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Feeding Behavior of American Shad during Spawning Migration in the York River, Virginia

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Abstract.—Throughout its native range, American shad *Alosa sapidissima* is thought to cease feeding during anadromous migration. We examined the feeding habits of American shad during spawning migration by documenting changes in diet composition and feeding that occur in mature fish in the York River, Virginia. American shad were collected prior to and after spawning at various locations on a gradient from open ocean waters to the freshwater spawning grounds. During the estuarine phase of migration, American shad fed predominantly upon mysid shrimp *Neomysis americana* and calanoid copepods. Feeding occurred during prespawning migration but decreased on the spawning grounds where plant matter comprised the majority of the stomach contents. After spawning, feeding intensity increased significantly as American shad resumed feeding on mysid shrimp and copepods during downstream migration through estuarine waters. Comparisons of diet composition and feeding intensity between the oceanic environment and the estuary indicate that calanoid copepods and planktonic shrimp dominated the diet in both environments, although feeding intensity was reduced within the estuary during the spawning migration. These results indicate that American shad in the York River feed during anadromous migration, most heavily in the middle estuary where there is an abundance of mysid shrimp. While shad lose somatic weight during migration, indicating insufficient consumption to maintain body condition, the ability to feed during some portion of migration and then soon after spawning may be important in decreasing postspawning mortality.

Introduction

The American shad *Alosa sapidissima* is an anadromous clupeid native to western North Atlantic waters from Canada to Florida. American shad spend the majority of their adult lives in open ocean waters of the continental shelf except during spawning migration when they ascend coastal tributary rivers. American shad are pelagic, filter-feeding fish that prey mainly on copepods, mysids, and euphausids (Leim 1924; Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953). During spawning migration, American shad are believed to cease feeding actively and to cease feeding entirely upon entering freshwater (Smith 1896; Leim 1924; Hatton 1940; Nichols 1959). Over the course of anadromous migration, shad experience significant energetic expenditures and weight losses, with the degree of energy loss commensurate with the level of iteroparity (Glebe and Leggett 1981a, 1981b).

The separation of spawning and feeding is a widely observed life history pattern in fishes and is particularly pronounced in the suite of diadromous fishes where adults and juveniles occupy vastly different habitats (McDowall 1987). While American shad undertake extensive migrations that remove them from their oceanic feeding habitat, they differ from obligatorily semelparous species, such as lampreys (Order: Petromyzontiformes) and Pacific salmonids *Oncorhynchus* spp., in that they retain the ability to feed during the entire spawning period, and the energetic losses that they experience are reversible when feeding resumes. Despite evidence indicating that no feeding occurs in freshwater, opportunistic feeding on insect hatches and juvenile fish (Chittenden 1969, 1976) and in experimental enclosures (Atkinson 1951) has been documented during the freshwater spawning period. This evidence, coupled with the observations that shad strike the fishing lures of anglers, indicates that American shad attempt to feed during the spawning period and suggests that the cessation of feeding represents a physical separation from suitable food sources rather then a behavioral or physiological reduction in feeding (Atkinson 1951). Presumably, those individuals that either feed to some extent during migration or resume

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feeding rapidly after spawning minimize their energetic losses. Thus, if the cessation of feeding during migration is temporary, the length of time and distance that shad are separated from food sources should be an important determinant of overall energetic expenditure and ability to repeat spawn.

This study describes the diets of American shad collected at various points during spawning migration, from coastal ocean waters to the freshwater spawning grounds of the York River, Virginia. In the York River, American shad must migrate through a lengthy brackish estuary prior to ascending to tidal freshwater spawning areas. Studies documenting the lack of feeding during migration have focused on the freshwater spawning grounds, whereas no studies have examined the feeding behavior from the ocean to the estuary to determine when feeding ceases during migration or when it resumes following spawning. The objectives of this study are (1) to examine the stomach contents of American shad at various stages of anadromous migration to determine when and where feeding ceases and resumes and (2) to compare the composition and intensity of feeding during migration with normal feeding patterns in the ocean.

Methods

American shad were collected in spring 1998 at various points along the course of spawning migration into the York River, Virginia, a tributary of the Chesapeake Bay (Figure 1; Table 1). Shad were also collected prior to spawning from coastal ocean waters off of the mouth of the Chesapeake Bay in the springs of 1998 and 2000. Oceanic samples of American shads came from fish collected by trawl in May 2000 from open ocean waters near Georges Bank. In addition, diet data from 52 shad collected in offshore waters from the Gulf of Maine to Delaware came from National Marine Fisheries Service groundfish trawl survey samples collected in 1979–2000. These data were received in raw form from the Northeast Fisheries Science Center, Fish Ecology Section. The entire collection of 456 fish (Table 1) spans a spatial gradient from offshore pelagic waters to freshwater tributaries, thus encompassing the areas encountered by adult and subadult American shad throughout their life history and particularly during spawning migration.

Fish collected by the authors in 1998 and 2000 were weighed and measured, and the sex and maturity stage were determined by macroscopic ex-

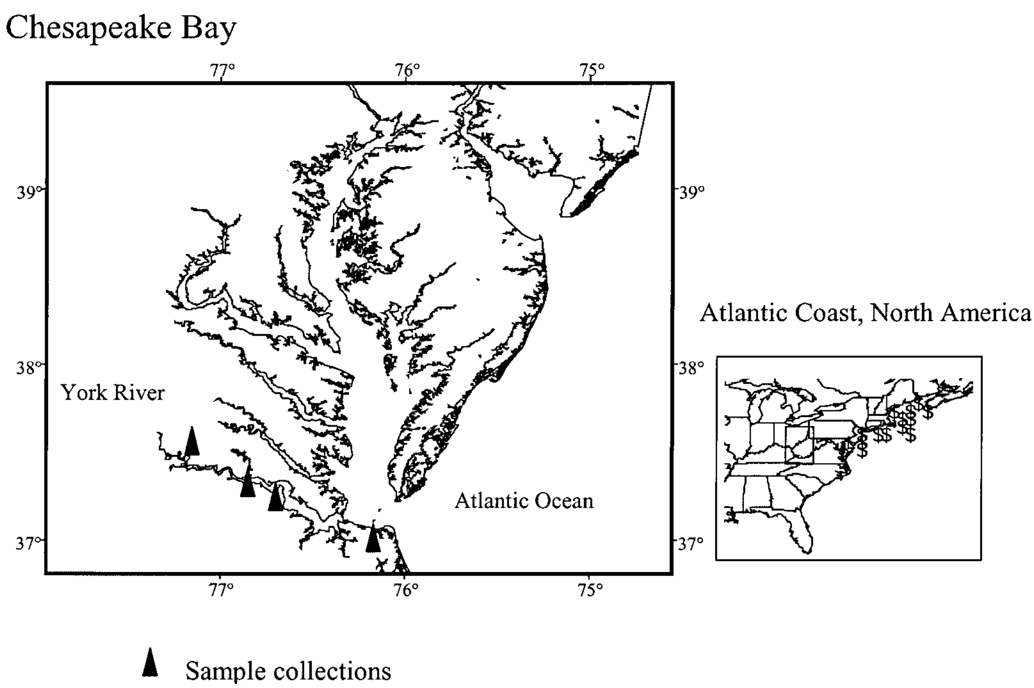

Figure 1. Map of collection locations of American shad. The left map depicts the Atlantic coast of North America with the Chesapeake Bay outlined and trawl sample collection locations (triangles) plotted. Sampling locations at the bay mouth, river mouth, river kilometers 24 and 90 on the Chesapeake Bay, and the York River, Virginia, are depicted on the right map ($).

Table 1. Distribution of American shad stomach samples by date, location, capture gear and spawning condition.

Dates	Category	Location	Gear	Spawning condition	Number
1979–1993	Open ocean	Offshore waters from Gulf of Maine to Cape Hatteras	NMFS groundfish trawl	Immature and mature, not spawning	52
23–25 May 2000	Open ocean	Hudson Canyon and Georges Bank	Trawl	Immature and mature, resting	33
12 February 2000 and 15 March 1998	Coastal ocean prespawn	Inshore coastal waters of Virginia	Gill net	Prespawning	20
17 March 1998–14 May 1998	River mouth prespawn	York River mouth	Pound net	Prespawning	74
16 March 1998–11 May 1998	km 24 prespawn	York River, km 24	Gill net	Prespawning	84
31 March 1998–6 May 1998	Spawning area	York / Pamunkey River, km 90	Gill net	Running ripe / hydrated	77
14 April 1998–11 May 1998	River km 24 postspawn	York River, km 24	Gill net	Partially or fully spent	26
22 April 1998–14 May 1998	River mouth postspawn	York River mouth	Pound net	Partially or fully spent	90

amination and confirmed for a limited number of fish by histology (Olney et al. 2001). For the purposes of this study, gonadal maturity stage was only reported as either prespawning or postspawning condition. Stomachs were removed and weighed with stomach contents, then opened and weighed empty to get stomach content weight. Stomach contents were then either frozen or placed in 5% formalin for further examination.

Stomach contents were sorted to lowest possible taxa, patted dry, and weighed wet (±0.001 g). Diet composition was analyzed using percent wet weight. Fish were sorted into seven categories for analysis based on location of capture and spawning condition (Table 1).

To measure the intensity of feeding, we used a stomach fullness index (SFI) modified from Hureau (1970, cited in Berg 1979) but with the fish total length (mm) used instead of fish weight:

$$\text{SFI} = \frac{\text{Stomach content weight}}{\text{Fish total length}^3} \times 100{,}000.$$

Stomach fullness index values were calculated for all fish regardless of the presence or absence of stomach contents. The percentage of full stomachs was also used to determine intensity of feeding. Length cubed was chosen as the denominator in the calculation of the SFI to approximate weight since shad lose significant weight during the spawning migration and are not known to decrease in length.

Nonparametric analysis of variance was performed with the Kruskal–Wallis test (Zar 1996) to test for significant differences in stomach fullness between fish collected at different locations and spawning stages. Corrections for tied ranks were employed using a correction factor. To test for differences between groups of fish, a posteriori nonparametric multiple comparisons were performed using a test proposed by Dunn (Zar 1996). A significance level of a = 0.05 was used for all tests.

Results

Of the 456 American shad sampled, 71.3% had food present. Of those fish with food present, 158 were randomly selected for diet composition analysis. Diet composition varied throughout the course of migration (Figure 2). Calanoid copepods dominated the diet in open ocean waters, accounting for 95% of the diet by weight (Table 2). *Calanus finmarchicus* was the most abundant copepod in the diet. A euphausid shrimp, northern krill *Meganyctiphanes norvegica*, accounted for 3% of the diet.

In inshore coastal waters, calanoid copepods remained the dominant component of the diet (65%), although the species consumed changed to *Centropages typicus* and *Acartia* spp. Mysid shrimp *Neomysis americana* accounted for 33% of the diet in inshore coastal waters.

Within the estuary, *N. americana* became the primary forage, accounting for 77% and 98% of the

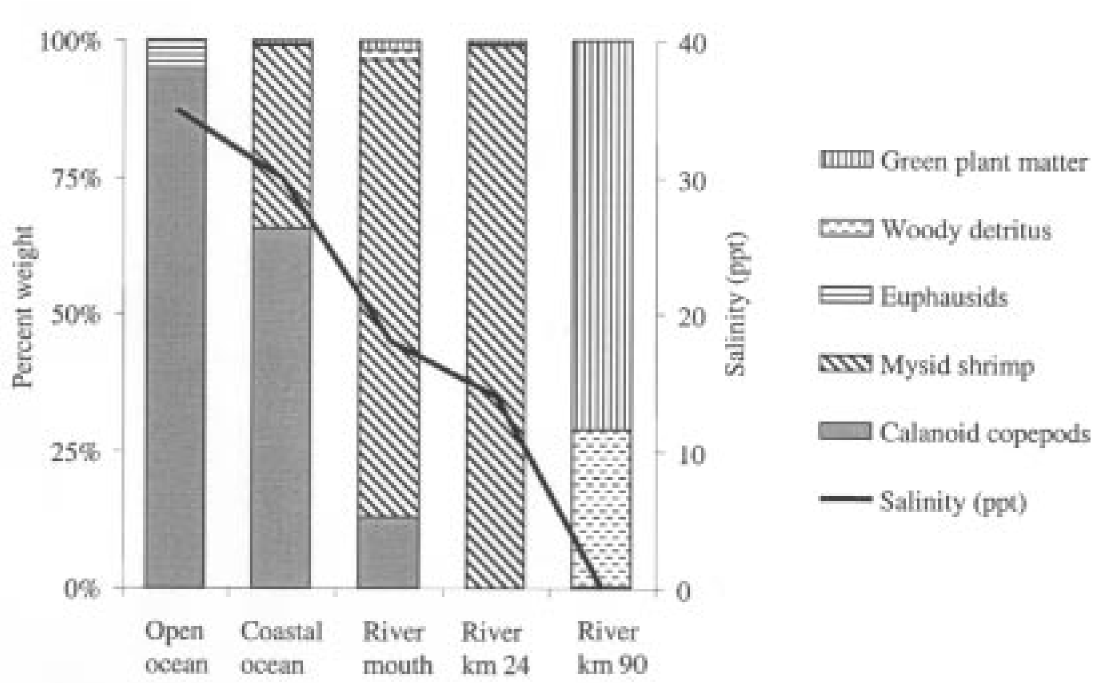

Figure 2. Percent diet composition of American shad by weight at each sampling location. The solid line denotes the salinity at each location in parts per thousand (ppt).

weight of stomach contents in fish at the river mouth and river kilometer 24, respectively. Calanoid copepods were second in importance by weight and consisted of *Acartia* and *Eurytemora* spp. Minor amounts of other crustaceans were found including cumaceans, sevenspine bay shrimp *Crangon septemspinosa,* and gammarid amphipods. On the spawning grounds, the stomach contents consisted almost entirely of woody and green plant matter.

Feeding intensity, as measured by both the stomach fullness index and the percentages of full stomachs, varied during the course of spawning migration (Figure 3). Stomach fullness values and the percentage of full stomachs decreased with proximity to the freshwater spawning grounds during the prespawning period and then increased as the fish completed spawning and migrated downstream. American shad captured in ocean waters had significantly higher SFI values than at all other locations and spawning stages (Tables 3, 4; Kruskal–Wallis nonparametric rank test, H = 144.25, df = 6, $P < 0.05$). Subsequent multiple comparisons indicate that fish in the open ocean had significantly higher SFI values than did all other fish with the exception of prespawning fish captured in coastal waters and postspawning fish captured at river mile 15. As the fish migrated into estuarine waters of the York River, mean stomach fullness values decreased along with the percentages of fish having food present in their stomachs. On the freshwater spawning grounds, fish had significantly lower SFI values than at other locations, with the exception of postspawning fish at the river mouth. The percentage of fish on the spawning grounds with full stomachs was also the lowest observed (18%), and the stomach contents consisted primarily of plant matter.

Discussion

Both the diet and the feeding intensity of American shad varied from open ocean waters to freshwater spawning grounds. Similar to other published reports of shad feeding (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953; Leim and Scott 1966), we found calanoid copepods and euphausid shrimp to be the dominant prey in the open ocean. While other food was present in the diet, the primary forage for shad in the ocean is

Table 2. Percent by weight of food items by location and spawning condition in the stomachs of American shad.

	All stages	Prespawning			Spawning	Postspawning	
Prey	Open ocean	Coastal ocean	River mouth	River km 24	River km 90	River km 24	River mouth
Phylum chaetognatha	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Class Osteichthyes							
Anchoa mitchilli	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Merluccius bilinearis	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Fish remains	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Fish eggs	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Class Cephalopoda	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Class Crustacea							
Order Thoracica	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Order Calanoida	67.3	65.0	17.7	0.1	0.0	0.2	0.0
Unknown copepods	27.2	0.0	0.0	0.0	0.0	0.0	0.0
Order Cumacea	0.0	0.0	0.0	0.2	0.0	0.1	0.0
Order Isopoda	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Order Amphipoda							
Gammaridae	0.0	0.0	0.0	0.4	0.0	0.0	0.0
Hyperiidae	0.01	0.0	0.0	0.0	0.0	0.0	0.0
Order Mysidacea							
Neomysis americana	0.0	33.1	77.0	97.9	0.2	97.6	96.9
Unknown mysids0.2	0.0	0.0	0.0	0.0	0.0	0.0	
Order Euphausiacea							
Meganyctiphanes norvegica	3.0	0.0	0.0	0.0	0.0	0.0	0.0
Unknown euphausids	2.0	0.0	0.0	0.0	0.0	0.0	0.0
Order Decapoda							
Crangon septimspinosa	0.0	0.2	0.1	0.3	0.0	0.0	0.0
Palaemonetes pugio	0.0	0.0	0.8	0.0	0.0	0.0	0.0
Unknown crustacean	0.0	0.3	0.0	0.0	0.4	0.0	0.0
Class Gastropoda	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Class Hydrozoa	0.0	0.0	0.4	0.3	0.2	0.0	0.9
Detritus							
Woody matter	0.0	0.1	2.3	0.6	28.4	0.0	1.1
Green plant matter	0.0	0.8	1.7	0.2	70.7	2.0	1.1
Total number of stomachs	85	20	74	84	77	26	90
Percent full stomachs	85	95	69	59	18	92	34
Mean stomach fullness index	2.798	0.506	0.154	0.44	0.046	1.236	0.164
(SD)	(2.45)	(0.59)	(0.27)	(0.54)	(0.06)	(1.35)	(0.29)
Mean observed fork length	301.7	489.6	461.4	477.7	478.8	508.2	446.4
(SD)	(82.7)	(28.4)	(32.5)	(32.5)	(31.4)	(50.3)	(56.7)

Calanus finmarchicus, a large (5–10 mm) calanoid copepod, andnorthern krill, a large euphausid shrimp. Both of these species are dominant planktonic fauna in the North Atlantic and exhibit diel vertical migrations which American shad are believed to follow (Neves and Depres 1979). In open ocean waters, American shad had the highest percentage of full stomachs and highest stomach fullness values, indicative of active feeding. Fish examined from the open ocean were large juveniles or adults captured during the nonspawning period and were assumed to exhibit natural feeding behavior to provide a contrast with fish captured during spawning migration. The inclusion of both subadult and mature American shad in the oceanic samples combines fish of differing ages; however, given the low sample sizes of fish available and the absence of documented ontogenetic differences in diet between large juveniles and adults, these fish were combined into a single sample.

American shad captured in nearshore coastal waters fed as intensely as fish captured in open ocean waters. These fish were captured in February and March , had enlarged, developing gonads, and were migrating into coastal rivers for spawning. The SFI values for fish in coastal waters were lower than for open-ocean fish but were not significantly different. Additionally, a higher percent-

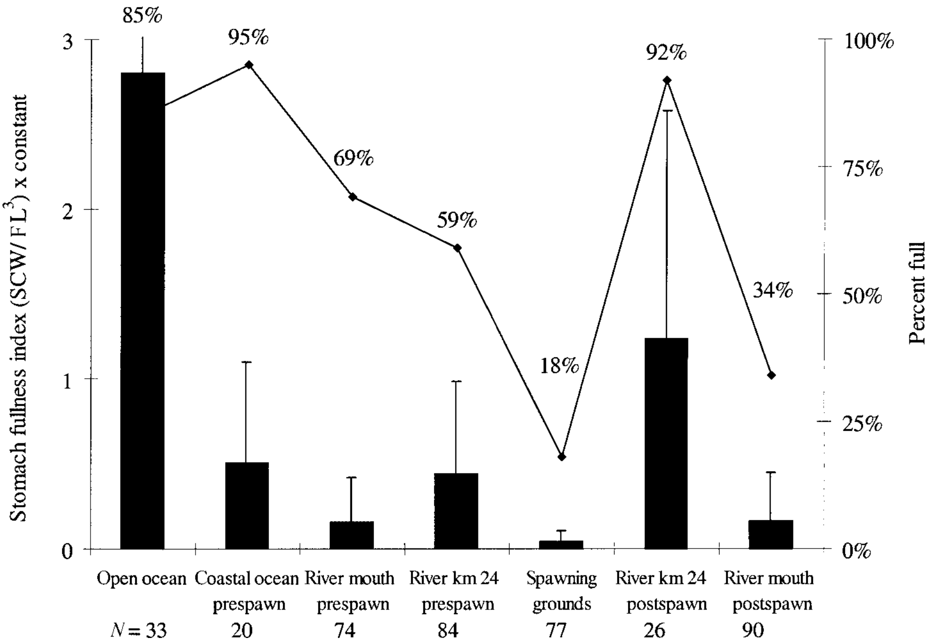

Figure 3. On the left vertical axis, the stomach fullness index calculated as (stomach content weight; SCW) / (fish fork length; FL^3) is plotted as solid bars for each location and spawning stage. Error bars represent standard deviations. On the right vertical axis, the percentage of full stomachs is plotted as a line for each location and spawning stage. Numbers below the locations are sample sizes.

age of fish from coastal waters had food in their stomachs, indicating that active feeding occurred. Diet composition changed when coastal and estuarine copepods (*C. typicus, Acartia* spp.) replaced the oceanic *C. finmarchicus* as the major constituents of the diet and the estuarine mysid shrimp *N. americana* increased in importance, replacing euphausids.

The species composition of the diet changed and feeding intensity decreased when American shad entered the estuary, though the overall pattern of feeding on the most abundant and larger planktonic crustaceans remained similar to that observed in oceanic waters. *Acartia* spp. and *C. typicus* replaced *C. finmarchicus* and *N. americana* replaced *M. norvegica* as dominant planktonic crustaceans both in the diet of American shad and in the environment. The increased importance of mysid shrimp reflects increased mysid density in the mid-estuary and compares with Stevens' (1971) study of American shad feeding in California rivers. Stevens found that mysid shrimp also dominated the diet, and he observed a significant positive relationship between the occurrence of food in shad stomachs and the concentration of zooplanktonic prey in the water. Shad experience different planktonic prey regimes as they migrate from the open ocean to the estuary, and their diet reflects these changes in zooplankton species composition but remains dominated by large copepods and larger planktonic shrimp.

While on the spawning grounds, American shad cease to feed except upon woody and green plant debris. This material is of little nutritional value, and it is unlikely that American shad can digest woody material. Numerous authors have documented a similar absence of feeding in freshwater (Smith 1896; Leim 1924; Hatton 1940; Nichols 1959). There remains, however, a question of whether the cessation of feeding is due to a change in behavior or solely to the absence of suitably-sized or abundant food, as Atkinson (1951) proposed. This latter hypothesis appears well founded since the freshwater zooplankton community is generally composed of far fewer species and in lower densities than communities in marine environments (Horne and Goldman 1994). Rivers, in particular, lack larger, holoplanktonic crustaceans suitable as prey for adult American shad. As for the act of striking a lure, this may be considered an attempted feeding act, and it is likely that, given sufficiently abundant and suitably-sized prey, American shad would feed during freshwater residency as they do in brackish estuaries. Chittenden's (1969,

Table 3. Kruskal-Wallis nonparametric rank test of stomach fullness by location and spawning condition. Median values are untransformed stomach fullness values. The Kruskal-Wallis test statistic (H) is corrected for tied ranks. $H = 144.25$, df = 6, $P = 0.000$.

Location (Spawning condition)	N	Median	Average rank	Z
1. Open ocean	85	1.767	337.5	8.76
2. Coastal ocean	20	0.191	296.8	2.42
3. River mouth (Prespawning)	74	0.045	225.5	-0.04
4. River km 24 (Prespawning)	84	0.051	210.9	-1.16
5. River km 90 (Spawning)	77	0.002	145.5	-5.95
6. River km 24 (Postspawning)	26	0.788	332.8	4.3
7. River mouth (Postspawning)	90	0.004	156.4	-5.58
Overall	456		226	

Table 4. Dunn's multiple comparisons based on the Kruskal-Wallis nonparametric ranks (Table 3).

Dunn's multiple comparisons	SE	Difference (R_b-R_a)	q	$Q_{(0.05,7)}$	Conclusion
1v2	33.07	40.7	1.23	2.936	NS
1v3	20.72	112	5.40	2.936	S
1v4	20.17	126.6	6.28	2.936	S
1v5	20.51	192	9.36	2.936	S
1v6	29.21	4.7	0.16	2.936	NS
1v7	19.82	181.1	9.14	2.936	S
2v3	33.52	71.3	2.13	2.936	NS
2v4	33.19	85.9	2.59	2.936	NS
2v5	33.39	151.3	4.53	2.936	S
2v6	39.34	-36	-0.92	2.936	NS
2v7	32.97	140.4	4.26	2.936	S
3v4	20.90	14.6	0.70	2.936	NS
3v5	21.22	80	3.77	2.936	S
3v6	29.71	-107.3	-3.61	2.936	S
3v7	20.56	69.1	3.36	2.936	S
4v5	20.68	65.4	3.16	2.936	S
4v6	29.33	-121.9	-4.16	2.936	S
4v7	20.01	54.5	2.72	2.936	NS
5v6	29.56	-187.3	-6.34	2.936	S
5v7	20.34	-10.9	-0.54	2.936	NS
6v7	29.09	176.4	6.06	2.936	S

1976) observations of American shad feeding on hatching insects supports this conclusion by indicating that shad will feed in freshwater when suitable prey are available. Leonard and McCormick (1999) observed higher proportional energy losses in American shad during the freshwater stages of spawning migration than in the estuarine stages and attributed these energy losses to the greater difficulty of migration in freshwater. It is likely, however, that the decline in food consumption during this period also accounts for the high rate of energy loss within freshwater.

American shad resumed feeding during postspawning migration with mysid shrimp accounting for almost all of the stomach contents. Stomach fullness values were similar to those of coastal and open ocean waters, and the percentage of full stomachs increased to 92% in the mid-estuary at river kilometer 24. Variability in stomach fullness remained high, indicating that not all fish actively fed, but some fish fed heavily. This resumption of feeding in spent or partially spent fish probably represents a return to natural feeding patterns and is likely important in beginning the process of reclaiming the energy expended in spawning migration.

As the ability to repeat spawn is correlated with the magnitude of energetic expenditures, those fish that feed closer to the spawning grounds and resume feeding rapidly after spawning would increase their likelihood of surviving the event. Estimates of repeat spawning in York River female American shad range from a 5-year average of 19% (Leggett and Carscadden 1978) to a 3-year average of 55% (Olney and Hoenig 2001), indicating that some, but not all, fish return to spawn again. Glebe and Leggett (1981b) observed that York River American shad experience lower total energy losses than do American shad in either the St. Johns River, Florida, or the Connecticut River. They attributed these differences to a shorter migration distance and lesser river gradient in the York River. However, the closer proximity of the spawning grounds to estuarine food sources coupled with the observation that many fish leave the river with partially spent ovaries (Olney et al. 2001) may also serve to decrease total energy expenditures. It is unknown, however, but likely that these fish resorb the partially spent gonadal material..

The low feeding intensity at the river mouth both prior to and after spawning likely was a result of pound-net confinement. American shad in this location were captured in fixed pound nets and confined for an undetermined time period of 1–4 d. Net feeding can complicate stomach content analysis for piscivorous fish that are captured in trawls and passive gear that captures and confines both predator and prey (Hodgson and Cochran 1988; Hayward et al. 1989), though no effects have been documented for planktivorous fish. In the case of shad, the pound net confined the predator while allowing planktonic prey to pass through, resulting in lower percentages of full stomachs and lower stomach fullness values, depending upon the time of confinement. The fish captured with gill nets in this study did not appear to suffer the same gear bias because gill nets confined the predator for a shorter period of 0–24 h

While American shad in the York River experienced a decrease in feeding during migration similar to decreases observed in other river systems, feeding did occur prior to and after spawning within the estuary. The cessation of feeding occurred on the freshwater spawning grounds, and it seems likely that the amount of time spent on the spawning grounds, coupled with the distance and difficulty of the route traveled, determine the magnitude of energy expenditure. American shad are not obligatorily semelparous as are Pacific salmon and lampreys, and the ability to survive spawning correlates with the degree of energy loss (Glebe and Leggett 1981b; Bernatchez and Dodson 1987). Shad that feed actively prior to and after spawning may mitigate their energy losses and have a higher likelihood of repeat spawning. Thus is it not surprising that, in the York River, where American shad have a relatively short migration and are not far removed from their food sources, there is a high frequency of repeat spawning and lower energy expenditures than in other rivers.

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