American Shad Feeding on Spawning Grounds in the St. Johns River, Florida

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Abstract.—We evaluated the feeding habits of American shad *Alosa sapidissima* on spawning grounds in the St. Johns River, Florida. Feeding intensity in freshwater was generally low but highly variable. The items consumed were mainly pelagic (cyclopoid copepods and woody debris), although benthic (mollusks and sand) and surface (adult insects [Coleoptera, Hemiptera, and Odonata]) organisms occurred occasionally. The stomach fullness index varied by location for males, suggesting that ingestion is related to prey availability. Feeding by females also varied by location and continued during final oocyte maturation and active spawning. Egg cannibalism was suggested by the presence of some eggs morphologically similar to American shad eggs in the stomachs of males and females collected when females were running ripe. The results from diel sampling suggested that individuals consumed approximately 1.727 kJ/d in freshwater, which represents only a small fraction of the estimated daily energetic expenditure during the spawning run. Unlike iteroparous populations, Florida's American shad probably do not conserve energy for out-migration. While this low incidence of freshwater feeding did not maintain fish weight, it may increase available energy and thereby increase fecundity.

American shad *Alosa sapidissima* are anadromous clupeids that spawn in rivers along the Atlantic coast from southern Canada to central Florida (Limburg et al. 2003). During their spawning run in freshwater, it is a common observation that adult American shad eat little or nothing and lose considerable weight (Chittenden 1976; Davis 1980). Leim (1924) summarized his observations and the opinions of other early writers stating that "shad did not feed actively [in freshwater], but only took such things as came their way" (Leim 1924:182). Chittenden (1976) observed opportunistic feeding by adult American shad in the Delaware River, but determined that such feeding was insufficient to maintain weight since males and females lost approx-

imately half their weight during the spawning run and some perished, probably as a result of starvation. Walter and Olney (2003) documented feeding by adult American shad in marine and estuarine habitats as well as during the complete spawning run in the York River, Virginia. Adult stomach fullness index was highest in marine followed by estuarine habitats, and was lowest in freshwater (Walter and Olney 2003). In marine and estuarine waters, American shad actively feed on a variety of presumably high calorie prey, including copepods, euphausids, and mysids (Leim 1924; Walter and Olney 2003). In contrast, items identified from American shad stomachs on the spawning grounds were plant based, either green plants or woody material (Walter and Olney 2003), which may yield relatively few calories. American shad ingest items in freshwater under experimental conditions when food or lures are made available; therefore, it has been suggested that they feed little in rivers because suitably sized prey are not abundant (Atkinson 1951; Chittenden 1976; Walter and Olney 2003).

The bioenergetic consequences of these feeding patterns are only beginning to be explored. Understanding bioenergetics during the spawning migration may require a river-specific approach since water temperature and distance to spawning grounds may contribute to the degree of weight loss during the spawning run (Glebe and Leggett 1981a, 1981b; Leonard and McCormick 1999; Leonard et al. 1999). Temperature appears to affect metabolic demands of migrating American shad, with individuals at higher water temperatures (mean = 21.3°C) exhibiting considerably higher metabolic rates than those at lower temperatures (mean = 15.6°C; Leonard et al. 1999). Most adults spawn in their natal systems (Melvin et al. 1986; Nolan et al. 1991; Epifanio et al. 1995) and life history traits, such as length at age, age at maturity, and degree of iteroparity, appear to be river specific (Carscadden and Leggett 1975; Leggett and Carscadden 1978; Limburg et al. 2003). In particular, few repeat spawners are observed in most systems south of the Carolinas.

The St. Johns River, Florida, is the southernmost system with a spawning population of American shad (Facey and Van Den Avyle 1986). It is slow flowing,

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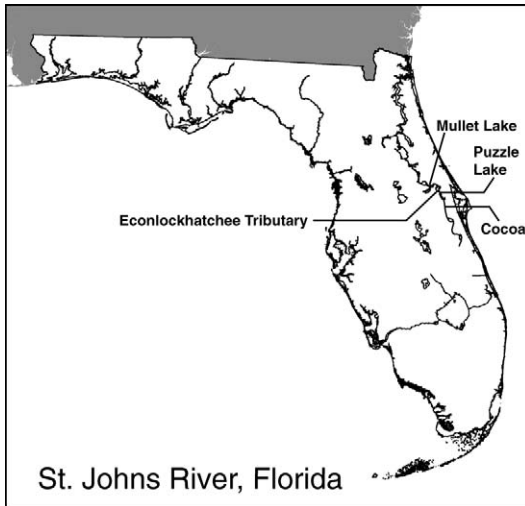
FIGURE 1.—Map of the St. Johns River, Florida, showing the sites at which American shad were collected by electrofishing during the 2003–2004 spawning season. All of these sites are lotic in nature and include three main-channel sites (Mullet Lake [river kilometer, rkm, 274–307], Puzzle Lake [rkm 308–315], and Cocoa [rkm 330 and 378]) and one tributary (Econlockhatchee Tributary, which enters the main channel of the St. Johns River at rkm 311).

runs approximately 500 km from headwaters to mouth, and has a substrate of mainly sandy sediments (Figure 1). American shad can migrate upstream in the St. Johns River nearly 400 river kilometers (rkm), with most spawning occurring between Lake Monroe (rkm 237) and Lake Poinsett (rkm 330; Williams and Bruger 1972; McBride and Holder 2008). The spawning period corresponds to the lowest annual water temperatures found locally, but individuals may be exposed to higher temperatures than those in more northern rivers at the start and end of the spawning run (Leggett and Whitney 1972). Warm water temperatures and a long spawning run may result in higher metabolic expenses for American shad in the St. Johns River than elsewhere.

If the St. Johns River population of American shad is semelparous, as is thought, then feeding in freshwater would not increase survival, but could increase egg production. This study was designed to examine freshwater feeding habits of this semelparous population of American shad. We collected fish from several locations on the spawning grounds in the St. Johns River to examine whether feeding intensity was related to location or an individual's sex or maturity class. In addition, we collected stomach samples at all hours of the day from one location to examine whether feeding was constant throughout the day and to estimate caloric

intake to evaluate possible energetic consequences of freshwater feeding.

Methods

Adult American shad were collected in the St. Johns River during their spawning migration in 2003–2004, as part of a larger study concerning stock status and biology of American shad in this system (Figure 1; McBride and Holder 2008). American shad were collected near and around the spawning grounds by electrofishing from a boat using a Wisconsin ring electrode apparatus (Reynolds 1996). Surface water temperature in the area of the river sampled was determined to the nearest 1°C with a thermometer at the start of most sampling dates.

To examine feeding habits on the spawning grounds, fish were collected from four locations from 2 December 2003 to 12 May 2004 during daytime hours (0700–1859 hours Eastern Standard Time [EST]). Fish were collected from three main-channel sampling areas: (1) a deep riverine area between Lakes Harney and Monroe referred to as "Mullet Lake" (rkm 274–307), (2) a shallow and diffuse riverine area called "Puzzle Lake" (rkm 308–315), and (3) two shallow main-channel areas, one south of Lake Cone (rkm 330) and the other just north of Lake Poinsett (rkm 378), collectively called "Cocoa" (Figure 1). Sampling occurred at least once every 6 weeks during the spawning run, but more frequently (every 2 weeks) in the Mullet Lake area. Sampling was also completed on two dates, one in March and one in April, within the Econlockhatchee Tributary, which enters the main stem in the Puzzle Lake area at rkm 311 (Figure 1). To examine diel patterns in feeding, American shad were collected every 1.5–2 h during nighttime (1900–0659 hours) on two occasions, 10–11 February and 9–10 March 2004, at Puzzle Lake and were examined in relation to daytime sampling (0700–1859 hours) at Puzzle Lake between 3 February and 17 March 2004. Puzzle Lake was selected for diel sampling because large numbers of American shad were collected there during previous sampling and it is a primary spawning site for American shad (Williams and Bruger 1972; McBride and Holder 2008).

American shad were immediately packed in ice and transported to the laboratory for collection of biological data. At the laboratory, fish were measured for total length (TL) to the nearest millimeter and body weight (BW) to the nearest gram. Gonads were removed and weighed (GW) to the nearest gram. Males were classified macroscopically as mature (spawning capable) or running ripe (milt freely expressed) and females were classified macroscopically as maturing (with vitellogenic oocytes), hydrated (with oocytes in final

maturation), running ripe (with ovulated eggs in the ovarian lumen), or spent (postspawning) following the criteria of Olney et al. (2001). Somatic–visceral weight (SVW), calculated as $SVW = BW - GW$, was used to identify weight loss over the season not related to loss of weight from gonads. A length–weight relationship, $SVW = a(TL)^b$, was calculated to obtain an expected SVW at TL for females and males separately. To evaluate SVW loss over the season, linear regression of the ratio of actual SVW to expected SVW (based on TL) by sampling day (the first collection date, 16 December 2003, was day 1) was completed. McBride and Holder (2008) found that American shad collected near the end of the season in the St. Johns River were shorter in length than those at the beginning and by using actual SVW divided by expected SVW (actual SVW/expected SVW) as the dependent variable, a change in condition over the season could be examined without a possible confounding effect of change in length. The gonadosomatic index (GSI) was calculated as $GSI = GW/(BW - GW) \times 100$. Linear regression was similarly used to examine the relationship between GSI and sampling day.

Stomachs of individual fish were removed whole and either fixed in 5% formalin (almost all samples) or frozen. Stomachs were later rinsed and cut open, and all contents were removed, sorted to the lowest taxonomic level possible, patted dry, and weighed wet to the nearest 0.0001 g. Since American shad lose considerable weight during the spawning season, a stomach fullness index modified by Walter and Olney (2003) for American shad in the York River, Virginia, was similarly used to measure feeding intensity for American shad in this study as: stomach fullness index $= 100 \times [(\text{total stomach content weight})/(\text{TL}^3)] \times 100{,}000$. This fullness index equation is the same as that used by Walter and Olney (2003), although their reported equation was missing the required multiplier ($\times 100$) to report the value as a percent (John Walter, personal communication). Instead of using BW as the denominator (as is standard in fullness indices), total length cubed then divided by 100,000 was used as an estimate of BW (modified BW) since actual BW would be affected by the extent of freshwater weight loss (Walter and Olney 2003; John Walter, personal communication).

Generally, stomach fullness index is calculated for each fish regardless of the presence or types of items consumed. We calculated an estimate of stomach fullness index using all types of contents (labeled SFI_{ALL}). This SFI_{ALL} was calculated to allow for the comparison between this study and that of Walter and Olney (2003). However, some items found in the stomachs were probably indigestible or otherwise

contributed little to the energetic budget (sand, woody debris, and green plant material). These indigestible or nonnutritive items were removed to calculate another stomach fullness index (hereafter labeled SFI), which was used in all further analyses.

Gonadosomatic indices (GSI) for males and females were compared for differences using a Student's t-test. American shad are batch spawners (Olney et al. 2001; Olney and McBride 2003); therefore, GSI presumably decreases successively with each spawning event over the duration of the spawning season, although cycles of hydration and spawning may lead to variability. Correlations between GSI and SFI for males and females separately were completed to evaluate whether feeding was related to time spent in the river and amount of spawning completed.

Analyses of variance (ANOVAs) were completed to examine for differences in SFI by sex, location, or maturity class. All males were running ripe, so no test for differences in SFI by maturity class for males could be completed. Females were a mix of maturity classes (maturing, hydrated, and running ripe; no spent females were observed), so differences by location were only tested for males due to possible interactions between maturity class and location. Where the null hypothesis was rejected, Tukey's multiple comparisons tests were completed to determine which groups differed significantly (Zar 1999).

To evaluate whether feeding intensity was constant throughout the day, diel catches were grouped into six periods: night (0000–0359 hours), sunrise (0400–0759 hours), morning (0800–1159 hours), afternoon (1200–1559 hours), sunset (1600–1959 hours) and evening (2000–2359 hours) and average SFI between periods were compared using an ANOVA. To examine for differences in consumption of specific items by period, a multivariate analysis of variance (MANOVA) was completed for all items that represented at least 1% by weight of the material found in all stomachs. All statistical tests were considered significant at the $\alpha = 0.05$ level.

To examine energetic consequences of freshwater feeding, daily ration was estimated using a method by Elliott and Persson (1978) from data collected during diel sampling at Puzzle Lake. Daily ration is the sum for all periods of

$$[(\text{SFI}_{t+1} - \text{SFI}_t \times e^{-Rt}) \times Rt]/(1 - e^{-Rt}),$$

where R is the evacuation rate by hour, t is the time interval between samples, SFI_t is the average SFI in one sample period and S_{t+1} is the average SFI during the following sample period. Two-hour time periods were used since periods no greater than 3 h are
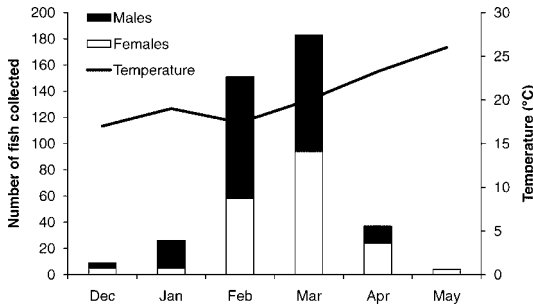
FIGURE 2.—Number of male and female American shad collected from all sampled locations in the St. Johns River, by month, and average river water temperature during each month.

suggested (Elliott and Persson 1978). Evacuation rates (R) by period were estimated by the following equation: $R = [\log_e(\text{SFI}_{t+1}) - \log_e(\text{SFI}_t)]/t$ and the highest R was applied to estimate daily ration (Boisclair and Leggett 1988; Boisclair and Marchand 1993; Brewster 2007). Daily ration was used to estimate total grams ingested by the average American shad in a day at Puzzle Lake. Caloric values for prey types multiplied by the proportion of those prey types in the diet and finally by total grams ingested was used to estimate total calories ingested in a day. Approximate caloric values for prey items were found in the literature (Cummins and Wuycheck 1971; Szeinfeld 1993). Since specific prey items in the St. Johns River were not tested for caloric value and the overall sample size was low, the average caloric intake is only a rough estimate and should be evaluated with caution until further research is completed.

Results

American shad were collected from mid-December to early May at temperatures between 15°C and 27°C, with most individuals collected during the peak of the run in February and March when temperatures ranged from 17°C to 24°C (Figure 2). Females ($n = 190$) ranged in size from 380 to 523 mm TL (mean = 451 mm TL) and males ($n = 220$) ranged in size from 308 to 475 mm TL (mean = 418 mm TL). Males and females were collected from each sampling location during daytime hours (0700–1859 hours EST), with most fish collected from Puzzle Lake (Table 1).

Material was frequently observed in the stomachs of American shad (77.1% of 410 fish) collected from the four sampling locations during daytime hours; however, feeding intensity was generally low (SFI_{ALL} ranged from 0 to 0.9156, with an average of 0.0243 [SD = 0.0669])). By weight, stomach contents were composed of woody debris (42.4%), zooplankton (31.7%),

sand (17.0%), green plant material (4.0%), insects (3.4%), other crustaceans (1.3%), benthic mollusks (0.1%), and fish eggs (0.1%). With indigestible and nonnutritive items excluded, SFI ranged from 0 to 0.4620, with an average of 0.0095 (SD = 0.0436). Nutritive items were mainly zooplankton, including small cyclopoid copepods and podocopid ostracods. Insects in the diet were mainly aquatic larvae and pupae from the orders Diptera (e.g., midges) and Trichoptera (e.g., caddis flies), but also included adult elmid beetles (Coleoptera), dragonflies (Odonata), and leaf hoppers (Hemiptera). Other crustaceans included palaemonid and mysid shrimp, gamaridean amphipods, and one xanthid crab. Fish eggs in the stomachs could not be identified with certainty, but some were the size, shape, and coloration of American shad eggs (Table 1).

Both males and females consumed prey items, but lost considerable weight during the freshwater migration. The percentage of females with stomach contents (85.3%) was higher than that of males (69.5%) and females had higher SFI (mean = 0.012, SD = 0.053) than did males (mean = 0.007, SD = 0.033), but the difference was not significant (t-test: $t = 1.07$, $P = 0.307$). Weight (actual SVW / expected SVW) declined significantly over time for both males and females ($R^2 = 0.39$, $F = 122.78$, $P < 0.001$ and $R^2 = 0.52$, $F = 236.73$, $P < 0.001$, respectively), illustrating that condition declined during the spawning season (Figure 3A). When examined by month, average SVW (g) of both males and females declined over the season by 40–50% (Figure 3B).

Like SVW, GSI generally declined during the spawning season. The GSI was significantly higher for females than for males (t-test: $t = 24.39$, $P < 0.001$) and declined significantly by sampling day for both females and males ($R^2 = 0.16$, $F = 36.03$, $P < 0.001$ and $R^2 = 0.31$, $F = 97.64$, $P < 0.001$). Female GSI averaged 25.0 in December and 7.8 in May, while male GSI averaged 6.9 in December and 3.6 in April (Figure 4A). The SFI was not significantly related to GSI for either females or males ($R^2 = 0.014$, $P = 0.107$ and $R^2 = 0.004$, $P = 0.328$, respectively) suggesting that feeding intensity was not related to the amount of time a fish spent in the river or how much spawning it completed.

Prey consumption appeared to be a factor of location and maturity class, although these two factors appear interdependent. The SFI differed significantly by collection location for males (ANOVA: $F = 24.71$, $P < 0.001$). Tukey's multiple comparisons tests indicated that SFI was significantly higher at Mullet Lake, the most downstream location, than at all other locations (all $P < 0.001$). Stomach fullness index was also higher for females collected at Mullet Lake, as compared with other areas (Table 1). Prey types also

TABLE 1.—Percent by weight of all items consumed by male and female adult American shad collected during the daytime in the St. Johns River, Florida, during the 2003–2004 spawning run, by sampling location (see Figure 1). Also shown are the number of stomachs examined, the percentage of stomachs with any items, and the means and SDs of stomach fullness indices including all items (SFI_{ALL}) and only nutritive items (i.e., excluding sand, woody plant material, and green plant material [SFI]). Fish scales were also found in the stomachs of some individuals.

Prey class	Prey type	Mullet Lake		Puzzle Lake		Econlockhatchee Tributary		Cocoa	
		Males	Females	Males	Females	Males	Females	Males	Females
Insecta	Coleoptera (adults)	0.00	0.00	6.14	<0.01	0.00	0.21	0.00	0.00
	Diptera (larvae and pupae)	0.00	0.00	0.02	0.06	0.00	0.11	0.04	0.01
	Hemiptera (adults)	0.00	5.95	0.00	0.00	0.00	0.00	0.00	0.00
	Odontata (adults)	0.00	0.00	0.00	0.00	0.00	0.99	0.00	0.00
	Trichoptera (larvae and pupae)	0.00	0.00	0.00	0.00	0.00	1.03	0.00	0.00
Copepoda	Cyclopoida	82.06	55.56	8.95	4.35	0.00	0.00	25.82	2.04
Ostracoda	Podocopida	7.96	0.00	0.38	0.02	0.00	0.00	0.00	0.24
Malacostraca	Amphipoda (Gammaridae)	0.00	0.00	0.06	0.05	0.00	0.00	0.00	0.00
	Decapoda (Palaemonidae)	0.00	2.60	0.00	0.00	0.00	0.00	0.00	0.00
	Decapoda (Xanthidae)	0.00	0.00	0.00	0.34	0.00	0.00	0.00	0.00
	Mysidacea	0.00	0.02	0.89	0.14	0.00	0.00	0.00	0.51
Gastropoda		0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.00
Bivalvia		0.00	0.00	0.02	0.06	0.00	0.07	0.00	0.00
Other	Fish eggs	0.00	0.00	6.04	8.27	0.00	0.00	0.00	0.00
	Woody debris	9.81	19.54	38.72	66.10	91.67	83.31	70.07	77.17
	Green plant material	0.00	0.00	5.79	6.59	8.33	14.29	0.00	12.18
	Sand–dirt	0.17	16.32	30.35	16.24	0.00	0.00	4.07	7.85
Number of stomachs examined		14	17	154	107	21	48	31	18
Percent with any contents		85.7	88.2	70.8	86.9	33.3	81.3	80.6	88.9
Mean SFI_{ALL}		0.080	0.177	0.015	0.026	0.002	0.008	0.007	0.010
SD of SFI_{ALL}		0.114	0.237	0.030	0.045	0.005	0.013	0.010	0.012
Mean SFI		0.072	0.113	0.005	0.004	0.000	<0.001	0.002	<0.001
SD of SFI		0.110	0.141	0.019	0.017	0.000	<0.001	0.006	<0.001

varied between sites, with a high percentage of cyclopoid copepods, by weight, consumed at Mullet Lake. Puzzle Lake was the only location where fish eggs were consumed (Table 1).

As well as varying by location, consumption may change with maturity class. Females were assigned to one of three classes: maturing ($n = 88$), hydrated ($n = 75$), or running ripe ($n = 20$). Maturing and hydrated females were found at all locations, but running-ripe females were only collected from Puzzle Lake ($n = 5$) and the Econlockhatchee Tributary ($n = 15$; Figure 4B) suggesting that maturity class is not independent of location and active spawning is more concentrated in some areas of the spawning reach, compared with others. To eliminate possible effects of location, only females from Puzzle Lake ($n = 56$ maturing, $n = 46$ hydrated, and $n = 5$ running ripe) were used to evaluate a relationship between maturity class and SFI. Mean SFI was highest for maturing females, but the relationship was not significant (ANOVA: $F = 2.40$, $P = 0.095$; Figure 4C).

Feeding intensity (as indicated by SFI) was generally low at Puzzle Lake and varied by diel period (ANOVA: $F = 2.42$, $P = 0.036$). The SFI was highest during sunset (Table 2), but Tukey's test did not find differences between specific periods. The top seven stomach items, by weight, varied significantly by diel period (see Table 2; Wilk's lambda: $F = 2.00$; Pillai's trace: $F = 1.97$; Hotelling–Lawley trace: $F = 2.02$; Roy's greatest root: $F = 6.29$; all $P < 0.001$; Zar 1999). When examined by prey type, weight of sand, green plant material, and fish eggs significantly differed by diel period and all others were not significant (Table 2; Figure 5). Sand was common in stomachs collected during all periods, but was highest at night. The SFI_{ALL} was also highest at night, probably as a result of increased sand ingestion (Table 2). Green plant material was found mainly during the afternoon, although to a small extent during the sunset and evening periods also (Table 2; Figure 5). Maturing and hydrated females were collected during all hours of the day at Puzzle Lake, but running-ripe females were only collected from 1620 to 1900 hours (Figure 6). Fish eggs were found in the stomachs of male ($n = 19$ of 154) and female ($n = 10$ of 107) American shad in all maturity classes. Most fish containing eggs in their stomachs were collected between 1620 and 1818 hours, the time range when females were running ripe (Figure
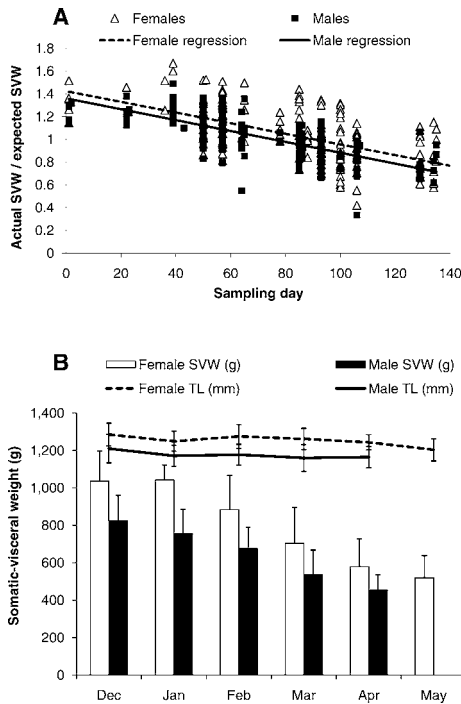
FIGURE 3.—**(A)** Ratio of actual somatic–visceral weight (SVW) to the expected SVW (based on the length–weight regression) for male and female American shad by sampling day (day 1 is the first collection date, 16 December 2003) and **(B)** average total length (mm) and somatic–visceral weight (g) for males and females by month; error bars represent SDs.

FIGURE 4.—**(A)** Gonadosomatic index for male and female American shad collected at all locations in the St. Johns River, by month, **(B)** percentage of females in different maturity classes by sampling location during daytime hours (see Figure 1), and **(C)** the stomach fullness index (SFI) for females at Puzzle Lake during daytime hours, by maturity class. Error bars represent SDs.

6). The number of eggs observed in a stomach ranged from 1 to 291 (mean = 27, SD = 53.84). The average number of eggs found in the stomachs of females was over twice the average found in the stomachs of males (mean = 49.1 and 20.8, respectively). The SFI at Puzzle Lake was highest during the diel time period when fish eggs were found in stomachs, as a result of their consumption (Table 2; Figure 6).

Diel data from Puzzle Lake and information from the literature on prey caloric values were combined to estimate daily energetic intake. Weight of nutritive stomach contents (excluding sand, woody debris, and green plant material) at Puzzle Lake ranged from 0 to 0.991 g with an average of 0.023 g (SD = 0.093). Gastric evacuation rate and daily ration estimated using SFI values were 0.880 and 0.043% of modified average BW, respectively. The modified average BW of American shad ($TL^3/100,000$) at Puzzle Lake during diel sampling was 806.8 g, which was only slightly higher than the actual average BW of fish collected (774.6 g). Using the modified average BW, average consumption was approximately 0.344 g/d at Puzzle
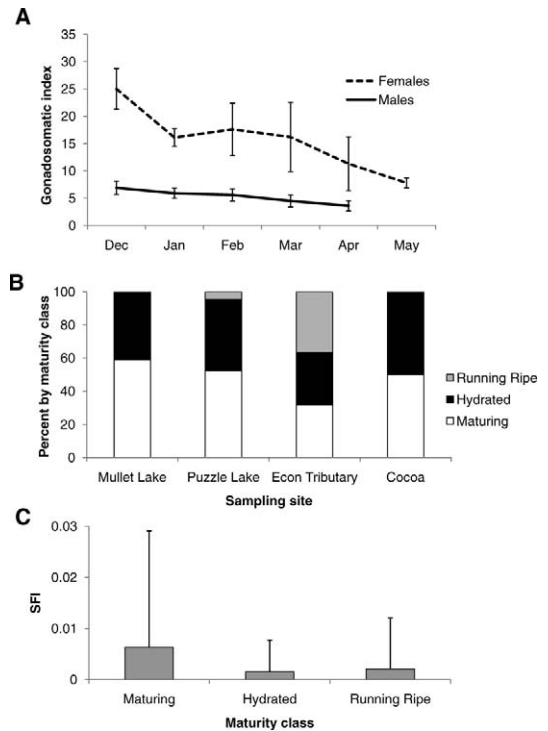
Lake. Thus, the average American shad at Puzzle Lake consumed about 412.85 calories or 1.727 kJ/d.

Discussion

American shad consumed a variety of prey types while on spawning grounds in the St. Johns River. As previously observed, individuals ingested mainly planktonic crustaceans such as copepods, ostracods, and mysids, but also opportunistically fed on adult and larval insects and benthic mollusks (Chittenden 1976; Walter and Olney 2003). In the present study, no fish prey were observed in the guts of American shad; however, unidentified fish larvae and larval and adult *Gambusia* sp. have previously been indentified from American shad stomachs in the St. Johns River, possibly during years when these prey were more available or abundant (A. R. Hyle, personal communication; R. S. McBride and A. Ross, unpublished data). The SFI$_{ALL}$ was considerably higher than SFI and the specific items consumed varied by location and diel time period (Tables 1, 2), suggesting that

TABLE 2.—Percent by weight of all items found in the stomachs of American shad collected at Puzzle Lake during the 2003–2004 spawning run, by diel period, and statistical significance of differences among periods. Night = 0000–0359 hours, sunrise = 0400–0759 hours, morning = 0800–1159 hours, afternoon = 1200–1559 hours, sunset = 1600–1959 hours, evening = 2000–2359 hours. Information on the number of stomachs collected and the mean and SDs of stomach fullness indices including all items (SFI_{ALL}) and only nutritive items (i.e., excluding sand, woody plant material, and green plant material [SFI]), by diel time period, are also included.

Prey class	Prey type	Night	Sunrise	Morning	Afternoon	Sunset	Evening	Statistic[a]
Insecta	Coleoptera	0.00	0.08	0.04	0.00	3.57	0.00	NS
	Diptera	0.08	0.12	0.00	0.10	0.10	0.81	
	Hemiptera	0.00	0.00	0.00	0.00	0.00	0.03	
Copepoda	Cyclopoida	0.28	13.97	9.24	12.03	2.72	5.48	NS
Ostracoda	Podocopida	0.35	0.08	0.00	0.56	0.00	0.03	
Malacostraca	Amphipoda (Gammaridae)	0.00	0.00	0.00	0.04	0.07	0.03	
	Decapoda (Palaemonidae)	0.00	1.41	0.00	0.00	0.00	0.00	
	Decapoda (Xanthidae)	0.00	0.00	0.00	0.00	0.31	0.00	
	Mysidacea	0.00	2.34	0.00	0.16	2.22	0.61	NS
Gastropoda		0.00	0.00	0.00	0.31	0.03	0.03	
Bivalvia		0.03	1.81	0.00	0.03	0.03	0.04	
Other	Fish eggs	0.47	0.00	0.00	0.00	10.38	0.00	0.012
	Woody debris	59.44	69.66	63.71	56.63	52.49	67.58	NS
	Green plant material	0.00	0.00	0.00	23.83	0.27	0.32	0.003
	Sand–dirt	39.36	10.54	27.02	6.29	27.83	25.03	0.001
Number of stomachs examined		32	56	18	106	125	62	
Mean SFI_{ALL}		0.033	0.014	0.011	0.012	0.027	0.011	
SD of SFI_{ALL}		0.037	0.023	0.020	0.019	0.048	0.015	
Mean SFI		<0.001	0.003	0.001	0.002	0.005	0.001	0.036
SD of SFI		0.001	0.008	0.003	0.006	0.018	0.004	

[a] Numbers are P-values, NS stands for not significant, blank rows indicate items not included in MANOVA (<1% of all contents by weight).

American shad consume mainly what they encounter, including items that are energetically rich (i.e., copepods), probably indigestible (i.e., woody debris), and energetically void (i.e., sand). American shad may consume prey both passively, by filtering as they swim, and actively, by feeding on insects at the water's surface.

One unexpected finding was the suggestion that American shad in the St. Johns River consume eggs of their own species. Various species of clupeids are thought to feed on eggs from unrelated conspecifics (Smith and Reay 1991) and blueback herring *A. aestivalis* have specifically been observed to feed on fish eggs in rivers (Simonin et al. 2007). Savoy and
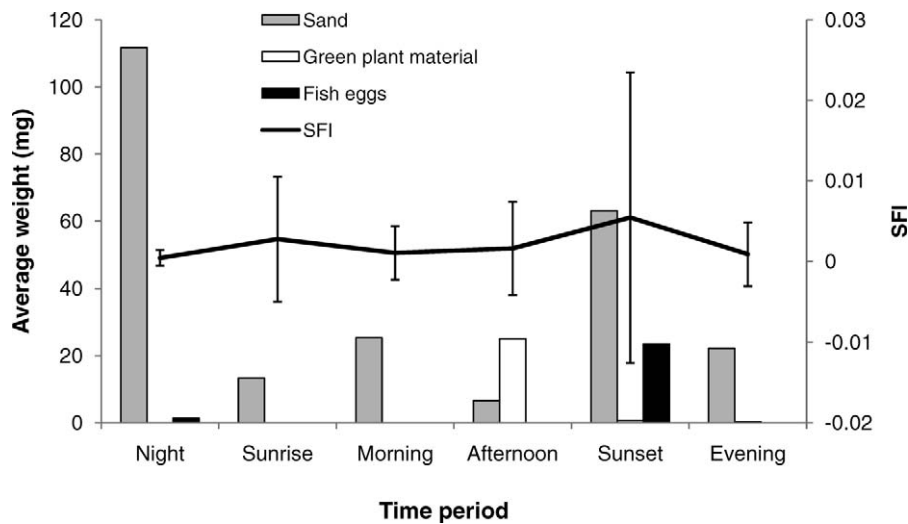

FIGURE 5.—Average weight of the stomach contents of male and female American shad combined found to differ significantly by diel time period (see Table 2) and average stomach fullness index (SFI), by diel time period. Error bars represent SDs.
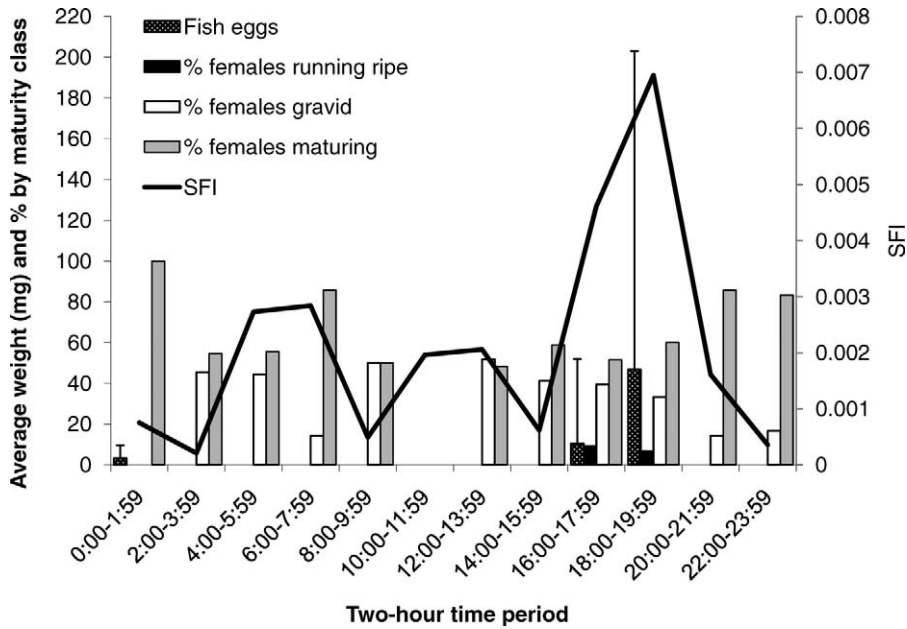
FIGURE 6.—Average weight of fish eggs collected in the stomachs of American shad and percentage of females in maturing, hydrated, and running-ripe maturity classes collected during diel sampling at Puzzle Lake in February and March, by 2-h time periods. Error bars represent SDs.

Crecco (1988) suggested that American shad consume little in freshwater and thus cannibalism of eggs and larvae was unlikely to affect the production of young. We found a low incidence of any species of eggs overall, although they did contribute considerably to the weight of contents consumed during sunset. American shad are pelagic spawners with semidemersal eggs (Jones et al. 1978), so eggs are presumably spawned in the water column and sink to the bottom. During spawning, American shad move rapidly and produce visible splashes (Walburg and Nichols 1967), which could stir fine sediments, such as sand, into the water column in shallow areas, such as at Puzzle Lake. Possibly during spawning acts recently spawned eggs are filtered incidentally along with commonly observed items, such as sand and woody debris. Additionally, splashes during spawning behavior may be one reason for sand consumption.

Variation in feeding intensity appeared mainly to be a factor of location within the St. Johns River, with maturity class being generally less influential. Feeding was highest at Mullet Lake, possibly because this area is surrounded by lakes and may have a higher concentration of zooplankton compared with other sites. Similarly, blueback herring feeding in the St. Johns River was highest at Mullet Lake compared with other areas (R. S. McBride, unpublished data). Feeding by alewife *A. pseudoharengus* in Lake Michigan is highly variable, but most consumption occurs during the fall when food is abundant (Stewart and Binkowski 1986). Feeding intensity may also be related to maturity class, with downstream fish being generally less ready to reproduce than are more upstream individuals and possibly more apt to actively feed. Although the average SFI was highest for maturing females, it was not significantly so and hydrated and running-ripe females had stomach contents also, demonstrating that while feeding may decline, it does not cease with active reproduction. Running-ripe females were collected during the early evening, suggesting that most spawning in the St. Johns River occurs during that time period, as has been observed for some individuals in the Mattaponi River (Hyle 2004); although, in many systems American shad spawn primarily between dusk and midnight (Leim 1924; Marcy 1972; Ross and Bennet 1993; Hyle 2004). The presence of running-ripe females suggests that Puzzle Lake and the nearby Econlockhatchee Tributary were often used for spawning during the 2003–2004 season. Actively spawning females may exhibit behaviors that cause them to encounter fewer items in the water column or they may be less actively filtering material. More research on the relationship between prey consumed and its abundance in specific areas would clarify feeding patterns in the spawning reach.

Although feeding clearly occurred in the freshwater

portion of the St. Johns River, consumption was low. Walter and Olney (2003) found that American shad feeding in the York River declined by almost two orders of magnitude as fish moved from the marine environment (SFI = 2.8), to the lower river (when fish were in prespawning condition, SFI = 0.5), and onto the spawning grounds (SFI = 0.05). Similarly, in the St. Johns River, feeding intensity was highest at the most downstream site. Slightly lower SFI_{ALL} values were obtained for American shad on spawning grounds in the St. Johns River (Table 1) compared with spawning grounds in the York River, but items in the stomachs of York River fish were almost exclusively plant derived and were probably indigestible. Differences in composition of stomach contents between the two systems may be a result of differences in prey abundances. Regardless, it is evident that consumption is low in freshwater systems for both iteroparous and semelparous populations of American shad.

Our study is the first that we know of to estimate daily consumption and caloric intake of American shad in any freshwater system. Estimated daily consumption is dependent on gastric evacuation rate, which is affected by water temperature, prey type, prey composition, and predator size (Kawaguchi et al. 2007; Berens and Murie 2008; Waddington 2008). Most importantly, differences in gastric evacuation rate for different prey types can affect their proportions in stomach content data, since easily digested items are removed more quickly and are thus less prevalent in the observed diet than in the actual diet. Bias in observed and actual proportions of different items can affect diet composition analysis and evaluation of daily caloric intake. Laboratory studies of gastric evacuation rates of different prey items for American shad would help better determine the differences between observed and actual consumption, as well as help obtain a more precise estimate of daily ration and the energetic benefits of freshwater feeding.

Our preliminary estimate indicates that caloric intake of American shad in the St. Johns River is low, but possibly not negligible. Bernatchez and Dodson (1987) use information from Glebe and Leggett (1981a, 1981b) to suggest that American shad in the St. Johns River require approximately 155 kJ/kg of body weight per day during the spawning migration. Using this estimate, the average American shad at Puzzle Lake consumes approximately 1.5% of the calories required daily. Considering that this percentage is very low, it is not surprising that American shad lost considerable weight during the spawning period. However, caloric intake in freshwater could still be important for biological processes, especially if it is considerably higher in some freshwater areas, such as at Mullet Lake, where the SFI was almost 20 times what it was at Puzzle Lake as a result of increased zooplankton consumption. Northern populations of American shad are iteroparous and there is evidence that many females hold back spawning and initiate active feeding soon after the spawning period to increase survival during out-migration (Olney et al. 2001; Walter and Olney 2003). In Florida, American shad literally spawn until they die, so saving or consuming energy for out-migration would not be advantageous. Besides survival and out-migration, energy from freshwater feeding could be allocated to reproduction. For white crappie *Pomoxis annularis* feeding before spawning affects egg production, with well-fed fish producing larger, but not more, eggs than starved fish (Bunnell et al. 2007). American shad are indeterminate spawners (Olney et al. 2001; Olney and McBride 2003) with high individual variability in female fecundity (Hyle 2004). Thus, it is possible that individuals in semelparous populations can spawn with greater frequency and for a longer duration, and produce larger batches or larger eggs, by assimilating calories from freshwater feeding.

In summary, despite low levels of consumption, our findings of sporadic freshwater feeding by American shad may be important for lifetime fecundity, either by increasing spawning during a specific year or by increasing survival to spawn in a future year for iteroparous populations. Although it cannot be determined with certainty, it appears that most prey intake in freshwater is done incidentally rather than actively, although fish may opportunistically consume items, such as insects, when available. Better estimates of caloric intake, feeding periodicity, and gastric evacuation are needed, especially for other river systems, since energetics may be river specific. Determining whether freshwater prey can be assimilated and used for growth of reproductive tissue would help address the bioenergetic consequences of freshwater feeding. American shad in the St. Johns River often appear emaciated later in the run, especially compared with individuals in other systems (authors' personal observation), and even a small amount of high calorie prey may help fish continue to develop oocytes throughout the spawning period.

Acknowledgments

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