish family, Centrarchidae, is the most important family of freshwater sport fish in Florida. This report presents a review of the literature for five selected centrarchid species—largemouth bass *Micropterus salmoides*, dollar sunfish *Lepomis marginatus*, redbreast sunfish *L. auritus*, spotted sunfish *L. punctatus*, and warmouth *L. gulosus*—to provide information for the determination of biologically meaningful MFLs. The species were chosen to cover a range of characteristics (e.g., size, habitat use, and diet) and, potentially, a range of responses to changes in water level or flow. This information will be used by the St. Johns River Water Management District for developing MFLs that will protect water resources from significant ecological harm caused by water withdrawal, consumptive use, or diversion and assure water for non-consumptive uses.

The largemouth bass is one of the best-known and most important freshwater fishes in the world. There are two subspecies—the northern largemouth bass *M. s. salmoides* and the Florida largemouth bass *M. s. floridanus*. The Florida largemouth bass is native to Peninsular Florida south of the Suwannee River system and there is a broad, natural zone of integration with the northern subspecies throughout the remainder of the state. The largemouth bass is a habitat generalist and is abundant in most freshwater and some brackish environments in Florida, including lakes, streams, floodplain wetlands, marshes, sloughs, and canals. This species is often associated with aquatic macrophytes or other structure, but may use open water with little or no cover. Although tolerant of a wide variety of physical and chemical parameters, largemouth bass is not well-adapted for periods of low oxygen and is one of the first fish species to succumb to hypoxic conditions. This species undergoes several ontogenetic shifts in diet, with fry feeding on zooplankton and juveniles and adults later switching to aquatic insects, crustaceans, and then fish. Although often considered piscivorous as adults, the largemouth bass is very adaptable and consumes a wide variety of prey. Largemouth bass males construct nests in shallow waters in the late winter to late spring, depending on region, where they court females and care for the eggs. The male will guard the schooling fry for a short period after swim-up (i.e., when fry become free-swimming). Growth is rapid and this species may live in excess of 16 years. Females tend to grow faster and live longer and therefore the largest, oldest individuals are female. Largemouth bass populations often are separated into groups that are sedentary or mobile and there may be inshore and offshore populations in lakes.

Water level fluctuations can produce positive or negative changes in largemouth bass populations. Inundation of floodplains or areas of terrestrial vegetation can increase access to prey, provide spawning and nursery habitat, and release nutrients that increase primary production. Nevertheless, fluctuations during and soon after spawning can be detrimental to largemouth bass recruitment by stranding nests or exposing fry to predation, adverse temperatures, or strong currents. Existing data, though limited for Florida, suggest more effect of hydrological variables on largemouth bass populations in streams than in lakes. Some effects of water level fluctuations, particularly in lakes, are mediated through effects on aquatic macrophytes. Due to the effects of changes in lake levels or stream flow on largemouth bass, water level manipulation can be a useful management tool.

The dollar sunfish is a coastal plain species and generally occurs in slow-moving or standing water habitats, often associated with macrophytes or woody debris, with sand, silt, or mud substrates. Very little is known about the life history of this species. It is uncommon in most habitats, but may reach relatively high abundance in floodplains, swamp streams, and long-hydroperiod wetlands. Dollar sunfish feeds on a variety of small organisms, with amphipods and insects being most important. The dollar sunfish spawns from April to September in Florida and the male tends the nest, eggs, and larvae. Little is known about the age and growth or movements of this small species in Florida. Being a short-lived species associated with floodplains, small streams, and other wetlands, dollar sunfish may be very susceptible to alterations of system hydrology.

The redbreast sunfish is a common stream-associated species and may be the most important sport fish in certain river systems in Florida. It is occasionally found in lakes connected to rivers, reservoirs, and riverine swamps. Redbreast sunfish commonly utilizes inundated floodplains in Florida. Habitat Suitability Index (HSI) criteria, including hydrological variables, have been developed for this species. Redbreast sunfish consumes a variety of prey, including insects, small crustaceans, and mollusks. Like other sunfish, males construct nests and guard eggs and larvae. Relatively low, stable current velocity is critical to redbreast sunfish spawning success and current HSI models may not adequately reflect this fact. Several studies have investigated redbreast sunfish age and growth in Florida and other states in the southeastern USA. Redbreast sunfish populations contain both sedentary and mobile individuals, some of the latter moving long distances. Being stream-associated, redbreast sunfish may be particularly sensitive to changes in stream hydrology. For example, abundance of this species was positively related to higher stream flows in the year prior to sampling.

Spotted sunfish is a coastal plain species that also is most commonly found in streams. This species is may be an important sport fish in lotic systems in Florida. This species occurs east of the Apalachicola River in Florida and intergrades with the very similar redspotted sunfish *L. miniatus* west of the Apalachicola River. Spotted sunfish is most abundant in streams, rivers, and floodplain wetlands, although it may be present in many different freshwater and brackish habitats. Insects are the dominant prey for spotted sunfish, but other invertebrate prey are eaten. Reproduction in spotted sunfish is similar to that of other centrarchids and this species spawns from March to September in Florida. Relatively little is known about the age and growth or movements of spotted sunfish in Florida. This species is stream-associated; therefore changes in flow and floodplain connectivity should be important for spotted sunfish dynamics. For example, abundance of spotted sunfish in the Oklawaha River was positively related to minimum stage in the year prior to sampling.

Warmouth is a relatively small sunfish that reaches its greatest abundance in slow-flowing streams or lentic systems with abundant vegetation. It is a littoral species and is rarely found in limnetic zones. Warmouth is a common component of the recreational fishery in some Florida systems. This species is adaptable to a wide variety of physical and chemical parameters and is the sunfish with the best ability to survive hypoxic conditions. Habitat Suitability Index criteria, including hydrological variables, have been developed for this species. Warmouth has a large mouth and consumes a variety of invertebrate and fish prey. Warmouth reproductive behavior is typical for sunfish and this species spawns from March to September in Florida. Although much information is available on growth of warmouth in Florida, little research exists documenting age. Very little is known about movement of warmouth, but this species is considered to be more sedentary than largemouth bass. The effects of changes in hydrology on warmouth populations have not been investigated. Hypothetically, alterations in hydrology that reduce floodplain-stream connectivity or reduce the abundance of aquatic macrophytes will negatively affect warmouth.

It is clear that hydrology has a considerable influence on centrarchid populations. Generally, periodic fluctuations in stream flow and lake levels will enhance centrarchid populations in the long-term. Water withdrawals resulting in changes to system hydrology will likely cause changes in centrarchid populations. Such changes will be linked to the magnitude, duration, frequency, and timing of withdrawals, the hydrological characteristics of the affected system, and the life history of the fish and other organisms present within the system. All things being equal, withdrawals of greater magnitude, duration, or frequency should have larger effects. Lakes, depending on morphometry, may be less impacted than streams or wetlands by water withdrawals; nevertheless, major changes in hydrological regime will negatively affect centrarchid populations in lakes. Stream fishes are particularly vulnerable to changes in hydrology due to reduced habitat, decoupled stream-floodplain connectivity, and decreased nutrient subsidies. For example, two important functions of inundated floodplains—nesting and nursery functions—require considerable time to complete. Water levels in inundated areas must be deep enough for nest construction and sustained throughout periods of courtship, spawning, and egg and larval development for inundated floodplains to be useful for centrarchid reproduction. For largemouth bass, total time for nest construction to swim-up ranges from 9 to 15 days and fry further school for 33 to 45 days prior to dispersing. Water level decreases during this time, especially prior to swim-up, can be detrimental to largemouth bass reproductive success and recruitment. Species that are dependent on floodplains (e.g., dollar sunfish) or are stream-associated (e.g., redbreast sunfish and spotted sunfish) may be especially sensitive to altered hydrology. Indeed major changes in lake or stream hydrology can lead to recruitment failures and potential loss of local populations of short-lived species. Rising water levels increase access to food resources for fish and promote primary production through nutrient inputs. These functions require sufficient time for fish to utilize the increased food resources and for flushing of nutrients and allochthonous materials into subsidized systems. Emphasis is often placed on the importance of relatively large changes in hydrology affecting fish populations; nevertheless, hydrological alterations of lesser magnitude also can negatively affect centrarchid populations.

There are considerable gaps in knowledge of basic life history of many Florida centrarchids. Even for relatively well-studied species, it is difficult to explicitly determine habitat suitability and sensitivity to changes in hydrology. Researchers are just beginning to develop empirically-derived predictive models of population indices based on hydrological data. In particular, there is a glaring lack of estimates of quantitative effects of specific hydrological regimes or events for fish populations. Until additional research provides quantitative data to build and test appropriate models, there is little hope of advancing beyond our current level of qualitative prediction.

Biological Synopsis of Five Selected Florida Centrarchid Fishes with an Emphasis on the Effects of Water Level Fluctuations

Introduction

Increasing demands for surface and groundwater resources due to human population increases can alter historic hydrological cycles and influence fish populations. Florida's Water Management Districts are charged with setting Minimum Flows and Levels (MFLs) for individual water bodies to prevent "significant harm" to ecological resources (e.g., fish populations) (Florida Statutes 2004).

Changing water levels and stream flows can have significant positive and negative effects on fish populations (reviewed in Hill and Cichra 2002a). Increases in stream flow or levels may enhance fish production by increasing available habitat, providing conditions conducive to spawning, making food resources available, and supplying nutrients to aquatic food webs. Nevertheless, acute flooding can directly kill or displace fish, degrade fish habitat, and reduce food resources. Low stream flow or water levels can reduce fish recruitment due to lack of suitable spawning conditions, increased predation, decreased habitat, increased competition, and degraded water quality.

Freshwater recreational fishing is a socio-economically important activity in Florida with expenditures estimated in excess of US$665 million in 2001 (USFWS 2003) for a total economic output of nearly US$1.9 billion (ASA 2002). Sunfishes of the family Centrarchidae (i.e., *Lepomis*, *Micropterus*, and *Pomoxis*) are the most important fishery species. Moreover, these species are abundant and ecologically important. Therefore, it is essential to consider such fishes when developing MFL criteria. Given the fishery and ecological importance of centrarchids in

Florida and much of North America, many species are well-studied (e.g., bluegill *Lepomis macrochirus* and largemouth bass *Micropterus salmoides*). Nevertheless, very little is known about other species (e.g., dollar sunfish *Lepomis marginatus*). Moreover, much of the available information on centrarchids is scattered in the literature and only occasionally is placed into a context of MFLs. The purpose of this report is to compile existing information on five selected centrarchids—largemouth bass, dollar sunfish, redbreast sunfish *Lepomis auritus*, spotted sunfish *Lepomis punctatus*, and warmouth *Lepomis gulosus*—into a biological synopsis, emphasizing the effects that fluctuating water levels have on their life histories and population dynamics.

This information will be used by the St Johns River Water Management District (SJRWMD), Water Supply Management Division for the development of ecological criteria for its MFLs Program. These MFLs will protect water resources from significant ecological harm caused by water withdrawal, consumptive use, or diversion and, at the same time, assure water for non-consumptive uses.

Methods

Five representative centrarchids were selected by the authors in consultation with biologists of the Florida Fish and Wildlife Conservation Commission (FWC). Each species occurs in the St. Johns River system of Florida. Indeed, all are found throughout much of Florida and are relatively widespread outside of the state. The species were chosen to cover a range of characteristics (e.g., size, habitat use, and diet) and, potentially, a range of responses to changes in water level or flow. For example, redbreast sunfish and spotted sunfish are considered to be stream-associated and potentially sensitive to changes in hydrology.

Literature included in this report was obtained by bibliographic database searches, discussions with university and agency biologists, internet queries, searches of gray literature sources, reference to published bibliographies, and perusal of the authors' personal libraries. Computer databases searched included Biosis (Biological Abstracts and Zoological Record), Cambridge Aquatic Science and Fisheries Abstracts, and the University of Florida Aquatic, Wetland, and Invasive Plants Database. Particularly useful printed bibliographies included Heidinger (1974) and Hill and Cichra (2002b). Additionally, the exhaustive review of Carlander (1977) provided significant information.

Largemouth bass *Micropterus salmoides* (Lacépède 1802)

General

The largemouth bass is one of the best known and most researched freshwater fishes in the world. It is a popular sport fish and has been introduced in many regions inside and outside of the USA. Given its long history of introductions, the exact limits of native distribution are not certain. Largemouth bass is presumed native to the Atlantic Slope drainages from North Carolina or Virginia (see Jenkins and Burkhead 1994), south throughout Florida, west into southern Texas and Mexico, and north in the Mississippi River and northern Gulf Coast drainages and in portions of the Great Lakes (MacCrimmon and Robins 1975; Lee 1980d).

Characteristics of the largemouth bass and taxonomic keys are provided in numerous works (e.g., Etnier and Starnes 1993; Jenkins and Burkhead 1994; Mettee et al. 1996; Pflieger 1997; Ross 2001; Boschung and Mayden 2004). High quality photos of largemouth bass are found in Robinson and Buchanon (1988), Etnier and Starnes (1993), Jenkins and Burkhead (1994), and Mettee et al. (1996), and illustrations in Page and Burr (1991), Pflieger (1997), and

Boschung and Mayden (2004). The largemouth bass is a large (up to 700 mm TL), heavy-bodied, perch-like fish with a large mouth. The body coloration is olive-green dorsally, fading to a whitish ventrally. There is a broad, blotched stripe along the side and dark lines radiating out on the cheek. South and east of the Suwannee River system in Florida, there is no native fish likely to be confused with largemouth bass. In systems from the Suwannee River system through the Panhandle, there are three additional *Micropterus*—shoal bass *M. cataractae*, spotted bass *M. punctulatus*, and Suwannee bass *M. notius*. The latter species are distinguished from largemouth bass by their well-connected spinous and soft dorsal fins (especially in specimens > 60 mm TL), lack of a distinct lateral stripe (in spotted bass it is generally much blotchier and less distinctly a stripe), upper jaw not extending far in back of eye (large juveniles and adults), and pyloric caeca not branched near their base (Boschung and Mayden 2004; C. R. Gilbert, FLMNH, unpubl. key). The most similar species is the spotted bass found in the Panhandle west of the Apalachicola River.

The largemouth bass was originally described by Lacépède in 1802 as *Labrus salmoides* (Eschmeyer 2004). Other synonyms commonly seen in older literature include *Grystes nobilis* Agassiz and *Huro salmoides* Hubbs and Bailey (see Jenkins and Burkhead 1994; Boschung and Mayden 2004). There are two well-distinguished subspecies—northern largemouth bass *M. s. salmoides* and Florida largemouth bass *M. s. floridanus* (Ramsey 1975). Florida largemouth bass is native to Peninsular Florida, south of the Suwanee River system (see Chew 1975 for a discussion of Florida largemouth bass). There is a broad, natural zone of integradation between northern and Florida subspecies in Georgia, southeast Alabama, and northern Florida (Etnier and Starnes 1993; Boschung and Mayden 2004). Some authorities consider the Florida subspecies to be distinct enough to elevate it to specific status (i.e., Florida bass *Micropterus floridanus*)

(Kassler et al. 2002); nevertheless, Nelson and co-authors (2004) retained this form as a subspecies of the largemouth bass. The Florida subspecies has been widely introduced into the native range of northern largemouth bass where it readily forms intergrades (e.g., Ross 2001).

Again, the largemouth bass is an extremely important sport fish in Florida and much of the USA. It grows large, is abundant, readily strikes bait and lures, and is a good food fish. The official record is a 7.83 kg fish caught in 1986 from an unnamed lake in Polk County (FWC 2004). However, there is a much larger, unofficial record fish—a 9.13 kg largemouth bass from Big Fish Lake, Pasco County, caught in 1923 (FWC 2004).

Habitat

Largemouth bass is a habitat generalist and is found in most freshwater and some brackish environments in Florida. Freshwater habitats include lakes, streams, reservoirs, ponds, swamps, marshes, and floodplains. Although the preference of largemouth bass for clear, non-flowing water with aquatic macrophytes is commonly repeated in the literature (Miller 1975; Carlander 1977; Lee 1980d; Trautman 1981; Pflieger 1997), this species is highly adaptable and thrives under a wide variety of environmental conditions (see Hoyer and Canfield 1994). The preferred temperature range is about 25-30°C (Coutant 1975).

McLane (1955) found largemouth bass throughout the St. Johns River system, Florida, except for sulphurous, hypoxic spring boils, very shallow habitats (e.g., shallow swamp streams), or ephemeral wetlands. Largemouth bass was found over all substrates and at all depths, with or without vegetation, in quiet waters or in moderate currents. Although McLane (1955) mentioned a lack of this species in certain spring boils, he and others have frequently collected largemouth bass in springs, runs, and spring-fed rivers (e.g., Caldwell et al. 1955; VanGenechten 1999).

Mesing and Wicker (1986) investigated habitat use of 22 radio-tagged largemouth bass in two central Florida lakes. They found that a segment of the population remained offshore whereas the other fish remained near shore. Largemouth bass occupied panic grasses *Panicum* spp., cattails *Typha* sp., and spatterdock *Nuphar luteum* more often than other available vegetation or open water. Bullrush *Scirpus* sp. and pickerelweed *Pontederia cordata* also were selected for when available. Colle and co-authors (1989) likewise documented inshore and offshore populations of largemouth bass in Lake Baldwin, Florida. Ager (1971) reported that largemouth bass were found in the littoral zone of Lake Okeechobee, Florida, in areas of eelgrass and pond weed.

Inundated floodplains of streams (Guillory 1979; Leitman et al. 1991; Baker and Killgore 1994; Light et al. 1995) and flooded areas of reservoirs and lakes are used as habitat by largemouth bass (e.g., Warden and Lorio 1975). Largemouth bass was common in floodplain wetlands of the Apalachicola (Light et al. 1995) and Ochlockonee (Leitman et al. 1991) rivers but rare in these habitats in the upper Suwannee River, Florida (Bass and Hitt 1973; cited in Light et al. 1995). This species was rare on inundated floodplains of the Apalachicola River (Light et al. 1995) but common in this habitat in the Ocklockonee River (Leitman et al. 1991). Only small numbers of larval and juvenile largemouth bass were collected in inundated hardwood floodplains along the Cache River, Arkansas (Baker and Killgore 1994).

Stream largemouth bass are commonly thought to inhabit mainly pools, backwaters, and other habitats with relatively low current velocity. Schramm and Maceina (1986) collected intermediate-sized largemouth bass (149-299 mm TL) in relatively low current velocity areas of the Santa Fe River, Florida. In the Chipola River, Florida, largemouth bass was most common in pool habitats and was most associated with areas of reduced current and higher-than-average amounts of woody debris (Wheeler and Allen 2003). Nevertheless, larger individuals (300 mm TL) in the Santa Fe River often were collected from turbulent, higher velocity habitats. Additionally, largemouth bass was found in shoals as well as in pool habitat in the Chipola River (Wheeler and Allen 2003). Based on such evidence, Wheeler and Allen (2003) concluded that largemouth bass may be more general in habitat use in streams than commonly thought.

In their survey of Florida lakes, Hoyer and Canfield (1994) documented largemouth bass from 59 of 60 lakes sampled. Lakes containing largemouth bass encompassed the entire range of variability in morphometry, water chemistry, and aquatic macrophyte coverage (Table 1). The only lake where largemouth bass was not found was Lawbreaker Lake, Lake County. The authors commented that this lake had a very low mean pH of 4.4, although other lakes that had largemouth bass also had low pH values (Table 1).

Table 1. Lake morphometry, water chemistry, and aquatic macrophyte variables for lakes (N = 59) in north and central Florida where Hoyer and Canfield (1994) collected largemouth bass.

Variables	Mean	Median	Minimum	Maximum	Standard Deviation
Surface area (ha)	413	55	2	12412	1767
Mean depth (m)	2.8	2.9	0.6	5.9	1.2
pH	7.0	7.6	4.3	9.7	1.6
Total alkalinity (mg/L as $CaCO_3$)	31.9	25.0	0.0	130.6	33.0
Specific conductance (µS/cm @ 25°C)	137	118	17	384	98
Color (Pt-Co units)	28	17	0	400	54
Total phosphorus (µg/L)	57	21	2	1043	149
Total nitrogen (µg/L)	938	702	82	3789	801
Total chlorophyll *a* (µg/L)	29	10	1	241	47
Secchi depth (m)	1.9	1.5	0.3	5.8	1.4
Percent area covered by macrophytes (%)	41	33	1	100	39

The largemouth bass is commonly associated with aquatic macrophytes (Miller 1975; Carlander 1977; Lee 1980d; Trautman 1981; Pflieger 1997) and many consider aquatic macrophytes essential to the maintenance of largemouth bass populations in lakes and reservoirs (see Hoyer and Canfield 1996). For example, Durocher and co-workers (1984) found a positive relationship between submerged aquatic macrophytes and largemouth bass standing crop and recruitment to harvestable size in 30 Texas reservoirs and recommended managing reservoirs for aquatic macrophytes, including the introduction of plants. Nevertheless, the results for Florida are mixed. Colle and co-workers (1987) found no correlation between coverage of submerged aquatic macrophytes and harvestable largemouth bass standing crop in Orange Lake, Florida. Moreover, in a study of 56 Florida lakes (< 300 ha surface area), Hoyer and Canfield (1996) reported no significant relations between macrophyte abundance and the abundance or standing crop of adult largemouth bass. However, condition of largemouth bass (Colle and Shireman 1980) and growth of age-1 and age-2 largemouth bass (Hoyer and Canfield 1996) were inversely related to coverage of submerged aquatic macrophytes in Florida lakes. On the other hand, there is a positive relationship between aquatic macrophyte coverage and abundance of age-0 largemouth bass (e.g., Hoyer and Canfield 1996).

Relatively little is known about specific habitat requirements of larval and juvenile largemouth bass. These requirements are likely similar to those of adults. Ager (1971) observed juveniles to occur farther inshore than adults and reach greatest abundance in shallow, clear water with spikerush in Lake Okeechobee, Florida.

Several authors have suggested that largemouth bass preferentially occupy clear waters (e.g., Ager 1971; Miller 1975; Carlander 1977; Lee 1980d; Trautman 1981; Pflieger 1997); however, largemouth bass seems to be more tolerant of turbidity than other *Micropterus* (e.g., Carver 1967; Miller 1975; Etnier and Starnes 1993). Miller (1975) speculated that negative effects of turbidity resulted from interference with spawning behavior and survival of eggs and fry rather than through effects on juveniles and adults.

Largemouth bass occur in low pH waters (i.e., 4.3) in Florida (Hoyer and Canfield 1994). However, growth and condition of fish in low pH lakes (< 5.0) was less than in neutral lakes (pH = 6.9-7.3) (Canfield et al. 1985). The lethal limits of pH are < 4.0 and > 10.2 (Eipper 1975).

Largemouth bass can tolerate low salinity environments. In the Florida Everglades, largemouth bass occurs in the vicinity of mangrove islands in "slightly" brackish water (Loftus and Kushlan 1987). Brockmann (1974) collected this species only once in a brackish canal (salinity < 4.9‰) in southwest Florida. Elsewhere in Florida, largemouth bass has been collected at salinities of 11.8‰ (rarely) in a Gulf Coast marsh (Kilby 1955) and 15.6‰ in the Ochlockonee River (Swift et al. 1977). Bailey and co-authors (1954) sampled largemouth bass at brackish water stations in Escambia River, Florida, with surface salinities of 4.5-24.4‰; however, the authors also mentioned a salinity wedge and did not record salinity at depth of capture. Carver (1967) reported largemouth bass in salinities up to 4.1‰ in Louisiana. In Mississippi, this species occurs in waters up to 10‰ (Ross 2001). Nevertheless, growth is slower in fish living at salinities greater than 4‰ (Peterson 1991) and largemouth bass cannot survive for extended periods at greater than 12‰ (Meador and Kelso 1990).

Largemouth bass is not resistant to low oxygen and is among the first species to die under hypoxic conditions (Kushlan 1974; Loftus and Kushlan 1987). Critical dissolved oxygen levels (i.e., the minimum level in which the fish survived 24 hr when transferred from oxygen-saturated water) in laboratory tests were 0.92 mg/L at 25°C, 1.19 mg/L at 30°C , and 1.40 mg/L at 35°C (Moss and Scott 1961). Similar experiments where largemouth bass were acclimatized to low oxygen water gave similar results but were confounded by differences in fish size (Moss and Scott 1961). Cech and co-authors (1979) described respiratory metabolism in largemouth bass. Bulkley (1975) discussed the effects of low oxygen on largemouth bass behavior.

Largemouth bass is a common to abundant species in many Florida systems. Hoyer and Canfield (1994) reported a mean of 517 fish/ha (SD = 1006) and 16.8 kg/ha (SD = 21.2 kg/ha) for north-central Florida lakes. In the same study, Petersen mark-recapture estimates for 51 lakes yielded a mean of 22 largemouth bass > 249 mm TL per hectare (SD = 12.9). Statewide mean abundance estimates of harvestable largemouth bass (i.e., 254 mm TL) for Florida systems based on rotenone or concussion blocknet sampling were 22.5 fish/ha (SE = 4.2) and 14.9 kg/ha (SE = 3.5) for canals, 23.4 fish/ha (SE = 4.2) and 11.3 kg/ha (SE = 2.4) for lakes, and 1.5 fish/ha (SE = 1.5) and 0.77 kg/ha (SE = 0.78) for streams (Hill 2003). Ten years of concussion blocknet sampling yielded composite estimates of 136 largemouth bass/ha and 5.0 kg/ha for Black Creek Canal, Miami-Dade County, Florida (Shafland 1999a). Jenkins (1975) reported that the mean standing crop of largemouth bass in 170 reservoirs in the USA was 10.0 kg/ha.

Electrofishing CPUE for 59 north-central Florida lakes was 43.1 largemouth bass/hr (SD = 42.7) and 9.1 kg/hr (SD = 7.4 kg/hr) (Hoyer and Canfield 1994). Statewide estimates for mean electrofishing CPUE of harvestable largemouth bass (i.e., 254 mm TL) for Florida systems were 0.292 fish/min (SE = 0.027) and 172 g/min (SE = 17) for canals, 0.489 fish/min (SE = 0.036) and 322 g/min (SE = 31) for lakes, and 0.243 fish/min (SE = 0.035) and 157 g/min (SE = 22) for streams (Hill 2003). In the Ocklawaha River, Florida, CPUE estimates for largemouth bass at two stations were 1.1 fish/min (SD = 0.56) and 296 g/min (SD = 231) for the first station and 1.1 fish/min (SD = 0.90) and 368 g/min (SD = 349) for the second station (Rogers and Allen

2004). In the same study, CPUE estimates for the Withlacoochee River were 0.46 fish/min (SD = 0.38) and 92 g/min (SD = 75).

Largemouth bass was the fifth most abundant species in electrofishing sampling in the Santa Fe River, Florida, making up 6.0% of the catch and was forth in the lower Suwannee River, Florida, at 5.8% (Bass and Hitt 1975). Bass (1990) reported a mean rank of 8.7 (ranged from 7-10) out of 15 common fishes in the Escambia River, Florida, for largemouth bass based on six years of electrofishing samples. Largemouth bass made up 8.92% of fish collected by boat electrofishing from six stations in the heavily-impacted Peace River, Florida (Champeau 1990).

Largemouth bass is uncommon in marshes and other shallow water habitats in southern Florida (Loftus and Kushlan 1987). Similarly, largemouth bass was collected only once in 288 throw trap samples from wet prairie and slough habitats in the Blue Cypress Marsh Conservation Area, upper St. Johns River system, Florida (Jordan et al.1998). This species is more common in deep water habitats such as canals, alligator ponds, airboat trails, and sloughs (Loftus and Kushlan 1987).

Feeding

Overall, largemouth bass is a generalist predator and preys on a wide variety of organisms—zooplankton (e.g., rotifers, copepods, and cladocerans), amphipods, insects (e.g., aquatic beetles, mayflies, midge larvae, odonate nymphs, water striders, and terrestrial insects), decapod crustaceans (e.g., grass shrimp and crayfish), fish, amphibians (e.g., frogs, tadpoles, and aquatic salamanders), reptiles (e.g., snakes and turtles), birds (e.g., ducklings), and mammals (e.g., rodents) (Carlander 1977). This species is opportunistic and readily adapts to various types of prey.

Studies in Florida systems have repeatedly documented largemouth bass diets composed of similar prey organisms (McLane 1947, 1955; Kramer and Smith 1960a; Chew 1974; Schramm and Maceina 1986; Cailteux et al. 1996; Shafland 1999b; Huskey and Turnigan 2001; Hill 2003; Wheeler and Allen 2003; see also Carlander 1977 for detailed diet descriptions for largemouth bass outside of Florida). The main differences have been in relative proportions of each prey category and in the timing of ontogenetic shifts. Largemouth bass undergoes ontogenetic dietary shifts, with fry consuming microcrustaceans and then progressing to larger prey (e.g., insects, decapod crustaceans, and fish) as growth increases body and gape size (Pasch 1975; Olson 1996; Hill 2003). Zooplankton is generally eaten by fry and small individuals up to about 50 mm TL, but may be eaten by largemouth bass up to nearly 80 mm TL (Hill 2003). Amphipods and insects, primarily ephemeropterans, corixids, odonates, chironomids, and gerrids, are important prey items for small fish (up to about 130 mm TL; Hill 2003) and may contribute heavily to the diet for fish up to about 200 mm TL (Cailteux et al. 1996). Crayfish (also *Macrobrachium* prawns in some systems [Shafland 1999b]) and fish become dominant prey categories for adults, making largemouth bass a top predator.

The interaction between prey availability and individual growth has a profound influence on population dynamics of largemouth bass (Shelton et al. 1979; Timmons et al. 1980; Davies et al. 1982; Gutreuter and Anderson 1985; Keast and Eadie 1985; Olson 1996; cf. Werner and Gilliam 1984; Garvey et al. 2000). Because largemouth bass is gape-limited (i.e., swallows prey whole; see Zaret 1980 for a discussion of gape limitation), the relationship of predator gape size to prey size is critical in determining the availability of food (Lawrence 1958; Hambright 1991;

Hill et al. in Press). Individual growth allows for consumption of larger, more energetically profitable prey (e.g., initiation of piscivory; Pasch 1975; Ludsin and DeVries 1997). Once largemouth bass individuals are large enough to consume fish prey, growth is accelerated and survival is enhanced (Aggus and Eliot 1975; Pasch 1975; Timmons et al. 1980; Gutreuter and Anderson 1985; Olson 1996; Ludsin and DeVries 1997). Several researchers have provided information on the relation of largemouth bass gape size and length (Table 2). Prey body depth is the constraining prey dimension for gape-limited predators (Hambright 1991), and Lawrence (1958), Hill (2003), and Hill and co-authors (in press) presented equations describing the relation of body depth and length for various prey fish.

Table 2. Relation of largemouth bass gape width to total length, including the total length range over which the predictive equation is valid.

Source	Gape Width Regression	Total Length Range (mm)
Lawrence (1958)	0.0775 TL + 1.88	< 100
	0.1113 TL – 1.88	100-199
	0.1289 TL – 5.16	200-299
	0.1371 TL – 7.96	300-399
	0.1961 TL – 29.41	400-499
	0.2477 TL – 56.36	500-595
Shireman et al. (1978)	0.0968 TL	< 200
	0.1567 TL – 11.102	> 200
Schramm and Maceina (1986)	0.11 TL – 1.25	75-430
Johnson and Post (1996)	$0.0507\ TL^{1.149}$	< 100
Hill (2003)	0.113 TL – 2.21	58-175
Hill et al. (in press)	0.14 TL – 5.59	17-423

Although there is individual variation in the timing when largemouth bass may include fish prey in their diet, Bettoli and co-authors (1992) defined true piscivory at the population level as the size at which 60% of individuals with food in their stomachs contain fish. The size at which largemouth bass becomes piscivorous is dependent on the characteristics of the prey base and habitat; however, largemouth bass exceed the 60% threshold at smaller total lengths in less-structurally complex habitats than in highly structured environments such as dense macrophyte beds. For example, largemouth bass did not become piscivorous until > 140 mm TL in heavily-vegetated Lake Conroe, Texas (Bettoli et al. 1992), and not until > 120 mm TL in vegetated Florida lakes (Cailteux et al. 1996) and canals (Hill 2003). In contrast, largemouth bass in non-vegetated lakes in Florida became piscivorous by 60 mm TL (Cailteux et al. 1996). Carlander (1977) noted that fish were important in the diet of largemouth bass of 80-100 mm TL or larger.

Although largemouth bass adults are considered to be highly piscivorous, decapod crustaceans may be of considerable importance in the diet of Florida largemouth bass after the onset of piscivory. In Florida streams, crayfish *Procambarus* spp. are heavily utilized (Schramm and Maceina 1986; Wheeler and Allen 2003). Grass shrimp *Palaemonetes* sp. may be important to largemouth bass in vegetated habitats of Florida lakes (McLane 1947; Chew 1974; Huskey and Turnigan 2001) and canals (Hill 2003). Additionally, Shafland (1999b) found *Macrobrachium* prawns in the stomachs of largemouth bass in Tamiami Canal, Miami-Dade County, Florida (see also McLane 1947 for a single specimen from the St. Johns River, Florida). Mud crabs *Rithropanopeus harrisii* were frequently found in largemouth bass stomachs from the St. Johns River, Florida (McLane 1947).

Largemouth bass can feed throughout the 24-hr day (Heidinger 1975), but relatively little feeding is documented during nighttime hours, and the highest percentages of empty stomachs have been found from 0200-0800 hr (Carlander 1977 and citations therein). Increased feeding activity has been observed in midmorning and afternoon periods (Heidinger 1975). Lilyestrom and Churchill (1996) additionally noted a lull in feeding activity as denoted by stomach contents analysis during the period of 1200-1600 hr in a Puerto Rican reservoir. Diet studies report that about 50% of largemouth stomachs were empty (Lewis et al. 1974); however smaller fish may have lower percentages of empty stomachs (e.g., about 13%; Hill 2003). Laboratory studies suggest that largemouth bass have crepuscular and mid-day active periods, are relatively inactive act night, and activity increases rapidly at the onset of light periods (Reynolds and Casterlin 1976).

Largemouth bass consumes its own body weight in about 15 days in laboratory trials (Hunt 1960). In tank prey selection trials, largemouth bass ate about 2.2% of body weight per day of prey fish (Lewis et al. 1961). However, average percentages of body weight for gizzard shad *Dorosoma cepedianum* prey were higher for smaller largemouth bass (9.2%) and decreased with increasing size (down to 2.1%) in specimens collected from an Illinois reservoir (Lewis et al. 1974). Food conversion rates of largemouth bass consuming natural foods ranged from 2.1 to 6.6 g of food to grow 1 g of largemouth bass (Carlander 1977 and citations therein). Digestion rates of bluntnose minnow *Pimephales notatus* prey ranged from 360 hours at 4°C (0.007-0.028 g/hr/100 g largemouth bass) to 10-12 hours at 34°C (0.33-0.72 g/hr/100 g largemouth bass) (Carlander 1977). Gastric evacuation times for 200- to 400-g largemouth bass fed gizzard shad at 3.0-4.1% of body weight was 20 hours at 27°C and 30 hours at 18°C (Carlander 1977).

Temperature has an important effect on largemouth bass feeding (see also Nesting and spawning below). Feeding and growth occur above 10°C (Adams et al. 1982) and increase up to temperatures of about 26°C. After this point, feeding and growth decline (Smagula and Adelman 1982).

Changing water levels can affect largemouth bass diet and feeding rates. In an Arkansas reservoir, rising waters lead to the increased inclusion of terrestrial organisms (e.g., terrestrial insects) in the diet (Mullan and Applegate 1968). On the other hand, reservoir drawdown increases the vulnerability of prey fishes by decreasing the amount of available cover, particularly in vegetated systems, and by concentrating prey in a smaller volume of water (Keith

1975). For example, daily food intake for a 454-g largemouth bass increased from 4.0 g per day in early July to 10.7 g per day in mid-July when vegetative cover was reduced by a drawdown (Heman et al. 1969).

Nesting and spawning

Spawning in largemouth bass is similar to that described for sunfishes (cf. Breder 1936). The spawning behavior of largemouth bass in Florida has been described in detail (Carr 1942; Clugston 1966; Chew 1974; see also Miller 1975). Largemouth bass generally spawn at temperatures from about 17.8-26.7°C, with most reproduction occurring between 20° and 23.9°C (Carr 1942; Clugston 1966; Chew 1974). Chew (1974) reported spawning activity in Lake Weir, central Florida, in February at a temperature of 15.6°C. Kramer and Smith (1960a) reported first spawning of largemouth bass 2-5 d after water temperatures reached 15.6°C in Lake George, Florida. Largemouth bass have spawned at temperatures as cool as 12.2°C in other regions (e.g., Allan and Romero 1975). In the St. Johns River, Florida, largemouth bass spawn from January until June (McLane 1955; Kramer and Smith 1960a). Peak spawning activity in north and central Florida may occur in March and April, earlier in much of south Florida (e.g., December or January to March). In southeast Florida canals, largemouth bass spawning peaks in March and April (Shafland 1999b). In the nearly constant temperature environment of Silver Spring, Florida, largemouth bass spawned in spring and early summer (Caldwell et al. 1955). Some off-season spawning may occur (Allan and Romero 1975). Among mature fish, larger individuals spawn earlier than smaller fish (Miranda and Muncy 1987). The annual reproductive hormonal cycle of Florida largemouth bass has been described for fish reared in hatchery ponds in north-central Florida (Gross et al. 2002).

The male constructs the nest by sweeping substrates such as sand, gravel, woody debris, or spatterdock *Nuphar luteum* roots (or other vegetation) clean of sediments (Chew1974; Carlander 1977; Kramer and Smith 1960a; Bruno et al. 1990). Vegetation may be important for largemouth bass in lakes with soft sediments (Bruno et al. 1990). Miller (1975) considered largemouth bass to be the most adaptable *Micropterus* in ability to spawn over a variety of substrates. The substrate of a typical nest in Lake Mead, Nevada, consisted of 2.5% rubble, 31.1% coarse gravel, 41.5% fine gravel, 16.4% sand, 7.4% silt, and 0.2% organic debris by volume (Allan and Romero 1975). No nests were observed on bare sand or silt, both dominant substrates in Lake Mead (Allan and Romero 1975), and egg survival was low for nests on bare sand in Lake Weir, Florida (Chew 1974). Nests are built in depths of 10-244 cm, with average depths ranging from 60-120 cm (Chew 1974). Heidinger (1975) reported a minimum nest depth of 15 cm. Many nests are situated near cover such as vegetation, woody debris, or docks (Allan and Romero 1975; Vogele and Rainwater 1975). Because of custodial male aggression, nests are seldom closer together than 1.8 m unless there is an intervening obstruction (Breder 1936; Carr 1942; Clugston 1966). Nests in Lake Weir, Florida, averaged about 1.7 times the diameter of the length of the constructing fish; however, small fish were found guarding large nests and large fish guarding small nests (Chew 1974).

Allan and Romero (1975) reported on the destruction of several largemouth bass nests due to bank erosion, heavy wave action, or lake drawdowns. Cool weather or storms may disrupt nesting and reduce nest survival (Allan and Romero 1975). Adverse weather or water level conditions can result in disjunctive spawning, leading to large differences between survival and growth of weekly cohorts of age-0 largemouth bass throughout the first year of life and potentially to reduced recruitment (Summerfelt 1975; Ozen and Noble 2002).

Although the female is the larger of the spawning pair, the smaller males aggressively court and harass the female throughout the spawning process (Chew 1974). The spawning act may be interrupted by the intrusion of rival males or egg predators—these are repelled by the resident male. Excessive intrusion during spawning or egg-guarding may cause the male to abandon the nest. An individual female may repeatedly spawn within a nest (Chew 1974) or may spawn with multiple males in their nests (Heidinger 1975). Males may spawn with multiple females (Miller 1975). For example, Allan and Romero (1975) report on single a nest containing eggs, yolk-sac larvae, and new swim-up fry. Females may be exhausted by the efforts of egg laying and require considerable recovery time before resuming normal activities (Chew 1974).

Largemouth bass lays adhesive eggs that are roughly spherical and contain a large oil globule (Chew 1974). Mean egg diameter for largemouth bass in Bivens Arm Lake, Florida, was 1.50 mm (Carr 1942). Mean egg diameter for 30 fertilized eggs from a Lake Weir, Florida, largemouth bass was 1.59 mm, ranging from 1.49 to 1.67 mm (Chew 1974). Merriner (1971) reported that mean egg size increased with female weight according to the following relationship—egg diameter = 1.51 mm + 0.000311 WT. Based on surprisingly few females, estimates of egg numbers taken from the literature were 8,800-176,000 (Heidinger 1975) and 2,000-15,000 (Carlander 1977) eggs/kg of body weight. Ova of all stages of development were found in ripe largemouth bass (Chew 1974).

Embryology and early development of largemouth bass in Florida was described by Carr (1942), Kramer and Smith (1960a), and Chew (1974); see also Meyer (1970). Water-hardening requires about 15 minutes (Chew 1974). Hatching takes place at about 45.5 hr post-fertilization at 22.2°C (Chew 1974), 47-64 hr at 17.2°C (Carr 1942), or in 3-4 d at 15.6-19.6°C (Kramer and Smith 1960a). Yolk-sac larvae began swimming at 167 hr at 22.2°C (Chew 1974) or in 5-8 days at a length of 6 mm (Kramer and Smith 1960a). Kramer and Smith (1960a) reported growth rates of 0.40-0.60 mm per day for yolk-sac larvae. Fry feed within 6 days (Heidinger 1975). Temperatures of 15.0°C are fatal to largemouth bass fry and growth rates increase with increasing temperature up to 27.5-30°C (Strawn 1961; Chew 1974). Eggs may be more resistant to cool temperatures, at least for short time periods (Heidinger 1975; Carlander 1977), but rapid or prolonged chilling of eggs can result in poor survival (Coutant 1975). Water temperatures 32.5°C are fatal to eggs (Strawn 1961). Dissolved oxygen levels < 2.0-2.8 mg/L decreased embryo survival in laboratory trials (Dudley and Eipper 1975). Eipper (1975) further discussed factors relating to the mortality of largemouth bass larvae.

Fry form schools are a guarded by the male for about two weeks after swim-up (i.e., stage when fry become free-swimming) (Miller 1975). Some have speculated that female Florida largemouth bass remain near the nest and assist the male in guarding the eggs, but this behavior is not confirmed and is considered unlikely (Miller 1975). Kramer and Smith (1960a) reported that schools remained intact for 26-31 days and dispersing fry had a mean total length of 32.5 mm. A school of fry (about 20-30 mm TL) observed for 24 hr moved very little, but the fry fed almost continuously, except at night (Elliot 1976). Broods ranging from about 500 up to > 12,700 fry have been reported (Carlander 1977).

Maturity is more related to size than to age (Heidinger 1975). Largemouth bass become sexually mature at about 250 mm TL (Chew 1974). Age at sexual maturity ranges from one to three years in Florida and other regions of the southern USA (Chew 1974; Carlander 1977). Florida largemouth bass can attain maturity in as little as nine months (Clugston 1964).

Other fish species in Florida may utilize largemouth bass nests as spawning substrates. Carr (1942) documented a substantial number of eggs of the lake chubsucker *Erimyzon sucetta* in a largemouth bass nest in Bivens Arm Lake, Florida. Chew (1974) found a high incidence of golden shiner *Notemigonus crysoleucas* eggs within largemouth bass nests in Lake Weir, Florida, as did Kramer and Smith (1960b) in Minnesota. Chew (1974) also reported on the nest association of taillight shiners *Notropis maculatus* with largemouth bass.

Age and growth

There are substantial data documenting age and growth for largemouth bass. Much of this material is summarized in Carlander (1977). Growth in largemouth bass is related to environmental factors such as temperature, water quality, and availability of prey. Growth of northern largemouth bass increases from zero at 10°C to optimum near 27°C and then declines back to near zero by 35.5°C (Coutant 1975).

Several authors have presented regression equations describing the relation of weight and length in largemouth bass. The typical form of these equations is $\text{Log}_{10}\text{WT} = a\text{Log}_{10}\text{TL} + b$, where a is the slope and b is the y-intercept. The higher the value of slope, the faster the weight of largemouth bass increases with length. Carlander (1977) compiled values from the literature and reported slopes that ranged from 1.343 to 3.962, with most being about 2.7 to 3.3. Intercept values ranged from -12.600 to -3.28, with most being about -6.0 to -4.8 (Carlander 1977). Caldwell and co-authors (1955), Clugston (1966), and Chew (1974) presented length-weight relations for Florida largemouth bass with parameters within these ranges. Hoyer and Canfield (1994) estimated length-weight regressions for 59 north and central Florida lakes and reported slopes ranging from 2.79 to 3.42 and intercepts ranging from -5.95 to -4.46. To obtain a better predictive equation for weight, Hoyer and Canfield (1994) included dorsal girth (DG) measurements into a multiple regression equation—$\text{Log}_{10}\text{WT} = 1.47\text{Log}_{10}\text{TL} + 1.52\ \text{Log}_{10}\text{DG} -$

4.53 (N = 208; weight ranged from 194 to 5550 g; $R^2 = 0.996$). The standard weight (WT_s) equation for largemouth bass is $Log_{10}WT_s = 3.191Log_{10}TL - 5.316$ (minimum TL of 150 mm) (Anderson and Neumann 1996).

Mean literature values for Fulton's condition factor (K) for standard length ranged from 1.90 to 3.06 and for total length ranged from 1.08 to 1.85 (Carlander 1977). Values of K for largemouth bass increase with increasing fish size (Carlander 1977). Mean weight at length data were presented by Hoyer and Canfield (1994) for north-central Florida lakes (Table 3).

Table 3. Mean weight for largemouth bass from Florida lakes, by total length size group. Data from Hoyer and Canfield (1994).

Size Group (mm)	Mean Weight (g)	Standard Deviation	N
40	<1	<1	2211
80	3	2	2474
120	12	9	818
160	30	9	436
200	65	9	384
240	120	16	352
280	203	32	275
320	325	55	237
360	489	65	166
400	693	84	123
440	985	154	86
480	1352	187	42
520	1779	264	36
560	2325	258	25
600	2975	460	22
640	2860	*	1
680	4245	926	2
720	4893	392	2

The relationship of season to K is unclear, but some studies report changes in K corresponding to increases or decreases in food availability or changes in environmental conditions (Carlander 1977; Adams et al. 1982). Extensive aquatic macrophyte coverage can affect condition of largemouth bass, probably due to its effect on prey availability (Colle and Shireman 1980). In two central Florida lakes, coverage of hydrilla *Hydrilla verticillata* > 30%

lead to reduced condition in harvestable largemouth bass; however, this effect was not manifested in smaller largemouth bass until hydrilla coverage exceeded 50% (Colle and Shireman 1980). Condition of largemouth bass > 305 mm TL was lower in acidic ($pH < 5.0$) Florida lakes than in neutral lakes ($pH = 6.9-7.3$) (Canfield et al. 1985). Clugston (1964) reported that K was positively correlated to growth, but several studies have found no such relationship and K should be regarded as a rough indicator of growth at best (Anderson and Neumann 1996).

The relation of total and standard length for largemouth bass in southern Florida was $TL = 1.23\ SL + 1.16$ and $SL = 0.814\ TL – 0.789$ ($R^2 = 0.999$; valid for individuals 17-423 mm TL) (Hill 1998). The ratio of total length to standard length for largemouth bass 18-242 mm TL in Silver Springs, Florida, was 1.24 (Caldwell et al. 1955). Carlander (1977) provided additional conversions of TL, SL, and fork length (FL) for largemouth bass outside of Florida. He assumed ratios of $TL = 1.22\ SL$ (for fish 200 mm TL), $TL = 1.215\ SL$ (for fish 201-380 mm TL) and $TL = 1.21\ SL$ (for fish > 380 mm TL) to be representative. Fishery length categories for largemouth bass are 200 mm TL (Stock), 300 mm (Quality), 380 mm (Preferred), 510 mm (Memorable), and 630 mm (Trophy) (Gabelhouse 1984). These category values are used to estimate fishery statistics such as proportional stock density (PDS) and relative stock density (RSD) (Anderson and Neumann 1996).

Sagittal otoliths are commonly used for determining the age of largemouth bass in Florida (Taubert and Tranquilli 1982; Hoyer et al. 1985; Porak et al. 1986; Crawford et al. 1989). Buckmeier and Howells (2003) validated the use of otoliths for largemouth bass of up to age-16. Annulus formation occurs from February to July in north-central Florida (see Hoyer et al. 1985) and April to July in Peninsular Florida (Crawford et al. 1989). Young (ages 2-3) and female fish formed annuli earlier than other largemouth bass and Crawford and co-authors (1989) speculated that annuli may form as early as March in some southern Florida populations. Sectioned otoliths gave better estimates of age but poorer relationships of otolith diameter to body length than did whole otoliths (Hoyer et al. 1985). Relations of otolith diameter and total length are reported by Hoyer and co-authors (1985) and Porak and co-authors (1986).

Mean back-calculated total lengths at age for male and female largemouth bass were different for six Florida systems; for males (N = 416) the estimated lengths were 170 mm at age-1, 264 mm at age-2, 313 mm at age-3, 339 mm at age-4, 373 mm at age-5, 404 mm at age-6, and 416 mm at age-7 and for females (N = 648) they were 179 mm at age-1, 286 mm at age-2, 356 mm at age-3, 410 mm at age-4, 464 mm at age-5, 504 mm at age-6, 530 mm at age-7, 558 mm at age-8, 556 mm at age-9, 572 mm at age-10, 586 mm at age-11, and 616 mm at age-12 (Porak et al. 1986). Hoyer and Canfield (1994) back-calculated length-at-age for largemouth bass from north-central Florida lakes using otolith-aging and reported mean total lengths of 155 mm at age-1, 258 mm at age-2, 330 mm at age-3, and 374 mm at age-4. Mean total length-at-age for 32 Florida populations was $TL = 626(1 - e^{-0.246[\text{age} + 0.139]})$ for females and $TL = 419(1 - e^{-0.435[\text{age} + 0.107]})$ for males (Allen et al. 2003a). Carlander (1977) compiled numerous additional length-at-age estimates for largemouth bass from various parts of the USA aged using scales or otoliths. Mean values of length-at-age for unweighted means from North American populations were 118 mm (age-1), 215 mm (age-2), 287 mm (age-3), 341 mm (age-4), 389 mm (age-5), 434 mm (age-6), 463 mm (age-7), 495 mm (age-8), 510 mm (age-9), 528 mm (age-10), 554 mm (age-11), 518 mm (age-12), 530 mm (age-13), 523 mm (age-14), and 523 mm (age-15) (Carlander 1977).

Largemouth bass generally live longer in northern parts of its range (e.g., 15 years in Wisconsin and only 11 in Louisiana). (Heidinger 1975). Total annual mortality (A) ranged from

37 to 54% for five Florida systems and averaged 51% for 45 Florida water bodies (Allen et al. 2003a). The oldest males were age-10 and the oldest females were age-12 in a Florida study (Porak et al. 1986). The percentage of males generally declines with age (Heidinger 1975; Porak et al. 1986). Nevertheless, Chew (1974) reported the ratio of males to females in Lake Weir, Florida, to be 1:1 for fish 200-300 mm FL, 1.80:1 for fish 300-374 mm FL (suggesting slowing growth and stockpiling of males), 0.31:1 for fish 375-475 mm FL, and no males were observed larger than 475 mm FL. Males grew slower than females in six Florida systems and few fish larger than 460 mm TL were males (Porak et al. 1986).

Growth is related to the density of prey and conspecific and heterospecific competitors. Growth of age-0 but not age-1 largemouth bass was correlated with density of zooplankton prey in North Carolina lakes (Lemly and Dimmick 1982).

Dispersal and migration

Largemouth bass are thought to remain in relatively restricted home ranges for long periods of time (Miller 1975). Home ranges in two central Florida lakes ranged from 0.01 to 5.16 ha and 50 to 2,364 m across (Mesing and Wicker 1986). In a small (7 ha) Florida limerock pit, largemouth bass mean home ranges were 3.04-4.09 ha (Thompson 2003). In 80-ha Lake Baldwin, Florida, largemouth bass either established relatively small home ranges in shallow areas (mean 4.1 ha) or large home ranges in offshore areas (mean 21 ha) (Colle et al. 1989). Lewis and Flickinger (1967) reported that of 200 fish marked and 96 recaptured, 92 were recaptured within 91 m and 57 were recaptured within 30 m of the initial point of capture in a Michigan lake. Home ranges in a Mississippi impoundment were < 100 m across (Warden and Lorio 1975). Hasler and Wisby (1958) suggested that largemouth bass were able to home and data collected by Lewis and Flickinger (1967) showed that largemouth bass that moved more than 100 m were still capable of homing. In Florida, Mesing and Wicker (1986) observed homing in radio-tagged fish. Research into home range has implied the existence of sedentary and mobile individuals (Funk 1957; Moody 1960)—about half of the largemouth bass in a Missouri stream were in each category (Funk 1957). A single fish tagged in Silver Springs, Florida, moved about 0.8 km in two days (Caldwell et al. 1955) and another in a Tennessee stream moved 4.5 km in two days (Gatz and Adams 1994).

There is little information on diurnal movements of largemouth bass. Miller (1975) speculated that largemouth bass in quiet waters become less active at night, but move very little. On the other hand, he suggested that largemouth bass in streams may undergo significant movements to and from feeding stations and quieter waters. In a Mississippi impoundment, largemouth bass moved more during the day in spring and fall and nocturnal movements increased in summer (Warden and Lorio 1975). No diurnal trends in movement were evident in a small (7 ha) Florida limerock pit (Thompson 2003). Based on tracking two Florida largemouth bass in a Texas reservoir, Wildhaber and Neill (1992) reported more activity at dawn than other times of day.

Little research has investigated seasonal movement of largemouth bass. Greatest average daily movements occurred during February, May, and June and least movements were observed in August in two central Florida lakes (Mesing and Wicker 1986). Some fish in these lakes moved up to 3 km during the spawning season. In a Mississippi impoundment, largemouth bass moved most in March and September and least in December and January (Warden and Lorio 1975). In more northern waters, largemouth bass move deeper during the winter months (Miller

1975 and citations therein). In more southern climates, particularly in subtropical portions of Florida, little information is available.

Largemouth bass are known to utilize inundated floodplains and long-hydroperiod floodplain wetlands (Guillory 1979; Leitman et al. 1991; Baker and Killgore 1994; Light et al. 1995), suggesting some degree of lateral dispersal with rising water levels. Although none of their tagged fish in a Mississippi impoundment moved outside of previously established home ranges during water levels above full pool, Warden and Lorio (1975) remarked that other largemouth bass individuals explored new areas inundated by the flood water.

Effects of water level fluctuations on largemouth bass

There is considerable evidence that water level fluctuations influence largemouth bass populations (see Hill and Cichra 2002a). Effects can be positive or negative depending on the timing and duration of fluctuations and are life stage-dependent.

Flooding of terrestrial vegetation coincided with improved largemouth bass production in a number of studies (Allan and Romero 1975; Summerfelt and Shirley 1978; Miranda et al. 1984). Increasing water levels allowed greater access to terrestrial organisms as a food source for largemouth bass in an Arkansas reservoir (Mullan and Applegate 1968). Flooded terrestrial vegetation also indirectly increases food availability through releases of nutrients and subsequent enhanced system productivity (Keith 1975). Additionally, areas of flooded terrestrial vegetation serve as good spawning habitat (Keith 1975; Meals and Miranda 1991; Raibley et al. 1997).

Water level fluctuations during and soon after spawning can have negative effects on largemouth bass spawning success and subsequent recruitment of young-of-year individuals. Generally, high, stable water levels during spawning benefit largemouth bass (Miranda et al.

1984; Meals and Miranda 1991; Kohler et al. 1993; Garvey et al. 2000; Ozen and Noble 2002). Garvey and co-authors (2000) suggested that high reservoir discharge was associated with reduced abundance of young-of-year in Ohio. Falling water levels can strand nests and lead to reduced fry production (Mitchell 1982; Kohler et al. 1993). For example, water withdrawals for irrigation and municipal use during largemouth bass spawning have led to complete recruitment failures in Hawaiian reservoirs (Devick 1980). Rising water levels early in the spawning season may reduce temperatures around nests enough to cause nest abandonment by the custodial male or poor survival of the eggs (Mitchell 1982; Kohler et al. 1993). Flooding events during nesting or while fry are schooling can result in increased mortality. Larimore (1975) discussed the influence of floodwaters on the fry of a congener, the smallmouth bass *Micropterus dolomieui*. Reduced recruitment due to water fluctuations during short portions of the spawning season may be overcome by successful nesting during more favorable portions of the spawning season (Kohler et al. 1993).

High water levels following spawning may enhance survival and increase abundance of age-0 largemouth bass (Miranda et al. 1984; Fisher and Zale 1991). However, growth may be less in such years, probably due to density-dependent mechanisms (Miranda et al. 1984).

In Florida, only a few studies have addressed trends in largemouth bass populations relative to system hydrology. Electrofishing CPUE for age-0 largemouth bass was inversely related to summer water levels in Orange Lake, but not Lochloosa Lake, Florida, potentially due to the negative effect of high water on hydrilla in Orange Lake (Tate et al. 2003). There were no significant correlations between flow variables and electrofishing CPUE for largemouth bass in the Oklawaha or Withlacoochee rivers in Florida (Rogers and Allen 2004). Year-class strength of *Micropterus* (included largemouth bass and Suwanee bass) was negatively related to spring median flow rates when data from the Ochlockonee, Withlacoochee (Panhandle), Santa Fe, and Withlacoochee (Peninsula) rivers were combined (Bonvechio and Allen 2005); this was perhaps due to spawning disruption or a reduction in aquatic macrophytes due to high spring flows. Conversely, year-class strength of largemouth bass in Florida lakes was positively related to fall (Lake Bonny and Crooked Lake) or annual (Lake Disston) water levels (Bonvechio and Allen 2005).

Although some studies have found a relationship between largemouth bass growth and flow variables, current velocity did not significantly correlate with largemouth bass growth in Illinois streams (Putnam et al. 1995). Reduced water levels in the late summer and fall can enhance largemouth bass growth (Keith 1975). Low water levels concentrate prey fish, increasing prey availability (Heman et al. 1969). Exposed substrates grow terrestrial vegetation, providing the benefits previously described following re-flooding.

Increases and decreases in water levels can negatively effect fish populations due to poor water quality. High water levels and floodplain inundation can lead to hypoxia due to decomposition of terrestrial vegetation and other organic materials (Toth 1993; Furse et al.1996; Sabo et al. 1999, Fontenot et al. 2001). Such harsh environmental conditions can lead to fish kills and affect movement and habitat use of largemouth bass and other species (Toth 1993; Furse et al. 1996; Sabo et al. 1999, Fontenot et al. 2001). Low water levels, particularly during hot periods, can reduce water quality and lead to fish kills as well (Jackson et al. 1982).

Water level manipulation is an important management tool for enhancing largemouth bass populations (Keith 1975). Planned flooding and drawdowns can be used to increase cohort strength and increase individual growth (Keith 1975). For systems where historic water level fluctuations have been stabilized by water control structures, restoration of historic hydrological regimes or periodic drawdowns (with or without muck removal) can result in improved fish habitat and abundance and growth of largemouth bass (Holcomb and Wegener 1971; Hill et al. 1994; Moyer et al. 1995; Allen and Tugend 2004; Allen et al. 2003b). However, Allen and co-authors (2003b) concluded that effects on adult largemouth bass are far more difficult to detect.

Dollar sunfish *Lepomis marginatus* (Holbrook 1855)

General

The dollar sunfish is considered a lowland or coastal plain species. It is found mostly below the Fall Line along the lower Atlantic Slope from North Carolina south through peninsular Florida, across the Gulf Coastal Plain to Texas, and up the Mississippi Embayment to extreme western Kentucky and southeast Missouri (Bauer 1980a; Pflieger 1997). There are a few scattered records of dollar sunfish above the Fall Line in the upper Mobile Basin of Alabama (Mettee et al. 1996) and the Tennessee River system of Alabama and Tennessee (Etnier and Starnes 1993; Mettee et al. 1996).

Characteristics of dollar sunfish and taxonomic keys are provided in numerous works (e.g., Etnier and Starnes 1993). High quality photos of dollar sunfish are found in Robinson and Buchanon (1988), Etnier and Starnes (1993), and Mettee et al. (1996), and illustrations in Page and Burr (1991) and Pflieger (1997). Dollar sunfish is small (< 125 mm TL), relatively deep-bodied, and colorful, with an orangey or reddish background and blue and green, iridescent vermiculations. The opercular flap is large, margined in pale greenish (may be lighter in other states), and slightly angled upward.

Dollar sunfish was originally described as *Pomotis marginatus* (Eschmeyer 2004). It belongs to the subgenus *Icthelis* along with the closely-related longear sunfish *Lepomis* *megalotis* (Bailey 1938, cited in Etnier and Starnes 1993). Longear sunfish in Florida occurs in the Florida Panhandle in the Choctawhatchee River and to the west (Bauer 1980b) (i.e., does not occur in the St. Johns River). In Florida, dollar sunfish is distinguished from the longear sunfish by range, pectoral fin rays (usually 12, rarely 13 in dollar sunfish versus 13 or 14 in longear sunfish), cheek scale rows (4, rarely 5 in dollar sunfish versus 6, rarely 5 in longear sunfish), and opercular flap margin (pale greenish in dollar sunfish versus whitish in longear sunfish) (C. R. Gilbert, Florida Museum of Natural History, unpublished key to Florida centrarchids). The number of pectoral fin rays and cheek scale row counts may vary in other states (cf. Robinson and Buchanon 1988). An additional distinguishing character is the presence of silver blotches on the dark field of the operculum of dollar sunfish (versus no silver blotches on longear sunfish) (see Etnier and Starnes 1993).

Beyond its distribution and systematics, very little information is known about the dollar sunfish. Primary sources are two unpublished works—a dissertation by McLane (1955) and an abstract by Lee and Burr (1985)—and the book by Etnier and Starnes (1993). This lack of information is due to several factors. Dollar sunfish is relatively rare in most habitats—it seems to be a habitat specialist or perhaps a poor competitor. Additionally, its small size (usually < 125 mm TL) and patchy distribution render this species unimportant as a pan fish.

Habitat

Dollar sunfish is a lowland species and generally occurs in slow-moving or standing-water habitats, often associated with macrophytes or woody debris, with sand, silt, or mud substrates. Being a lowland species, it is often associated with floodplains. This species was collected from floodplains of the Appalachicola (Light et al. 1995) and Ochlockonee (Leitman et al. 1991) rivers in the Florida Panhandle. Toth (1993) mentions the presence of dollar sunfish in FWC collections from the historic (i.e., pre-channelized) Kissimmee River floodplain, Florida.

Chable (1947) remarked that in northern Peninsular Florida, dollar sunfish reaches its greatest abundance in flatwoods streams, and is less commonly found in other types of streams and in lakes. In the St. Johns River, Florida, it is more abundant in the southern half of the system and in swamp stream tributaries of the Oklawaha River (McLane 1955). McLane (1955) found this species mostly in small, sluggish, and highly-colored tributary streams draining forested areas. He also collected small numbers of dollar sunfish in littoral areas of the main river and associated lakes, typically in vegetation (e.g.,*Vallisneria*, *Najas*, or floating vegetation) over sand or mud bottoms. Additionally, McLane (1955) collected dollar sunfish on one occasion near the middle of the channel in vegetation in Alexander Springs Creek, a clear spring run. Likewise, VanGenechten (1999) reported collections of dollar sunfish from vegetated habitats of the Wekiva River, another spring-fed system within the St. Johns River basin. Also within this basin in Florida, dollar sunfish may be common in small cypress ponds (authors, pers. obs.) and are found (occasionally common) in long-hydroperiod ponds with emergent vegetation (e.g., pickerelweed) (J. E. Hill, pers. obs.).

Dollar sunfish was collected in 20 of 60 Florida lakes sampled by Hoyer and Canfield (1994). The statistical means and ranges of lake morphometry, water chemistry, and aquatic macrophyte variables for these 20 lakes were nearly identical to the entire 60 lake dataset (Table 4).

Brockmann (1974) categorized dollar sunfish as a facultative invader of brackish water in a southwest Florida canal where he collected this species at salinities up to 8.9‰.

Although information is lacking, larval and juvenile dollar sunfish likely have habitat requirements that are similar to adults.

Table 4. Lake morphometry, water chemistry, and aquatic macrophyte variables for lakes (N = 20) in north and central Florida where Hoyer and Canfield (1994) collected dollar sunfish.

Variables	Mean	Median	Minimum	Maximum	Standard Deviation
Surface area (ha)	366	87	9	5580	1230
Mean depth (m)	2.9	2.8	0.6	5.7	1.3
pH	7.0	7.5	4.5	9.0	1.4
Total alkalinity (mg/L as $CaCO_3$)	25.6	20.0	0.1	86.5	26.3
Specific conductance (µS/cm @ 25°C)	139	120	17	323	93
Color (Pt-Co units)	20	18	0	68	16
Total phosphorus (µg/L)	23	13	2	166	35
Total nitrogen (µg/L)	795	730	192	1808	457
Total chlorophyll *a* (µg/L)	15	9	1	102	23
Secchi depth (m)	2.0	1.5	0.6	5.3	1.3
Percent area covered by macrophytes (%)	49	46	1	100	38

Dollar sunfish is one of the rarer centrarchids in many areas (McLane 1955; Robinson and Buchanon 1988). For example, out of 8195 fish collected in the Ochlockonee River using electrofishing, traps, and nets, only 22 were dollar sunfish (Leitman et al. 1991). Similarly, dollar sunfish made up only 1.4% of 218 fish collected by electrofishing in tupelo gum *Nyssa aquatica* swamp habitat in the Cache River, Arkansas (Baker and Killgore 1994). Extensive sampling by additional gears and in other floodplain and channel habitats failed to collect additional specimens. Dollar sunfish made up a mean of only 0.28% of fish sampled by electrofishing at six stations in the heavily-impacted Peace River, Florida (Champeau 1990). Although usually found in relatively low numbers, it can be common in some habitats (Hoyer and Canfield 1994; authors, pers. obs.; see also Appendix III, Light et al. 1995). For example, dollar sunfish achieved an “exceptionally large population” in an artificial pond lacking predators (or other fishes?) in North Carolina (Lee and Burr 1985). Hoyer and Canfield (1994) reported a mean abundance of 765 dollar sunfish/ha (SD = 1647), ranging from 2.9-6547 dollar sunfish/ha, for 20 Florida lakes based on rotenone-blocknet collections; this species was not collected in an additional 40 Florida lakes. Biomass estimates from this dataset yielded a mean of 1254 g/ha (SD = 2306), ranging from < 0.1-9340 g/ha (Hoyer and Canfield 1994).

Feeding

Dollar sunfish feeds on benthos and at the surface based on stomach contents (Etnier and Starnes 1993). Based on 20 individuals from northern Peninsular Florida, Chable (1947) found *Hyalella azteca* (amphipod) in 100% and insects (mayfly nymphs, chironomids, and beetles) in 40% of stomachs by frequency of occurrence. In the most comprehensive study (i.e., 42 stomachs), McLane (1955) reported that dollar sunfish in the St. Johns River, Florida, is mainly insectivorous, with chironomids dominating numerically. Other food items were copepods, cladocerans, ostracods, amphipods, mayfly nymphs, odonate nymphs, clams, snails, grass shrimp, and marine polychaetes. North Carolina specimens had eaten small crustaceans and aquatic insects (Lee and Burr 1985) and Tennessee specimens contained detritus, filamentous algae, and terrestrial insects (Etnier and Starnes 1993).

Nesting and spawning

Dollar sunfish spawn during the warmer months—from April to September in Florida (McLane 1955) and May to August in North Carolina (Lee and Burr 1985). Typical of centrarchids, dollar sunfish is a substrate spawner and a paternal guarder—males guard nests, eggs, and young larvae. Males built nests on sand substrates and nested colonially (3-5/m^2) in a constructed pond in North Carolina (Lee and Burr 1985). Spawning occurs repeated through the warmer months and males may simultaneously guard overlapping broods of eggs and larvae (Lee and Burr 1985). Lee and Burr (1985) briefly described spawning behavior, including male aggression. McLane (1955) reported that three ripe females contained 280 (34 mm standard length [SL]), 310 (36 mm SL), and 414 (41 mm SL) ova. The author was not explicit about length measurements, but SL was assumed based on other portions of the manuscript—Robinson and Buchanon (1988) also interpreted this length as SL. Lee and Burr (1985) estimated that 150-200 larvae hatched per spawning in North Carolina. Sexual maturity is reached by age-2 in North Carolina (Lee and Burr 1985).

Age and growth

Very little information is available on growth of dollar sunfish. Young attained a length of about 10 mm TL in a month in North Carolina (Lee and Burr 1985). Based on scale annuli in Tennessee collections, mean lengths during August were 57 mm TL for age-1, 75 mm TL for age-2, 83 mm TL for age-3, and 95 mm TL for age-4 (Etnier and Starnes 1993). Lee and Burr (1985) reported a maximum age of 6 years in North Carolina and sexual maturity at 2 years (60 mm TL). Although lacking a conversion of standard length to total length for this species, dollar sunfish in Florida may reach sexual maturity at slightly smaller sizes (McLane 1955; see Nesting and spawning, above).

Hoyer and Canfield (1994) provided estimates of mean weight for dollar sunfish in 20 Florida lakes of 0.8 g for 40 mm, 2.5 g for 80 mm, and 13.0 g for 120 mm TL groups.

Dispersal and migration

There is only scarce information on dispersal and migration of dollar sunfish. In a constructed pond in North Carolina, dollar sunfish lived in deeper water during winter and moved into shallow water to spawn by mid-May (Lee and Burr 1985). Females and juveniles spent much of the breeding season in deeper water away from colonies of the spawning males (Lee and Burr 1985). It should be noted that the pond lacked predators and the authors did not describe the habitat, therefore this pattern of movement might differ under predation threat.

Dollar sunfish have been collected in long-hydroperiod wetlands that occasionally dry out (J. E. Hill, unpubl. data), suggesting some degree of dispersal ability in re-colonizing such habitats. Nevertheless, this fact does not suggest any special dispersal ability relative to other fishes (e.g., ability to move overland) given the occurrence of 5 to 12 other fish species—including other centrarchids such as the flier *Centrarchus macropterus*, bluespotted sunfish *Enneacanthus gloriosus*, and warmouth—in these collections (J. E. Hill, unpubl. data).

Effects of water level fluctuations on dollar sunfish

No studies have investigated the effects of water level or flow fluctuations on dollar sunfish. From the limited habitat information, dollar sunfish would be expected to respond most to changes in hydrology of swamp forest streams and their associated wetlands. Theoretically, floodplain inundation benefits dollar sunfish by increasing habitat, food resources, and food web productivity. Moreover, periodic floodplain inundation facilitates dollar sunfish dispersal by maintaining wetlands connectivity and refilling wetlands, preventing potentially catastrophic losses due to predation and desiccation (cf. Tramer 1977). Nevertheless, hypoxic conditions that may accompany floodplain inundation (Sabo et al. 1999; Fontenot et al. 2001; see also

Welcomme 1979) could have significant negative effects on dollar sunfish populations at local scales. However, the effects of hypoxia on dollar sunfish autecology have not been investigated. Being a short-lived species associated with floodplains, small streams, and other wetlands, dollar sunfish may be very susceptible to alterations of system hydrology.

Redbreast sunfish *Lepomis auritus* (Linnaeus 1758)

General

The redbreast sunfish is a stream-associated species of the Atlantic Slope ranging from the Maritime Provinces of Canada, south to central Florida, and west to the Apalachicola River system (Lee 1980a). This species has been widely introduced and the exact limits of its natural range are unclear. For example, Lee (1980a) concluded that redbreast sunfish may be native to the Choctawhatchee River (just west of the Apalachicola River) and introduced into the Mobile Bay system. Conversely, Metee and co-authors (1996) considered Choctawhatchee River populations to be introduced and Coosa and Tallapoosa system (eastern Mobile Bay drainage) populations to be possibly native. Boschung and Mayden (2004) also considered eastern Mobile Bay basin populations native. Nevertheless, there is current debate on the status of these populations (C. R. Gilbert, FLMNH, and J. D. Williams, USGS, pers. comm.).

The southern range limit of the redbreast sunfish in Florida is unclear in the literature (i.e., “central Florida”) and distributional maps often show a nearly straight line running east and west near Ocala (e.g., Lee 1980a; Page and Burr 1991). Nevertheless, the species is widespread in the St. Johns River system (McLane 1955; FLMNH 2004) and is found in the Kissimmee River (Toth 1993; FLMNH 2004). A single record exists for a coastal drainage of the Indian River in Indian River County (FLMNH 2004). Redbreast sunfish is apparently absent from Lake

Okeechobee (Ager 1971), Gulf of Mexico coastal drainages south of the Little Manatee River (e.g., Peace River, Champeau 1990), southeast Florida coastal drainages (Loftus and Kushlan 1987), and the Greater Everglades (Loftus and Kushlan 1987) (see also FLMNH 2004).

Characteristics of the redbreast sunfish and taxonomic keys are provided in numerous works (e.g., Etnier and Starnes 1993; Jenkins and Burkhead 1994; Boschung and Mayden 2004). High quality photos of redbreast sunfish are found in Etnier and Starnes (1993), Jenkins and Burkhead (1994), and Mettee et al. (1996), and illustrations in Page and Burr (1991) and Boschung and Mayden (2004). This small-to-medium sized sunfish (up to about 200 mm TL) is very colorful and is characterized by an orangey-red or yellow breast and venter, blue-green, wavy lines on the face and operculum, bluish, greenish, and orange spots on the body, and an elongated, opercular flap that is black to its posterior margin and often has pale blue upper and lower margins.

Redbreast sunfish was originally described as *Labrus auritus* by Linnaeus in 1758 and is the type species for the genus *Lepomis* (Eschmeyer 2004). Mitchell's original description of *Labrus pallidus* was actually based on *Lepomis auritus*; however, subsequent uses of *Labrus pallidus* are clearly referable to *Lepomis macrochirus* (C. R. Gilbert, FLMNH, pers. comm.). In Florida, the redbreast sunfish is often called "redbelly" or "redbelly sunfish".

Redbreast sunfish genetics were discussed by Avise and Smith (1974a, 1977) in their investigation of centrarchid genetics and phylogentic relationships. Generally, dendrogram branching patterns suggested that redbreast sunfish is most closely related to pumpkinseed sunfish *Lepomis gibbosus* and spotted sunfish.

The redbreast sunfish is a common panfish of Atlantic Slope and Florida streams. It may be the most important sport fish in some stream systems (e.g., Davis 1972). The Florida record is a 942 g (2.08 lb.) fish caught in the Suwannee River, Gilchrist County, in 1988 (FWC 2004).

Habitat

The redbreast sunfish is highly-associated with stream systems (Chable 1947; Jenkins and Burkhead 1994; Mettee et al. 1996; Boschung and Mayden 2004). This species is also found in lakes with connecting riverine habitats (McLane 1955; Hoyer and Canfield 1994), in reservoirs (Mettee et al. 1996), and in riverine swamps (Aho et al. 1986). However, redbreast sunfish is absent from extensive swamps and marshes and from isolated lakes (McLane 1955; Jenkins and Burkhead 1994). Although typically considered a species of moderate to low elevations, redbreast sunfish occurs in reservoirs up to 1067 m and in headwater streams exceeding this elevation in North Carolina (Shannon 1967). Aho et al. (1986) incorrectly cited Shannon (1967) as the source for redbreast sunfish being found up to 1345 m. This species typically occurs over sandy or rocky substrates and woody debris or aquatic macrophytes may be used as cover.

McLane (1955) reported that redbreast sunfish was collected most frequently in the main river course, large tributary streams, springs, and connecting lakes in the Oklawaha and St. Johns rivers, Florida. Common substrates were silty or bare sand and fish were often found associated with *Vallisneria* and *Najas* beds. Chable (1947) reported similar habitat characteristics for redbreast sunfish throughout northern Peninsular Florida. In the St. Johns River system, redbreast sunfish was more abundant in the northern half of the drainage, particularly in the Oklawaha River (McLane 1955). Hellier (1966) listed redbreast sunfish as the most common centrarchid in the Santa Fe River system, Florida; it was most abundant in sand-bottomed creeks and less so in vegetated backwaters.

The redbreast sunfish is known to utilize floodplains and floodplain wetlands in Florida. This species is common to abundant in Apalachicola River (Light et al. 1995) and Ochlockonee River (Leitman et al. 1991) backwaters and inundated floodplains. For example, it was the most abundant centrarchid and made up about 11% by number of total fishes (ranking 3rd) in electrofishing samples from the inundated Ocklockonee River floodplain (Leitman et al. 1991). Redbreast sunfish was the most abundant species by number in the inundated Santa Fe River floodplain (Bass and Hitt 1973, cited in Light et al. 1995). Toth (1993) listed redbreast sunfish occurring on the historic Kissimmee River floodplain. The use of inundated floodplains by this fish is undoubtedly more widespread than reported, probably due to the few studies investigating fish use of floodplains in Florida. It is worth noting that redbreast sunfish is not native or widely introduced in the Mississippi River system, a region where many studies of temperate fish floodplain use have occurred.

Being primarily a stream centrarchid, redbreast sunfish was only collected in 5 of 60 north and central Florida lakes sampled by Hoyer and Canfield (1994). These lakes had associated streams, were relatively large and alkaline, and had low aquatic macrophyte coverage compared to the entire 60 lake dataset (Table 5).

Redbreast sunfish is a freshwater species but may tolerate low levels of salinity. Peterson (1988) provided a graphic representation of centrarchid salinity tolerances and showed a continuum from salt-tolerant to salt-intolerant species—redbreast sunfish was listed as relatively intolerant of elevated salinity (up to 7‰). Shannon (1967) reported redbreast sunfish from waters with up to 8‰ salinity. Richmond (1940) documented redbreast sunfish nests in the tidal lower Chickahominy River, Virginia, in water that ranges from fresh to "perceptibly brackish".

Table 5. Lake morphometry, water chemistry, and aquatic macrophyte variables for lakes (N = 5) in north and central Florida where Hoyer and Canfield (1994) collected redbreast sunfish.

Variables	Mean	Median	Minimum	Maximum	Standard Deviation
Surface area (ha)	1176	80	24	5580	2463
Mean depth (m)	3.2	3.6	1.7	4.5	1.2
pH	8.4	8.5	7.3	9.0	0.7
Total alkalinity (mg/L as $CaCO_3$)	68.4	69.0	18.8	104.7	32.1
Specific conductance (µS/cm @ 25°C)	222	182	117	384	102
Color (Pt-Co units)	30	17	12	68	24
Total phosphorus (µg/L)	53	28	21	98	38
Total nitrogen (µg/L)	1570	1550	530	3228	1051
Total chlorophyll *a* (µg/L)	66	37	18	173	65
Secchi depth (m)	0.8	0.6	0.4	1.6	0.5
Percent area covered by macrophytes (%)	9	3	1	27	11

Little is known about other water quality tolerances of redbreast sunfish. This fish has been collected in waters with low pH (range from 4.0 to 8.4) (Shannon 1967), but this is likely an extreme value rather than a normal value for the species. Redbreast sunfish may tolerate temperatures of 33-35°C in thermally enriched waters (Aho et al. 1986 and citations therein). Redbreast sunfish is not known to be especially tolerant of hypoxia relative to other centrarchids.

Aho and co-authors (1986) provided riverine, lacustrine, and palustrine Habitat Suitability Index (HSI) models for redbreast sunfish. These models incorporated variables used to estimate life requisites and ultimately habitat suitability. The riverine model incorporated a "food/cover" component (% hard structural cover and % vegetative cover), a "water quality" component (turbidity, pH, dissolved oxygen, and temperature during growing season), a “reproduction” component (% hard structural cover, current velocity, substrate composition, and temperature during spawning season), and an “other” component (stream width). The lacustrine model incorporated a “food” component (total dissolved solids during growing season), a “cover” component (% hard structural cover, % vegetative cover, and % area as littoral zone), a “water quality” component (turbidity, pH, dissolved oxygen, and temperature during growing season), and a “reproduction” component (% hard structural cover, substrate composition, % area as littoral zone, and temperature during spawning season). The palustrine model incorporated a “food/cover” component (% hard structural cover, % vegetative cover, and % vegetated wetland exceeding critical water depth), a “water quality” component (pH, dissolved oxygen, turbidity, and temperature during growing season), and a “reproduction” component (% hard structural cover, temperature during spawning season, current velocity, and substrate composition). The authors gave interpretations of Suitability Index (SI) values of “poor” (0.0-0.1), “fair” (0.2-0.4), “good” (0.5-0.7), and “excellent” (0.8-1.0). Aho and co-authors (1986) provided graphs estimating SI for a range of values of each habitat variable. The overall HSI value for each model is the minimum SI value among the variables included in the model. Increasing percent vegetated wetland at a depth 20 cm, percent of stream during spawning season with a current velocity 20 cm/s and at least 20 cm in depth, percent bottom area at preferred spawning depth (0.2-1.5 m) composed primarily of coarse sand and fine gravel favor redbreast sunfish abundance (Table 6). Habitat suitability is highest at intermediate levels of percent hard structure cover, percent vegetative cover, maximum temperature during spawning, turbidity, pH, and maximum growing season temperature, mean total dissolved solid concentration, and percent littoral zone (Table 6). Caution must be exercised in interpreting HSI model output. Some values are based on incomplete or inconclusive information from literature sources, are inferences based on related species (often at the familial level), or are arbitrary values based on biological intuition. These models had not been tested in the field to compare model outputs to population responses such as growth, survival, or abundance. Moreover, these models were developed specifically for a system with warm effluents (i.e., the Savannah River, Georgia) and the emphasis on the thermal environment may not be appropriate for Florida systems.

Table 6. Habitat Suitability Index (HSI) habitat variable values to achieve an "Excellent" (i.e., 0.8-1.0) Suitability Index (SI) for redbreast sunfish (Aho et al. 1986). Values based on interpretation of graphs.

Habitat Variable	Excellent Value
% Hard Structure Cover during Average Spring-Summer Flow	15%
% Vegetative Cover during Average Spring-Summer Flow	20-85%
% Vegetated Wetland with Depth 20 cm	50%
Maximum Water Temperature at Spawning Depth	20-29°C
% of Stream Area during Spawning with 20 cm/s Current Velocity and 20 cm in Depth	35%
% Bottom Area during Spawning at Depth of 0.2-1.5 m Composed Primarily of Coarse Sand or Fine Gravel	35%
pH during Spawning/Growing Season	4.5-9.5
Minimum DO during Spawning/Growing Season	Seldom < 5.0 mg/L
Maximum Monthly Average Turbidity during Spawning/Growing Season	40-140 JTU
Maximum Weekly Water Temperature (1-2 m deep) during Growing Season	20-30°C
Mean Total Dissolved Solids Concentration during Growing Season	90-550 ppm
% Littoral Zone Area at Average Summer Water Level	30%
Mean Stream Width at Average Summer Flow	5-40 m

Although there is little information in the literature, larval and juvenile redbreast sunfish are assumed to have similar habitat requirements to adults (Aho et al. 1986). Anecdotally, juveniles may occupy areas with bare substrates more often than other centrarchids (Chable 1947). In contrast, Hellier (1966) noted that young redbreast sunfish were found in association with vegetation.

Redbreast sunfish is common to abundant in many systems in Florida, particularly in streams. In electrofishing samples, it was the dominant species numerically in the lower Suwannee River (33.8%; CPUE = 39.0/hr) and in the Santa Fe River (29.8%; CPUE = 34.0/hr) (Bass and Hitt 1975). Rogers and Allen (2004) reported mean electrofishing CPUE of 6.14 fish/min (225.9 g/min) and 1.74 fish/min (55.8 g/min) for two stations on the Oklawaha River and 2.76 fish/min (64.6 g/min) for one station on the Withlacoochee River, Florida. In blocknet-rotenone sampling of five Florida lakes, Hoyer and Canfield (1994) found a mean abundance of 187 redbreast sunfish/ha (SD = 210), ranging from 5.4 to 417/ha, and mean biomass of 1862 g/ha (SD = 2334), ranging from 40 to 5670g.

Feeding

There is considerable information on the diet of redbreast sunfish. This species is a generalist feeder, consuming a wider variety of invertebrates, and occasionally, fish. Stomach contents suggest feeding on the benthos, drift, and surface.

There are three studies of food habits of redbreast sunfish in Florida. Chable (1947) examined 21 individuals (7 empty) from northern Peninsular Florida and found insects (57% by occurrence), mainly chironomids, crustaceans (33%), mainly amphipods, plant material (33%), and molluscks (19%). In the same study, by number crustaceans (mostly amphipods) were 79% and insects (mostly chironomids) were 17%. McLane (1955) reported the stomach contents of 152 redbreast sunfish collected from the St. Johns River, Florida. Chironomid larvae frequently occurred in the stomachs (83.6%). By number, insects were predominant with 44.4% (mostly chironomids), followed by fish eggs at 32.6%, amphipods at 17.5%. Of lesser importance were copepods, cladocerans, ostracods, isopods, decapods, branchiurans (i.e., *Argulus,* a fish parasite), terrestrial insects, mollusks, bryozoans, plant material, and sand. In the lower Suwannee River, insects (mostly midge larvae) made up 69.4% by number and 42.1% by volume, isopods made up 15.4% by number and 8% by volume, and plant material was 32.2% by volume of stomach contents of 979 redbreast sunfish (Bass and Hitt 1975). In the Santa Fe River, insects (mostly midge and caddisfly larvae) made up 97.8% by number and 55.4% by volume, and plant material and debris were 36.2% by volume of stomach contents of 774 redbreast sunfish (Bass and Hitt 1975). Of lesser importance in the lower Suwannee River and Santa Fe River were oligochaetes, mollusks, spiders, water mites, ostracods, copepods, amphipods, grass shrimp, crayfish, crabs, fish, and fish eggs.

The food habits of redbreast sunfish outside of Florida have been well studied. Larval and small juvenile redbreast sunfish feed on zooplankton (Lemly and Dimmick 1982; Johnson and Johnson 1984; Perez-Fuentetaja et al. 1996). Growth of age-0 and age-1 redbreast sunfish was correlated with zooplankton density in North Carolina lakes (Lemly and Dimmick 1982). Aquatic insects generally dominate the stomach contents of larger fish, with the most frequently occurring and important (numerically and volumetrically) taxa including Diptera (especially chrionomids), Trichoptera, Ephemeroptera, Odonata, and Coleoptera (Flemer and Woolcott 1966; Shannon 1967; Davis 1972; Coomer et al. 1977; Cooner and Bayne 1982; Kirby 1982; Thorp et al. 1989; Johnson and Dropkin 1993, 1995). Nevertheless, redbreast sunfish in these studies consumed a wide variety of other organisms, including crustaceans, arachnids, mollusks, fish (including nest cannibalism [DeWoody et al. 2001], and plant material. Terrestrial arthropods may be important prey items in some systems (Cloe and Garman 1996). Plant material and detritus are assumed to be eaten incidentally while pursuing invertebrate prey

(Davis 1972). Sand in redbreast sunfish stomachs may come from ingestion of caddisfly larvae and their cases (Davis 1972).

Johnson and Dropkin (1993, 1995) studied the diel feeding periodicity of redbreast sunfish in a Pennsylvania river. They found that mayflies dominated the diet over most 4-hour periods and across the entire 24-hour period. Feeding in July peaked at 1600 h and feeding was minimal at night (Johnson and Dropkin 1995). In contrast, feeding peaked at 0400 h in October and was low but stable throughout the remainder of the 24-hour period (Johnson and Dropkin 1993).

The redbreast sunfish has been the subject of study for ecological and functional morphology of fishes. For example, Gatz (1979a, b, 1981) included redbreast sunfish in his investigations of the links between morphology, niche differentiation, and community structure of stream fishes in North Carolina. Lauder (e.g., 1980, 1983) provided functional analyses of redbreast sunfish feeding morphology in his broader investigations of comparative sunfish functional anatomy.

Nesting and spawning

Like other centrarchids, redbreast sunfish males construct a nest and guard the eggs and fry (Breder 1936; Miller 1964). In the Suwannee River system, Florida, spawning takes place from April until October with a peak from May to August (Hellier 1966; Bass and Hitt 1975). Spawning in the St. Johns River, Florida, occurs from May to August (McLane 1955). Similar, but less protracted, spawning seasons have been reported for redbreast sunfish in other regions of its range from Georgia to New York (Breder 1936; Richmond 1940; Davis 1972; Sandow et al. 1975; Helfrich et al. 1991; Lukas and Orth 1993). Spawning occurs at temperatures of 20-29°C

(Sandow et al. 1975; Helfrich et al. 1991; Lukas and Orth 1993). Interestingly, Lukas and Orth (1993) found that variation in nest density (nests/ha = y) in Virginia was almost fully explained by the number of degree-days accumulated after water temperatures first reached 20°C ($\log_{10} y = 109.1 – 14.7 \log_{10}$ degree-days; $R^2 = 0.99$). Lukas and Orth (1993) contrasted characteristics of successful and unsuccessful nests in Virginia (Table 7).

Table 7. Summary statistics for nest habitat characteristics for 30 successful redbreast sunfish nests in Virginia. Table adapted from Lukas and Orth (1993). Degree-days denote the number of degree-days after reaching 20°C. Mean velocity is average water column velocity and Bottom velocity is velocity 5 cm above spawning substrate. Cover in 1 m and Cover in 2 m refers to the number of structural surfaces within these distances. The "***" denotes a significant two-sample t-test (i.e., $p < 0.05$) which indicates a statistical difference between successful and unsuccessful nests. Unsuccessful nests had a mean discharge of 4.17 m^3/s (SD = 1.28) and 6.7 nests per colony (SD = 3.5).

Variable	Mean	SD	Minimum	Maximum
Degree-days	737.6	250.3	507	1312
Mean temperature (°C)	24.3	1.2	23.5	27.5
Minimum temperature (°C)	22.3	0.8	21.7	24.9
Maximum temperature (°C)	26.6	1.5	25.6	30.2
Temperature change (°C)	4.3	0.8	3.9	7.1
Water depth (m)	1.08	0.37	0.42	1.81
Mean velocity (m/s)	0.050	0.046	0	0.15
Bottom velocity (m/s)	0.0008	0.009	0	0.03
Nest diameter (cm)	47	9.5	32	76
Nest depth (cm)	4.3	1.6	2	9
Distance to shore (m)	12.6	4.1	1.5	18
Distance to cover (m)	0.43	0.44	0	1.7
Cover in 1 m	5.4	2.65	0	11
Cover in 2 m	10.8	4.89	2	20
Mean discharge (m^3/s)***	3.17	1.54	1.26	4.77
Maximum discharge (m^3/s)	5.02	1.44	1.39	5.69
Minimum discharge (m^3/s)	1.16	0.02	1.16	1.22
Change in discharge (m^3/s)	3.86	1.44	0.17	4.53
Nests in colony***	3.8	3.5	1	11
Distance to next nest (m)	9.1	18.7	1	100

Spawning behavior is well known for redbreast sunfish (Breder 1936; Miller 1964; Lukas and Orth 1993). Generally reproductive behavior of this species is consistent with other members of the genus (see Breder 1936 for a detailed description of sunfish reproductive behavior). Miller (1964) noted that redbreast sunfish males have a highly developed habit of removing large gravel from the nest, leaving rather uniform gravel size. The resulting uniformity was a useful characteristic in differentiating redbreast sunfish nest from some other *Lepomis* nests. In contrast to other sunfish observed, the redbreast sunfish male does not make sounds during courtship (Gerald 1971).

Males construct nests in relatively shallow water (25-150 cm) (Breder 1936; Davis 1972; Bass and Hitt 1975; Sandow et al 1975; Aho et al. 1986). Nest depths were 15-46 cm in New York (Breder 1936), were 36-38 cm in North Carolina (Davis 1972), and had a mean nest depth in Virginia of 63.7 cm (Helfrich et al. 1991). More than 50% of 128 nests were found in water of 30-60 cm depth in Virginia (Helfrich et al. 1991). Nest diameters were 25-61 cm in New York (Breder 1936), were 30-76 cm in Virginia (Lukas and Orth 1993), were 60-125 cm in New York (Thorp 1988), and had means of 91 cm in North Carolina (Davis 1972) and 94 cm in Georgia (Sandow et al. 1975). Breder (1936) noted that nests built in areas of current were oval, rather than round.

Water velocity is an important environmental variable for redbreast sunfish nesting. In North Carolina, redbreast sunfish nests were found when river gauge velocities were 3.4-56.1 cm/s with a mean of 18.0 cm/s (Davis 1972). Actual velocities at the nest sites were not measured (Davis 1972) and current velocities may differ between nest sites and non-nest sites (Helfrich et al. 1991). In their HSI modeling efforts, Aho and co-authors (1986) considered current velocities 20 cm/s to be optimal for nesting, largely based on information from Davis (1972). Nevertheless, a mean current velocity of only 0.9 cm/s was found for 128 redbreast sunfish nests in Virginia (Helfrich et al. 1991). Furthermore, Lukas and Orth (1993) recorded a mean water column velocity of 5 cm/s and mean velocity 5 cm above the nest of 0.8 cm/s for 30 successful nests in Virginia (Table 7). These results from Virginia suggest that current velocities in the upper portion of HSI model ranges actually may not have high suitability (see also Leonard and Orth 1988). Overall, low, stable current velocities during spawning season enhance redbreast sunfish reproductive success (Helfrich et al. 1991).

Nests are generally built on relatively firm substrates such as sand or gravel (Davis 1972; Sandow et al. 1975; Lukas and Orth 1993). Davis (1972) conducted a limited experiment in a pond that suggested a preference for sand-gravel substrates over silt. Indeed, Helfrich and co-authors (1991) stated that redbreast sunfish requires sand-gravel substrates to successfully spawn. Nevertheless, redbreast sunfish may construct nests where softer substrates overlay firmer substrates (e.g., silt over sand or shell), if the softer sediments are not excessively deep (Breder 1936; Richmond 1940; McLane 1955). The activities of the custodial male alters the composition of the substrate within the nest by the removal of fine sediments, leaving a greater proportion of coarse and intermediate substrates within the nest relative to non-nest sites (Helfrich et al. 1991).

Several authors have noted the frequent association of nests with cover such as aquatic vegetation, rocks, or woody debris (e.g., Davis 1972; Bass and Hitt 1975; Sandow et al. 1975). Breder (1936) suggested that redbreast sunfish construct nests immediately downstream of obstructions because of reduced current velocity in these locations. Nevertheless, Sandow and co-authors (1975) noted that redbreast sunfish nests in Georgia were upstream of obstructions. Current velocities were not provided in either paper, but Breder (1936) suggested rather high current velocity in their New York study. Nests in Virginia were located in areas with a mean of 30% cover within 2 m of the nest site, with nearly 60% of nests in the category of 0-25% cover

(Helfrich et al. 1991). There was no difference between the percentages of nests associated with hard structures versus aquatic vegetation (Helfrich et al. 1991).

Nesting activities reduce the food intake of custodial males and alter the characteristics of the local benthic invertebrate fauna. Thorp and co-authors (1989) found that non-nesting redbreast sunfish had fuller stomachs than nesting males in a New York impoundment. The construction of nests and increased localized predation pressure reduce the density and diversity of benthic invertebrate prey (Thorp 1988). These localized effects on benthic invertebrates were dramatic during the spawning season and were still detectable for slightly less than a year (Thorp 1988). Persistent effects were likely due to changes in sediment composition accompanying nest construction (cf. Helfrich et al. 1991).

Total fecundity (F) was strongly correlated with total length ($\text{Log}_{10}F = 3.16\text{Log}_{10}TL - 3.88$; $R^2 = 0.71$) and weight ($\text{Log}_{10}F = 1.13\text{Log}_{10}WT - 0.955$; $R^2 = 0.75$) for female redbreast sunfish (N = 79) in the Satilla River, Georgia (Sandow et al. 1975). Mean ova count was 3302, ranging from 322 to 9206 in 79 females of 115-265 mm TL and 24-278 g. Mean ova diameter was 1.20 mm and ranged from 0.90 to 1.64 mm. Larval development was described by Buynak and Mohr (1978).

The smallest sexually mature male and female were both in the 89-113 mm TL size class in the Satilla River, Georgia (Sandow et al. 1975). All males >165 mm TL and all females > 191 mm TL were mature. There was 1 male for every 1.5 females.

Genetic evidence using microsatellites has documented the parentage of offspring within nests and the occurrence of cannibalism in redbreast sunfish. DeWoody and co-authors (1998) conducted a detailed study of a nesting colony in South Carolina. They found that nests contained offspring from a mean of 3.7 females (ranged from two to six). More than 95% of the offspring were sired by the guarding male. Nevertheless, about 40% of nests contained small percentages (< 10%) of offspring that were sired by nest parasites (cf. Gross and Charnov 1982; Gross 1982). Two nests contained no offspring sired by the guarding male, suggesting nest takeover. Observations of guarding male redbreast sunfish cannibalizing eggs within their own nests (e.g., DeWoody et al. 1998) were shown to include eggs sired by parasites (i.e., heterocannibalism) as well as eggs sired by the guarding male (i.e., filial cannibalism) (DeWoody et al. 2001). This suggests that male redbreast sunfish can maximize lifetime reproductive output by indiscriminately consuming a portion of eggs from their nests.

Centrarchid nests are often used by cyprinids (e.g., Carr 1946; Kramer and Smith 1960b; Chew 1974). Fletcher (1993) reported on the nest association of dusky shiners *Notropis cummingsae* and redbreast sunfish.

Age and growth

Some research has investigated the relation of length and weight of redbreast sunfish in Florida and adjacent regions of the southeastern USA. Bass and Hitt (1975) reported regression equations for redbreast sunfish in the Santa Fe River ($\text{Log}_{10}\text{WT} = 2.89\text{Log}_{10}\text{SL} - 4.20$; $R^2 = 0.98$; N = 913) and Suwannee River ($\text{Log}_{10}\text{WT} = 2.81\text{Log}_{10}\text{SL} - 4.06$; $R^2 = 0.89$; N = 974), Florida. Males and females had slightly different length-weight relations in the Satilla River, Georgia (Sandow et al. 1975). The equation for redbreast sunfish in the Satilla River, Georgia was $\text{Log}_{10}\text{WT} = 3.24\text{Log}_{10}\text{TL} – 5.28$; $R^2 = 0.99$; N = 893 (Sandow et al. 1975). In Alabama, an equation based on 3,937 fish was $\text{Log}_{10}\text{WT} = 3.01\text{Log}_{10}\text{TL} – 4.69$ (Carlander 1977). In South Carolina beaver ponds, the relation of weight and length for 534 redbreast sunfish was $\text{Log}_{10}\text{WT} = 3.12\text{Log}_{10}\text{TL} – 5.06$ (Levine et al. 1986).

Hoyer and Canfield (1994) reported mean weights for redbreast sunfish of six size classes collected in five Florida lakes (Table 8). Mean values of Fulton's condition factor (K) for redbreast sunfish in the Satilla River, Georgia, were 1.80 for males, 1.76 for females, and 1.79 for all fish (N = 893) (Sandow et al. 1975). Sandow and co-authors (1975) calculated mean condition for redbreast sunfish in Alabama from the literature and found a mean K of 2.61. Bass and Hitt (1975) reported substantially higher values for K for redbreast sunfish in the Santa Fe and Suwannee rivers in Florida (i.e., 3.58 to 4.01), but these estimates were based on standard length rather than total length. The length conversion is TL = 1.22 SL (Carlander 1977). Generally, K factor values increase with increasing fish size (e.g., Bass and Hitt 1975).

Table 8. Mean weight for redbreast sunfish from Florida lakes, by total length size group. Data from Hoyer and Canfield (1994).

Size Group (mm)	Mean Weight (g)	Standard Deviation	N
40	<1	<1	93
80	7	1	339
120	15	4	53
160	31	7	34
200	65	11	7
240	170	*	1

Sandow and co-authors (1975) used scales to age redbreast sunfish from the Satilla River, Georgia. They reported mean total length-at-age to be 59 mm for age-1, 90 mm for age-2, 125 mm for age-3, 153 mm for age-4, 181 mm for age-5, 205 mm for age-6, and 222 for age-7 individuals. They reported numerous checks and false annuli and suggested that at least some of these marks were the result of slow growth during low water periods. Annuli (on scales?) form in March to May in Georgia (Carlander 1977). However, otoliths are more appropriate for use in Florida (Mantini et al. 1992). Mean total length-at-age estimates for redbreast sunfish collected in Florida streams were 61 mm for age-1, 104 mm for age-2, 115 mm for age-3, and 119 mm for age-4 (Mantini et al. 1992). The estimates were highly variable, especially among streams. For example, the minimum length at age-4 was 118 mm and the maximum was 152 mm. The authors commented that similar estimates were reported for populations in other states. Nevertheless, Georgia redbreast sunfish were considerably longer than Florida redbreast sunfish at all ages after age-3 if the data from Georgia based on scales is comparable to data from Florida based on otoliths. Values summarized by Carlander (1977) for Georgia and North Carolina systems ranged from 32-102 mm for age-1, 58-127 mm for age-2, 120-161 mm for age-3, 148-188 mm for age-4, 166-173 mm for age-5, and 180-211 mm for age-6. Petrimoulx (1983) reported mean length-at-age for redbreast sunfish in Virginia of 73 mm for age-1, 108 mm for age-2, 122 mm for age-3, and 141 mm for age-4. Again, the comparability of these data, presumably obtained from reading scales, with Florida otolith-based data is unknown.

Dispersal and migration

Redbreast sunfish occupy home ranges, yet will frequently move large distances in streams (Hudson and Hester 1976; Gatz and Adams 1994). The longest movement recorded for this species in a North Carolina stream was 6.1 km (Hudson and Hester 1976). A minority of tagged redbreast sunfish were found in small home ranges in Tennessee streams (Gatz and Adams 1994). Some Tennessee individuals moved from 3-10 km from the capture site and several of these eventually returned to their capture site. Estimated home ranges (i.e., stream length) were from < 50 m to 9,650 m. Movements peaked in spring and were shorter during the winter. Larger redbreast sunfish moved longer distances than smaller fish. Individuals tended to be either short-distance or long-distance movers, suggesting the occurrence of sedentary and mobile individuals (sensu Funk 1957). Freeman (1995) studied movements of juvenile redbreast sunfish in a Georgia stream and reported relatively short movements for most individuals. She found most movements were along stream banks (although some individuals crossed the stream).

Very little is known about seasonal movements of redbreast sunfish. Based on a tagging study in a North Carolina stream, redbreast sunfish moved more in May and June and less in January and February than in other months (Hudson and Hester 1976). This species forms aggregations during cold periods, often in deep water (Breder and Nigrelli 1935). Redbreast sunfish is a common inhabitant of inundated floodplains, suggesting lateral dispersion from stream channels to floodplains.

Effects of water level fluctuations on redbreast sunfish

Although little directed study has occurred, redbreast sunfish may be expected to respond to fluctuations in stream flow and water levels in a manner similar to largemouth bass. Mechanisms increasing overall fish populations resulting from periodic increasing water levels such as enlarged habitat, access to additional food resources, and enhanced food-web productivity (Hill and Cichra 2002a) also should benefit redbreast sunfish. Redbreast sunfish is commonly found using inundated floodplains for nursery and feeding habitat (Leitman et al. 1991; Light et al. 1995), therefore periodic inundation should provide positive responses in population parameters. These benefits may be immediate or may be manifested after a time lag. For example, electrofishing CPUE for lotic sportfish (i.e., redbreast sunfish and spotted sunfish combined) was positively correlated with minimum stream stage during the prior year in the Oklawaha River, Florida, and was described by $\mathrm{Log}_e\mathrm{CPM} = -1.60\mathrm{Log}_e + 2.70\ \mathrm{Log}_e\ (\mathrm{MIN})$ ($R^2 = 0.98$) and $\mathrm{Log}_e\ \mathrm{BPM} = 2.38\ \mathrm{Log}_e + 2.32\ \mathrm{Log}_e\ (\mathrm{MIN})$ ($R^2 = 0.94$), where CPM is number of fish per minute, BPM is weight of fish in grams per minute, and MIN is minimum stage during the prior year (Rogers and Allen 2004). Likewise, year-class strength of redbreast sunfish in four Florida rivers was positively related to median stream flow in the fall of the prior year (Bonvechio and Allen 2005).

Conversely, increased water levels and flow may have negative effects on redbreast sunfish. For example, poor water quality such as hypoxic conditions on floodplains is detrimental to redbreast sunfish. In addition, redbreast sunfish nesting success is sensitive to current velocity (Aho et al. 1986; Helfrich et al. 1991; Lukas and Orth 1993). Successful nests were closely associated with relatively slow, stable current velocity (Helfrich et al. 1991; Lukas and Orth 1993) and increased currents during this time may lead to catastrophic loss of eggs or larvae. Moreover, year-class strength of *Lepomis* spp. (i.e., bluegill and redbreast sunfish data combined) in four Florida rivers, although positively related to pre-spawn fall median flow, was negatively related to fall median flow (Bonvechio and Allen 2005). They suggested managing for high flows on a 3-year cycle to produce periodic strong *Lepomis* spp. year-classes.

Spotted sunfish *Lepomis punctatus* (Valenciennes 1831)

General

The spotted sunfish is a lowland or coastal plain species and is often considered to be stream-associated. Nevertheless, the spotted sunfish is found in a variety of freshwater and slightly brackish habitats. This species occurs from southeastern North Carolina (Cape Fear River), south along the Atlantic Coastal Plain to the Ochlockonee River in the Florida Panhandle and southwestern Georgia, as well as throughout Peninsular Florida (Warren 1992). Spotted sunfish has a natural contact zone containing hybrids with redspotted sunfish *Lepomis miniatus* in northern Gulf of Mexico drainages from the Apalachicola River west to the Perdido River

(Warren 1992) (see Lee et al. 1980c and Warren 1992 for distribution of redspotted sunfish). Discordant populations occur in the upper Coosa River drainage of Alabama and northwestern Georgia and in the Tennessee River drainage in Lookout Creek, Georgia (Warren 1992). The source of hybrids in these systems is not completely understood—alternatives include introduction of spotted sunfish as contaminants with redbreast sunfish stocking programs, stream capture events (particularly regarding the possibility of genes from Lookout Creek populations entering the upper Coosa), and the existence of relicts of an ancestral, eastern epiphenotype (Warren 1992). Etnier and Starnes (1993) also listed spotted sunfish in the Conasauga River, Tennessee (upper Coosa River system), and South Chickamauga Creek (tributary to the Tennessee River and adjacent to Lookout Creek). These are presumably hybrids as well.

The spotted sunfish was originally described as *Bryttus punctatus* by Valenciennes in 1831 (Eschmeyer 2004). Spotted sunfish was long considered to have two subspecies, eastern spotted sunfish *L. p. punctatus* and western spotted sunfish *L. p. miniatus* (Bailey 1938), until Warren (1992) elevated both to species rank as blackspotted sunfish *L. punctatus* (Valenciennes) and redspotted sunfish *L. miniatus* Jordan (see Nelson et al. 2004 for an explanation of omitting parentheses around the name Jordan). Bermingham and Avise (1986) had previously investigated genetic structuring in spotted sunfish populations and their data supported Warren's (1992) conclusions based on an analysis of morphology. Some authorities disagree with elevating these to species rank, arguing that the broad natural zone of contact in Alabama, Florida, and Georgia is more correctly a zone of intraspecific introgression (Nelson et al. 2004; C. R. Gilbert, Florida Museum of Natural History and University of Florida, pers. comm.). Although Warren (1992) suggested blackspotted sunfish replace spotted sunfish as the common name for *L. punctatus* (e.g., Boschung and Mayden 2004), Nelson and co-authors (2004) retain spotted sunfish as the recognized common name. In Florida, spotted sunfish is often called "stumpknocker".

Characteristics of the spotted sunfish are provided in Page and Burr (1991 [as *L. p. punctatus*]) and Warren (1992). Several slightly older works (i.e., before these species were separated) present diagnostic characteristics of redspotted sunfish or mix characteristics of both species in their accounts of spotted sunfish. Spotted sunfish is a relatively small (up to about 200 mm TL), chunky sunfish with numerous dark spots on the body, a black opercular flap that is stiff to the margin, relatively short, rounded pectoral fins, and moderate gill rakers (Page and Burr 1991; Warren 1992).

Surprisingly little ecological information is available for spotted sunfish—one of the more detailed accounts being McLane's (1955) dissertation on the fishes of the St. Johns River. In addition, some data on spotted sunfish are actually for redspotted sunfish (e.g., Robison and Buchanan 1988). Spotted sunfish is an common species in Florida and in streams, rivers, and oxbows of the southeastern Atlantic and northeastern Gulf slopes. Although relatively small, it is an aggressive feeder and willingly strikes lures or natural baits; it is a common panfish in Florida. The Florida record is a 376 g (0.83 lb.) fish caught in the Suwannee River, Columbia County, in 1984 (FWC 2004).

Habitat

The spotted sunfish often is abundant in streams, rivers, and floodplain wetlands (McLane 1955; Lee et al. 1980c; Leitman et al. 1991; Light et al. 1995). Additionally, spotted sunfish occurs in the littoral zones of lakes, in canals, and in grassy and broadleaf marshes (McLane 1955; Ager 1971; Kushlan and Lodge 1974; Loftus and Kushlan 1987; Hoyer and

Canfield 1994). Loftus and Kushlan (1987) considered this species to be the most ubiquitous and abundant centrarchid in southern Florida, and concluded that the spotted sunfish was one of the few centrarchids that is adapted to life in the southern Everglades.

Chable (1947) collected spotted sunfish in greatest abundance in small streams, rivers, and springs in northern Peninsular Florida and failed to collect this species in lakes or ponds. He indicated that spotted sunfish was seldom found in locations without vegetation or woody debris for cover. McLane (1955) found spotted sunfish to be most abundant in the St. Johns River system, Florida, in streams with cover such as aquatic macrophytes, woody debris, or snags or in deeper pools of sluggish, swamp streams. Kilby (1955) also emphasized the presence of submersed vegetation where spotted sunfish were found in Florida coastal marshes. McLane (1955) also collected spotted sunfish from Florida spring heads and runs, as did Caldwell and co-authors (1955) in Silver Springs and VanGenechten (1999) in the Wekiva River. McLane (1955) noted that no spotted sunfish were collected from totally isolated water bodies within the St. Johns River system. McLane (1955) collected this species over a variety of substrate types including mud, sand, gravel, and rock in water that ranged from clear to highly-colored.

Hoyer and Canfield (1994) collected spotted sunfish from only 19 of 60 north and central Florida lakes. Based on inspection of the data, they concluded that this species tends to occur in moderately hardwater, nutrient-rich lakes (Table 9).

Although primarily freshwater, spotted sunfish may tolerate low to moderate salinity. In Florida, spotted sunfish have been collected at salinities up to 11.8‰ in a coastal marsh (Kilby 1955) and at salinities up to 12.5‰ in the Everglades (Loftus and Kushlan 1987). Chable (1947) commented that spotted sunfish is frequently found in brackish water, including the mouth of the Weekiwachee River at Bayport and the mouth of the Suwannee River; however, no salinity data were given. Bailey and co-authors (1954) noted that natural hybrids between redspotted sunfish and spotted sunfish had a marked tolerance for salinity based on collections at all brackish water stations along the lower Escambia River, Florida. Unfortunately, the station descriptions mention salinity wedges of up to 24.4‰ salinity, but the reference is not clear about the salinity of the water at capture depths for spotted sunfish.

Table 9. Lake morphometry, water chemistry, and aquatic macrophyte variables for lakes (N = 19) in north and central Florida where Hoyer and Canfield (1994) collected spotted sunfish.

Variables	Mean	Median	Minimum	Maximum	Standard Deviation
Surface area (ha)	522	137	19	5580	1325
Mean depth (m)	3.1	3.5	0.9	5.7	1.3
pH	8.0	8.0	6.6	9.5	0.7
Total alkalinity (mg/L as $CaCO_3$)	45.2	46.0	3.9	104.7	26.6
Specific conductance (µS/cm @ 25°C)	196	187	45	384	95
Color (Pt-Co units)	34	27	7	116	29
Total phosphorus (µg/L)	107	26	10	1043	242
Total nitrogen (µg/L)	1169	935	389	3228	749
Total chlorophyll *a* (µg/L)	40	22	4	173	45
Secchi depth (m)	1.2	1.0	0.4	2.7	0.7
Percent area covered by macrophytes (%)	34	13	1	100	37

In contrast to these studies indicating salinity tolerance of spotted sunfish, other data suggest that this species may be inconsistent in its use of brackish environments. For example, Brockman (1974) found no individuals at salinities > 4.9‰ in a southwestern Florida coastal canal. More compelling evidence is found in data for centrarchid salinity tolerances (Peterson 1988, and references therein). These data show that species in this family form a continuum from salinity intolerant species (e.g., dollar sunfish) to highly tolerant species (e.g., redear sunfish *Lepomis microlophus*). Spotted sunfish is near the center of this continuum. In experimental studies, redspotted sunfish experience increases in blood plasma osmolality and decreases in hematocrit values when subjected to increasing water salinity. Recovery or acclimation times were up to 36 hours at salinities < 8‰ and 72 hours at 8‰ (Peterson 1988). Therefore, the tolerance of spotted sunfish (if indeed similar to redspotted sunfish) to salinity is likely dependent on rate of change. This could lead to differing distributional patterns between systems where salinity is more tidally regulated (e.g., estuaries, coastal marshes) versus seasonally regulated (e.g., river mouths). Spotted sunfish in seasonally regulated systems may be able to tolerate higher salinities because the inherent acclimation ability of the species is not overwhelmed by rapidly changing salinity regimes. Peterson and Meador (1994) reviewed the effects of salinity on freshwater fishes, including centrarchids, in the southeastern USA.

Little is known about other environmental tolerances of spotted sunfish (e.g., pH). Kushlan (1974) found that centrarchids, including spotted sunfish, were among the first species to die under low oxygen conditions in a natural Florida pond in the Big Cypress Preserve. Additionally, larger individuals succumbed before smaller individuals. Hypoxia may therefore limit the use of inundated floodplains by spotted sunfish (see Sabo et al. 1999; Fontenot et al. 2001).

Spotted sunfish may be common to abundant in preferred habitat and relatively rare in other habitats. Several authors made qualitative statements concerning the abundance of spotted sunfish in Florida. McLane (1955) commented that it was the most abundant sunfish in sluggish swamp streams, but noted that several other centrarchids (i.e., bluegill, redear sunfish, black crappie, largemouth bass, warmouth, and redbreast sunfish) exceeded spotted sunfish in numerical and biomass abundance throughout the St. Johns River system, Florida. Light and co-authors (1995, and references therein) summarized information on relative abundance of spotted sunfish in various floodplain habitats and described this species as common in backwaters of the

Apalachicola and Ochlockonee rivers and rare in these habitats in the upper Suwannee River and in the Santa Fe River. Also, spotted sunfish was considered rare on inundated floodplains of the Apalachicola, Ochlockonee, Suwannee, and Santa Fe Rivers, Florida (Light et al. 1995). In electrofishing samples, spotted sunfish made up < 0.7% by number of fish collected along margins of main channel habitat, 2.1% in backwater habitats with slack water, and only 0.2% in inundated floodplains of the Ochlockonee River, Florida (Leitman et al. 1991).

Spotted sunfish was the second most numerically dominant species in the Santa Fe River (12.9%) and third in the lower Suwannee River (11.4%) (Bass and Hitt 1975). Bass (1990) found spotted sunfish hybrids to have a mean rank of 7th (range 5-9) out of 15 common fish species in electrofishing samples from the Escambia River, Florida. Rogers and Allen (2004) reported mean electrofishing CPUE of 3.59 fish/min (93.6 g/min) and 1.72 fish/min (36.5 g/min) for two stations on the Oklawaha River and 7.01 fish/min (145.5 g/min) for one station on the Withlacoochee River, Florida. In electrofishing samples in the heavily-impacted Peace River, Florida, spotted sunfish made up a mean of six stations of 12.4% (SD = 8.7%) of fish sampled (Champeau 1990).

In blocknet-rotenone sampling of 60 lakes, Hoyer and Canfield (1994) found spotted sunfish in 19 lakes. In these lakes, mean abundance was 149 spotted sunfish/ha (SD = 332), ranging from 0.9 to 1332/ha, and mean biomass was 2009 g/ha (SD = 5262), ranging from 20 to 22910 g/ha. Spotted sunfish made up about 0.9% of total fish biomass. Similarly, spotted sunfish made up 5% by number (139/ha) and 1% by biomass (1.7 kg/ha) of fish collected by blocknet and detonator cord in Black Creek Canal (C-1, C-1N), Miami-Dade County, a heavily human-modified habitat (Shafland 1999a).

Spotted sunfish is often the most abundant sunfish in the Florida Everglades (Kushlan and Lodge 1974; Loftus and Kushlan 1987). It was the most abundant *Lepomis* in throw trap samples from wet prairies and sloughs of the Blue Cypress Marsh Conservation Area, St. Johns River system, Florida, but was only 1% or less of the total fish numbers (Jordan et al. 1998).

Feeding

Spotted sunfish consumes a wide variety of invertebrate prey, with insects being the dominant food category. Chable (1947) reported that insects were found in 100% of 19 spotted sunfish from northern Peninsular Florida—aquatic beetles (47.4%), chironomids (31.6%), hemipterans (15.8%), mayfly nymphs (15.8%), and terrestrial hymenopterans (15.8%) were the most frequently occurring. Chable (1947) also found amphipods (15.8%), decapods (10.5%), and snails (10.5%) in the stomachs. McLane (1955) examined stomachs of 73 specimens from the St. Johns River, Florida. Insects were found in 85% of the 67individuals with stomach contents. Chironomids, mayfly nymphs, odonate nymphs, and terrestrial insects were commonly eaten by spotted sunfish. By frequency of occurrence, amphipods (34.3%) and aquatic plant fragments (mostly filamentous algae) (26.9%) followed insects in importance. By number, amphipods dominated (38.5%), followed by insects (29.3%), cladocerans (22.5%), and copepods (6%). Small numbers of isopods, decapod crustaceans, water mites, snails, and fish eggs were found. McLane (1955) commented that he found relatively large quantities of twigs and leaf fragments in the stomachs (28% of stomachs), but did not provide data on volume or mass of food items.

Caldwell and co-authors (1955) reported that the stomach contents of spotted sunfish in Silver Springs within the St. Johns River system, Florida, resembled the plant and animal constituents of the periphyton covering beds of *Sagittaria*. Although not specific, the authors mention chironomids and caddisfly larvae as being the most abundant invertebrates. The reference also implies that amphipods and grass shrimp were eaten. Similar to McLane (1955), Caldwell and co-authors (1955) remarked on the relatively large quantity of algae in the stomachs and intestines of spotted sunfish. The authors doubted that spotted sunfish receive much nutrition from algae. Items such as algae, twigs, and leaf fragments are likely consumed incidentally during the pursuit of invertebrates.

Hunt (1953) reported on the stomach contents of 20 spotted sunfish (combined with the stomach contents of two bluegills) in the Tamiami Canal, Miami-Dade County, Florida. He found copepods (77.3% by frequency of occurrence), ostracods (72.7%), dipteran larvae (59.1%), cladocerans (45.5%), and a low incidence of rotifers, mayfly larvae, damselfly nymphs, water mites, snails, and *Argulus* (a parasitic branchiuran), but no plant material.

Very little is known about the diet of spotted sunfish in brackish water habitats. Desselle and co-authors (1978) found a variety of invertebrates and a few small fishes in stomachs of the closely-related redspotted sunfish in the Lake Pontchartrain Estuary, Louisiana. Likewise, redspotted sunfish in brackish waters of Davis Bayou, Mississippi, consumed zooplankton, insects, amphipods, and other small invertebrates (VanderKooy et al. 2000).

Wainwright and Shaw (1999) studied prey-capture kinematics of spotted sunfish and found its characteristics to be intermediate between largemouth bass and bluegill.

The vulnerability of spotted sunfish to gape-limited predators (e.g., largemouth bass) is related to its ratio of body depth to length (i.e., $BD = 0.42\ TL - 3.84$) (Hill 1998; Hill et al. In press).

Nesting and spawning

In his seminal work on sunfish reproductive habits, Breder (1936) indicated that nothing at that time was known about the spawning of spotted sunfish (i.e., *Sclerotis punctatus*); subsequently, studies of spotted sunfish reproductive behavior in Florida were conducted. Like other centrarchids, spotted sunfish is a substrate nester with paternal care.

A brief mention was made by Hubbs and Allen (1943) of grouped spotted sunfish nests over hard substrates during April and June in Silver Springs, Florida. Caldwell and co-authors (1955) also studied aspects of spotted sunfish reproduction in Silver Springs and reported an extended spawning period during summer but limited spawning during winter in the near constant temperature environment. Their data on gonad development suggested that the peak of spawning activity was May to June.

Carr (1946) provided detailed observations of spotted sunfish spawning behavior and nests during the months of May and June in Hogtown Creek, Alachua County, Florida. Water temperatures during the study were 20-24°C. The study site was a small stream having a maximum depth of < 1 m and a sandy substrate with organic detritus and occasional limestone sections, flowing through a hardwood hammock. Nests generally were not aggregated, but occasionally two to four nests were observed in close proximity. Nests were about 30-60 cm in diameter, excavated about 2.5-5 cm into the substrate, and found in water depths of 10-38 cm (mean depth = 15 cm). Most nests were in the main channel and current of the stream. Like other centrarchids, the male constructs the nest by strong undulations of the body and fins (see also Breder 1936; McLane 1955). Spawning usually took place soon after nest completion and the male expels the female from the area after spawning. Males were observed to spawn with multiple females (Carr 1946). Multiple paternity and maternity of eggs in individual nests has been confirmed using genetic evidence (DeWoody et al. 2000). Eggs from the Hogtown Creek, Florida, population were 1.4-1.8 mm in diameter (mean = 1.6 mm), round, adhesive, and an amber color with a dark oil globule on the yolk (Carr 1946). Incubation lasted from 48-52 hours and the larvae were 4 mm at hatching. The 6.5-7 mm larvae began to feed by nine days post-hatch and they began to leave the nest by day 10. The larvae formed loose schools on days 10-13 and then dispersed.

Spotted sunfish has an extended spawning period of March to September in northern Florida (McLane 1955). McLane (1955) made observations of spotted sunfish spawning behavior and nesting in Hogtown Creek in the same area as Carr (1946) and in springs of the Suwannee River (e.g., Ichetucknee Springs) and St. Johns River (e.g., Silver Glenn Springs) systems.

Spotted sunfish females can spawn at a relatively small size. Based on an observed (but not measured) individual, Carr (1946) reported breeding by a female of approximately 51 mm (TL?). The smallest ripe female collected by Caldwell and co-authors (1955) was 55 mm SL.

Carr (1946) observed golden shiners *Notemigonus crysoleucas* spawning over spotted sunfish nests. Some eggs were consumed by the guarding male spotted sunfish. She noted that the duration of development of the golden shiner larvae was similar to that of the spotted sunfish larvae and both species left the nest at about the same time. Golden shiners also have been reported to spawn over the nests of largemouth bass (Kramer and Smith 1960b; Chew 1974).

Age and growth

Relatively little is known about age and growth of spotted sunfish. For example, few relations of length and weight have been published (Table 10). Caldwell and co-authors (1955) provided means and ranges of observed weights along with calculated weights for fish collected from Silver Springs, Florida (see Table 10 for the regression equation used to calculate weight). The relation of length and weight did not vary significantly from month to month or between sexes (Caldwell et al. 1955). Canfield and Hoyer (1994) reported mean weights of five 40-mm TL size classes of spotted sunfish collected from 19 Florida lakes (Table 11).

Table 10. Relations of standard length and weight for spotted sunfish. The SL range for each equation was not presented in the reference.

Location	N	Equation	Reference
Florida	NA	$\text{Log}_{10}\text{WT} = 3.002\text{Log}_{10}\text{SL} - 4.32$	Caldwell et al. 1955
Florida	29	$\text{Log}_{10}\text{WT} = 3.05\text{Log}_{10}\text{SL} – 4.53$	Wainwright and Shaw 1999

Table 11. Mean weight for spotted sunfish from Florida lakes, by total length size group. Data from Hoyer and Canfield (1994).

Size Group (mm)	Mean Weight (g)	Standard Deviation	N
40	0.6	0.2	88
80	4	1.0	485
120	20	2	213
160	47	10	74
200	96	2	6

Spotted sunfish was not included in the summary of fish standard weight equations in Anderson and Neumann (1996). However, Fulton’s condition factor (K) was determined for 756 spotted sunfish from Silver Springs, Florida (Caldwell et al. 1955). The mean K for all spotted sunfish was 4.82, ranging from 4.38 to 5.59, and there was no obvious increase in K with fish size.

An attempt to age spotted sunfish with scales was made from specimens collected in the nearly constant-temperature environment of Silver Springs, Florida (Caldwell et al. 1955). The authors reported the presence of presumed annuli and provided some information on standard lengths at these “distinct rings”. Nevertheless, the authors suggested a number of difficulties with scale reading, including numerous false annuli, conflicting age estimates from a single reader between scales within a fish, and the development of the first annulus being more related to size than to age. These problems, along with the lack of proper validation of the technique (see Beamish and McFarlane 1983), effectively limit the utility of scales in aging spotted sunfish in Florida.

The available information on growth of spotted sunfish is limited both in quantity and quality. Based on very limited data from tagged fish maintained in cages and a single individual tagged and recaptured within the spring, Caldwell and co-authors (1955) suggested growth rates of 0.12 mm/day and 44 mm/year for spotted sunfish of 90-120 mm SL in Silver Springs, Florida. Given their observations, it is clear that the study was hampered by serious loss of tags and tagging mortality. Furthermore, they assumed that spotted sunfish growth ceased in winter, even in the near constant temperatures of the spring head. Given the limited information available, additional study is needed to investigate the basic aspects of spotted sunfish age and growth in Florida.

Dispersal and migration

Very little is known about movements or dispersal of spotted sunfish. This species is known from floodplain wetlands, suggesting some degree of lateral dispersal. Genetic data document that spotted sunfish populations in Everglades wetlands subject to wet-dry cycles do not experience bottlenecks (e.g., due to severely reduced populations surviving drought) and suggest re-colonization from surrounding areas (McElroy et al. 2003). However, spotted sunfish were found in less than one third of Florida lakes sampled by Hoyer and Canfield (1994) and are often absent from isolated wetlands (McLane 1955; J. E. Hill, unpubl. data).

Effects of water level fluctuations on spotted sunfish

Water level fluctuations should have effects on spotted sunfish that are similar to those described earlier for largemouth bass (see also Hill and Cichra 2002a). This species is stream-associated; therefore changes in flow and floodplain connectivity should be important for spotted sunfish dynamics. Otherwise, little species-specific information for spotted sunfish exists.

Spotted sunfish abundance, as indicated by electrofishing CPUE, was related to the minimum river stage achieved in the previous year in the Oklawaha River, Florida (Rogers and Allen 2004; see also redbreast sunfish above). The relationships were $\mathrm{Log}_e\,\mathrm{CPM} = -1.10\mathrm{Log}_e + 2.81\ \mathrm{Log}_e\ (\mathrm{MIN})$ ($R^2 = 0.84$) and $\mathrm{Log}_e\,\mathrm{BPM} = 5.83\ \mathrm{Log}_e - 6.31\ \mathrm{Log}_e\ (\mathrm{MIN})$ ($R^2 = 0.86$), where CPM is number of fish per minute, BPM is weight of fish in grams per minute, and MIN is minimum stage during the prior year (Rogers and Allen 2004).

Warmouth *Lepomis gulosus* (Cuvier 1829)

General

The warmouth is often considered to be a lowland or coastal plain species, but it is also found in more upland river systems (e.g., Cumberland River, Tennessee; Etnier and Starnes 1993). This species is native to the Atlantic Slope from the James River, Virginia (Jenkins and Burkhead 1994) throughout the Gulf Coastal Plain and Florida, west to Texas, and north into the upper Mississippi River, Ohio River, Tennessee River, and Lake Erie basins (Lee 1980b). The apparent absence of warmouth in much of Georgia in Lee (1980b) is perhaps due to a combination of sampling bias and an absence of specimens in the museums that submitted data for the publication rather than a true break in the distribution (e.g., see Mettee et al. 1996 for Georgia records from the upper Mobile Basin).

Characteristics of the warmouth and taxonomic keys are provided in numerous works (e.g., Etnier and Starnes 1993; Pflieger 1997). High quality photos of warmouth are found in Robinson and Buchanon (1988), Etnier and Starnes (1993), Jenkins and Burkhead (1994), and Mettee et al. (1996), and illustrations in Page and Burr (1991) and Pflieger (1997). The warmouth is a small-to-medium (< 250 mm TL), chunky, dark sunfish. Body color is brownish, olivaceous, or brassy yellow with profuse dark mottling on the body and fins (Etnier and Starnes 1993). The mouth is very large for a *Lepomis* and there are dark streaks extending backwards from the eye. It is unlikely to be confused with other Florida species.

The warmouth was originally described as *Pomotis gulosus* by Cuvier (Eschmeyer 2004). It was considered a member of the genus *Chaenobryttus* prior to the publication of Bailey et al. (1970). This name was placed into synonymy with *Lepomis*, largely due to the ability of warmouth to hybridize with various *Lepomis* species and its apparent morphological similarity with the green sunfish *Lepomis cyanellus* (see discussions in Etnier and Starnes 1993 and Jenkins and Burkhead 1994). Another factor influencing this issue is the varying interpretations of biochemical and genetic data presented by Avise and Smith (1974a, 1977). Because of conflicting interpretations of morphological and genetic data, some workers retain *Chaenobryttus* as valid. However, based on recent genetic evidence (Roe et al. 2002), warmouth is retained in the genus *Lepomis* by Nelson and co-authors (2004). Also, older literature often uses the name *Chaenobryttus coronarius* (Bartram) (e.g., McLane 1955), a junior synonym for *C. gulosus*. Using mitochondrial DNA evidence, Bermingham and Avise (1986) found genetic structuring of warmouth populations in southeastern USA, with some Mobile Basin populations clustering with Florida and Atlantic Slope populations and thus representing a lineage distinct from western populations. However, this degree of structuring was not enough to declare subspecific status (cf. bluegill *L. m. purpurescens*; Avise and Smith 1974b).

The warmouth is a common panfish in Florida and throughout much of its range. Its large mouth, broad diet, and willingness to strike a lure or bait overcome its relatively small size and make it a common part of the recreational fishery (e.g., Robinson and Buchanon 1988). This species is often caught incidentally by “bream” anglers pursuing other sunfishes (Etnier and Starnes 1993). The Florida record is a 1105.3 g (2.44 lb) fish caught in the Yellow River in 1985 (FWC 2004).

Habitat

The warmouth has been considered a habitat specialist (Larimore 1957; Guillory 1978; Savitz 1981; McMahon et al. 1984); nevertheless, the warmouth occurs in a wide variety of habitats. It is often found in lowland lakes, sluggish streams, ponds, and marshes, typically associated with aquatic macrophytes or woody structure and sand, silt, or mud substrates (Etnier and Starnes 1993; Mettee et al. 1996; Pflieger 1997). Warmouth also inhabits reservoirs, river margins, and faster-flowing streams (Robinson and Buchanon 1988; Etnier and Starnes 1993). It often occurs on inundated floodplains and in floodplain wetlands (Guillory 1979; Leitman et al. 1991; Toth 1993; Light et al. 1995). Warmouth is a littoral species and is rarely found in limnetic zones.

In northern Peninsular Florida, Chable (1947) concluded that warmouth reaches its maximum abundance in smaller rivers, flatwoods streams, and vegetated lakes, often in vegetation and over soft substrates. In the St. Johns River, Florida, McLane (1955) found warmouth to occur in nearly all aquatic habitats, although it was most abundant in sluggish or standing water habitats with abundant vegetation, often stained water, and silty or muddy bottoms.

Hoyer and Canfield (1994) collected warmouth from 59 of 60 lakes sampled in north and central Florida. Lakes containing warmouth encompassed the entire range of variability in lake morphometry, water chemistry, and aquatic macrophyte coverage (Table 12). The authors concluded that warmouth increased in relative abundance with increasing aquatic macrophtye coverage. Similarly, Guillory (1978) reported that warmouth was exclusively associated with dense stands of aquatic macrophytes (e.g., *Vallisneria*, *Potomogeton*) and was most prevalent in such areas with organic detritus or silt substrate and water depths > 30 cm in Lake Conway, Florida.

Table 12. Lake morphometry, water chemistry, and aquatic macrophyte variables for lakes (N = 59) in north and central Florida where Hoyer and Canfield (1994) collected warmouth.

Variables	Mean	Median	Minimum	Maximum	Standard Deviation
Surface area (ha)	411	55	2	12412	1767
Mean depth (m)	2.8	2.9	0.6	5.9	1.2
pH	7.0	7.6	4.3	9.7	1.6
Total alkalinity (mg/L as $CaCO_3$)	31.5	22.0	0.0	130.6	33.2
Specific conductance (μS/cm @ 25°C)	136	117	17	384	98
Color (Pt-Co units)	28	17	0	400	54
Total phosphorus (μg/L)	56	19	1	1043	149
Total nitrogen (μg/L)	925	687	82	3789	808
Total chlorophyll *a* (μg/L)	28	9	1	241	47
Secchi depth (m)	2.0	1.5	0.3	5.8	1.5
Percent area covered by macrophytes (%)	41	33	1	100	39

Although there is little information in the literature, larval and juvenile warmouth are assumed to have similar habitat requirements to adults, particularly regarding the importance of vegetative or woody cover (McMahon et al. 1984).

The warmouth is found in fresh water, but may tolerate low to medium salinity waters. McLane (1955) collected warmouth in Salt and Mullet lakes in the St. Johns River system, Florida, at salinities of 5-10.7‰. Loftus and Kushlan (1987) reported warmouth from waters of 12.5‰ in the Florida Everglades. Brockmann (1974) collected warmouth at salinities up to 8.9‰ in a southwest Florida coastal canal. In Florida and Louisiana coastal marshes (Carver 1967) and in the Lake Pontchartrain estuary, Louisiana (Desselle et al. 1978), collections have occurred at salinities up to 4.1‰. In Alabama, warmouth are abundant in the lower Mobile Delta during periods of low freshwater discharge and high tidal intrusion at salinities of 1-15‰ (Mettee et al. 1996). In contrast, Bailey and others (1954) remarked that the salinity tolerance of warmouth was less than that of other sunfishes given a lack of collections at brackish water stations in the Escambia River, Florida. Similarly, Kilby (1955) never collected warmouth at salinities above 1.8‰, but considered this species to be resident (i.e., not transient) in Salt Creek at Bayport, Florida, with a salinity of 1.5‰. He felt that the lack of warmouth in higher salinity marsh habitat adjacent to Salt Creek indicated a restriction to fresh water.

The warmouth occurs across a range of pH values. McMahon et al. (1984) considered approximate minimum and maximum pH values of about 5 to 9.5 to be tolerable and 6 to 8.5 as optimal. They also pointed out that warmouth may be tolerant of pH fluctuations given the species common occurrence in heavily-vegetated systems where diurnal pH variation may be large. Canfield and Hoyer (1994) collected warmouth from Florida lakes with pH ranging from 4.3 to 9.7.

The warmouth is noted for its ability to survive brief periods of hypoxia and is one of the last species to die under hypoxic conditions (Larimore 1957; Kushlan 1974). Warmouth survived DO concentrations of 0.7-1.3 mg/L when allowed access to the surface (Baker 1941).

In laboratory studies, warmouth tolerated DO levels of 1.0 mg/L without mortality (Gould and Irwin 1965) and DO concentrations of 0.3 mg/L for brief periods (Larimore 1957). Nevertheless, Larimore (1957) suggested that a DO level of 3.6 mg/L is critical for long term survival. Increasing turbidity may reduce warmouth abundance and growth, perhaps indirectly due to its negative influence on aquatic macrophtyes (McMahon et al. 1984).

McMahon et al. (1984) provided riverine and lacustrine Habitat Suitability Index (HSI) models for warmouth. Both models incorporate variables used to estimate life requisites and ultimately habitat suitability. The riverine model incorporates a “food/cover” component (% pools, % cover, and average current velocity), a “water quality” component (turbidity, pH, dissolved oxygen in pools, and summer temperature), a “reproduction” component (% pools, % cover, dissolved oxygen near spawning substrate, and temperature during spawning), and an “other” component (gradient). The lacustrine model incorporates a “food/cover” component (% shoreline cover), a “water quality” component (turbidity, pH, dissolved oxygen along shoreline, and temperature), and a “reproduction” component (% shoreline cover, dissolved oxygen near spawning substrate, and temperature during spawning). The authors give interpretations of Suitability Index (SI) values of “poor” (0.0-0.1), “fair” (0.2-0.4), “good” (0.5-0.7), and “excellent” (0.8-1.0). McMahon et al. (1984) provided graphs estimating SI (Suitability Index) for a range of values of each habitat variable. Increasing % pools, % cover, and dissolved oxygen concentrations and decreasing current velocity and stream gradient favor warmouth abundance (Table 13). Habitat suitability is highest at intermediate levels of turbidity, pH, and temperature (Table 13). The riverine model predicts optimum warmouth habitat to be characterized by summer temperatures of 25-30°C, 70% pool area, and high amounts of aquatic macrophytes or other cover present. The lacustrine model predicts optimum warmouth habitat to be characterized by summer temperatures of 25-30°C, extensive shallow littoral area, and high amounts of aquatic macrophytes or other cover along the shoreline. Caution must be exercised in interpreting HSI model output. Some values are based on incomplete or inconclusive information from literature sources, are inferences based on related species (often at the familial level), or are arbitrary values based on biological intuition. Additionally, the authors state that the models are "generalized descriptors" of warmouth habitat requirements and that no relationship between these models and population abundance should be assumed.

Table 13. Habitat Suitability Index (HSI) habitat variable values to achieve an "Excellent" (i.e., 0.8-1.0) Suitability Index (SI) for warmouth (McMahon et al. 1984).

Habitat Variable	Excellent Value
% Pools during Average Summer Flow	75%
% Cover during Summer	40%
Average Current Velocity in Summer	10 cm/sec
Stream Gradient	~ 0 m/km
Maximum Monthly Average Turbidity in Summer	0-80 JTU
Minimum or Maximum pH Value	6-9
Average Daily Minimum DO in Summer	6 mg/L
Average Daily Minimum DO at Spawning Substrate	6 mg/L
Mean Weekly Water Temperature in Summer	25-30°C
Mean Weekly Water Temperature during Spawning	21-27°C

Hester (2001) analyzed data for 60 Florida lakes (see Canfield and Hoyer 1992 for the original data collection) and investigated the relationship of selected habitat variables and the abundance of warmouth using simple linear regression techniques. She found that warmouth abundance (fish/ha) had a positive relationship with percent area covered by vegetation (R^2 = 0.4703) and percent volume infested by vegetation (R^2 = 0.3615). Relationships of other variables (i.e., benthic invertebrate prey biomass, fish prey biomass, phosphorus, nitrogen, chlorophyll, and Secchi depth) to warmouth abundance were not significant or only explained a minute fraction of the variability in warmouth abundance. A relationship between warmouth abundance and lake trophic state was presented, but no analysis was given. Variability and maximum abundance seem to increase with increasing trophic state. A re-examination of the data using more sophisticated regression techniques and incorporating additional variables might reveal more significant factors (see Allen et al. 1998, 2000 for this approach taken for other species using the same dataset).

Several authors have observed that warmouth is not abundant numerically, but occurs in collections at a high frequency (e.g., Chable 1947; McLane 1955; Pflieger 1997). As previously mentioned, some authors consider warmouth to be habitat specialists and food generalists, suggesting that these aspects of warmouth ecology influence its interactions with other species and ultimately its population size. Although not studied for warmouth, it is tempting to generalize from the case of largemouth bass, bluegill, and green sunfish in temperate lakes of the northern USA (Werner 1974, 1977; see also Savitz 1981). Green sunfish also is a habitat specialist and food generalist. This species possesses a relatively large mouth, is intermediate between largemouth bass and bluegills in shape, and is similar to bluegills in size (i.e., similar in those respects to warmouth). Largemouth bass and bluegills are categorized as habitat generalists and food specialists, overlapping extensively in habitat use with one another, but partitioning food resources based on prey size. Green sunfish cannot successfully compete with either species for food and is thus relegated to marginal habitats and occurs in relatively low densities in most lakes.

In boat electrofishing samples over six years in the Escambia River, Florida, Bass (1990) found warmouth to have a mean rank abundance of only13 (ranged from 10.5 to 14) out of 15 common fish species. Also using boat electrofishing samples, Champeau (1990) reported that warmouth made up a mean of only 0.33% of fish collected at six stations along the heavily human-impacted Peace River, Florida. Composite estimates for warmouth abundance based on

10 years of concussion blocknet sampling in Black Creek Canal, Miami-Dade County, Florida, were only 9 fish/ha and 0.1 kg/ha (Shafland 1999a).

On the other hand, warmouth can be common to abundant and can reach high densities (i.e., over 10,000/ha) in vegetated Florida lakes (Hoyer and Canfield 1994) and in swamps. Based on blocknet rotenone collections, 59 Florida lakes had a mean warmouth abundance of 1796 warmouth/ha (SD = 2239), ranging from 0.7-10047/ha (Hoyer and Canfield 1994). An estimate of mean biomass from the same study was 10510 g/ha (SD = 12897), ranging from 10-73,500 g/ha. In Lake Conway, Florida, warmouth was the sixth most abundant fish by number (482 fish/ha) and fifth by biomass (3,270 g/ha) in blocknet rotenone samples (Guillory 1978).

Feeding

Warmouth has a relatively large mouth for a sunfish and consumes a wide variety of prey. Studies have reported stomach contents consisting of zooplankton, amphipods, isopods, insects (primarily aquatic), mysid shrimp, decapod crustaceans, and fish. Additionally, traces of plant material have been found.

Chable (1947) reported on the stomach contents of 55 warmouth (81-203 mm fork length [FL]) from lakes and 81 warmouth (53-205 mm FL) from streams in northern Peninsular Florida. A high percentage of stomachs were empty (i.e., 89.1% in lakes and 77.8% in streams), resulting in a small sample of stomachs (i.e., 6 from lakes and 18 from streams). Grass shrimp (67%), crayfish (50%), fish (50%), and insects (33%) in lake warmouths and grass shrimp (33%), insects (28%), fish (22%), crayfish (17%), and crabs (17%) in stream warmouths were the most frequently occurring food items.

McLane (1955) examined 111 warmouth ranging in size from 18-219 mm SL from the St. Johns River, Florida. Warmouth up to 75 mm SL ate small crustaceans (mostly copepods) and insect larvae. Individuals   76 mm SL consumed insect larvae, decapod crustaceans, and fish. Predominant dietary items by number (30 items) were copepods, fish eggs, mysid shrimp, chironomids, odonate nymphs, grass shrimp, and amphipods. Fish prey included fundulids, poeciliids, pygmy sunfishes, centrarchids, and gobies.

Guillory (1978) described the stomach contents of 280 warmouth from Lake Conway, Florida. He found cladocerans, ostracods, amphipods, decapod crustaceans (i.e., grass shrimp and crayfish), aquatic insects (i.e., odonate nymphs, coleopterans, corixids, dipteran larvae, and tricopterans), oligochaetes, snails, fish, fish eggs, and vegetation fragments. Warmouth < 76 mm TL primarily ate aquatic insects (68.8%), especially chironomids and trichoperan larvae, but included a variety of prey in their diet. For fish 76-125 mm TL, aquatic insects (54.4%) again dominated the diet (i.e., chironomids, trichopteran larvae, and odonate nymphs), with fish (16.1%) as the second most numerous prey category (i.e., bluefin killifish *Lucania goodei*, eastern mosquitofish, and bluespotted sunfish *Enneacanthus gloriosus*). Crayfish (34.9%) dominated the diet of warmouth 126-175 mm TL, followed by aquatic insects (21%; i.e., odonate nymphs and dipteran larvae) and fish (20.9%; i.e., brown bullhead *Ameiurus nebulosus* and bluespotted sunfish). The largest size class (176-225 mm TL) ate mainly crayfish (73.3%) and amphipods (13.4%). The author concluded that smaller warmouths feed more frequently and on smaller organisms whereas larger warmouth feed less frequently on larger prey.

In a study in southeast Georgia in the Okefenokee Swamp and adjacent upper Suwannee River, Germann and co-workers (1975) reported a varied predatory diet for warmouths. The authors divided their specimens into four, 50-mm TL size classes (25-76 mm, 77-127 mm, 128-

178 mm, and 179-229 mm). Fish from the river and swamp were reported separately. They examined 348 warmouths ranging from 27-228 mm TL from the Suwannee River. The percentage of stomachs with food was about 50% for all size classes except for the 77-127 mm size class (i.e., 60%). By occurrence, insect larvae (79%; primarily odonate nymphs and chironomids) were dominant, followed by fish (14%; eastern mosquitofish *Gambusia holbrooki*, pirate perch *Aphredoderus sayanus,* pygmy sunfish *Elassoma* sp., and swamp darter *Etheostoma fusiforme*), in the smallest size class. Warmouth 77-127 mm TL mainly consumed insects (73%; odonates, coleopterans, and trichopterans), decapod crustaceans (31%; grass shrimp and crayfish), and fish (17%; pirate perch). Crustaceans (43%; particularly crayfish) were the most common food items for warmouth 128-178 mm TL, followed by insects (35%; odonate nymphs) and fish (35%; pickerel *Esox* sp., bullhead catfish *Ameiurus* sp., and bluespotted sunfish *Enneacanthus gloriosus*). Crayfish (74%) again dominated the diet of warmouths 179-229 mm TL, followed by insects (29%; odonate nymphs) and fish (14%; eastern mosquitofish, pygmy sunfish, and bluespotted sunfish). A total of 104 warmouth from the Okefenokee Swamp were examined and 63% contained food items. By occurrence, insects (82%) dominated the diet of warmouths 25-76 mm TL—grass shrimp also were eaten (27%). Similarly, insects (mainly odonate nymphs and coleopterans) were the principle food for warmouths of 77-127 mm (64%) and 128-178 mm TL (59%). Decapod crustaceans were found in about 45% of warmouths from both size groups. Fish (eastern mosquitofish, bluespotted sunfish, and unidentified *Lepomis* spp.) increased in frequency from 9% in the 77-127 mm TL group to 27% in the 128-178 mm TL group. Crayfish were the main food items for the largest size class of warmouths (179-229 mm TL). Insects (45%), primarily odonate nymphs, were second in importance for this group, followed by fish (14%). Fish eaten by warmouths of this size group were bluespotted sunfish

and *Lepomis* spp. The results show an overall similarity in diet of river and swamp warmouth. Nevertheless, swamp warmouths relied more on crustaceans and less on fish than did river warmouth.

Hunt (1953) examined 25 warmouths collected in Tamiami Canal, Miami-Dade County, Florida. Of the 12 (48%) with stomach contents, food items included odonate and mayfly nymphs, dipteran larvae, amphipods, ostracods, and grass shrimp.

In his detailed life history study of warmouth in two Illinois lakes, Larimore (1957) examined 391 specimens from Park Pond and 356 specimens from Venard Lake. Food items listed as abundant were a snail *Physa* sp., cladocerans, copepods, ostracods, amphipods, isopods, decapods, ephemeropterans, odonates, coleopterans, trichopterans, and chironomids. Common food items were clams, snails, hemipterans (corixids, gerrids, and veliids), coleopterans, and fish (bluegills, warmouth, and largemouth bass). A seasonal diet analysis was presented for both lakes. Fish and crayfish were important prey volumetrically in Park Pond in all seasons, but fish were unimportant and crayfish were only important during summer and fall in Vernard Lake. Insects made up a significant percentage of the diet during all seasons in both lakes in the frequency of occurrence and volumetric data. Based on 21 warmouth, Savitz (1981) reported consumption of aquatic insects (72% by number), fish (17%), crayfish, amphipods, and molluscs in a northern Illinois lake.

Limited information is available concerning the diet of warmouths in brackish water environments. Desselle and others (1978) examined the stomach contents of 13 warmouths from the Lake Pontchartrain estuary, Louisiana, and found amphipods (*Gammarus* sp.), blue crabs, grass shrimps (mostly *Palaemonetes* sp.), fish (bluegill and naked goby *Gobiosoma bosc*), plant material, and organic detritus.

Relatively little is known about the feeding behavior of warmouth. Etnier and Starnes (1993) noted that diet studies suggest a bottom-oriented feeding behavior in warmouth because terrestrial insects are lacking from stomach contents and no other evidence of surface feeding is published. Conversely, Larimore (1957) previously mentioned surface feeding behavior of warmouth in laboratory studies and the use of surface lures (e.g., poppers) for warmouth angling. Although Larimore (1957) only discussed suction feeding, the large mouth of warmouths suggests some measure of ram feeding as well (cf. Norton and Brainerd 1993). Hunt (1960) reported that warmouth would actively ("avidly") feed on prey fish in experimental aquaria.

Hunt (1960) investigated digestion rates of warmouth of 153-179 mm TL and 72-113 g in weight. He found that warmouth digested between 0.053 and 0.127% of their own body weight in food per hour. Digestion was evident in consumed prey after 3.5 h and was complete by 24-28 h post-feeding. These results were obtained using an average force-fed meal size of 2.69% of warmouth body weight (eastern mosquitofish prey) and temperatures of 23-26° C. This rate was about 1.6 times greater than Florida gar *Lepisosteus platyrhincus*, but about 1.5 times less than largemouth bass, under identical laboratory conditions. Similarly, voluntary feeding trials revealed that warmouth take about 24 days to consume their own body weight in prey fish in contrast to about 15 days for largemouth bass. Warmouth in the voluntary feeding trials ate additional prey while still digesting previous prey (i.e., had overlapping meals).

A single study investigated diets of warmouth during high and low water periods in a river. Germann and others (1975) reported that warmouths in the Suwannee River, Georgia, consumed more decapod crustaceans and fewer insects during high water periods than during low water periods (Table 14).

Table 14. Frequency of occurrence of prey categories in stomachs of warmouths collected during high water and low water periods from the upper Suwannee River, Georgia. The high water period was December to May and low water was June to November. Frequency is the number of warmouths containing the food type; percent is frequency divided by N and multiplied by 100; N is the number of fish examined that contained food items. Because an individual warmouth may contain more than one type of food, the values for frequency do not add up to N and the percentages do not add up to 100%. Data obtained from Germann et al. (1975).

	High Water		Low Water	
Food Category	Frequency	Percent (%)	Frequency	Percent (%)
Insects	5	17	111	76
Crustaceans	19	66	29	20
Fish	8	28	24	16
	N = 29		N = 147	

The vulnerability of warmouth to gape-limited predators (e.g., largemouth bass) is related to its ratio of body depth to length (i.e., BD = 0.38 TL – 5.85) (Hill 1998; Hill et al. In press).

Nesting and spawning

Warmouth spawn at least from March through September in Florida based on observations of nests and newly hatched fry (McLane 1955). Moreover, ripe individuals have been collected as late as October (males) and November (females) in the St. Johns River, Florida (McLane 1955). In the Suwannee River and Okefenokee Swamp, Georgia, warmouth spawning began in April, peaked in May, and ended by late July or August (Germann et al. 1975). Warmouth spawned from April to August, with a peak in late April to May, in Lake Conway, Florida, at temperatures of 15-32°C (Guillory 1978). In Illinois, warmouth spawn from May to August, peaking in June (Larimore 1957).

Spawning behavior has been described for warmouth in Biven’s Arm, a lake within the St. Johns River system, Alachua County, Florida (Carr 1939), and for warmouth in laboratory aquaria (with supporting observations from lakes in Illinois) (Larimore 1957). Breder (1936) provided a general description of the spawning behavior of sunfishes. Like other centrarchids, warmouth males construct the nest and guard the eggs and fry.

Carr (1939) observed about 100 nests along a 50-m stretch of shoreline of Biven's Arm from 14 March to 1 April. Water temperatures ranged from 13-22°C. The nests were in an area of open water, scattered clumps of vegetation with a substrate of sand covered by 2.5-12.5 cm of fine organic silt. He suggested that other areas of the lake were not suitable for spawning because of deeper silt. Nests were 15-20 cm in diameter, in 5-25 cm of depth, and close to shore. Many nests were adjacent to some form of cover (e.g., root, vegetation). A single bed was found in a dense bed of vegetation where the male had created a spherical chamber about 11.5 cm in diameter. McLane (1955) likewise observed warmouth nesting in vegetation above the bottom in the St. Johns River, Florida. Carr (1939) observed that beds were more spread out in open areas (i.e., 60-90 cm apart) than in cover (i.e., as close as 7.5-10 cm). Males courted females soon after completing nest construction and eggs were generally found in the nest within 12 hours (but up to 36 hours). Males seldom left the nest, even at night, except when disturbed by human presence or to chase away egg predators. Although feeding during this time is apparently limited, suitable prey in the vicinity of the nest were eaten.

Larimore (1957) provided a detailed description of the reproductive cycle and spawning behavior of warmouth in Illinois. Larger fish (i.e., > 137 mm TL) attained spawning condition earlier and spawned over a longer period than did fish of 89-137 mm TL. Many of the smaller fish failed to engage in reproductive activity whereas all of the large fish spawned. Additionally, males matured earlier in the season and were reproductively active longer than were females. Spawning began at a water temperature of about 21°C. Larimore (1957) concluded that females spawn over an indefinite period of time and implied that warmouth may spawn multiple times per year. The latter implication agreed with observations reported by Toole (1946, cited in Larimore 1957) in Texas of multiple spawnings within a year by a single warmouth pair. Also, Guillory (1978) reported several stages of ova within warmouth in Florida. Warmouth nests in Illinois were not constructed on clean sand, but otherwise were found on a variety of substrate types (e.g., rubble with silt, sand covered by silt). Nests were invariably closely associated with cover of some type (e.g., tree roots, rocks, vegetation), but were of varying distance from shore. Nest depths ranged from 15-152 cm, but most were found in depths of 60-75 cm. However, the author commented that deeper nests were more difficult to locate and hence may have been more common than estimated. In contrast to earlier investigators, including Carr (1939), Larimore (1957) suggested that apparent colonial nesting was likely due to limited nesting habitat based on observations of a scattered distribution of nests in Vernard Lake. Nests were usually 10-20 cm in diameter. Larimore described typical sunfish nest construction and courtship behavior for warmouth based on laboratory observations. Interestingly, he observed a single, isolated female construct a small nest in a laboratory tank.

Larimore (1957) categorized warmouth ova into seven size classes, with mature or nearly mature ova being   0.80 mm (i.e., Stages V, VI, and VII). Ova of multiple size classes were regularly present within a single ovary. The total number of ova (i.e., all size classes) was a highly correlated function of total length; nevertheless, the relationships differed between the two study lakes (see Figure 10 in Larimore 1957). Estimated total ova numbers for warmouth in Illinois ranged from 4,500 for a female of 89 mm TL to 63, 200 for a female of 137 mm TL (Larimore 1957). In the Suwannee River and Okefenokee Swamp of southern Georgia, estimates of mature or nearly mature ova ranged from 3,030 to 22,850 in 43 females in the 150-240 mm TL groups (Germann et al. 1975). In Lake Conway, Florida, fecundity ranged from 304 to 8504 mature ova per fish (mean = 1981) (Guillory 1978). In this study, the relation of fecundity and female size was $\text{Log}_{10}\text{F} = 0.1619 + 1.418\text{Log}_{10}\text{SL}$, where F is fecundity; however, this equation only explained 13.7% of the variability in egg numbers. Although the numbers for Florida and Georgia are considerably smaller than those reported for Illinois, the Illinois estimates included all ova sizes, not just mature ova. Warmouth eggs averaged 1.01 ± 0.087 mm (Merriner 1971) and ranged from 1.0-1.1 mm (Carr 1939), 0.95-1.03 mm (Larimore 1957), and 0.81-1.19 mm (Merriner 1971). Eggs hatch in 25-45 hours, depending on temperature (Carr 1939). Larimore (1957) reported a mean time to hatch of 34.5 hours for a temperature range of 25.0-26.4°C. Sudden drops in temperature during development can lead to fungus growth and mortality of eggs (Larimore 1957).

Larimore (1957) provided a detailed description of larval development of warmouth under laboratory conditions at temperatures of 24-25°C, with supporting observations from Illinois lakes. The yolk-sac was exhausted by the forth day post-hatch and larvae began active swimming by the fifth day.

Age and growth

Fairly substantial data are available describing age and growth in warmouth. Much of this literature is summarized in Carlander (1977). Primary references include Larimore (1957) for Illinois and Germann and co-authors (1975) for southern Georgia.

Considerable information is known about the relations of length and weight in warmouth (Table 15). Hoyer and Canfield (1994) reported mean weights of Florida lake warmouths of seven 40-mm size classes ranging from 40mm to the 280 mm TL group (Table 16). Nevertheless, warmouth was not included in the summary of fish standard weight equations in

Anderson and Neumann (1996). However, Fulton's condition factors (C or K) have been reported in the literature (e.g., Carlander 1977). Condition in warmouths increases with increasing fish size (Larimore 1957; Germann et al. 1975; Guillory 1978). For example, average K for warmouth of 40-49 mm TL was 1.93, of 140-149 mm was 2.25, and of 240-249 mm was 2.77 (Germann et al. 1975). Larimore (1957) also noted seasonal differences in condition and attributed them to the consumption of food types—low C in winter corresponded to a more limited diet of dragonfly nymphs and fish whereas high C during summer corresponded with increased consumption of other insect larvae and crayfish. This is similar to observations by Germann and co-authors (1975) where south Georgia warmouth had highest condition in spring and lowest in late fall. There were no consistent differences between condition factors of males and females (Larimore 1957). Condition factor values of K from 1.29 to 2.20 were reported for Florida (Guillory 1978), 1.39 to 3.06 for Georgia (German et al. 1975) and 1.74 to 2.36 for Alabama (Swingle 1965 cited in Carlander 1977).

Table 15. Relations of length and weight for warmouth. The TL ranges for equations from Germann et al. (1975) were estimated from a figure. Conversion of SL to TL is TL = 1.24SL (Larimore 1957).

Location	TL Range	N	Equation	Reference
Alabama	51-215	3,860	$\log_{10}WT = -4.841 + 3.08\log_{10}TL$	Swingle 1965
Florida	40-100	250	$\log_{10}WT = -4.661 + 2.953\log_{10}TL$	Guillory 1978
Florida	101-225	225	$\log_{10}WT = -5.567 + 3.400\log_{10}TL$	Guillory 1978
Georgia	85-225	443	$\log_{10}WT = -5.4996 + 3.3726\log_{10}TL$	Germann et al. 1975
Georgia	82-220	184	$\log_{10}WT = -5.2395 + 3.2736\log_{10}TL$	Germann et al. 1975
Illinois	81-208	866	$\log_{10}WT = -4.499 + 3.049\log_{10}SL$	Larimore 1957

The relations of total length and standard length for warmouth in southern Florida are TL = 1.21 SL + 3.89 and SL = 0.83 TL – 3.11 (valid for specimens 18-190 mm TL) (Hill 1998). Fishery length categories for warmouth are 80 TL mm (Stock), 150 mm (Quality), 200 mm (Preferred), 250 (Memorable), and 300 (Trophy) (Gabelhouse 1984). These category values are used to estimate fishery statistics such as proportional stock density (PSD) and relative stock density (RSD) (Anderson and Neumann 1996).

Table 16. Mean weight for warmouths from Florida lakes, by total length size group. Data from Hoyer and Canfield (1994).

Size Group (mm)	Mean Weight (g)	Standard Deviation	N
40	0.6	0.2	11208
80	3	1	13539
120	18	4	3209
160	48	10	870
200	102	12	229
240	191	29	28
280	320	*	1

Although not commonly used in southern parts of the USA, the scale method to determine age in warmouth has been validated in Illinois (Larimore 1957) and Georgia (Germann et al. 1975). Larimore (1957) provided an illustration of a warmouth scale to assist in aging. In Georgia, annulus formation occurred from March through April and the scales of about 85% of sampled warmouths could be read (Germann et al. 1975). Nevertheless, the scale method should be validated in Florida systems prior to its use in the state (see Beamish and McFarlane 1983). For example, Guillory (1978) attempted to use scales to age warmouth from Lake Conway in central Florida. He reported that defined annuli were not discernible and concluded that validation was not possible. Indeed, most age determinations for centrarchids in Florida are conducted using otoliths (e.g., Mantini et al. 1992).

Mean total length at age for warmouth from the Okefenokee Swamp, Georgia, for ages 1 through 7 were 54, 90, 127, 154, 179, 179, and 190 mm (Germann et al. 1975). Mean total length at age for Illinois warmouth for ages 1 through 8 were 42, 86, 125, 163, 189, 204, 215, and 217 mm (Larimore 1957). In the same study, mean weights at age for ages 1 through 8 were 1.8, 12, 40, 91, 153, 196, 231, and 239 g. Carlander (1977) summarized a number of additional studies that included length at age data for warmouth. Maximum age reported is age-8 (Larimore 1957; Carlander 1977).

Dispersal and migration

Very little is known about dispersal and migration of warmouth. This species is known from floodplain habitats and long-hydroperiod wetlands, suggesting some degree of lateral migration and dispersal (see Dollar sunfish, above). Pezold (1998) reported warmouth from an artificial, permanent, and isolated wetland in a Louisiana floodplain.

Free-swimming fry tended to disperse into surrounding vegetation or other cover rather than remain in schools as is common with some other centrarchids (Larimore 1957).

Movements of warmouth have been studied using mark-and-recapture techniques over a three-year period in an eastern Tennessee stream (Gatz and Adams 1994). Of 123 warmouths tagged, 20 (16.3%) were recaptured at least once. Warmouth were more sedentary than bluegill or largemouth bass, and less sedentary than redbreast sunfish. The maximum recapture distance was 300 m and 65% of movements were upstream.

Effects of water level fluctuations on warmouth

There is very little species-specific information on the effects of water level fluctuations on warmouth. It may be inferred that changes will have effects mimicking those seen in largemouth bass and other sunfish. Given the frequent association of warmouth and floodplains and small wetlands, periodic high water levels should aid in warmouth dispersal and re-colonization. Hypothetically, alterations in hydrology that reduce floodplain-stream connectivity or reduce the abundance of aquatic macrophytes will negatively affect warmouth.

Summary of Effects of Water Level Fluctuations and Water Withdrawals on Centrarchid Populations

It is clear that hydrology has a considerable influence on centrarchid populations. Generally, fluctuations in flow or water levels enhance centrarchid populations over the long-term. Increased water levels in streams, lakes, or wetlands increases fish habitat, allows access to increased food resources, and provides additional nutrients to fuel primary production (Hill and Cichra 2002a). These factors generally lead to increases in centrarchid abundance, survival, and growth. Nevertheless, the timing and duration of hydrological events greatly influences direction and magnitude of their effects (Hill and Cichra 2002a). Lowered water levels, particularly events of long duration, can be detrimental to centrarchid populations. Extended or more frequent events can produce poor water quality, reduce the amount of available habitat, crowd individuals (potentially increasing predation risk and competition), decouple floodplains from streams, prevent fish dispersal to wetlands, and allow salinity intrusion into the lower courses of rivers.

Although there has been relatively little empirical evaluation, predictions of the effects of water withdrawals can be made based on well-founded theoretical principles (Hill and Cichra 2002a). For example, it is known that the effects of environmental variability, particularly in stream flow, can overwhelm biotic influences (e.g., predation and competition) and reduce the importance of habitat limitation in stream fish assemblages (Grossman et al. 1998). Water withdrawals usually will result in changes to system hydrology and therefore will likely cause changes in centrarchid populations. Furthermore, the magnitude of changes to centrarchid populations will be closely linked to the magnitude, duration, frequency, and timing of withdrawals, the hydrological characteristics of the affected system, and the life history of the fish and other organisms present within the system.

Logically, water withdrawals of greater magnitude, duration, and frequency will have greater effects. For many fish species, habitat models show that decreased stream flow directly diminishes available habitat (e.g., Orth and Maughan 1982). Hypothetically, centrarchid adults being large-bodied fishes (with some exceptions) may be more resilient to these effects than fry and juveniles, particularly if the withdrawals are of limited duration relative to the fish's generation time (i.e., the storage effect; Warner and Chesson 1985). There are likely species-specific threshold levels of habitat that correlate to varying degrees of effect (e.g., Orth and Maughan 1982; Zorn and Seelbach 1995). Withdrawals that are poorly-timed or too frequent may impact reproduction (e.g., by nest stranding), impair nursery habitat, deprive stream systems of floodplain-based nutrient subsidies, or degrade water quality. Each of these mechanisms should reduce abundance, survival, or growth of centrarchids over short- or long-term scales.

Water withdrawals can reduce the duration of high water events and therefore negatively affect centrarchid populations. High water levels must be maintained for sufficient time to obtain the benefits associated with high water (e.g., floodplain inundation). Water levels in inundated areas must be deep enough for nest construction and sustained throughout periods of courtship, spawning, and egg and yolk-sac larval development for inundated floodplains to be useful for centrarchid reproduction. For example, largemouth bass construct nests in water averaging 60-120 cm in depth, and require about four days for eggs to hatch and 5-8 days for larvae to leave the nest (Kramer and Smith 1960a; Chew 1974) (Table 17). Obviously, short duration inundation events will not promote significant reproduction and can in fact be detrimental if centrarchids attempt to nest but fail due to falling water levels. Inundated floodplains are frequently cited as important nursery habitat (e.g., Leitman et al. 1991 for the Apalachicola River floodplain). The nursery function requires an extended period of inundation to encompass larval development (e.g., weeks) (Table 17). Although the absolute importance of flooded nursery areas for larval development of centrarchids is not known, falling water levels may concentrate larvae, potentially increasing competition and vulnerability to predation. Rising water levels increase access to food resources for fish and promote primary production through nutrient inputs. These functions require sufficient time for fish to utilize the increased food resources and for flushing of nutrients and allochthonous materials into subsidized systems.

Table 17. Sequence and duration of largemouth bass spawning and development events. There can be multiple egg clutches resulting in considerable overlap in batches of eggs and yolk-sac larvae. Total time for nest construction to swim-up ranges from 9 to 15 days. Schooling of fry prior to dispersal ranges from 33 to 45 day post-swim-up. Water level decreases during this time, especially prior to swim-up, can be detrimental to largemouth bass reproductive success and recruitment. Data for other centrarchids were incomplete but suggested somewhat shorter durations than for largemouth bass.

Largemouth bass spawning and development (in days)				
Nest construction/Spawning	Time to egg hatch	Time to swim-up	Schooling fry guarded by male parent	Schooling fry after abandonment
1-3	3-4	5-8	7-14	26-31

Water withdrawals can likewise reduce the frequency of high water events. Decreased frequency can lead to negative changes in centrarchid populations. For example, less frequent high water can dramatically alter riverine, floodplain, and littoral habitats, often by influencing plant communities. Less frequent high waters decrease floodplain-river connectivity, thereby reducing allochthonous subsidies and increasing the isolation of floodplain wetlands. Isolated pools can be important fish habitats, but extended periods of isolation can lead to declines in food availability (i.e., increasing competition), greater losses to predation (including higher vulnerability to terrestrial and avian predators), lower species richness, and higher risk of desiccation. For systems where flooding is necessary to maintain system productivity, enhance habitat, or to provide for spawning or nursery functions, reduced frequency of high water events will have negative effects on centrarchid populations, potentially including highly variable growth, survival, recruitment, and population abundance. For long-lived species (e.g., largemouth bass), this effect may be lessened with the occurrence of periodically favorable conditions allowing for occasional strong cohorts. These cohorts then can carry the largemouth bass population through periods of poor recruitment (cf. Warner and Chesson 1985). For shorter-lived species (e.g., dollar sunfish), reduced frequency of favorable conditions for recruitment can lead to significant reductions in abundance and to local extirpations.

The hydrological characteristics of the aquatic system will influence the effect of water withdrawals on centrarchids. Except for isolated wetlands, lakes may be the least affected aquatic systems, depending on lake morphometry. Lakes with small littoral zones would probably experience larger effects than systems with more extensive littoral zones because the loss of portions of the littoral zone in the latter systems would not be as critical. Nevertheless, even on lakes with extensive littoral zones, major changes in hydrological regime such as decreased magnitude, duration, and frequency of high water levels will reduce centrarchid populations and potentially limit their socio-economic value through denial of physical access to the fishery (e.g., Orange Lake, Florida, during recent drought conditions; pers. obs.). Streams would be affected in relation to stream order, the relative importance of floodplain-stream connectivity to stream productivity, and the presence of flow-sensitive habitats and species. Shallow water habitats are more affected by alterations in flow regime than are deeper habitats (Travnichek and Maceina 1994). Smaller streams can support less withdrawal than larger streams. Streams that derive a significant proportion of productivity from inundation-mediated floodplain subsidy (as opposed to primarily instream- or allochthonous-derived productivity) should be negatively affected by water withdrawals that decouple stream-floodplain connectivity (e.g., Thorp and Delong 1994; Thorp et al. 1998). Although perhaps not as important for centrarchids, riffles and other shallow, flowing habitats are vulnerable to decreases in stream flow (Aadland 1993).

The life history of centrarchids, other fishes, and various prey taxa will influence how water withdrawals affect centrarchids. Based on their close association with stream systems, redbreast sunfish and spotted sunfish may be particularly affected by changes in stream flow. For example, abundance of these centrarchids in the Oklawaha River, Florida, was positively related to river stage in the prior year (Rogers and Allen 2004). Obviously, centrarchids that are dependent on floodplain wetlands (e.g., dollar sunfish) would be highly vulnerable to water withdrawals that reduce or eliminate periodic connectivity with stream systems due to effects of crowding, poor water quality, and potential desiccation. Changes to flow or fluctuating water levels during critical periods such as nesting can have profound implications for centrarchid populations. Such effects can be as drastic as eliminating entire year-classes. Effects of water withdrawals on centrarchids also could be indirect and mediated through effects of competitors, predators, or prey. Reduction in the abundance of competitors or predators could allow for increased abundance of centrarchids. However, changes that negatively influence populations of competitors and predators would likely negatively influence centrarchid populations as well and overwhelm any advantage conferred by release from these biotic constraints. For example, water withdrawals would more likely reduce than increase food resources and therefore negatively affect centrarchids.

Emphasis is often placed on the importance of relatively large changes in hydrology affecting fish populations; nevertheless, hydrological alterations of lesser magnitude also can negatively affect centrarchid populations. It is assumed that small shifts in hydrology will have minor impacts, but this has not been evaluated empirically. Hypothetically, cumulative effects of relatively minor water withdrawals could produce effects on centrarchid populations that mimic the effects of much larger alterations to hydrology. Such impacts should be dependent on biological and hydrological characteristics of the altered system. On the other hand, the stochastic nature of the hydrology of many Florida systems might mask any variation in centrarchid populations that result from slight alterations in hydrology, make the detection of such effects difficult, and ameliorate the potential long-term significance of these effects. Therefore, it may be difficult to establish thresholds for small changes over the range of natural variation in the hydrologic regime. Nevertheless, it is prudent to test the assumption that small changes yield small effects and to consider the potential influence of even relatively minor changes in system hydrology when setting MFL levels.

In summary, changes in hydrology due to water withdrawals, especially reductions in the magnitude, duration, and frequency of high water events, can lead to negative changes in centrarchid populations. Larger changes in hydrology should produce greater effects on centrarchid populations, but the potential impacts of lesser water withdrawals should not be overlooked. The effects of altered hydrology are dependent on the nature of the withdrawals, characteristics of the altered system, and the centrarchid species present in the system.

Management Implications and Future Research

Given the observed and theoretical effects of changes in hydrology on centrarchids, it is obvious that water flow or level manipulation can be an effective tool in fishery management. It is equally obvious that such important biotic and socio-economic resources (i.e., centrarchids) must be considered when determining allowable consumptive use of surface waters or ground waters strongly coupled to surface waters (i.e., when setting MFLs).

It is clear from the species accounts that there are considerable gaps in our basic understanding of centrarchid life history. This lack is particularly acute with respect to Florida environments. Climate and other abiotic and biotic factors contribute to Florida's uniqueness. For example, the use of scales for aging fish is a common practice in most of the USA. Nevertheless, due to climate, otoliths are the structures of choice in Florida. Therefore, focused research is needed for Florida populations of centrarchids to document basic life history, population dynamics, and ecology.

Even for relatively well-studied species, it is difficult to explicitly determine habitat suitability and sensitivity to changes in hydrology. Redbreast sunfish and warmouth have been the subjects of reports outlining habitat suitability models (McMahon et al. 1984; Aho et al. 1986). Nevertheless, numerous parameters were based on incomplete or inconclusive data, were biological intuition, or were inferred from related species. Similar efforts were lacking for largemouth bass, dollar sunfish, and spotted sunfish. Although the present review attempted to compile these types of basic information, no effort has been made to explicitly and quantitatively link the data with estimates of habitat quality.

Hill and Cichra (2001a) suggested the development of predictive models of fish population indices based on hydrological data. VanGenechten (1999), Rogers and Allen (2004), and Bonvechio and Allen (2005) have successfully developed such models for a few Florida systems. This effort should continue and expand to incorporate more systems and increase temporal coverage. Such an effort could provide practical dividends in the field of minimum flows and levels similar to what the large database of Florida lakes (e.g., Hoyer and Canfield 1994) has done for limnology.

What are glaringly lacking are estimates of quantitative effects of specific hydrological regimes on centrarchid populations. For example, the effect that specific water withdrawals will have on centrarchid populations is simply not known. Quantitative models are lacking and therefore reliance on conceptual models is necessary. As pointed out by Hill and Cichra (2002a) in an earlier review, there is a strong theoretical base for building predictive models, yet there has been relatively few empirical studies providing data documenting the magnitude of effects. Until additional research provides such quantitative data to build and test models, there is little hope of advancing beyond our present level of qualitative prediction.

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Appendix. Lake morphometry, water chemistry, and aquatic macrophyte variables for lakes (N = 60) in north and central Florida sampled by Hoyer and Canfield (1994).

Variables	Mean	Median	Minimum	Maximum	Standard Deviation
Surface area (ha)	406	55	2	12412	1752
Mean depth (m)	2.8	2.9	0.6	5.9	1.2
pH	7.0	7.6	4.3	9.7	1.6
Total alkalinity (mg/L as $CaCO_3$)	31.4	13.6	0.0	130.6	33.0
Specific conductance (µS/cm @ 25°C)	136	118	17	384	97
Color (Pt-Co units)	28	17	0	400	53
Total phosphorus (µg/L)	56	20	1	1043	148
Total nitrogen (µg/L)	924	694	82	3789	802
Total chlorophyll *a* (µg/L)	28	10	1	241	47
Secchi depth (m)	2.0	1.5	0.3	5.8	1.5
Percent area covered by macrophytes (%)	40	30	1	100	39