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A REVIEW OF THE POTENTIAL EFFECTS OF WATER LEVEL FLUCTUATION ON DIADROMOUS FISH POPULATIONS FOR MFL DETERMINATIONS

ST. JOHNS RIVER WATER MANAGEMENT DISTRICT

Final Report
For

A review of the potential effects of water level fluctuation on diadromous fish populations for MFL determinations

St. Johns River Water Management District
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A review of the potential effects of water level fluctuation on diadromous fish populations for MFL determinations

Executive Summary

This report summarizes information concerning the life histories of three diadromous fishes in the St. Johns River, Florida—American shad, hickory shad and American eel—that may be affected by changing water flows and levels, to support the establishment of appropriate minimum flows and levels (MFLs) for the St. Johns River system. Information regarding basic life history, population dynamics and habitat requirements for each species is included, as well as a discussion focused on how alteration of water velocity and depth in the St. Johns River, Florida, could affect the health of each population.

Minimum flows and levels (MFLs) were established to protect Florida's water resources, aquatic ecosystems, and fish and wildlife habitats from withdrawals that could prove "significantly harmful." Diadromous fishes are those that migrate between salt and freshwater habitats during specific periods of their life histories. The St. Johns River populations of American shad, hickory shad and American eel are affected by water flows and levels during their residences in the river, as well as when they are migrating into and out of the river system. Certain current velocities, temperatures and dissolved oxygen levels may be critical for survival, optimal growth and migratory behavior during one or more stages in the life history of each species examined.

For American shad, appropriate flow levels are essential for maintenance of a healthy and abundant population. In particular, current velocity appears to affect growth and survival of eggs and larvae. Flow rates within the St. Johns River, Florida, are at or below those known to contribute to high growth and survival rates of American shad larvae in the Connecticut River;

therefore, a reduction in current velocity may reduce survival or otherwise negatively impact the development of larval American shad in the St. Johns River. Flow also affects the timing of downstream migration of juvenile American shad. Maintenance of positive flow rates during their fall and winter migration period may be important for juveniles. In addition, water flows and depths that maintain adequate water temperatures and dissolved oxygen levels may be important for young American shad, especially during summer months when the young may experience peak temperatures and levels of dissolved oxygen that may approach their tolerance limit.

Comparatively little research has been conducted on the biology of hickory shad; therefore, the affects of altered current velocity and water depth on the population in the St. Johns River is somewhat unclear. Hickory shad may behave like American shad and require comparable flows and depths during periods of migration; however, migration by juvenile hickory shad has been observed to take place much earlier than that for juvenile American shad. The development of hickory shad eggs and larvae may be more dependent upon appropriate water depth than it is on water velocity, though this is not known for certain. Although specific flow and depth requirements for hickory shad eggs are unknown, flows low enough to significantly reduce dissolved oxygen levels may adversely affect the population. For both species of shad, dissolved oxygen levels of at least 5 mg/L are suggested for the proper development of eggs and larvae.

American eels are ecological generalists; however, they may be affected by flow rates during seasonal periods when the young are migrating up the St. Johns River and when the adults are migrating down river, on their way to their oceanic spawning grounds. Upstream migration of young American eels into river systems in northern Florida occurs from early January to

March. The exact timing of the spawning migration of American eels in the St. Johns River is not known. In the Cooper River, South Carolina, American eels conduct their migration during the fall. Most likely, the spawning migration takes place at a similar time of the year for American eels in the St. Johns River. Therefore, during these seasonal periods, flow rate in the St. Johns River, Florida, may be an important factor affecting movement and migration of American eels.

Further research needs to be conducted on American shad, hickory shad and American eel before the effects of water removal on their populations in the St. Johns River can be accurately understood or predicted. Removal of some amount of water may be acceptable during periods of high flow. Flow and water level reduction during low water periods may lead to significant declines in the populations of these three diadromous species in the St. Johns River.

Introduction

Minimum flows and levels (MFLs) were required to be established in Florida as a result of the 1972 Florida Water Resources Act to protect water resources and aquatic ecosystems from "significantly harmful" anthropogenic freshwater withdrawal (Wade and Tucker 1996). Minimum flows represent the least amount of water required to protect the resources of a specific aquatic system, or conversely, could be understood as the maximum extent to which flows in a system could be depleted or altered by human activities. The current MFL paradigm states that many aquatic organisms require certain "natural" hydrologic regimes and that magnitude, frequency, duration, timing, and rate of change are considered important components of those flow regimes (Neubauer et al. Unpublished Manuscript)

The authority to establish MFLs and to allocate freshwater resources in Florida is held by the five Florida Water Management Districts; among these is the St. Johns River Water Management District. Each Water Management District determines water use within its own jurisdiction (Section 373.042, Florida Statue). No statue dictates methods that must be used to establish MFLs; however, Water Management Districts are required to use the best available information and to consider the protection of water resources, water quality, natural flows and levels, recreation, navigation, fish and wildlife habitats, and the passage of fish, among other environmental values associated with the health of the system (Wade and Tucker 1996, Section 373.042, Florida Statute).

Many aquatic organisms are adapted to seasonal hydrologic regimes, rather than having one specific water flow requirement. Therefore, it is important to consider seasonal changes in water flows and levels when establishing an MFL, in order to insure that such populations remain healthy and abundant (Neubauer et al. Unpublished Manuscript). In addition, inflow changes can alter productivity in coastal systems (Livingston 1997; Livingston et al. 1997). For diadromous fish species, changes in flow rates, durations, and water levels can be very important for survival, growth, and reproduction within a river system. In addition, sufficient flow rates can be essential during migration periods (Clayton 1979; Bergeron et al. 1998; Vadas 2000; Hembre et al. 2001; Robards and Quinn 2002). Flow models have been used to predict the responses of diadromous fishes to changes in water levels and flows (Heggenes et al. 1996; Hatfield and Bruce 2000); however, no stream flow models have been completed for diadromous species of concern in the St. Johns River, Florida.

The St. Johns River is a northward flowing, tannin-stained river in Florida (Figure 1) with a diverse icthyofauna assemblage. Occupying an area of approximately 8,350 square miles, the St. Johns River is close to 315 miles long from the headwaters to the mouth. With a stream gradient of only 6.1 m, the river's current is slow and sometimes reversed by winds and tides (McLane 1955). A complex salinity pattern exists in this river system due to current reversals, at times to half the river's length, and a network of lakes and springs. As a result, the fish assemblage in the St. Johns River includes a mixture of freshwater, diadromous and marine species. Annually, a low water period usually occurs during the months of March to June and high water arises from October to December. Low water levels can be at or slightly below sea level (Moody 1963). Therefore, fish community structure varies by stretch of river and may also vary by season due to tidal and flow characteristics.

The purpose of this study was to organize, summarize and elucidate aspects of the life histories of three diadromous fishes—American shad, hickory shad and American eel—that may be affected by changing water flows, levels, frequencies and durations in the St. Johns River, Florida. These three species were selected because they are common in the St. Johns River and they represent both anadromous (i.e., fish that migrate from the sea into freshwater to spawn) and catadromous (i.e., fish that migrate from freshwater into the sea to spawn) life cycles. The life history, population dynamics and habitat requirements of each species in the St. Johns River, Florida, will be reviewed to characterize how alteration of water flows and levels in this river system may potentially affect the health of each population.

American shad, *Alosa sapidissima*

American shad is an anadromous clupeid native to the Atlantic coast of North America, from Florida to Newfoundland (Facey and Van Den Avyle 1986; Bentzen et al. 1993). The St. Johns River population of American shad is the southern most population of the species. At the turn of the nineteenth century, American shad supported one of the most valuable commercial fisheries in the United States with millions of pounds landed each year (Smith 1894; Walburg and Nichols 1967; McBride 2000). On the St. Johns River, a small gill net fishery for American shad began in the 1850's. This fishery increased greatly in size with the construction of railroad systems which enabled the fish to be transported up the Atlantic coast and sold earlier in the season than more northern populations could be harvested (Walburg 1960; McBride 2000). The introduction of the 'net ban' amendment to the Florida Constitution, effective July 1995, as well as other gear restrictions, severely reduced Florida's commercial landings of American shad. The recreational fishery for American shad has declined in recent decades but continues to persist on the St. Johns River, Florida (McBride 2000).

Spawning activity and habitat:

After feeding in the Bay of Fundy, Canada (Melvin et al. 1986), American shad migrate down the east coast of North America in the late winter and spring to spawn in their natal rivers when river temperatures range from 10 to 21 °C (Leggett and Whitney 1972; Facey and Van Den Avyle 1986; Melvin et al. 1986). Although straying may occur (Godwin 1968), populations of

American shad are presumed to be reproductively isolated and spawn following a latitudinal pattern, with fish native to southern rivers spawning earlier than those from more northern systems (Leggett and Whitney 1972). Repeat spawning (i.e., iteroparity) is observed for individuals in populations in rivers north of and including the Neuse River, North Carolina. In more southern rivers, American shad spawn only once and then die (i.e., semelparity) (Facey and Van Den Avyle 1986). Both olfactory and visual factors are thought to cue philopatry (i.e., the tendency of an individual to return to its home area or birthplace) (Dodson and Leggett 1974; Facey and Van Den Avyle 1986; Klauda et al. 1991). Flow rate has been observed to affect upstream migration. During periods of reversed or zero flow, American shad may terminate active "upstream" migration and begin meandering, holding station or migrating back downstream (Leggett 1976). Additionally, flow rate may affect the abundance of shad in a river. Annual flow in the Santee River, South Carolina, was reduced from 525 m^3/s to 63 m^3/s in 1941, but water was redirected in 1985, increasing the river's annual flow rate to 295 m^3/s, and a fish passageway was installed. These changes led to an increase in passage counts and commercial landings of American shad starting in the early 1990's, about one generation after the water re-diversion (Cooke and Leach 2003). Water temperature is thought to be the primary factor that triggers spawning, but photoperiod, current velocity and turbidity may also be influential (Klauda et al. 1991; Quinn and Adams 1996).

American shad broadcast spawn their eggs in water depths ranging from 1 to 10 m onto mostly sand, gravel, or mixed substrates when temperatures range from 8 to 26 °C (Limburg et al. 2003). Most spawning is thought to take place between sunset and midnight (Marcy 1972) and peak between 2100-0100 h (Ross et al. 1993) although, when rivers are turbid or highly colored, spawning may take place during all hours (Klauda et al. 1991). Eggs are demersal (i.e., located on the bottom), non-adhesive (Rulifson 1994) and require dissolved oxygen levels of at least 4 mg/L. Survival is greatest when eggs are spawned in water temperatures between 13 and 22 °C and in waters with dissolved oxygen levels above 5 mg/L (Koo 1977; Facey and Van Den Avyle 1986; Klauda et al. 1991; Leach and Houde 1999). Spawning usually occurs in areas with water velocities of 30.5 to 91.4 cm/s (Facey and Van Den Avyle 1986; Hightower and Sparks 2003). In the Delaware River, egg abundance has been associated with areas characterized by moderate to high current velocities and shallow depths (Ross et al. 1993), and in some Virginia streams, more eggs were found in locations with velocities between 61.0 and 88.4 cm/s than were found in areas with lower velocities (Massmann 1952).

In the St. Johns River, Florida, American shad are semelparous and usually spawn from late November to March between Lakes Monroe and Poinsett (Figure 1) (Walburg 1960; Williams and Bruger 1972; Glebe and Leggett 1981a). Analysis of data collected by Williams and Bruger (1972) indicated that American shad eggs collected by a 1 m plankton net set on the river bed were found in water temperatures that averaged 18.9 °C and ranged between 12.4 and 27.8 °C, in depths from 1.2 to 7.0 m. Water current in areas where American shad eggs were collected ranged from 7.62 to 60.7 cm/s and water current was positively correlated with the abundance of American shad eggs collected per hour (Spearman *Rho* = 0.314, *P* = 0.005) (Figure 2). During a low water year, a higher proportion of eggs/h were located between Lakes Harney and Poinsett, an area with higher flow rates, than between Lakes Monroe and Harney, an area with lower flow rates (Table 1; Figure 1). In contrast, a higher proportion of eggs/h were found between Lakes Monroe and Harney during a higher flow year (Figure 1) (Williams and Bruger 1972; Williams et al. 1975). Catch per unit effort (CPUE) of adult American shad collected by electrofishing in the St. Johns River, Florida, was greater for a spawning area characterized by relatively high flow located between Lakes Harney and Puzzle, as compared to a spawning location with lower flow between Lakes Monroe and Harney (McBride, Unpublished data) (Table 1; Figure 1). Williams and Bruger (1972) suggested that the area between Lakes Harney and Poinsett may be very important for American shad because the elevation gradient in the area insures suitable flow for the survival and development of eggs, even during periods of low flow.

Habitat requirements, behavior, and feeding of larvae, juveniles and adults:

The timing and location of spawning and the subsequent production of American shad eggs and larvae in the Connecticut River have been closely linked to water temperature and zooplankton abundance encountered by first-feeding larvae (Crecco and Savoy 1987). In this river, annual changes in year-class strength were observed to be inversely related to river flow and rainfall and positively related to temperature during the month when most larvae begin feeding (Crecco and Savoy 1987). Survival and growth of larvae were greatest when flows were low (50-100 m^3/s) and temperatures were high (10-14 °C) (Crecco and Savoy 1985; Crecco and Savoy 1987). Authors suggested that survival might decrease with increased flow because increased flow is correlated with increased turbidity, which may be harmful to larvae (Crecco et al. 1986).

Juvenile American shad reside in their natal river systems after hatching. While in rivers, the juveniles are opportunistic feeders, consuming dipteran larvae, as well as a variety of other insects and crustaceans (Davis and Cheek 1966; Domermuth and Reed 1980). The index of stomach fullness for juveniles was highest at sunset, followed by day, night and lastly sunrise (Grabe 1996). Often, juveniles are found in riverine areas with dissolved oxygen levels of 5.0 mg/L or above and current velocities ranging from 6 to 75 cm/s (Klauda et al. 1991). Juveniles usually migrate down river between 1400 and 2400 h in the fall, when temperatures drop to 15.5-19 °C and flow increases (Davis 1973; Stevens and Miller 1983; O'Leary and Kynard 1986). A decrease in water temperature, increase in flow rate, or a combination of both, is thought to cue this downstream migration (O'Leary and Kynard 1986; Klauda et al. 1991). However, evidence suggests that some juveniles migrate out of rivers during the summer, before the fall decrease in temperature occurs (Limburg 2001) and may use estuarine areas for overwintering (Hawkins 1980; Milstein 1981). Additionally, longer residence times for juveniles in fresh water may reduce cohort strength (Klauda et al. 1991; Limburg 2001).

In the St. Johns River, Florida, during a low flow year, some juveniles were found in close proximity to spawning grounds during their first summer, fall and winter, whereas during a higher flow year, all juveniles were found in lower areas of the river during the summer and fall. In addition, during that same low flow period, many juveniles were collected within the river through March, indicating that they did not migrate to estuarine areas during their first winter. In a higher flow year, no juveniles were found in any area of the river after January, despite considerable sampling effort. Authors suggested that the lack of current may have resulted in some juveniles being unable to find their ways downstream (Williams and Bruger 1972).

Adult American shad are thought to eat very little during the riverine portion of their spawning migration (Leggett 1972) and, therefore, lose weight during the spawning migration (Chittenden 1976; Glebe and Leggett 1981b; Leonard and McCormick 1999; Walter and Olney 2003). The reason for their fasting is unknown (Leggett 1972; Walter and Olney 2003).

Growth and mortality of larvae and juveniles:

In the Connecticut River, water temperatures between 15 and 20 °C, low and stable flow rates (<566.3 m^3/s), and high zooplankton densities result in high growth rates and low mortality of larval American shad (Crecco et al. 1983; Crecco and Savoy 1985; Leach and Houde 1999). Larval growth rates decreased as temperatures increased above 23 °C (Crecco and Savoy 1985). Growth and mortality rates did not vary with salinity (Limburg and Ross 1995). In this river system, larvae experienced more density-independent mortality than density-dependent mortality (Savoy and Crecco 1988). Juvenile mortality rates were low and independent of year-class strength, but positively correlated, in some cases, to recruitment levels of adult females 4-6 years later (Crecco et al. 1983). Juveniles reared in ambient temperatures (24-28 °C) died when temperatures were quickly raised to 32.5 °C (Moss 1970).

Aspects of life history requiring future study:

Additional information concerning population dynamics and abundance of this southern most population of American shad in relation to environmental conditions would be of interest. In particular, research examining the abundance of eggs, young and adults during different environmental and hydrologic conditions, especially during periods when flow rates are highly variable or reversed or when depths in spawning areas, like that between Lakes Harney and Poinsett, are greatly variable or shallow, would be useful in understanding how alterations in water flows and levels may affect this population.

Hickory shad, *Alosa mediocris*

Compared to American shad, far less research has been conducted concerning the life history of hickory shad. Hickory shad are anadromous (Mansueti 1962) and spawn along the east coast of North America, from Maryland south to Florida (Rulifson 1994). Occasionally, hickory shad are caught off the coast of southern New England states, suggesting that they may conduct a migration similar to that of American shad, but this has not been confirmed (Richkus and DiNardo 1984). As for American shad, hickory shad in the St. Johns River are spawning in the most southern portion of their range. Hickory shad are considered “inferior in flavor” to American shad (Hildebrand 1963), but are fished recreationally in some systems (Pate 1972). Hickory shad are generally less abundant in most rivers than are American shad (Godwin 1968) and are often misidentified and mixed with catch of American shad, so their harvest may often be underestimated (Richkus and DiNardo 1984; Klauda et al. 1991).

Spawning activity and habitat:

In systems from Virginia south to Florida, hickory shad are the first of the *Alosa* species to enter freshwater in the winter to spawn (Adams 1970; Sholar 1977; Williams et al. 1975). Spawning takes place in areas with dissolved oxygen levels between 5 and 10 mg/L (Hawkins 1980). Hickory shad eggs have been found in the main channels of rivers, but are more often collected in tributaries and lakes (Godwin and Adams 1969; Street 1970; Pate 1972; Davis 1973; Marshall 1976; Klauda et al. 1991). Areas where eggs are found are often characterized as deep and dark with slow currents (Street 1970; Hawkins 1980). The eggs of hickory shad are slightly adhesive, semi-demersal, and only buoyant in flowing water (Mansueti 1962). Eggs have been found in areas with temperatures ranging from 9.5 to 20.6 °C (Pate 1972; Marshall 1976; Hawkins 1980), but most eggs have been collected from temperatures of 16.7 to 18.9 °C (Pate 1972). After spawning, hickory shad return to the ocean, where their movements are largely unknown (Klauda et al. 1991).

Hickory shad migrate into the St. Johns River, Florida, to spawn from November to March (McLane 1955; Williams et al. 1975; McBride Unpublished data). Unlike American shad, freshwater marks on scales indicate that hickory shad in the St. Johns River are iteroparous. In this population, spawning begins at age two or three and continues each year until a maximum age of seven (McBride Unpublished data). No hickory shad eggs have been located in the St. Johns River; therefore, their spawning locations in that system are still unknown (Williams et al. 1975). In the St. Johns River, hickory shad have been found more often in deeper areas (1.2-3.4 m) as compared to more shallow areas (0-1.2 m), but their abundance has been negatively correlated with temperature and water level (Moody 1961).

Habitat requirements, growth, behavior, and feeding of larvae, juveniles and adults:

Juvenile hickory shad are not often found in areas with juveniles of other *Alosa* species (Mansueti 1962), and their nursery habitats are thought to be in estuarine areas outside their natal river systems (Godwin and Adams 1969; Adams 1970; Street 1970; Pate 1972). In the Altamaha River system, Georgia, Adams (1970) captured only 38 juvenile hickory shad from 551 hauls seines pulled from July to November within the Altamaha River. However, Adams (1970) collected 1067 juveniles from 66 trawl hauls conducted during the same months in Altamaha Sound and offshore areas, suggesting that juvenile hickory shad migrate to estuarine and offshore areas sooner in the season than do American shad. Also, freshwater marks on scales indicate that very little growth occurs in freshwater; hence, juvenile hickory shad are thought to leave rivers very soon after metamorphosis (Street and Adams 1969). Juvenile hickory shad are more often found in areas with higher current, as compared to juvenile American shad (Street 1970; Marshall 1976). Very little is known about the growth and mortality rates of juveniles, but it appears that growth rates of hickory shad are higher than those of American shad (Street 1970).

Adult hickory shad are picivorous (i.e., fish-eating), and they eat while in the St. Johns River, Florida. Common food items consumed by adult hickory shad in this system are bay anchovy *Anchoa mitchilli*, threadfin shad *Dorosoma petenense*, and inland silverside *Menidia beryllina*, as well as other antherinids and clupeids (McLane 1955; Williams et al. 1975).

Aspects of life history requiring future study:

Very little research on hickory shad has been conducted in any river system. Information concerning basic life history, behavior, and population dynamics of larvae, juveniles and adults would contribute considerably to our understanding of this poorly studied species. Specifically, data relating to adult abundance, location and characteristics of spawning and nursery habitats, as well as population dynamics of juveniles in the St. Johns River and other systems would improve our understanding of this species and how changing water depths and flow levels may impact the health of the St. Johns River population.

American eel, *Anguilla rostrata*

American eels are distributed in coastal river systems of the western Atlantic Ocean from the southern tip of Greenland to the northern portion of South America and in rivers along the Gulf of Mexico coast from Florida to Mexico (Williams and Koehn 1984; Van Den Avyle 1984). No genetic divergence was found among fish collected from Maine to Louisiana, suggesting that this species is truly panmictic (Avise et al. 1986). Presently, American eel support important commercial fisheries and are harvested from rivers, estuaries and the ocean throughout their geographic range. American eels are caught and can be sold in either foreign or domestic markets during most of their life history stages (American Eel Plan Development Team 2000). Harvest of American eels, however, has decreased since its peak in the 1970's (American Eel Plan Development Team 2000; Munger et al. 2002) and since 1991, Florida's commercial landings of America eel have been well below 1% coast wide (Munger et al. 2002; Crumpton and Johnson 2003). Few recreational anglers specifically target American eel, yet eels are used recreationally as bait for larger game fish in some areas (Munger et al. 2002).

<u>Spawning migration and river entrance:</u>

Unlike American and hickory shad, American eels are catadromous. Eels spawn at sea, but most individuals spend the majority of their lives in rivers, estuaries, and lakes (Van Den Avyle 1984). Catadromy in *Anguilla anguilla* and *A. japonica* may be facultative, with some individuals exhibiting a completely marine life history pattern; however, this has not been confirmed specifically for American eels (Tsukamoto et al. 1998). When American eels mature, they migrate from river systems all along their range to meet in the Sargasso Sea to spawn during only one season before dying (Kleckner and McCleave 1985; Richkus and DiNardo 1984). This downstream migration may take place after river temperatures drop below 17-20 °C (Haro 1991), usually between sunset and midnight (Hain 1975), and often after heavy rains (Winn et al. 1975). In freshwater tank experiments, migrating American eels preferred a downstream current to an upstream current or no current (Hain 1975). The peak spawning time for American eels is thought to take place in February in areas of the Sargasso Sea where water temperatures approximate 25 °C (Kleckner et al. 1983; Kleckner and McCleave 1985).

After hatching from March to October (Wang and Tzeng 2000), larval leptocephalus stage eels are carried by currents towards the east coast of North America. Later, individuals undergo metamorphosis and become glass eels. At this stage, eels actively migrate towards freshwater areas. After larval metamorphosis is complete, the eels, now called elvers, arrive in estuaries (Van Den Avyle 1984). Young eels usually arrive in these brackish water inshore areas in the spring, during the year after they were spawned in the Sargasso Sea (Sorensen 1986; Castonguay et al. 1994).

Elvers may wait in estuarine areas for a short period until conditions are favorable (water temperature and discharge rate) for upstream migration (Jessop 1998). In tank experiments, elvers showed preference for fresh compared to salt water. In addition, most elvers preferred water from the river where they were collected to water from other rivers or water filtered through ‘active’ charcoal, well water, tap water, or distilled water (Miles 1968; Sorensen 1986). Natural river water is thought to contain organic attractants, which serve as orientation cues for young eels (Sorensen 1986). Elvers begin migrating up river when water temperatures reach 10-12 °C (Jessop 2003), and migration continues as river temperatures increase to 19 °C (Sorensen and Bianchini 1986). For European eels, this upstream migration often occurs when sea and river temperatures are similar (difference not exceeding 3-4 °C) (Gandolfi et al. 1984). Increased river temperature and tidal height and reduced river flow rate may enhance upstream migration of elvers (Martin 1995; Jessop 2003), although increased flow rate and rainfall prior to accent may help initiate upstream migration (Smith and Saunders 1955). Elvers appear to maintain a constant upstream migration, regardless of current velocity (Barbin and Krueger 1994).

Very little research or monitoring of American eels has been completed in river systems in Florida, but results suggest that young eels may respond to specific flow rates. At the Guana River dam, St. Augustine, Florida (Figure 1), most glass eels entered from early January to early March when temperatures ranged from 13 to15 °C. Catch rates of elvers were highest when temperatures ranged from 10 to 13 °C. Young eels were captured in the brackish water during a period when water flow was low, often a few days after a period when water releases were high (Figure 3). The highest catch rates occurred when flows were less than 0.1 m/s, but a few eels were captured when flows exceeded 1.5 m/s (Crumpton and Johnson 2003).

Habitat requirements, behavior, and feeding of juveniles and adults in rivers:

American eels are ecological generalists. As immature or 'yellow' eels, they remain in rivers and coastal systems for anywhere from 5 to 20 years before returning to the ocean to spawn (Haro et al. 2000). This species exists in incredibly diverse habitats from small, clear, unproductive streams to large, turbid, productive rivers. In addition, American eels have been located in black water swamps, estuaries, lakes, subterranean springs and caves (Helfman and Bozeman 1984; Helfman et al. 1987). Many immature eels migrate periodically between riverine and estuarine habitats within a coastal system (Jessop 2003). American eels are also dietary generalists, consuming both living and recently dead prey (Helfman et al. 1987). Examination of stomach contents revealed that eels consume aquatic vertebrates and aquatic and terrestrial invertebrates, with aquatic invertebrates being the most common prey for small eels, and fish and crayfish for larger eels (Godfrey 1957; Ogden 1970; Wenner and Musick 1975;

Lookabaugh and Angermeier 1992). In areas influenced by tides, yellow eels usually moved either upstream or closer to shore during high tides, possibly to move into areas with higher water temperatures (Dutil et al. 1988) or increased abundance of prey (Helfman et al. 1983). In addition, eel movement is greater at night than during the day and peaks between 2100 and 2300 h (Edel 1976; Dutil et al. 1989). Eels are most often found in temperatures between 13 and 27 °C, salinities below 12 ppt, depths of 1 to 10 m, and dissolved oxygen levels between 5 and 9 mg/L (LaBar and Facey 1983; Dutil et al. 1988; Geer 2003). At temperatures below 8 °C, American eels become inactive, metabolic needs are reduced, and feeding is diminished or ceased (Walsh et al. 1983).

There is debate as to whether sex determination in American eels is genetically determined, environmentally determined, or a combination of both (Helfman et al. 1987; Krueger and Oliveira 1999). High population density or high recruitment may result in late differentiation and a lower proportion of females (Holmgren and Mosegaard 1996; Krueger and Oliveira 1999). In European eels, higher ambient temperatures produced a higher frequency of females (Holmgren 1996). Growth rates in American eels may impact future sex, with those achieving faster growth rates earlier in life more likely differentiating into females (Oliveira and McCleave 2002).

Growth and mortality of larvae and juveniles:

Most spawning occurs in February and the leptocephali (i.e. the slender transparent larvae of some fishes) grow at a rate of about 0.24 mm per day until October, when growth slows or stops. Subsequently, metamorphosis into the glass eel stage usually occurs at lengths of 55-65 mm and ages of 8-12 months (Kleckner and McCleave 1985).

Evidence suggests that growth rates in yellow eels may be influenced by environmental parameters and habitat characteristics. Eels may grow faster in more southern climates compared to northern latitudes, possibly because higher temperatures cause the growing season in the south to be longer (Bieder 1971; Harrell and Loyacano 1982; Hansen and Eversole 1984). However, maximum female length has been observed to increase with latitude (Hansen and Eversole 1984; Helfman and Bozeman 1984; Helfman et al. 1987; Barbin and McCleave 1997) and distance from the Sargasso Sea (Helfman et al. 1987), because more northern eels will spend more years growing in rivers. American eels have been observed to grow faster in systems with larger compared to smaller watersheds (Bouillon and Haedrich 1985). Also, within a single coastal system, growth is higher in estuarine compared to freshwater locations (Helfman and Bozeman 1984; Morrison et al. 2003). In freshwater, eels are generally longer, heavier, and older at maturation than are eels in estuaries (Helfman et al. 1987). Eels may select freshwater habitats because densities are lower and predators are less prevalent, reducing cannibalism and predation and increasing survival rates (Moriarty 1987). Also, females usually have higher early growth rates (Oliveira and McCleave 2002) and are more prevalent in upstream locations as compared to males, which are slower growing at younger ages and more frequently found in downstream and estuarine areas (Oliveira 1999). It may be that males and females have evolved different life history strategies, with females attaining a larger size at maturity and males reaching maturity at a younger age (Helfman et al. 1987; Oliveira and McCleave 2002).

Aspects of life history requiring future study:

Although much research on American eels has been completed, little is known about this species in Florida. Examination of the distribution, abundance and population dynamics of American eels in Florida would aid in management decisions regarding this species. Also, basic life history information, such as age and size at maturity, sex-specific growth rates and timing of downstream migration of adult eels, is currently unavailable and will be critical to understanding the potential effects of flow and water level alteration on this species. Current velocity is possibly an important environmental factor triggering the downstream migration out of rivers, before the oceanic migration to the spawning grounds.

Discussion

Modification of the flow regime in a river can affect aquatic ecosystems by changing the natural current velocity and depth, as well as by altering the physical and chemical characteristics of the water body (Bain and Finn 1988; Richter et al. 1996; Poff et al. 1997). Decreases in water flow rate and depth in aquatic systems have been observed to alter water temperature and to reduce dissolved oxygen levels (Sykes and Lehman 1957; Richter et al. 1996). During some life history stages, all three diadromous species discussed occur in areas with dissolved oxygen levels of at least 5 mg/L and this is the minimum concentration suggested for egg and larvae development of American and hickory shad (Koo 1977; Hawkins 1980; Facey and Van Den Avyle 1986; Klauda et al. 1991). Flow rates that reduce dissolved oxygen below 5 mg/L in areas of the St. Johns River where these species spawn or grow may reduce their population abundances. Appropriate levels of dissolved oxygen are likely most important in areas where spawning of American and hickory shad takes place, because eggs and larvae probably have little tolerance to low oxygen events. Additionally, specific temperatures and appropriate seasonal temperature changes in the St. Johns River may be necessary for high growth and survival rates, as well as for triggering seasonal migrations. Average dissolved oxygen levels and temperatures during each month collected from a US Geological Survey gage station located near Lake Harney on the St. Johns River, an area where gravid (i.e., actively spawning) female American shad have been collected (McBride Unpublished data), are presented in Figure 4. Specific temperatures may be particularly important for these populations of American and hickory shad, which are spawning in the southern most river system within their ranges (Facey and Van Den Avyle 1986; Bentzen et al. 1993; Rulifson 1994). Flow should be maintained at velocities that retain appropriate temperatures and dissolved oxygen levels, especially during summer months when young American shad may be experiencing the upper levels of their temperature tolerance and low concentrations of dissolved oxygen (Figure 4).

For American shad, previous studies suggest that specific water velocities and depths are critical to the survival and development of eggs and larvae (Massmann 1952; Williams and Bruger 1972; Williams et al. 1975; Crecco and Savoy 1985; Facey and Van Den Avyle 1986; Crecco and Savoy 1987; Klauda et al. 1991; Ross et al. 1993; Hawkins 1980). Maintaining appropriate flow rates during the period of the year (December to May) when eggs and larvae are developing in the St. Johns River (Figure 5) may be very important to this population of American shad. In the St. Johns River, eggs were found in areas with water currents ranging from 7.62 through 60.7 cm/s (Williams and Bruger 1972). In this system, current velocity was weakly but positively correlated with the abundance of shad eggs collected per hour (Figure 2) and in other rivers, eggs were found in locations with moderate to high current velocities, compared to those with lower current velocities (Massmann 1952; Ross et al. 1993). In the Connecticut River, the growth and survival of American shad larvae was higher in areas with lower flow (50-100m^3/s) compared to those with higher flows (Crecco and Savoy 1985); however, flows considered low in the Connecticut River would be better described as average in some areas where American shad spawn in the St. Johns River. Flow rates during each month collected from four US Geological Survey gage stations located in different areas on the St. Johns River are presented in Figure 6. Mullet Lake, Harney and Cocoa, are areas where gravid female American shad have been collected (McBride Unpublished data). Flow rates from December to May, when eggs and larvae would be developing in these three locations, are at or below those described by Crecco and Savoy (1985) to contribute to high growth and survival rates of larvae in the Connecticut River. A reduction in stream velocity, therefore, is not predicted to aid in the survival or development of larval American shad in the St. Johns River, Florida.

Upstream migration and spawning location of adult American shad and downstream migration of juveniles may be affected by flow rate in river systems, especially if flows are slowed or reversed (Williams and Bruger 1972; Williams et al. 1975; Leggett 1976). Adults have been observed to alter upstream migration rates in response to periods of halted or reversed flows (Leggett 1976) and to differentially select spawning habitat in relation to flow rates and water levels (Williams and Bruger 1972; Williams et al. 1975). Juvenile American shad have been found in water velocities between 6 and 75 cm/s (Klauda et al. 1991) and have been located in closer proximity to upstream spawning sites during a lower versus a higher flow year. In addition, during a year when water flows and levels were low, juveniles were located in the river until March, several months after their fall and winter downstream migration should have taken place (Williams and Bruger 1972). Increasing the river residence time of juveniles, by delaying downstream migration, may reduce cohort strength (Klauda et al. 1991; Limburg 2001). It has been suggested that an increase in flow rate may cue the downstream migration of juveniles (Klauda et al. 1991). There is a natural increase in flow rate starting in the late summer and ending in the late fall in upper areas of the St. Johns River (Figure 6) and this hydrologic pattern may signal juveniles to migrate downstream. Maintenance of positive flow rates in the river during the fall and winter migration period of both adults and juveniles may be important to their migrations.

Far less is known about the specific flow rates and water levels needed for hickory shad during any life history stage. No gravid adults (McBride Unpublished data), eggs, or larvae of hickory shad have been located in the St. Johns River (Williams et al. 1975). In other river systems, however, hickory shad eggs are usually found in small tributaries and lakes, rather than in the main stem of the river (Godwin and Adams 1969; Street 1970; Pate 1972; Davis 1973; Marshall 1976; Klauda et al. 1991). Areas where eggs have been located have been characterized as deep and dark with slow moving currents (Street 1970; Hawkins 1980). In the St. Johns River, adult hickory shad have been found in higher abundances in deeper areas, most especially in Lake George (Moody 1961). It is possible that hickory shad may be spawning in more lacustrine areas or small tributaries that have not been well sampled in previous studies of anadromous fishes in the St. Johns River (Williams and Bruger 1972; Williams et al. 1975). Therefore, it is unknown if alteration of flow rates or water levels would adversely affect the eggs and larvae of hickory shad; however, it could be hypothesized that water depth may be more important than water velocity. Adult hickory shad conduct an upstream migration similar to that of American shad, except that their migration occurs earlier in the season than that of American shad, with peak migration occurring from December to February (McLane 1955; Williams et al. 1975). In addition, juvenile hickory shad migrate downstream as do juvenile American shad, though this migration also most likely takes place earlier in the year. If juvenile hickory shad migrate downstream before the summer months, they may not be exposed to long periods of low dissolved oxygen and high water temperature, as are American shad (Figure 4). Maintenance of positive flow rates during migration periods may be important for hickory shad. Further research on hickory shad is necessary to more fully understand how this species would respond to changes in natural water depths and flow rates.

American eels in the St. Johns River may be seriously affected by alteration in natural water flows and depths only when they are conducting migrations into and out of the riverine environment. However, general declines in the abundance of American eels along the Atlantic coast calls for a precautionary approach to any decision making, including the alteration of habitat or flow regimes in river systems (Castonguay et al. 1994; Haro et al. 2000; Geer 2003). American eels are ecological generalists. They live in many different habitats (Van Den Avyle 1984), eat a variety of prey organisms (Godfrey 1957; Ogden 1970; Wenner and Musick 1975; Helfman et al. 1987; Lookabaugh and Angermeier 1992), and can survive in a range of temperatures (Van Den Avyle 1984). Glass eels and elvers enter rivers in Florida from January to March. Previous research suggests that American eels may preferentially migrate upstream when water velocities are low, shortly after instances of high current (Smith and Saunders 1955; Crumpton and Johnson 2003). As they prepare for and initiate this upstream migration, elvers are attracted to river water (Miles 1968; Sorensen 1986). In addition, elvers may remain in estuarine areas for short periods until conditions are favorable for upstream migration (Jessop 1998). It is possible that glass eels can detect chemical components from rivers more easily when flow rates are higher, which may help to bring the eels near the river system, but wait in estuarine areas until lower currents are present to proceed with upstream migration when it would be more energy efficient. Flow rates in Jacksonville from January to March are moderate and variable, which may be beneficial for young eels. Downstream migration of adult American eels has not been well studied in Florida, but in other states, American eels have been observed to migrate downstream after heavy rains when temperatures decrease and flow rates increase (Hain 1975; Winn et al. 1975; Haro 1991). It is not known specifically when American eels conduct their downstream migration in the St. Johns River; however, in the Cooper River, South

Carolina, the downstream migration of adult eels is thought to take place during the fall (Hansen and Eversole 1984). Likely, the timing of the spawning migration of American eels in the St. Johns River is similar. Flow rates may be important to American eels during their seasonal migration.

Conclusion

The populations of American shad, hickory shad and American eel in the St. Johns River are affected by river flow rate and water depth during their residencies in this system as well as during their migrations into and out of the river environment. Although these species seem to be mainly channel fish and do not appear to require high flows to reach foraging or spawning habitats, each species is affected by current velocity, temperature and dissolved oxygen during one or more stages of its life history. American shad are the most thoroughly studied of the three species, both in terms of the St. Johns River population and in response to flow rate and water depth, and it appears that appropriate flow levels for eggs and young individuals are essential for maintenance of a healthy and abundant population. Current velocity appears to affect growth and survival of eggs and larvae and the downstream migration of juveniles. The ecology of hickory shad is still a mystery in Florida and many other states. Hickory shad may behave like American shad and require comparable flows and depths during periods of migration, but the requirements of eggs are unknown, except that flows low enough to significantly reduce dissolved oxygen levels may have negative repercussions for the population. American eels are ecological generalists, able to withstand environmental fluctuations while in rivers; however, they may be affected by flow rates during seasonal periods when young eels are migrating up the St. Johns River and adult eels are migrating down river on their way to spawn in the Sargasso Sea.

Further research needs to be conducted on these three diadromous species in the St. Johns River, Florida, before the effects of removal of water from this river system on these populations can truly be understood or predicted. Much of the research and modeling on the effects of flow rates and durations on these specific and other diadromous species has been conducted in more northern systems, often in rivers with lower average temperatures and higher flow rates. However, the species covered in this report are affected by changes in water current and depth during their residences in the St. Johns River, especially during times of migration and during periods when flows are low. Therefore, maintenance of a natural flow regime in the St. Johns River may be an important consideration for these populations, and maintenance of adequate flows may be essential during droughts. Removal of some amount of water may be acceptable when flow rates are high. However, flow and water level reduction during periods with low water may lead to significant population declines.

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Table

Table 1—Catch per unit effort of American shad eggs (Williams and Bruger 1972) and adults (McBride Unpublished) at spawning areas in the St. Johns River, Florida, during seasons of comparatively high and low flow. Williams and Bruger (1972) collected eggs using ½ m plankton nets in 1969 and 1 m plankton nets in 1970. McBride (Unpublished data) collected adults both seasons by electrofishing.

Study	Spawning Season	Location	Flow during the spawning season (comparative)	Catch	Effort (h)	Catch/Effort
Williams and Bruger	1970	Lake Monroe-Lake Harney	High	5755	454.73	12.66
Williams and Bruger	1970	Lake Harney-Lake Poinsett	High	10938	1068.13	10.24
Williams and Bruger	1969	Lake Monroe-Lake Harney	Low	46	45.58	1.01
Williams and Bruger	1969	Lake Harney-Lake Poinsett	Low	419	139.10	3.01
McBride	2003	Lake Monroe-Lake Harney	High	189	65	2.91
McBride	2003	Lake Harney-Lake Puzzle	High	208	4.17	49.88
McBride	2004	Lake Monroe-Lake Harney	Low	32	92	0.35
McBride	2004	Lake Harney-Lake Puzzle	Low	304	9.5	32.0

Figure Captions

Figure 1—The St. Johns River, Florida, including locations and lakes addressed in the text.

Figure 2—The correlation between American shad eggs collected per hour and current velocity in locations where eggs were located in the St. Johns River, Florida. Eggs were collected and current velocity was measured by Williams and Bruger (1972) during the 1969-1970 sampling season using a 1 m plankton net set on the bottom of the river bed.

Figure 3—Catch rates of young American eels and current velocity at Guana River Dam, Florida, February and March 2002, during their upstream migration. Glass eels were collected using dip nets every half hour at the start of incoming tides at night. Figure from Crumpton and Johnson (2003).

Figure 4—Average dissolved oxygen levels and water temperatures during each month collected from a US Geological Survey gage station located in Geneva, Florida, near Lake Harney on the St. Johns River, Florida.

Figure 5—Eggs and larvae of American shad collected per hour by month by 1 m plankton net sets on the river bottom by Williams and Bruger (1972) during the 1969-1970 spawning season in the St. Johns River, Florida.

Figure 6—Flow rates during each month collected from four US Geological Survey gage stations located in different areas on the St Johns River, Florida.

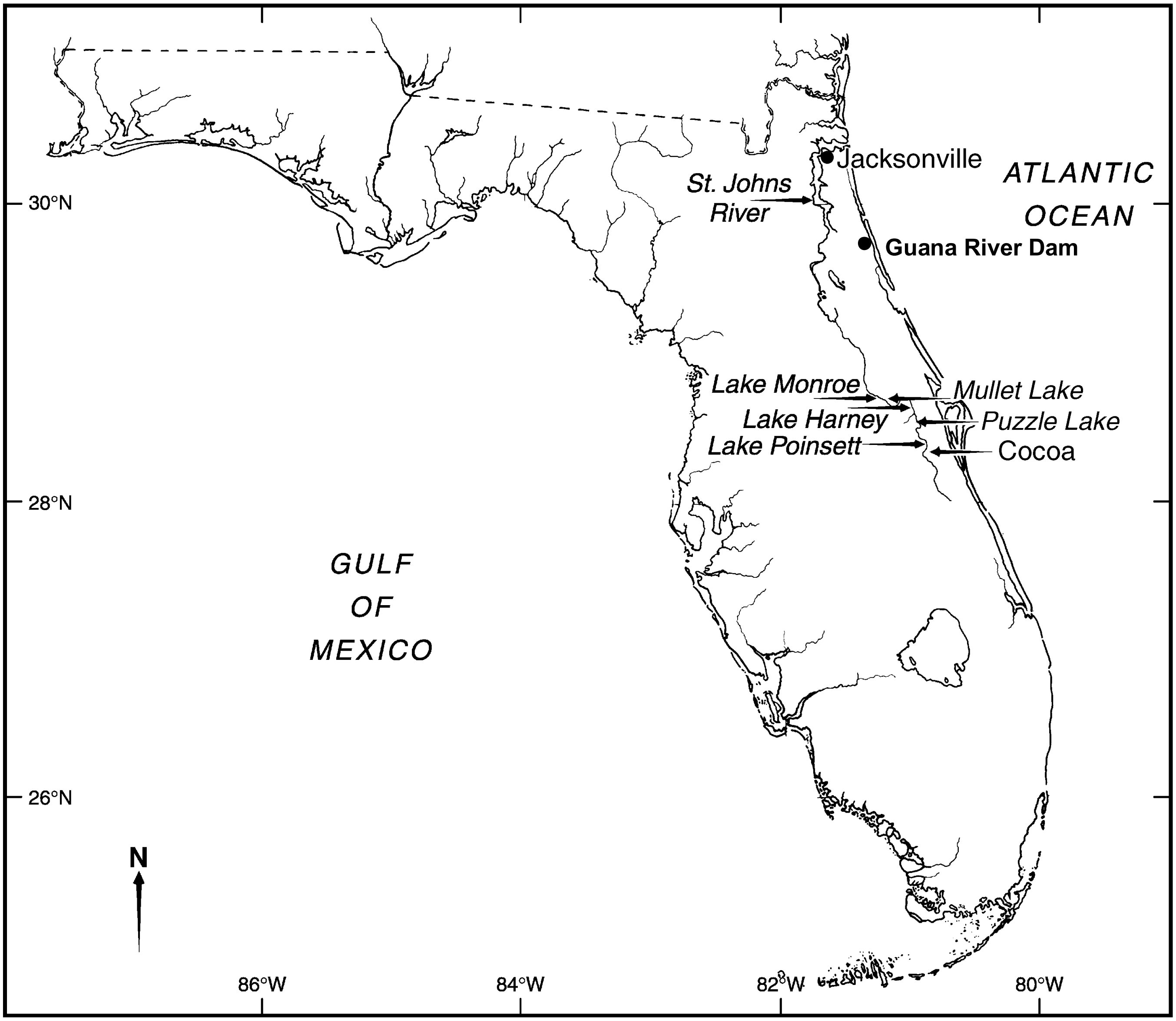
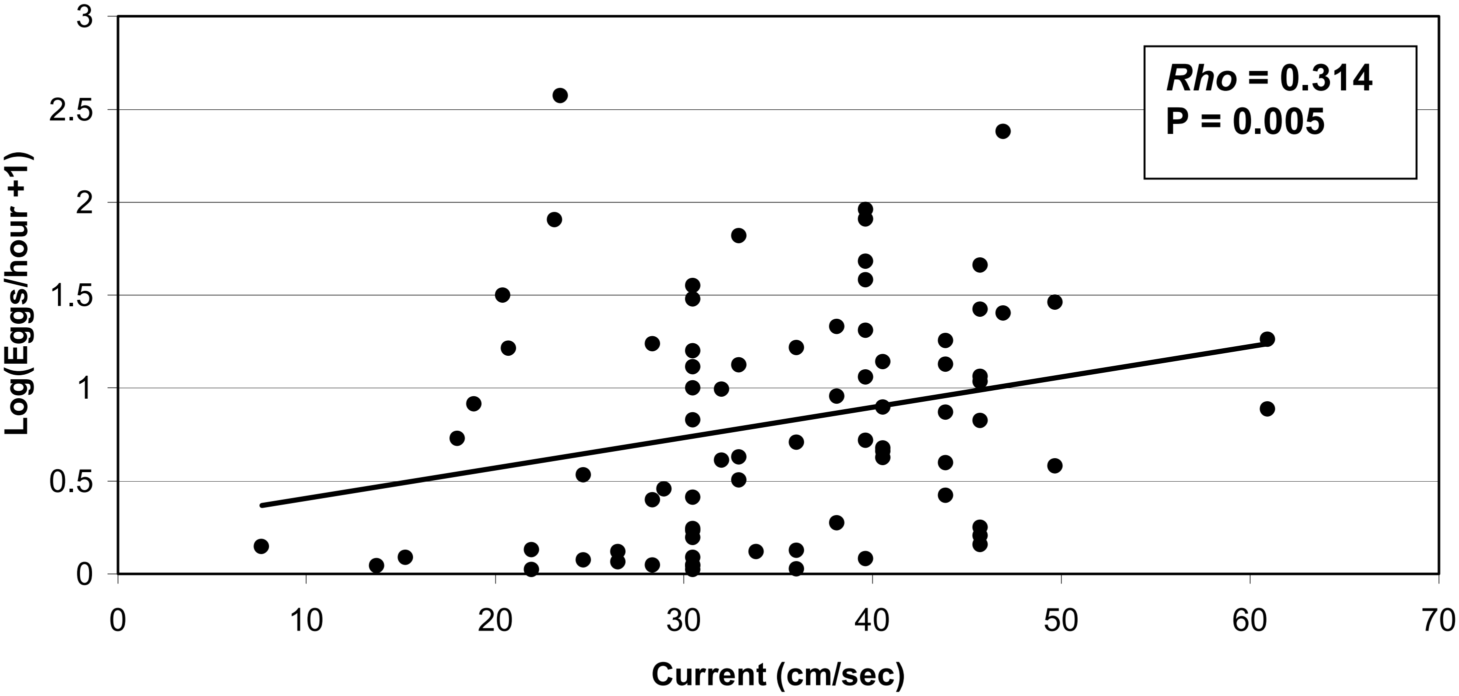

30°N
28°N
26°N
86°W
84°W
82°W
80°W
Jacksonville
ATLANTIC OCEAN
St. Johns River
Guana River Dam
Lake Monroe
Mullet Lake
Lake Harney
Puzzle Lake
Lake Poinsett
Cocoa
GULF OF MEXICO
N

Figure 1



Rho = 0.314
P = 0.005
Log(Eggs/hour +1)
3
2.5
2
1.5
1
0.5
0
0
10
20
30
40
50
60
70
Current (cm/sec)

Figure 2

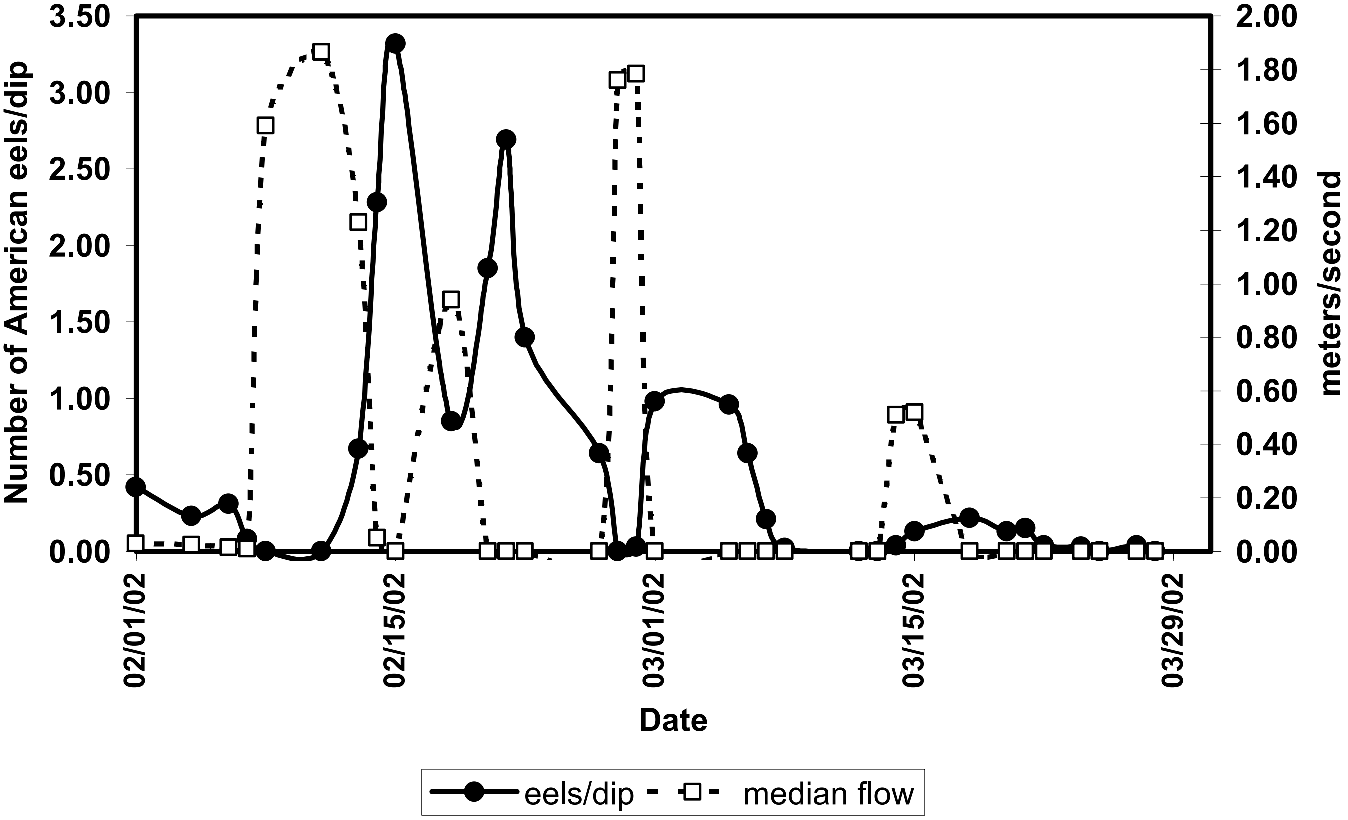

3.50
3.00
2.50
2.00
1.50
1.00
0.50
0.00
Number of American eels/dip
2.00
1.80
1.60
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0.00
meters/second
02/01/02
02/15/02
03/01/02
03/15/02
03/29/02
Date
eels/dip
median flow

Figure 3

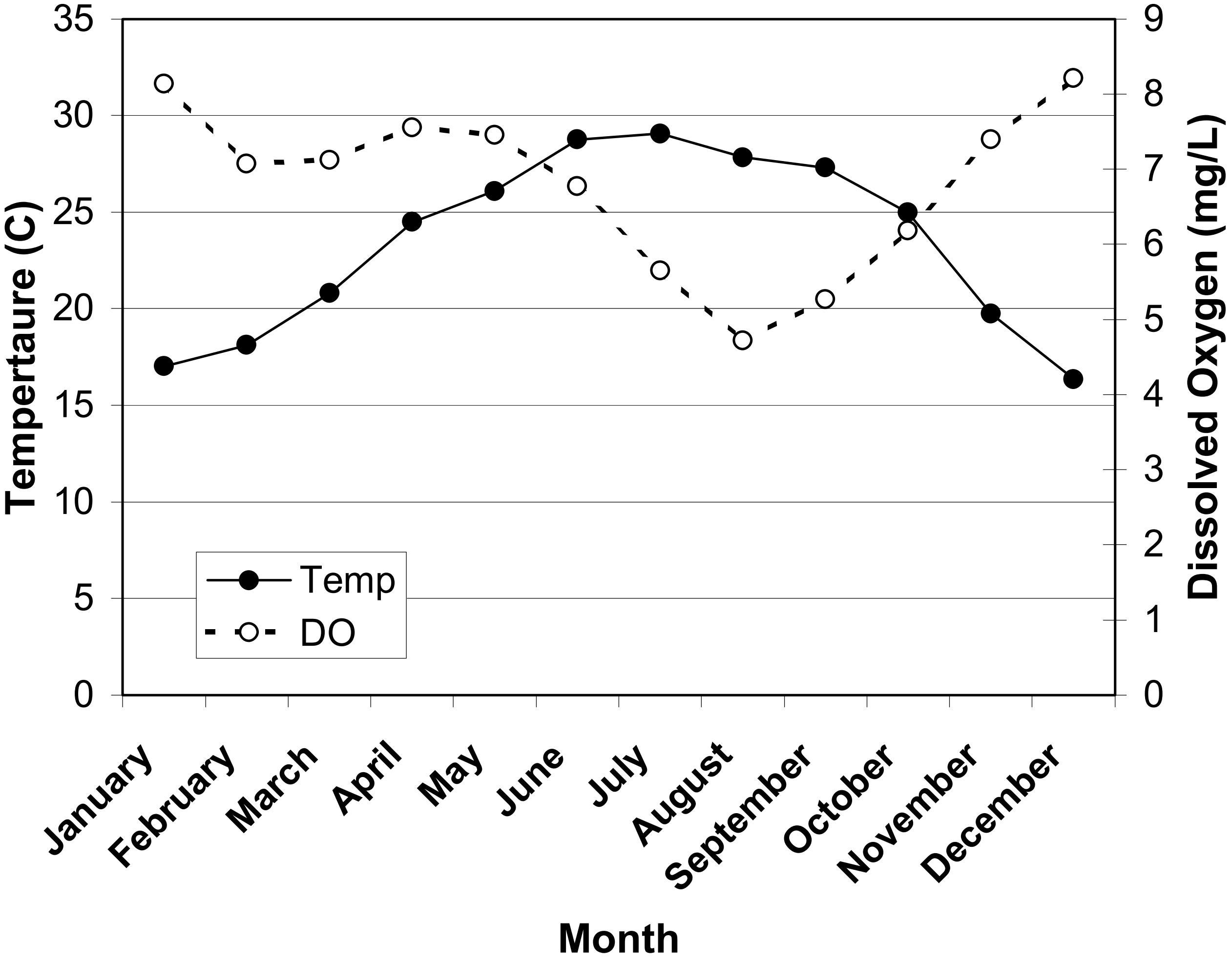
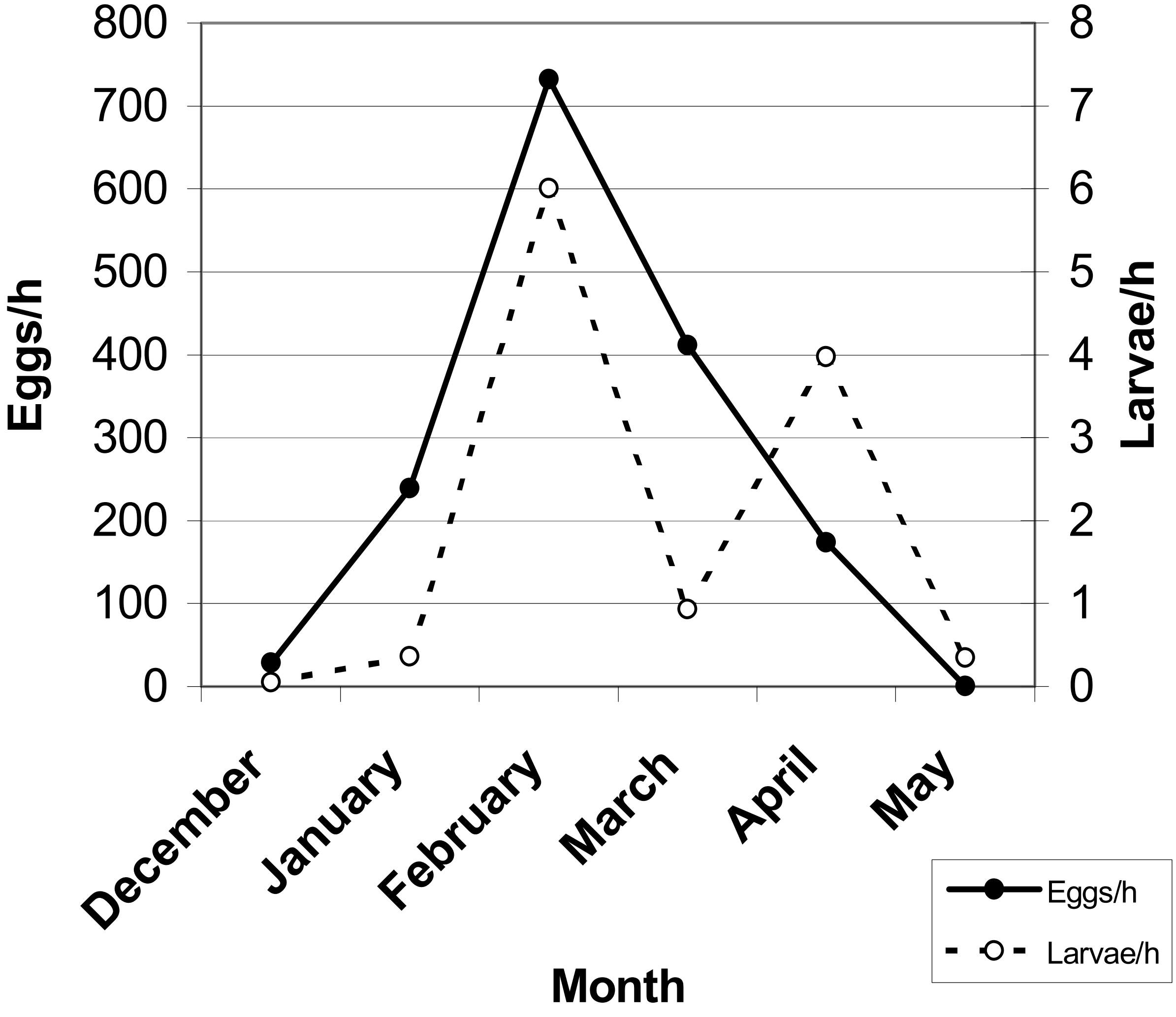

Tempertaure (C)
Dissolved Oxygen (mg/L)
35
30
25
20
15
10
5
0
9
8
7
6
5
4
3
2
1
0
Temp
DO
January
February
March
April
May
June
July
August
September
October
November
December
Month

Figure 4



800
700
600
500
400
300
200
100
0
Eggs/h
8
7
6
5
4
3
2
1
0
Larvae/h
December
January
February
March
April
May
Month
Eggs/h
Larvae/h

Figure 5

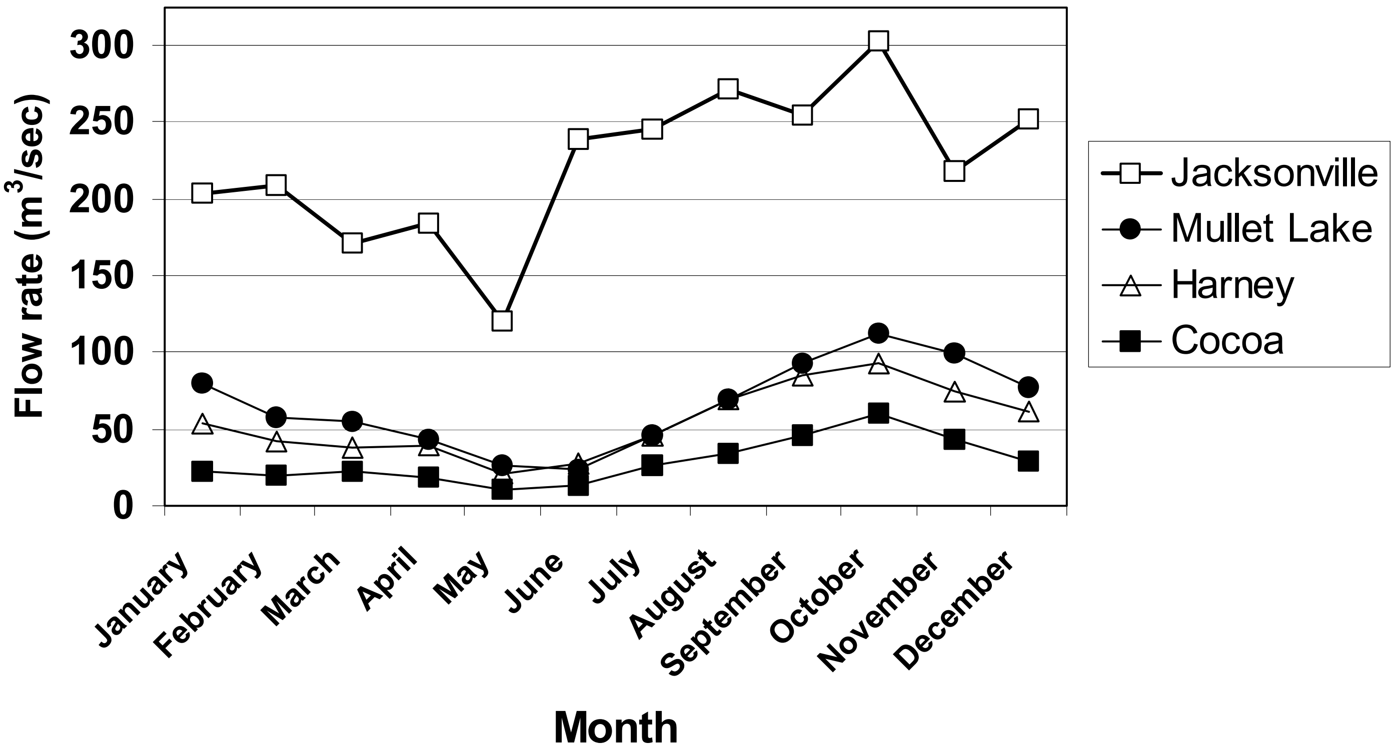

300
250
200
150
100
50
0
Flow rate (m³/sec)
Jacksonville
Mullet Lake
Harney
Cocoa
January
February
March
April
May
June
July
August
September
October
November
December
Month

Figure 6