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American Shad in the Columbia River

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Abstract.—American shad *Alosa sapidissima* from the Hudson River, New York, were introduced into the Sacramento River, California, in 1871 and were first observed in the Columbia River in 1876. American shad returns to the Columbia River increased greatly between 1960 and 1990, and recently 2–4 million adults have been counted per year at Bonneville Dam, Oregon and Washington State (river kilometer 235). The total return of American shad is likely much higher than this dam count. Returning adults migrate as far as 600 km up the Columbia and Snake rivers, passing as many as eight large hydroelectric dams. Spawning occurs primarily in the lower river and in several large reservoirs. A small sample found returning adults were 2–6 years old and about one-third of adults were repeat spawners. Larval American shad are abundant in plankton and in the nearshore zone. Juvenile American shad occur throughout the water column during night, but school near the bottom or inshore during day. Juveniles consume a variety of zooplankton, but cyclopoid copepods were 86% of the diet by mass. Juveniles emigrate from the river from August through December. Annual exploitation of American shad by commercial and recreational fisheries combined is near 9% of the total count at Bonneville Dam. The success of American shad in the Columbia River is likely related to successful passage at dams, good spawning and rearing habitats, and low exploitation. The role of American shad within the aquatic community is poorly understood. We speculate that juveniles could alter the zooplankton community and may supplement the diet of resident predators. Data, however, are lacking or sparse in some areas, and more information is needed on the role of larval and juvenile American shad in the food web, factors limiting adult returns, ocean distribution of adults, and interactions between American shad and endangered or threatened salmonids throughout the river.

Introduction

American shad *Alosa sapidissima* are native to eastern North America, spawning and rearing in rivers from Florida to Newfoundland. Juvenile American shad migrate downriver, and adults spend 3–6 years in the western Atlantic Ocean before returning to spawn in their natal stream (Judy 1961; Olney and Hoenig 2001). American shad are iteroparous, and individuals may live to at least 13 years (M. King, Virginia Commonwealth University, personal communication). During the late 1800s and early 1900s, numerous stocks of American shad declined in their native rivers, and conservation efforts have been developed to recover populations (e.g., Hightower et al. 1996; see Olney et al. 2003, this volume; St. Pierre 2003, this volume). American shad have, however, become abundant in several river systems in western North America, following their transcontinental introduction in the late 1800s.

In 1871, Seth Green, an enterprising fish culturist, was asked by the California Fish Commission to transport and release American shad into the Sacramento River (Green 1874). During June 1871, Green used the recently-completed transcontinental railway to move 12,000 fry across the country in seven days. Fry were transported in four 30.3-L (8-gal) milk cans, and Green made stops for freshwater or cooling ice in Illinois, Nebraska,

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and Utah. Although air temperatures were occasionally over 38°C during the trip, Green arrived with about 10,000 surviving fry that he released 443 km upriver from Sacramento into the Sacramento River (Green 1874).

The transplanted fry survived, and the population grew and expanded its range. Adult American shad migrated north and south along the Pacific coast and soon became established in rivers from southern California to Alaska. The northward range extension from San Francisco Bay was likely aided by the Davidson Current, which could transport fish up to 72 km per day (Burt and Wyatt 1964). Juvenile or adult American shad probably moved southward in the California Coastal Current. David Starr Jordan collected adult American shad in the Columbia River in 1880, and spawning American shad were first recorded in the Columbia River in 1885 (Smith 1896). American shad occur as far south as Baja California, Mexico (Hart 1973), and have been reported in the Anadyr' River, Russia, although fish were recorded there only during 1 year (Chereshnev and Zharnikov 1989).

In this paper, we summarize the current information on American shad in the Columbia River. We review historical data on adult distribution, abundance, and fisheries in the river and present some new data on the ages of returning adults. We present new data on the distribution of larval and juvenile American shad and the diet of juveniles. We review existing data from published reports, compare our understanding of American shad in the Columbia River to studies in eastern North America, and identify information needs.

Study Area

The Columbia River is the third largest river in North America, with an average annual flow rate at the river's mouth of about 6,655 m^3/s, draining a watershed of 671,000 km^2 (Ebel et al. 1989). The river originates in the Rocky Mountains of British Columbia, flows southward through Washington, turns westward through the Cascade Mountains, and enters the Pacific Ocean (Figure 1). Beginning in 1933, a series of large hydroelectric dams were

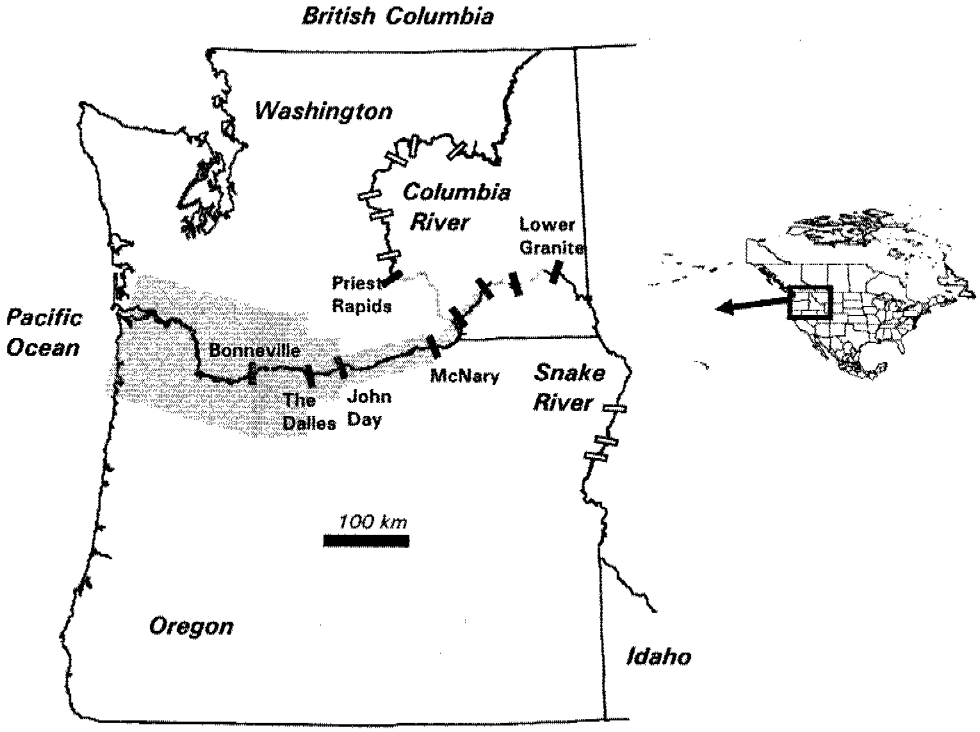

Figure 1.—The range of adult American shad in the Columbia River. American shad have successfully migrated past five dams on the Columbia River (Bonneville, The Dalles, John Day, McNary, and Priest Rapids) and four dams on the Snake River (as far as Lower Granite). American shad have not passed dams shown as open rectangles. For 2000, the percent of the adult American shad run migrating past dams is indicated by the width of the light gray bars relative to Bonneville Dam passage as 100%.

built on the Columbia River and its largest tributary, the Snake River (Figure 1). Most of these dams created "run-of-the-river" reservoirs with flushing times less than 4 d (Ebel et al. 1989). From the late 1930s to the present, water temperature in the lower Columbia River has averaged 16.1–18.2°C during the summer period (June 1–August 15), with some of this variation correlated with climatic regime shifts (Petersen and Kitchell 2001).

Methods

Dams on the lower Columbia and Snake rivers have fish ladders and methods for counting adult Pacific salmon *Oncorhynchus* spp. as they migrate upriver, and these systems have been used to enumerate adult American shad passage at dams. Daily and annual counts of adult and juvenile American shad at dams were collected by the U.S. Army Corps of Engineers (CBR 2001) and the Fish Passage Center (FPC 2001). Commercial and recreational catch statistics are from state agency summaries (ODFW and WDFW 2000).

Mobile hydroacoustic surveys for juvenile American shad were conducted in John Day Reservoir between river kilometers (rkm) 382 and 389 on September 7 and September 24, 1994. Prior to a survey, cross-sectional transects were plotted on a map at 161-m intervals, and subsamples of transects were randomly selected. Surveys were conducted on selected transects, moving from downstream to upstream in the study area. Hydroacoustic data were collected using a Bio Sonics, Inc. model ES2000 echosounder operating at 420 kHz. The echosounder transmitted a 0.4-ms pulse at 5 pings/s through a 6°/15° dual-beam transducer aimed vertically. Additional hydroacoustic equipment consisted of a model 151 chart recorder and a portable computer equipped with Bio Sonics ESP_Dbm software (Bio Sonics, Inc. 1990). To determine species composition of fish detected during hydroacoustic surveys, we deployed a midwater trawl randomly within the study area. Both shallow (5-m) and deep (15-m) strata were sampled with the trawl.

American shad larvae and early juveniles were sampled in the John Day Reservoir and below Bonneville Dam during June–September in 1995 and 1996. Larvae were collected in pelagic waters at night using surface ichthyoplankton tows. In shoreline areas, larvae and juveniles were collected during daytime with a small beach seine (15.2 × 1.2 m; see Gadomski and Barfoot 1998; Barfoot et al. 1999; and Gadomski et al. 2001 for detailed methods).

The diet of juvenile American shad was determined from fish collected with midwater trawls in John Day Reservoir (rkm 384) during September 1994. Samples were frozen and dietary items were identified to the lowest possible taxon with the aid of a dissecting microscope.

Adult American shad were sampled on June 25, 2001, at the Bonneville Dam fish ladder, and scales and otoliths were removed for aging. Whole otoliths were aged and scales were mounted for reading.

Adult American shad have been captured as bycatch between about 34°N and 49°N latitude in bottom trawl surveys conducted by the National Marine Fisheries Service in the Pacific Ocean (M. E. Wilkins, National Marine Fisheries Service, personal communication). Surveys have been conducted during summer months every 3 years since 1977 using a high-opening Nor'eastern trawl fished at depths ranging from 55 to 500 m. American shad, and other pelagic or semipelagic fishes, are captured while the net is being set and retrieved. The number of American shad collected during 1995, 1998, and 2001 were used to describe the general distribution of shad on the continental shelf (inside the 500-m isobath) along the coast from California to British Columbia.

Results

Adult Abundance, Distribution, and Exploitation

The number of adult American shad migrating up the lower Columbia River has increased greatly in the last 60 years from an average of 16,700 adults between 1938 and 1957 to over 2 million adults between 1988 and 1992 (Figure 2; Quinn and Adams 1996). In recent years, as many as 4 million adult American shad have migrated past Bonneville or The Dalles dams (Figure 2). The total number of adult American shad entering the Columbia River is not known, but the run is probably much higher than the dam counts since many adults spawn below Bonneville Dam (see below), which is 235 km from the river's mouth. The dramatic increase in the number of adult American shad coincided quite closely with construction of dams on the lower Columbia and Snake rivers (Figure 2).

Catches of American shad in the ocean trawl surveys ranged from 0 (74% of all hauls; $N = 1{,}559$ hauls) to 620 in a single haul in 1998 off the northern Washington coast. During the 3 years examined, American shad occurred primarily along the coasts of Washington and southern Vancouver Island, British Columbia, although small numbers were also caught off Oregon and California (Figure 3). The

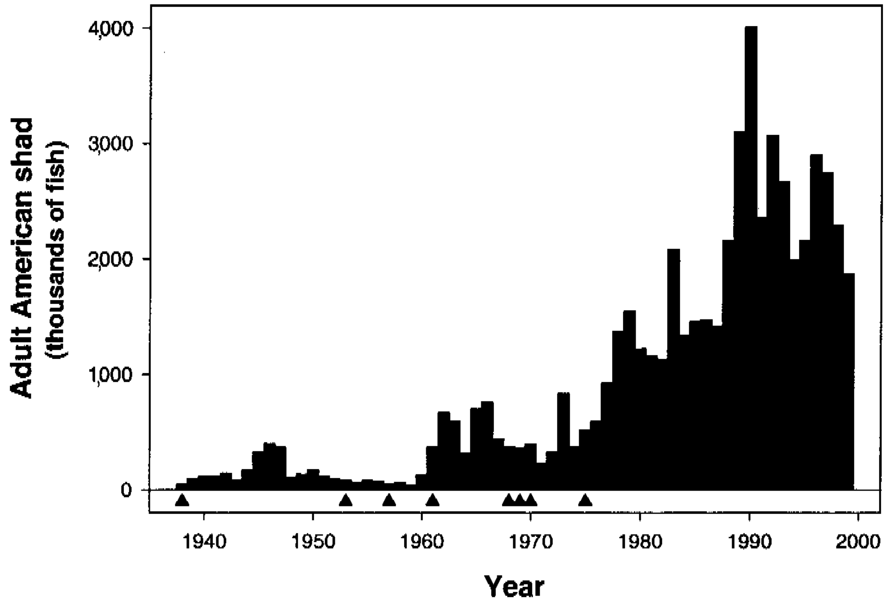

Figure 2.—Counts of adult American shad in the Columbia River at Bonneville Dam (1938–1999) and construction dates (triangles, bottom axis) for dams on the lower Columbia and Snake rivers.

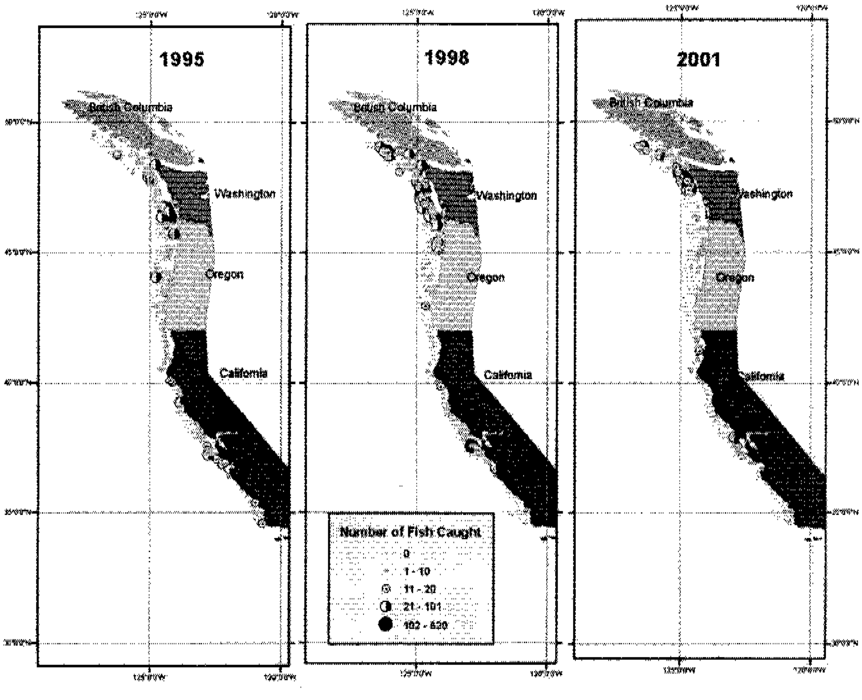

Figure 3.—Relative number of adult American shad caught as bycatch in bottom trawl surveys during 1995, 1998, and 2001. All trawls were conducted on the continental shelf, within the 500-m isobath.

average catch per haul was almost an order of magnitude higher off the coast of Washington and British Columbia in each year compared to catches off the coast of Oregon and California. For example, the catch per trawl haul in 1998 was about 19 shad off Washington and British Columbia but was less than 2 shad off Oregon and California. American shad collected off the Washington and British Columbia coasts averaged 347 mm fork length (FL; range = 190–500 mm; $N = 705$) and 331 mm FL (range = 110–480 mm; $N = 696$) during 1998 and 2001, respectively; fish were not measured during the 1995 and earlier surveys. Length–frequency distributions suggested at least three, and perhaps four, age-classes during the 1998 and 2001 surveys.

Adult American shad migrate into the Columbia River from May through July, and adults spawn soon after migration (Figure 4). Adult passage at Bonneville Dam (rkm 235) is generally highest during mid-June, while adult passage peaks slightly later at John Day Dam (rkm 347; Figure 4). Adults do not appear to feed during their migration up the river (Hammann 1980), although this has not been examined in detail.

Based on otoliths, returning adult American shad ranged from 2 to 6 years old, although the sample size was small ($N = 25$). Most aged adults (56%; 14 of 25) were 3 years old, with one 2-year-old fish and ten fish aged 4–6 years old. Three-year-old fish averaged 392 mm FL (938 g; $N = 14$), which was similar to the average size of 4–6 year-old fish (384 mm FL; 833 g; $N = 10$). Based on spawning checks on otoliths, eight fish (32%) were repeat spawners, five were spawning for the first time, and three were spawning for the second time.

Counts of adult American shad were highest at Bonneville and The Dalles dams, with fairly rapid declines in percent passage at the next few dams upriver (Figure 1); 53% of adults migrated into John Day Reservoir while 22% reached McNary Reservoir. Adult American shad have been observed as far upriver as Priest Rapids Dam (rkm 639) on the Columbia River and Lower Granite Dam on the Snake River (695 km from the ocean; Figure 1), although passage at these dams is less than 1% of the total adult count. Since 1993, adult passage counts at Priest Rapids and Lower Granite dams have remained fairly constant (FPC 2001), suggesting little ongoing range extension further up the Columbia or Snake rivers.

From 1990 to 1995, the average annual commercial harvest rate was 4.2%, and the recreational catch (kept) was 4.8% (ODFW and WDFW 2000). During the last 10 years, the commercial and recreational catch of American shad has remained quite stable, with one peak in the commercial fishery during 1996 (Figure 5). American shad are caught in a commercial gill-net fishery below Bonneville

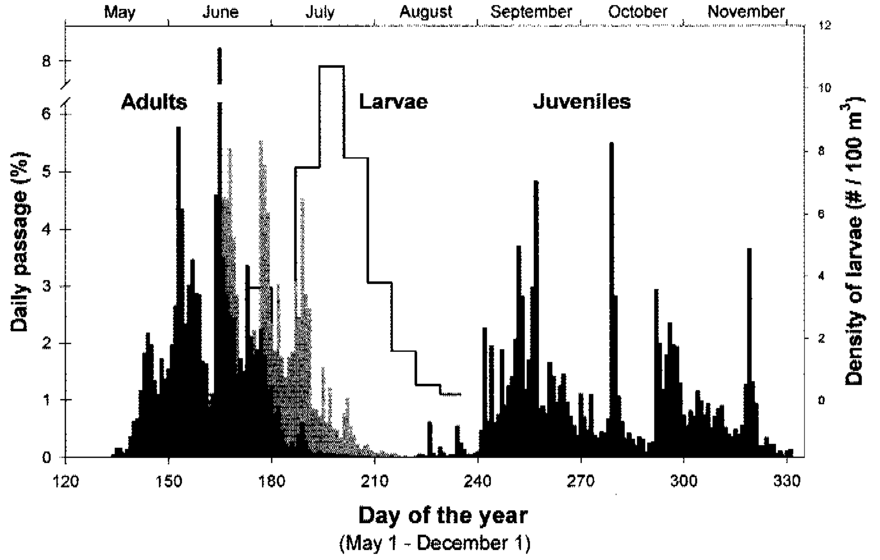

Figure 4.—Daily passage (%) of adult American shad at Bonneville (black bars; left distribution) and John Day (gray bars) dams and juvenile American shad at McNary Dam (black bars; right distribution) during 2000. The stepped line shows the density of American shad larvae in plankton tows in John Day Reservoir (1995–1996; see Figure 6A). Juvenile data for John Day Dam are not shown since counts at this dam do not continue into November.

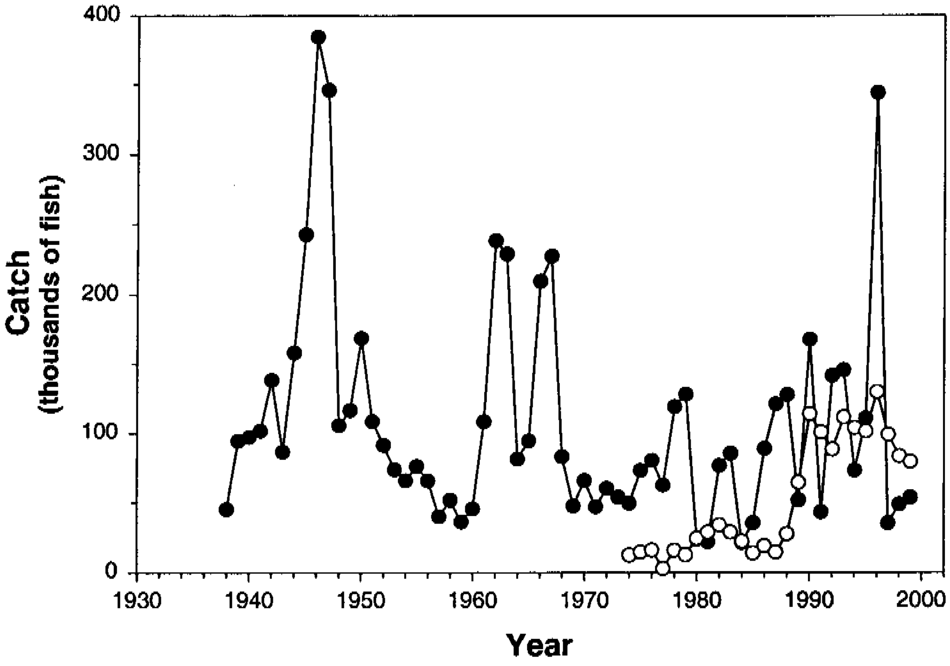

Figure 5.—Catch of adult American shad in the commercial (solid circles) and the recreational (open circles) fisheries in the Columbia River, 1934–1999. Data are from ODFW and WDFW (2000).

Dam, which takes place during the peak of the adult American shad migration in late May and early June.

Early Life History

During 1995 and 1996, American shad larvae and early juveniles were among the five most abundant taxa collected by plankton tows and beach seine hauls in main channel and backwater habitats in the John Day Reservoir and below Bonneville Dam (D. M. Gadomski, unpublished data). In the main channel, American shad larvae (8–25 mm total length; TL) first appeared in plankton in late June, were most abundant in July, and diminished in early August (Figure 6A, B). Larvae apparently recruited to shorelines during July and August (Figure 6C, D). Young-of-the-year juveniles were observed in nearshore samples from late July through September (Figure 6E, F), suggesting transformation of most individuals during this period. For the 2 years sampled, larval and juvenile densities varied considerably, especially below Bonneville Dam (Figure 6). Larval and juvenile American shad have also been observed in small numbers in slough habitats of the Hanford Reach, a free-flowing section of the Columbia River below Priest Rapids Dam (Gadomski, unpublished data).

Juvenile American shad were observed throughout the water column using trawl and hydroacoustic surveys (Figures 7, 8). Estimated densities of juvenile American shad were higher during nighttime hydroacoustic surveys than during daytime surveys (Figure 7). During the early September surveys, fish density was as much as 10–12 times higher at night than during the day. The density of fish was highest at about 7 m deep, and the majority of fish occurred between 5-m and 20-m water depths (Figure 7A). Later in September, nighttime fish density was only about 2 times higher than daytime fish density, and a subsurface peak in density was less obvious (Figure 7B). Cross-channel transects conducted during day and night, combined with trawl surveys to verify species, suggested that juvenile American shad stayed near the bottom or were in inshore areas during the day and dispersed throughout the water column at night (Figure 8). The hydroacoustic system used was not able to resolve targets within 30 cm of the bottom. Juvenile American shad were 100% ($N = 38$ fish) of midwater trawl catches in early September and 97% ($N = 215$ fish) of the catch during late September.

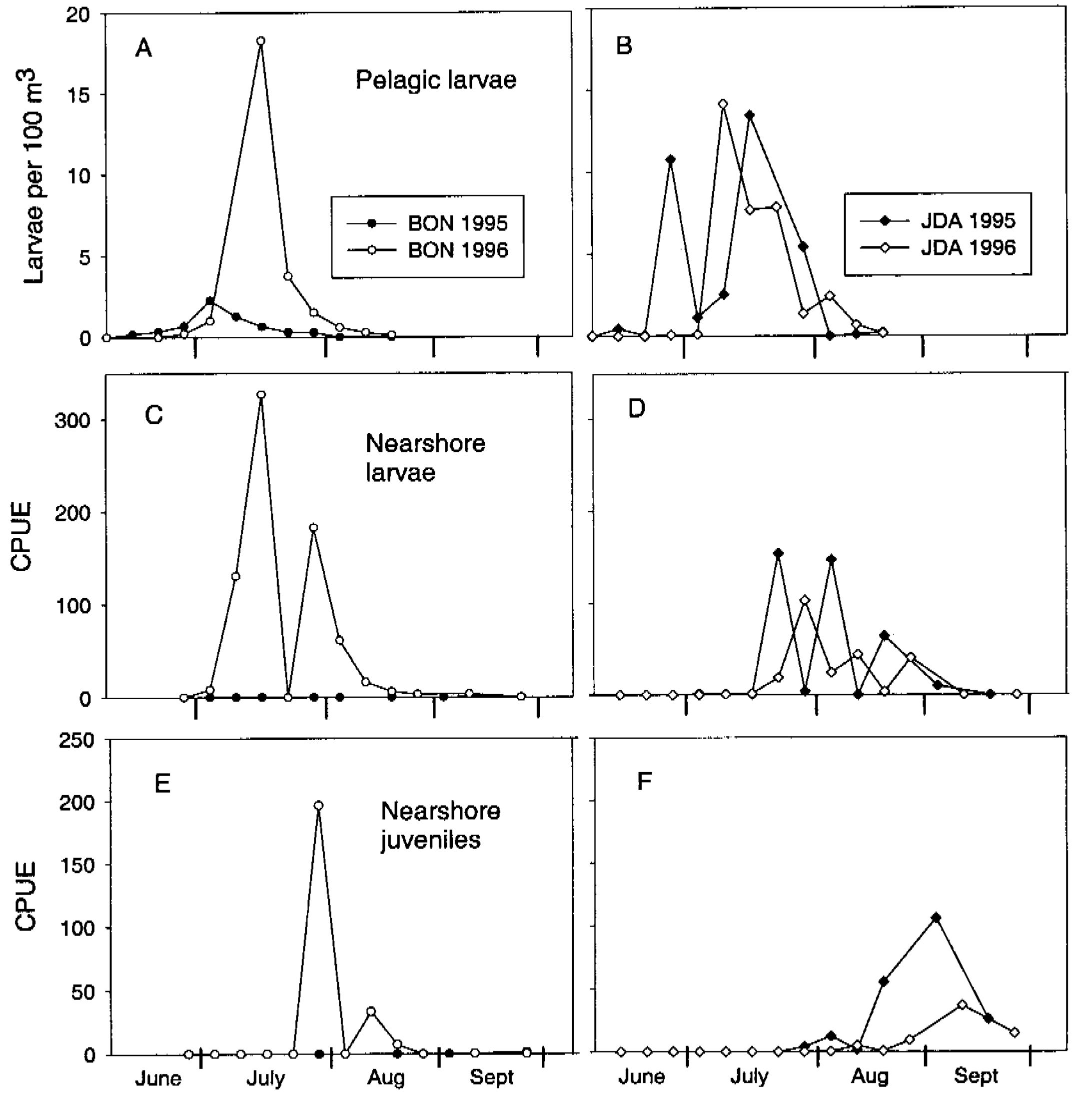

Figure 6.—Mean weekly abundances of American shad larvae sampled in nighttime ichthyoplankton tows (A and B), and larvae (C and D) and juveniles (E and F) in daytime beach seine hauls. Collections were during 1995 and 1996 in main-channel areas below Bonneville Dam (BON; A, C, and E) and in the John Day Reservoir (JDA; B, D, and F). Sample sizes were 12–24 for ichthyoplankton averages (A and B) and 2–6 for beach seine averages (C–F); CPUE = catch per unit effort.

Other species commonly caught in midwater trawling included juvenile chinook salmon *O. tshawytscha*, juvenile steelhead *O. mykiss*, and northern pikeminnow *Ptychocheilus oregonensis*.

The diet of juvenile American shad collected in John Day Reservoir consisted primarily of cyclopoid copepods (Table 1). Calanoid copepods, numerous taxa of cladocerans, dipteran larvae, and a few other items were observed in the diet of juveniles (Table 1).

Discussion, Synthesis, and Information Needs

Success of American Shad in the Columbia River

The reasons for the success of American shad in the Columbia River have not been identified, but several hypotheses might be proposed; low fishing pressure, successful passage at dams, appropriate adult spawning habitat, and good conditions for

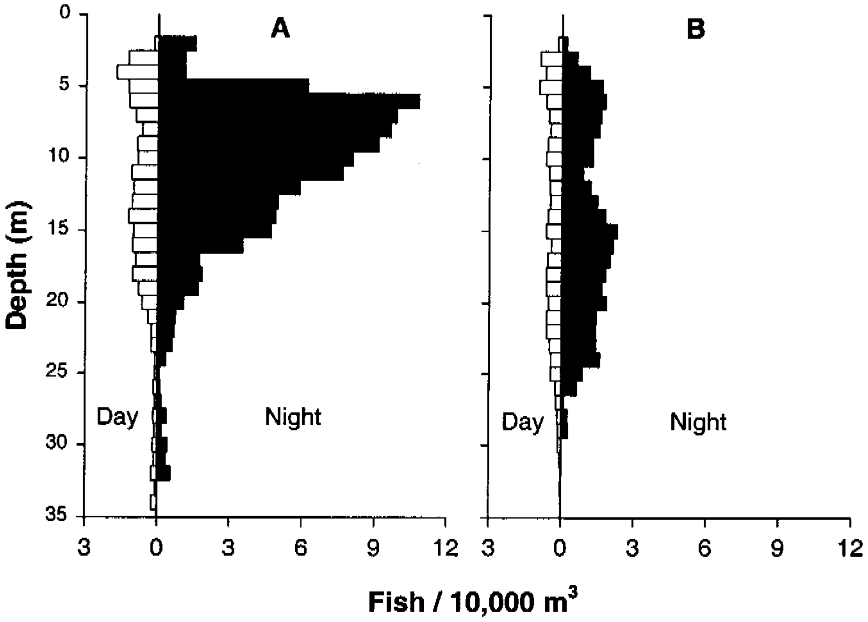

Figure 7.—Diel vertical distribution of juvenile American shad in John Day Reservoir on (A) September 7, 1994 and (B) September 27, 1994. In each panel, the daytime distribution is to the left (white bars) and the nighttime distribution is to the right (black bars).

survival of early life history stages may be especially relevant factors.

Historically, the exploitation of American shad has been limited, partly due to its low value as a food fish on the Pacific coast. Craig and Hacker (1940) noted that some American shad were consumed locally, and occasionally some were shipped to Atlantic coast cities, but demand was never sufficient for a strong commercial fishery. Columbia River American shad (and roe) were first canned in the late 1800s. During 1913–1936, a total of 168,222 cases were packed (Craig and Hacker 1940). Currently, the Columbia River American shad are exploited through only limited sport and commercial harvest. Markets have not kept pace with the supply of American shad on the Columbia River. The American shad are sold in small niche markets that remain a closely guarded secret of the fishers (S. King, Oregon Department of Fish and Wildlife, personal communication). The American shad fishery in the Columbia River coincides with depressed runs of spring and summer chinook salmon, sockeye salmon *O. nerka*, and summer steelhead. Thus, even if a large market were to de-

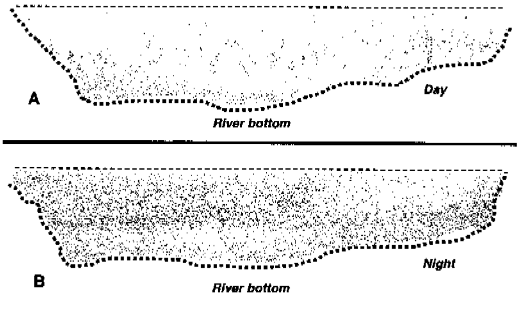

Figure 8.—Vertical and horizontal distribution of juvenile American shad in John Day Reservoir during (A) day (1200 hours) and (B) night (2200 hours), from cross-river hydroacoustic transects. The water surface is the dashed line and the river bottom is the heavy dotted line.

Table 1.—Frequency of occurrence and diet by weight of juvenile American shad ($N = 24$) collected in John Day Reservoir, Columbia River.

Taxa	Occurrence (%)	Diet (wet weight; %)
Cyclopoid copepods	100	85.8
Calanoid copepods	95	5.7
Bosmina	95	4.2
Daphnia	83	2.2
Alona	75	0.1
Leptodora	63	1.8
Sida	29	0.1
Moina	8	<0.1
Chydorus	8	<0.1
Dipteran larvae	4	<0.1
Pelecypoda	4	<0.1
Corophium	4	<0.1
Ilyocryptus	4	<0.1
Other		0.4

velop for Columbia River American shad, harvest by gill nets or nonselective gear might be restricted in order to protect valued salmon.

Fish ladders at Columbia River dams, constructed to allow passage of adult Pacific salmon, have been used successfully by American shad adults in their upstream migration. In fact, the ladders at some dams have been modified to facilitate American shad passage since high numbers of American shad congregated at ladder entrances were believed to impede adult Pacific salmon passage (Monk et al. 1989). The ladders at John Day Dam, completed in 1968, had only submerged orifices, and American shad had poor passage through these ladders, with as few as 18% of adults passing successfully (Monk et al. 1989). John Day Dam ladders were modified in the early 1970s with overflow slot weirs which improved American shad passage to more than 70% (Monk et al. 1989). Fish ladders at other dams have also been modified to facilitate the migration of American shad. Although these modifications were ultimately for the benefit of adult salmon migrants, they also opened up large reservoirs for spawning shad and contributed to American shad success in the system.

Impoundment of the Columbia and Snake rivers may have improved conditions for American shad spawning and early life stages. Although American shad spawn in a variety of habitats, spawning is usually observed where water velocity is less than 0.7 m/s and temperature ranges between 14°C and 24.5°C (Stier and Crance 1985; Ross et al. 1993). Water velocities in reservoirs and much of the free-flowing river below Bonneville Dam meet these criteria. Additionally, impoundment has created earlier seasonal warming and later cooling of water in the Columbia River during the last 60 years (Quinn and Adams 1996; Quinn et al. 1997). Since water temperature regulates the timing of American shad migration (Leggett and Whitney 1972), this has resulted in earlier upriver migrations of American shad, as much as 38 d earlier in 1993 compared to 1938 (Quinn and Adams 1996). The consequence of this earlier spawning date for the population dynamics of American shad has not been examined.

Impoundment of the Columbia and Snake rivers may also have improved conditions for growth and survival of larval and juvenile American shad. Year-class strength of American shad is established during the early larval stage, with the late juvenile stage possibly being another critical period (Crecco et al. 1983; Crecco and Savoy 1984; Limburg 2001). However, conditions required for optimal growth and survival of larvae and juveniles are complex and vary somewhat with the river system. In the Connecticut River, Crecco and Savoy (1987) reported that larval cohorts of American shad had greater survival when they emerged during periods with higher temperatures (>18°C), low flows, and higher water transparency, all conditions common in shorelines of impounded areas of the Columbia River (Barfoot et al. 1999). In the upper Delaware River, Ross et al. (1997) found that premigratory juvenile American shad (<72 mm TL) used all habitat types, but maximum suitability was in shallow shorelines (0.5–1.5 m) with warmer waters (19.5–24.5°C) and lower turbidities. Conversely, in the Sacramento–San Joaquin River system, the abundance of young American shad was positively correlated with river flow, which may have increased quality and quantity of nursery habitat and provided better dispersal of young fish (Stevens and Miller 1983).

Separation of the Columbia River and eastern North American stocks of American shad for over 100 years may have resulted in an evolutionary adaptation in juvenile growth rate (Rottiers et al. 1992). Columbia River fish had higher growth rates (mass per day) than did Delaware River fish when reared in ponds for 91 d (Rottiers et al. 1992), and the two stocks differed genetically (one locus; creatine kinase). American shad from the Columbia River grew from 0.2 g (31 mm TL) to 6.1 g (95 mm TL) during the experiment while water temperature was declining fairly steadily from about 23°C to11°C. The average monthly water temperature at Bonneville Dam for 1980–1996 ranged from about 21.5°C in August to about 7.0°C in December (Petersen, unpublished analyses). Other data on the growth rate of juvenile American shad in the Columbia River are not available.

Little is known about American shad during their time in the Pacific Ocean, including their distribution and movement, growth rate, feeding, and other factors. American shad was not one of the target species in the trawl data that we analyzed, but many other pelagic and semipelagic fishes are caught while the net is descending or being recovered from some depth. The relatively high catches of American shad observed north of the Columbia River mouth suggests that a significant portion of the population migrates into these waters. This pattern is also observed in Atlantic stocks of American shad, which tend to migrate northward from their spawning streams (Leggett and Whitney 1972). The slightly higher numbers of adult American shad observed off central California (Figure 3) were likely migrants from the Sacramento River system. The distribution pattern that we observed, higher numbers off the Washington and British Columbia shores, may have been partially caused, however, by the timing of the surveys beginning in early June and proceeding from central California northward, concluding in August (1998 and 2001) or September (1995). Many adult shad may have been in freshwater during June and July when the ocean trawling was being conducted, thus reducing the observed numbers off California and Oregon.

Finally, the rapid increase in American shad within the Columbia River also coincides fairly well with the 1977 climatic regime shift in the north Pacific Ocean and in the Pacific Northwest (Beamish et al. 1999; Petersen and Kitchell 2001). Improved survival of juvenile and adult American shad in the ocean might have contributed to the rapid rise in the numbers of shad returning to the Columbia River during the 1970s and 1980s (Figure 2). If American shad occupy areas of the north Pacific Ocean different from Pacific salmon, then they might have better survival than salmon during specific climatic periods.

Trophic Relationships

Larval and juvenile American shad have relatively high densities in the Columbia River, which may be sufficient to produce changes in trophic levels. Our maximum density estimate for juvenile American shad in John Day Reservoir (1.2 fish/1,000 m^3; Figure 7A) was greater than total prey fish densities (all species combined) in Lake Tahoe (0.07 fish/1,000 m^3) and Lake Washington (0.9 fish/1,000 m^3) but was less than the density measured in Strawberry Reservoir, Utah (2.4 fish/1,000 m^3; Beauchamp et al. 1999). Rainbow smelt density in Horsetooth Reservoir, Colorado, averaged about 1 fish/1,000 m^3 during 1990–1996 (Johnson and Goettl 1999). The maximum density of American shad larvae in John Day Reservoir, measured with plankton nets, was about 150 fish/1,000 m^3 (Figure 6A). Gadomski and Barfoot (1998) found American shad larvae to be the second most abundant taxon in the upper John Day Reservoir (main channel, plankton tows) and the most abundant taxon in a backwater area.

The effects of American shad on the aquatic community in the Columbia River have not been studied, but invasive planktivores, especially clupeids and osmerids, have been shown to cause dramatic effects at several trophic levels in other large aquatic systems (Crowder 1980; Johnson and Goettl 1999). Haskell et al. (2001) observed a decline in the abundance and size of *Daphnia* spp. during August and September in two Columbia River reservoirs, which they speculated was caused by feeding of abundant American shad. The relatively high density and widespread distribution of juvenile American shad throughout the water column (Figures 7, 8) suggest they could have a strong influence on the lower trophic levels in these reservoirs.

Besides these direct trophic influences, larval and juvenile American shad may also compete with native and introduced fishes for habitat or food resources during the late summer and fall period. Juvenile American shad consume a diet similar to many other species whose larvae or juveniles cooccur in backwater or main-stem river habitats. For example, Rondorf et al. (1990) found that zooplankton (mostly *Daphnia* spp.) were a primary component of subyearling chinook salmon diets in reservoir habitats. Most stocks of salmon have migrated out of the system before American shad become abundant, but the median date of passage at McNary Dam of wild subyearling chinook salmon from the Snake River occurs in early August (W. Connor, U.S. Fish and Wildlife Service, personal communication), when larval American shad are transitioning into the juvenile phase (Figure 4). American shad may also compete with resident species whose larvae or juveniles use main-stem rivers (Gadomski and Barfoot 1998; Gadomski et al. 2001). Further complicating the feeding relationships, small American shad are occasionally eaten by subyearling chinook salmon (K. Tiffan, U.S. Geological Survey, unpublished data), although the details of this interaction are unknown.

The spatial and temporal overlap of American shad and other species is not limited to the reservoirs. Large numbers of juvenile American shad migrate into the Columbia River estuary where they continue to feed and grow (McCabe et al. 1983; Bottom and Jones 1990). Bottom and Jones (1990) collected American shad during all months of the year and in a variety of habitats in the estuary. Multivariate analysis suggested that American shad habitat was similar to the habitat of salmonid species (Bottom and Jones 1990). McCabe et al. (1983) identified *Corbicula maniliensis*, an introduced bivalve, and calanoid copepods as the principal prey of American shad in pelagic samples from the estuary. Diet overlap and habitat indices were moderate to high in the estuary between American shad and chinook salmon, coho salmon, and steelhead (McCabe et al. 1983). In the pelagic zone of the estuary, the average size of American shad sampled was 172 mm TL in May and 239 mm TL in August

(McCabe et al. 1983); these fish were 1 or 2 years old. In the intertidal zone, the average length of American shad collected in September was 62 mm TL, and these fish would have been young of the year (McCabe et al. 1983).

Juvenile American shad are abundant during late summer and fall throughout the lower Columbia River, and are thus a potential source of food for both fish and avian predators. Studies in several rivers in eastern North America demonstrate the role of juvenile American shad in predator diets (e.g., Juanes et al. 1993; Johnson and Ringler 1998). Major fish predators in the Columbia River are northern pikeminnow, smallmouth bass *Micropterus dolomieu*, and walleye *Stizostedion vitreum* (Rieman et al. 1991; Ward et al. 1995). Northern pikeminnow have been intensively studied as predators of juvenile salmon in the Columbia and Snake rivers (Thompson 1959; Rieman et al. 1991; Ward et al. 1995; and many others). Thompson (1959) examined the gut contents of over 3,500 northern pikeminnow collected throughout 1955 and early 1956. He does not mention observing American shad in any samples, although much of his data were pooled into broad taxonomic categories. In more recent studies, the diet of northern pikeminnow during late summer and fall often includes a high proportion of juvenile American shad. Based on a 4-year study in John Day Reservoir, Poe et al. (1991) found that northern pikeminnow "switched to nonsalmonid fishes—primarily prickly sculpin *Cottus asper* and American shad" during August. Petersen et al. (1994) sampled northern pikeminnow below Bonneville Dam in late August and early September of 1990 and 1991. In 1990, juvenile American shad were 78% of the diet, while in 1991, juvenile American shad were about 5% of the diet of northern pikeminnow. The high percentage of American shad in the diet during 1990 coincided with high passage indices of American shad at Bonneville Dam, while the low diet percentage observed during 1991 occurred when American shad passage was relatively low (Petersen et al. 1994). Recent sampling of northern pikeminnow have further confirmed that juvenile American shad are often a significant component of the diet of northern pikeminnow (Petersen and S. Sauter, U.S. Geological Survey, unpublished data).

The occurrence of juvenile American shad in the diet of northern pikeminnow could be producing faster rates of growth, and larger predators at a given age. Juvenile American shad have a relatively high energy density compared to crayfish or other fishes, which they likely replace in the diet of omnivores such as northern pikeminnow. For example, the energy density of crayfish, juvenile salmonids, and juvenile American shad are about 4.5, 4.7, and 5.7 kJ/g wet mass, respectively (Cummins and Wuycheck 1971; Rondorf et al. 1985; Roby et al. 1998). Using a bioenergetic model (Petersen and Ward 1999), the predicted growth of northern pikeminnow increased significantly when the proportion of juvenile American shad in the diet was increased from zero to 30% during August through October (Petersen, unpublished analyses). This increased availability of a high-energy prey could produce significantly faster growth during fall months, and potentially larger size-at-age.

Similar results might be expected for other predator species if American shad are replacing low-energy prey types or stimulating faster feeding rates than occurred on native prey communities. Poe et al. (1988) observed American shad in the diets of smallmouth bass and walleye during August, although not in great numbers, perhaps because their sampling was earlier than the peak abundance of juvenile American shad (Figure 4). American shad may also compose part of the diet of other predators or omnivores that occur in the river, such as white sturgeon *Acipenser transmontanus* (M. Parsley, U.S. Geological Survey, personal communication).

The potential importance of larval and juvenile American shad in the diets of predaceous birds is largely unstudied since most work has been conducted during spring and summer months, focusing on juvenile salmonids as prey. Avian predators include Caspian terns *Sterna caspia*, double-crested cormorants *Phalacrocorax auritus*, brown pelicans *Pelecanus occidentalis*, and various gulls *Larus* spp. (Ruggerone 1986; Roby et al. 1998; D. Roby, Oregon State University, personal communication). American shad have been detected in the diets of double-crested cormorants and gulls, and brown pelicans are abundant in the estuary during August and September when American shad are abundant (Roby, personal communication).

Management Considerations and Information Needs

Adult American shad have become so abundant in the Columbia River that concerns have been raised about their effects on the migration of adult and juvenile salmon, chiefly at dams. The upstream migration of adult sockeye and summer chinook salmon, in particular, coincides with the return migration of adult American shad. Accumulations of large numbers of adult American shad has caused avoidance or delay of salmon at fish ladder entrances (Monk et al. 1989). Adult American shad in the juvenile bypass system at McNary Dam blocked subyearling chinook salmon passage and caused mortality in the collection system (Basham et al. 1982, 1983). Most of these passage problems have been resolved with modifications to fish ladders or collection facilities (Monk et al. 1989; Merchant and Barila 1998).

Specific recommendations for overall management of the American shad population in the Columbia River Basin would appear to be premature, until there is a better understanding of the role of this species. If management of American shad is deemed necessary in the future, however, some information is available to develop controls on the population. American shad adults are reluctant to enter submerged orifices and also have difficulty negotiating some weirs (Monk et al. 1989; Haro and Kynard 1997). Various studies on factors affecting American shad behavior at passage facilities have been conducted (e.g., Haro and Kynard 1997; Kynard and Buerkett 1997), which might be used to develop systems that discourage adult passage. A system for collecting and disposing of large numbers of American shad would be required during the beginning years of the removal operation. Huppert and Fluharty (1995) roughly estimated the cost of such a program at US$1 million annually for about five years (in 1995 dollars). Expansion or further development of the commercial and recreational shad fisheries might also be considered.

Considering the widespread occurrence of American shad in the Columbia River, it is surprising that several management plans and ecosystem reviews for the Columbia River Basin fail to even mention American shad, much less its potential importance (e.g., ISG 1996; NRC 1996; USFWS 2000; NWPPC 2001). These documents are generally oriented toward salmon recovery, but they discuss introduced predators, changes in temperature, conditions for salmonid passage, and a large array of topics—but fail to mention the most abundant anadromous fish in the river system! Some management plans (e.g., SRSRT 1994; NMFS 1995), on the other hand, recognize the potential importance of American shad in the aquatic community and to salmon recovery. These plans recommend studies on the population ecology of American shad, elimination of American shad above Bonneville Dam, and minimization of their abundance below Bonneville Dam (e.g., SRSRT 1994).

Our understanding of how the American shad population influences riverine and reservoir communities in the Columbia River Basin is poor. We have summarized the principal data that exist, but much of these data were collected during 1 or 2 years at a few sites. Little information exists on long-term trends or spatial variation in patterns. No attempts have been made to test the hypotheses that we have suggested, plus many others that could be proposed about the role of introduced American shad in the Columbia River. More information is needed on the role of larval and juvenile American shad in the food web, factors limiting adult returns, ocean distribution of adults, and interactions between American shad and endangered or threatened salmonids throughout the river.

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