# Ocean distribution of the American shad (*Alosa sapidissima*) along the Pacific coast of North America

**William G. Pearcy (contact author)**[1]
**Joseph P. Fisher**[2]

Email address for contact author: wgpearcy@coas.oregonstate.edu

[1] College of Oceanic and Atmospheric Sciences
Oregon State University
Corvallis, Oregon 97331

[2] Cooperative Institute for Marine Resources Studies
Hatfield Marine Science Center
Oregon State University
Newport, Oregon 97365

**Abstract**—We examined the incidental catches of American shad (*Alosa sapidissima*) taken during research cruises and in commercial and recreational landings along the Pacific coast of North America during over 30 years of sampling. Shad, an introduced species, was mainly found over the shallow continental shelf, and largest catches and highest frequency of occurrences were found north of central Oregon, along the coasts of Washington and Vancouver Island, and in California around San Francisco Bay. Migrations to the north off Washington and Vancouver were seen during spring to fall, but we found no evidence for large-scale seasonal migrations to the south during the fall or winter. The average weight of shad increased in deeper water. Sizes were also larger in early years of the study. Most were caught over a wide range of sea surface temperatures (11–17°C) and bottom temperatures (6.4–8.0°C). Abundance of shad on the continental shelf north of 44°N was highly correlated with counts of shad at Bonneville Dam on the Columbia River in the same year. Counts were negatively related to average weights and also negatively correlated with the survival of hatchery coho salmon (*Oncorhynchus kisutch*), indicating that survival of shad is favored by warm ocean conditions. Examining the catch during research cruises and commercial and recreational landings, we concluded that American shad along the Pacific coast have adapted to the prevailing environmental conditions and undertake only moderate seasonal migrations compared with the long seasonal migrations of shad along the Atlantic coast of North America. We suggest that the large spawning populations in the Columbia River and San Francisco Bay areas explain most of the distributional features along the Pacific coast.

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American shad (*Alosa sapidissima*), the largest member of the family Clupeidae, is a euryhaline, anadromous fish native to the east coast of North America, where it ranges from Florida to the Bay of Fundy. American shad undertake extensive ocean migrations along the east coast of North America to the north in the summer, and south in the fall and winter, before returning to natal rivers in the spring to spawn. Adults usually spend 3–6 years in the ocean before returning to spawn in natal rivers. Juveniles migrate downstream in the fall, but some may reside in estuaries more than a year (Talbot and Sykes, 1958; Walburg and Nichols, 1967; Leggett, 1973). According to tagging studies, their extensive ocean migrations, of sometimes thousands of kilometers during one season, are closely correlated with 13–18° sea surface isotherms (Leggett, 1973; Leggett and Whitney, 1972) and 7–13°C bottom temperatures (Neves and Depres, 1979).

Little is known about the ocean life of American shad (hereafter referred to as "shad") along the west coast of North America, although long migrations, like those in the Atlantic, have been postulated (Leggett and Whitney, 1972; Moyle, 1976; Petersen et al., 2003). We examine recent catches of American shad along the Pacific coast of North America from research surveys, 1977–2008, as well as from landings of shad by commercial or sport vessels, thus expanding the data provided for the Pacific coast by Petersen et al. (2003) and Leggett and Whitney (1972). We compare similarities in distributions and seasonal migrations along the Pacific coast with those along the Atlantic coast of North America.

American shad were first introduced to the Pacific coast of North America from the eastern United States in 1871. About ten thousand shad from the Hudson River were released into the Sacramento River after shipment across the country in 8-gallon (31.3-L) milk cans by the California Fish Commission (Green, 1874). Several other shipments were made between 1871 and 1881 (Smith, 1896). Shad migrated rapidly to the north and south. They were introduced into the Columbia River, and the Willamette and Snake rivers, in 1885 and 1886 (Skinner, 1962; Craig and Hacker, 1940). However, shad had appeared in the Columbia River several years before these introductions, and this occurrence indicated the rapid movements of fish planted earlier in California (Welander, 1940; Oregon Fish Commission, 1951). Shad eventually were found in British Columbia in 1891, and later as far north as Alaska and as far south as Baja California (Hart, 1973). They have been reported as far west as Kamchatka, Russia, but established spawning populations there are not known (Chereshnev and Zharnikov, 1989).

Adult and juvenile shad have been reported in many bays and estuaries along the west coast of United States from Grays Harbor, Washington, to San Francisco Bay, California (Emmett et al[1]). Their distribution in inland and coastal waters along the Pacific coast is known mainly from fishery landings. Large commercial catches of shad have been made in rivers in Oregon, Washington, and California. A fishery existed in the Columbia River, as well as in Oregon coastal streams in the early 1900s. Landings in other rivers (Siuslaw, Umpqua, Smith, Coos, and Coquille) in Oregon, where shad spawned, averaged 192 metric tons per year (t/yr) during 1962–72 (Mullen and Conover[2]). The fishery in the Umpqua River landed an average of 180 t annually after 1923 (Skinner, 1962). Each of these rivers apparently supported its own spawning run of shad, although some recoveries of tagged fish have been reported in other rivers (Mullen[3]). In the Columbia River, counts of shad passing Bonneville Dam to spawn during May through July have increased greatly over the past 70 years because of the completion of dams and creation of large reservoirs, from fewer than 17,000 before 1960 to over 2–5 million after 1990 (www.cbr.washington.edu/dart/, accessed November 2010). Several hundred thousand shad are landed annually by commercial and sport fisheries in the Columbia River (Petersen et al., 2003). Adults are even found in the Snake River above Lower Granite Dam, 600 km from the ocean (Quinn and Adams, 1996). However, the major spawning areas for shad in the Columbia River are thought to be below Bonneville Dam where large numbers of juvenile shad are found in the estuary (Cleaver, 1951; Oregon Fish Commission, 1951; Hamman, 1981; Petersen et al., 2003). In Washington, breeding populations of shad are known from Puget Sound, the Chehalis River, and Willapa Bay (Wydoski and Whitney, 2003; Emmett et al.[1]).

In California, large runs of shad migrate into the Sacramento–San Joaquin River Delta to spawn where juvenile shad have been collected. Smaller runs are found in the Klamath, Eel, Salinas, and Russian rivers (Skinner, 1962; Allen et al., 2006; CDFG[4]). The shad fishery in the San Francisco Bay area peaked in 1917 when over 2500 t were landed. Between 1918 and 1945 the catch averaged 362 to 1800 t and then declined. In 1957 the commercial fishery in the bay was closed and there now exists only a sport fishery (Skinner, 1962; Moyle, 1976).

Shad were first reported in British Columbia in 1891; small numbers were caught between 1914 and 1946 in fresh water. They were also reported from several regions in the ocean along the coast (Carl et al., 1959), but according to McPhail (2007), there is no evidence of reproduction in British Columbia.

Our objectives were to document the distributional patterns of American shad along the Pacific coast of North America and to compare these patterns with those known from the Atlantic coast.

## Materials and methods

American shad were captured incidentally in both pelagic and benthic research surveys from 1977 through 2008 from California to British Columbia, as well as in commercial and recreational fisheries. National Oceanic and Atmospheric Administration's (NOAA) Alaska Fisheries Science Center (AFSC) triennial bottom trawl surveys from 1977 to 2004 provided extensive data on shad catches. Nor'eastern trawls (with 27.4-m head-rope and 12.7-cm mesh in the body, 9-cm mesh in the codend and a 3.2-cm stretch mesh liner) were fished during the day at about 5.6 km/h for one half hour and from depths of 55 to 500 m during the months of May through September, 1977–2004 (Stauffer, 2004). Cruises began during different months of the year, beginning in California and progressing northward to Vancouver Island.

Shad were also caught by the Northwest Fisheries Science Center (NWFSC) in bottom trawls (Aberdeen-style high-opening net, 26-m head rope, 3.8 cm liner in the codend), fished during the daytime to depths of 55–1280 m at a nominal tow duration of 15 min on the bottom at 4.0 km/h, mainly from late May to late July (early cruise) and again from late August to late October (late cruise), 2003–08. The trawl surveys were conducted according to a random-stratified sampling design (Keller et al., 2008). Biomass caught in both the AFSC and NWFSC trawls was converted to average weight per shad by dividing the total biomass by the total number of shad caught. Stepwise multiple regression models were used to relate size of shad to bottom depth, day of year, sea surface temperature (SST), and bottom (gear) temperature during the 10 years of AFSC surveys, and to bottom depth and day of year during the six years of the NWFSC surveys (SST data for the NWFSC cruises were not available). Catches were also related to the Pacific Decadal Oscillation (Mantua et al., 1997), Oregon Production Index (OPI) survival estimates generated from hatchery releases of coho salmon (*Oncorhynchus kisutch*) smolts and returns of adult coho salmon to hatcheries, and counts of shad passing the Bonneville Dam. Shad were also caught in pelagic surveys targeting juvenile salmonids from 1981 to 2008 off Oregon and Washington. The purse

[1] Emmett, R.L., S.A. Hinton, S.L. Stone and M.E. Monaco. 1991. Distribution and abundance of fishes and invertebrates in west coast estuaries. Volume 11: species life history summaries. ELME Report 8, 329 p. NOAA/NOS Strategic Environmental Assessments Division, Rockville, MD.

[2] Mullen, R. E., and K. R. Conover. 1973. Ecology of shad and striped bass in coastal rivers and estuaries, 12 p. Fish Comm. Oregon, Project No. AFC 53, Portland, OR.

[3] Mullen, R. E. 1974. A summary of American shad (*Alosa sapidissima*) tagging studies on the coastal streams of Oregon, 1946–70. Coastal Rivers Investigation, Inf. Rep. 74-3, 43 p. Fish Comm. Oregon, Portland, OR.

[4] CDFG (California Department of Fish and Game). 2010. Effects of delta inflow and outflow on several native, recreational, and commercial species. DFG Exhibit 1, unpubl. report, 39 p. California Department of Fish and Game, 830 S Street, Sacramento, CA 95811.

seine used during 1981–85 was 457–496 m long, had 32-mm or finer mesh, fished to a depth of 30–65 m, and sampled about 20,000 $m^2$ (Pearcy and Fisher, 1988). The midwater trawl deployed during 1998–2008 was a Nordic rope trawl that fished near the surface mainly during the day with a mouth opening 30 m wide×20 m deep and had a 0.8-cm fine mesh liner in the codend (Brodeur et al., 2005).

Shad catches and sizes were available from both commercial midwater and bottom trawling, 1997–2009, off British Columbia (Davidson and Fargo[5]), from commercial landings from bottom and midwater trawls and from gill nets, set nets, dip nets, and hook-and-line gear fished in the Columbia River and the Oregon coast, 1978–2009 (Karnowski and Hurtado[6]) and California (Larinto[7]). Catches in all regions were highly variable and shad discarded as bycatch were not reported. In addition, observer data on shad catches in the limited-entry trawl groundfish fishery in Washington, Oregon, and California for "summer" (April–October) and "winter" (November–March) seasons, 2002–2009 were also examined (Majewski and Bellman[8]; Olson[9]).

Shad, a schooling pelagic fish, undertake diel vertical migrations in the Atlantic (Neves and Depres, 1979). Such migrations are not known, however, for shad in the Pacific Ocean. We assumed that they would be more susceptible to capture during the daytime in bottom tows, or as the net descended or ascended to surface waters than in surface waters. Because schooling behavior may result in a few extremely large catches and many zero catches, we restricted our analyses mainly to $\log_{10}$ transformed numbers for fish caught and presence–absence data to deemphasize the rare catches of large numbers of shad. Although bottom trawls are designed to capture demersal species, catches may reflect major changes in abundance or availability of pelagic species, such as shad (Neves and Depres, 1979). In addition, shad migrate into estuaries and freshwater to spawn during May, June, and July along the Pacific coast (Hamman, 1981; Petersen et al., 2003) and hence adults and some juveniles were not available during the early months of ocean sampling. Also, small and young-of-the-year shad are unlikely to be retained by all sampling nets.

[5] Davidson, J., and J. Fargo. 2010. Personal commun. Department of Fisheries and Oceans, 200-401 Burrand St., Vancouver, British Columbia, Canada V6C 3S4.

[6] Karnowski, M., and N. Hurtado. 2010. Personal commun. Oregon Department of Fish and Wildlife, 2040 Southeast Marine Science Dr., Newport, OR 97365, and 3406 Cherry Ave NE, Salem, OR 97305.

[7] Larinto, T. 2010. Personal commun. California Department of Fish and Game, 4665 Lampson Ave Los Alamintos, CA 90720.

[8] Majewski, J., and M. Bellman. 2010. Personal commun. Northwest Fisheries Science Center, 2725 Montlake Blvd. E., Seattle, WA 98112.

[9] Olson, J. 2010. Personal commun. Pacific States Marine Fisheries Commission, 7600 Sand Point Way, Seattle, WA 98115.

## Results

Shad were caught in 1178 of the 5612 tows by the AFSC (frequency of occurrence, FO=21%), and in 403 of 3762 tows by the NWFSC (FO=11%). Highest $\log_{10}$ catches were noted along the continental shelf off Washington and Vancouver Island and off San Francisco Bay during the AFSC cruises (Fig. 1A). Catches in NWFSC early season and late season tows were more uniformly distributed along the coast from northern Washington to northern California than were AFSC catches, but again with highest catches off Washington and lower catches to the south, with a cluster of catches off San Francisco (Fig 1, B and C). Large catches appeared to shift from Oregon to off Washington up to Vancouver Island between the early and late NWFSC cruises. This shift was consistent with the high catches off Vancouver Island also in late summer during the AFSC cruises (see also Fig. 2).

When the $\log_{10}(catch+1)$ and FO data were pooled across years, clusters of high shad catches became evident off the Washington coast (45–49°N lat.) and along the central California coast (37–38 °N lat.) during the AFSC sampling (Fig. 2A). Similar latitudinal trends in abundance were shown with the late-May to late-July NWFSC sampling (Fig. 2B), and this northward shift in abundance was also documented with the late-August to late-October NWFSC sampling (Fig. 2C). In addition to the two latitudinal centers of abundance seen in the AFSC sampling, the NWFSC sampling indicates a third center of abundance in northern California (41–42°N lat.). Despite interannual variations in the distribution of catches along the coast among years of sampling, this fairly consistent distributional pattern emerged. Note that catches in the AFSC tows were sometimes orders of magnitude higher than those in the NWFSC tows (Fig. 2), a difference related to the faster tow speeds, longer tow durations on the bottom, and the higher net opening of the AFSC tows.

Shad were also collected in purse seine surveys off Oregon and Washington during cruises conducted by Oregon State University from 1981 through 1985 (summarized by month in Fig. 3). Over 1100 shad were caught in 29 sets. Catches had a restricted distribution mainly near the Columbia River plume and close to shore. The largest catch comprised 883 shad in one purse seine set off Cape Disappointment in August 1981. In the daytime surface trawls by the NWFSC, only 139 shad were captured from 43 tows out of a total of 1536 tows (FO=2.8%) from central Oregon and the Washington coast during 1998–2008 (Fig. 4). These numbers and frequencies of occurrence were much lower than those seen during the demersal sampling (Fig. 2), supporting the observations in the Atlantic that shad undertake diel vertical migrations and are more available in subsurface than in surface waters by day.

An inshore–offshore gradient in abundance of shad was significant; most shad were caught in AFSC and NWFSC tows on the continental shelf (≤200 m) (Fig. 5,

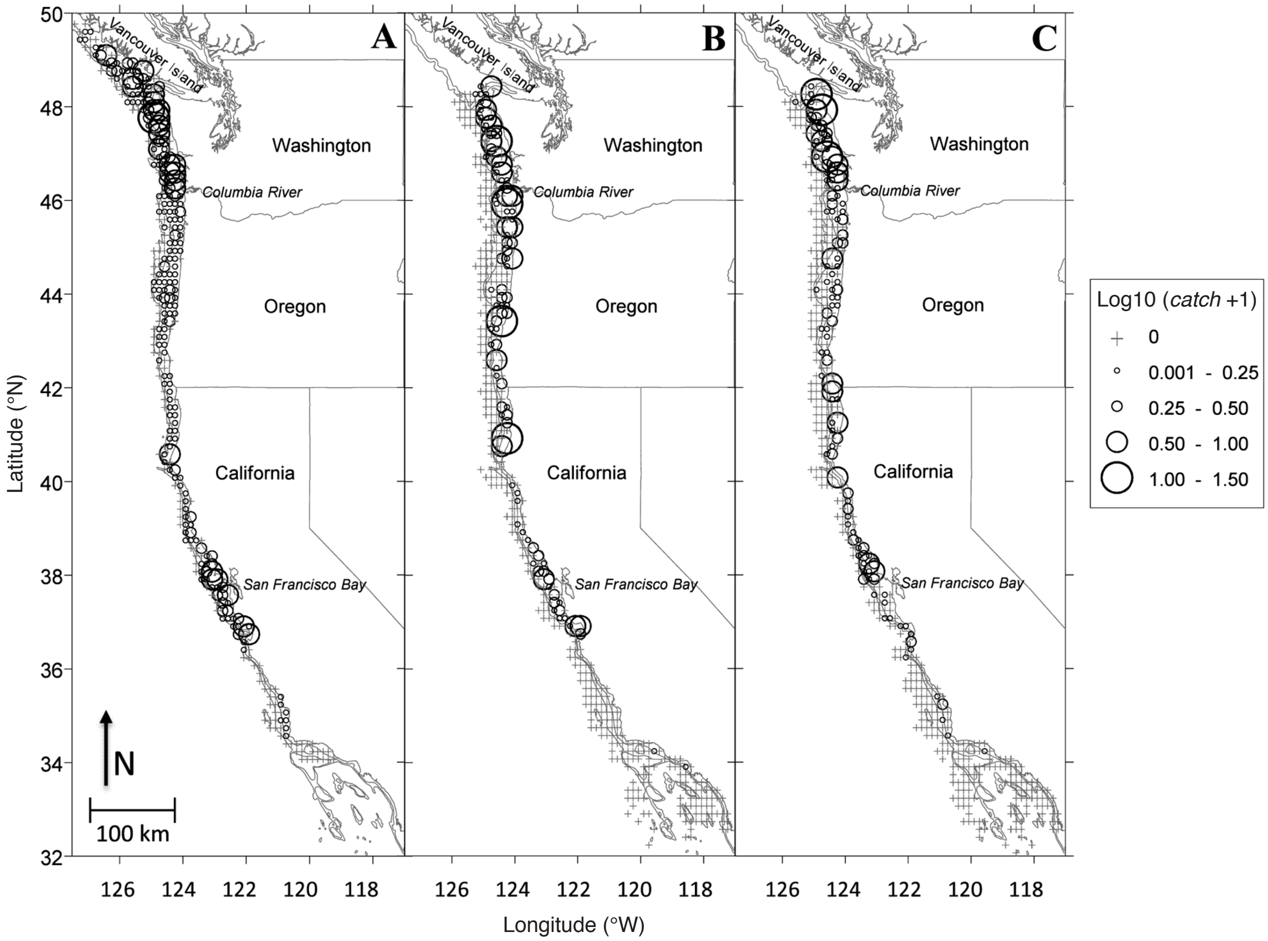


**Figure 1**

Average catch of American shad (*Alosa sapidissima*) in 10′ latitude×10′ longitude sampling areas during (**A**) 30-minute bottom tows conducted by the Alaska Fisheries Science Center for the years 1977–2004 combined, and (**B**) during 15-minute bottom tows conducted by the Northwest Fisheries Science Center for the years 2003–08 combined in early season sampling (May–July), and (**C**) late season sampling (August–October). Isobaths are 200 m and 500 m. Catch is transformed by $\log_{10}(catch{+}1)$.

Table 1). On the shelf shad were found in 28% of AFSC tows (1132 of 4010), whereas, off the shelf in deeper water they were found in only 2% of tows (36 of 1586). Similarly, shad were found in 24% of NWFSC tows (394 of 1669) on the shelf, but in <1% of off shelf tows (9 of 2093).

The average weight of individual shad caught in AFSC trawls increased with both latitude and day of year (Fig. 6, A and B). However, because latitude and day of year were highly correlated during each AFSC cruise (correlation coefficient [$R$]=0.90–0.99), it was impossible to separate the effects of these two variables on size. Average weight consistently increased with depth during both surveys and often with day of year during the AFSC sampling. An effect of sea surface temperature on size was evident in only a few years (Table 1). Similar increases in weight were obtained when latitude was substituted for day of year (not shown in Table 1). The increase in size of shad with depth was consistent in all sampling collections that we examined. Besides the increase in average weight of shad with depth in the AFSC and NWFSC tows (Table 1), shad weight in purse seines was also positively correlated with depth ($R$=0.40, $n$=43 hauls, $P$=0.007), and in the limited-entry trawl fisheries off Washington, Oregon, and California during both summer and winter seasons (linear regressions of average weight of shad by 5-m tow depth intervals: summer, $n$=36, slope =0.0026 kg/m, coefficient of determination [$r^2$]=0.53, $P$<0.001; winter, $n$=33, slope=0.0016 kg/m, $r^2$=0.56, $P$<0.001).

The weight of shad caught in later years, uncorrected for date of sampling or depth of tow, was also significantly less than that in early years (Fig. 7A). To correct weight for depth and date of sampling in the different years a general linear model was applied to the weight data from both the AFSC and NWFSC demersal surveys combined (Fig. 7B). Even when adjusted for bottom depth and date of capture (much earlier for 1995–2004),

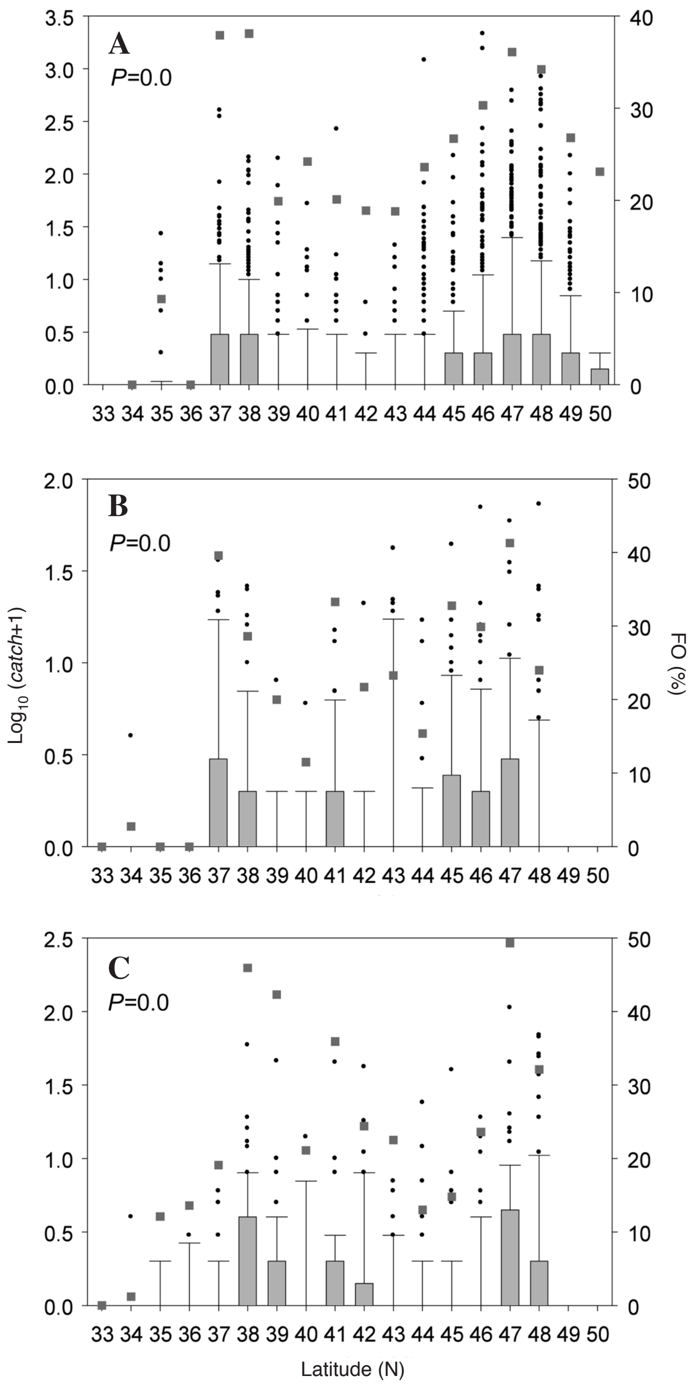


**Figure 2**

$Log_{10}$-transformed catch of American shad (*Alosa sapidissima*) and percent frequency of occurrence (FO) out to the 200-m isobath by one degree latitude ranges during (**A**) the 1977–2004 Alaska Fisheries Science Center triennial surveys, (**B**) the 2003–08 Northwest Fisheries Science Center early season (May–July) sampling, and (**C**) late season (August–October) sampling. Box plots show the 50th–75th percentile (shaded columns), the 10th–90th percentiles (whiskers), and outliers (dots). Small squares indicate FO of shad in tows. Kruskal-Wallace tests showed that catch differed by latitude ($P<0.05$) for all three studies.

a decline in size with year was still apparent (Fig. 7B). Shad caught in the surface trawls in 1998 were larger than those in the four subsequent years (2001, 2004, 2007, and 2008) when more than 10 fish were caught (Kruskal-Wallace test, $P=0.001$) and therefore also indicated a possible decrease in average weight of shad during this decade.

During the AFSC sampling survey over the shelf (≤200 m), shad were caught in tows over a wide range of sea surface temperatures (SSTs), from about 9° to 18°C, with the 10th and 90th percentiles of $\log_{10}(catch+1)$ occurring at 11.2° and 16.5°C, respectively (Fig. 8A). Cumulative frequency curves of $\log_{10}(catch+1)$ vs. SST and presence–absence vs. SST closely followed that of sampling, indicating that shad were widespread across most sea surface temperatures sampled on the shelf. However, the raw catch of shad (numbers per tow) indicated that the largest catches tended to occur where SSTs were from 13° to 17°C (Fig. 8A). This finding indicates that large schools of shad may be more abundant in areas where the SST is above 13°C. Conversely, the largest catches of shad also tended to occur where the bottom temperature (where gear was situated) was colder than that found in most other areas sampled; 80% of the raw catch occurred between 6.4°C and 8.0°C, whereas only 56% of sampling was in water that cold (Fig. 8, B and C). During both AFSC and NWFSC sampling surveys, bottom temperature was strongly negatively correlated with latitude ($R=0.78$ and 0.86, respectively). SST was weakly positively correlated with latitude ($R=0.36$). Therefore, the shad abundance vs SST patterns seen in Figure 8 (largest catches where bottom temperature is cool and SST is warm) are consistent with the generally larger catches seen north of 44°N and the smaller catches seen off central California (Fig. 2).

## Discussion

Shad undertake long distance seasonal migrations along the Atlantic coast of the United States, swimming thousands of kilometers north in the summer and south in the winter (Talbot and Sykes, 1958; Walburg and Nichols, 1967; Leggett and Whitney, 1972; Leggett, 1973). Although little is known about shad migrations in the Pacific Ocean (Moyle, 1976), Leggett and Whitney (1972) speculated that shad in the Pacific Ocean migrate long distances within their preferred SST range of 13–18°C as they do in the Atlantic—migrating south of Point Conception into southern

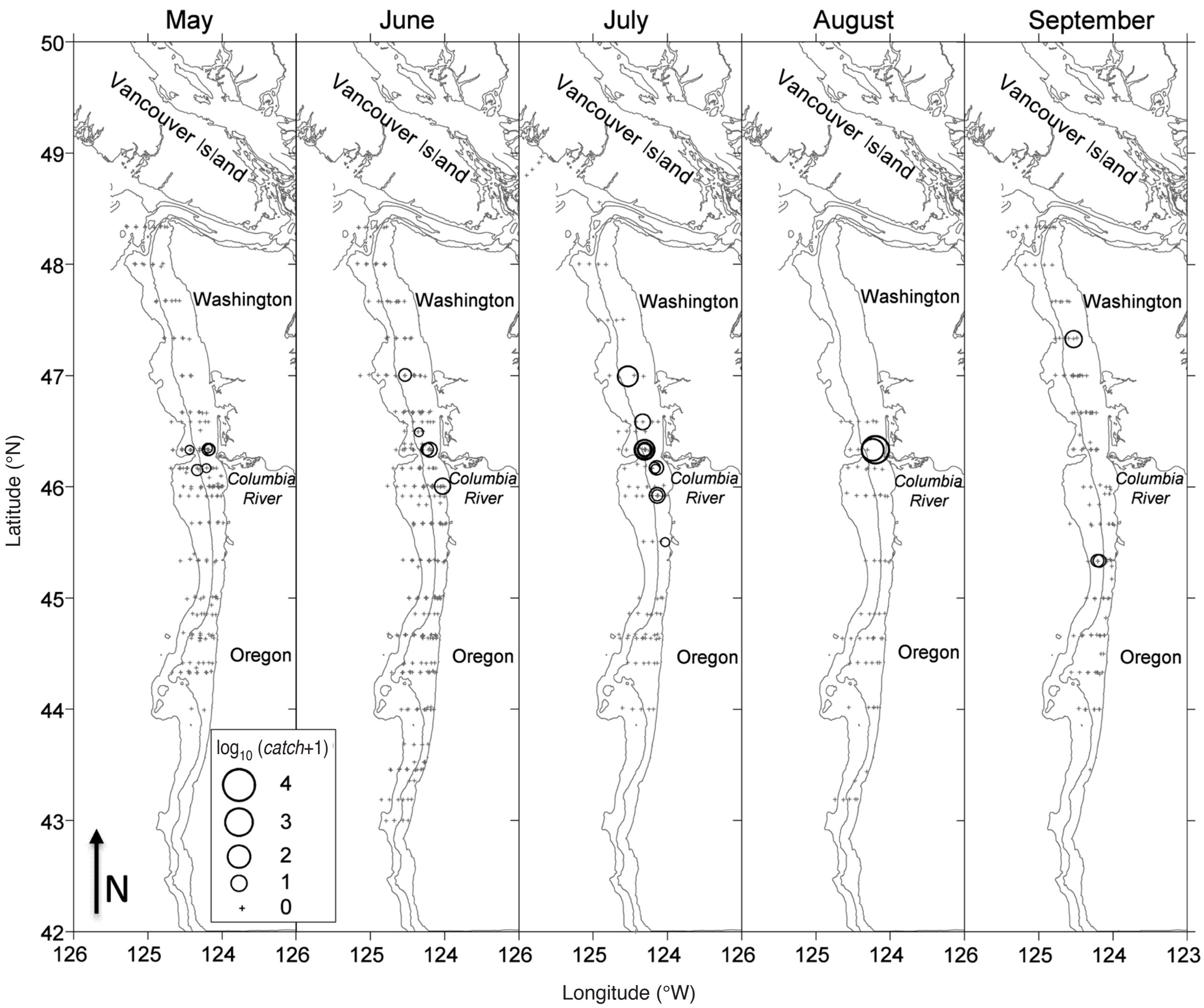


**Figure 3**

Catch of American shad (*Alosa sapidissima*) in round haul purse seine sets conducted by Oregon State University by month, for the combined years 1981–85. Catches are $\log_{10}$-transformed. Isobaths are 100 m and 200 m.

California and Baja Mexico during January–June, followed by migrations far to the north during July–October. Because ocean temperatures along the coast are often cooled by coastal upwelling during July, Leggett and Whitney thought that northward movements were diverted offshore to avoid these cool coastal waters. Data from our research surveys were collected mainly during the spring and summer; however, other data lend little support for shad migrations in the Pacific Ocean far to the south during the winter months. Data from commercial and sport landings of American shad along the Pacific coast indicate limited seasonal migrations along the West Coast.

In British Columbia, over 100 t of shad have been landed in some years in bottom and midwater trawls from 1997 to 2009 (Davidson andFargo[5]). This figure includes large catches from "unknown management" ocean areas in British Columbia (not shown in Table 2). From known ocean management areas, about 85% of the weight landed occurred between April and October ("summer" in Table 2) and most of these landings (95%) occurred during the months of August and October (see Figs. 1 and 2A). Shad were 260–580 mm fork length, most 400 mm or larger (about 0.8–3.0 kg; Davidson and Fargo [5]), mature, and over three years of age according to Petersen et al. (2003) and Hamman (1981). Large numbers of shad would not be expected in British Columbia waters during the fall when cool water temperatures below 13°C prevail if their migration patterns were similar to those predicted or shown for the Atlantic coast by Leggett and Whitney (1972). These large catches often found off the northern Washington and British Columbia coasts (Figs. 1 and 2) indicate that many shad from the Columbia River region move to the north after spawning. Surface currents to the north along the coast during winter months, or the deep

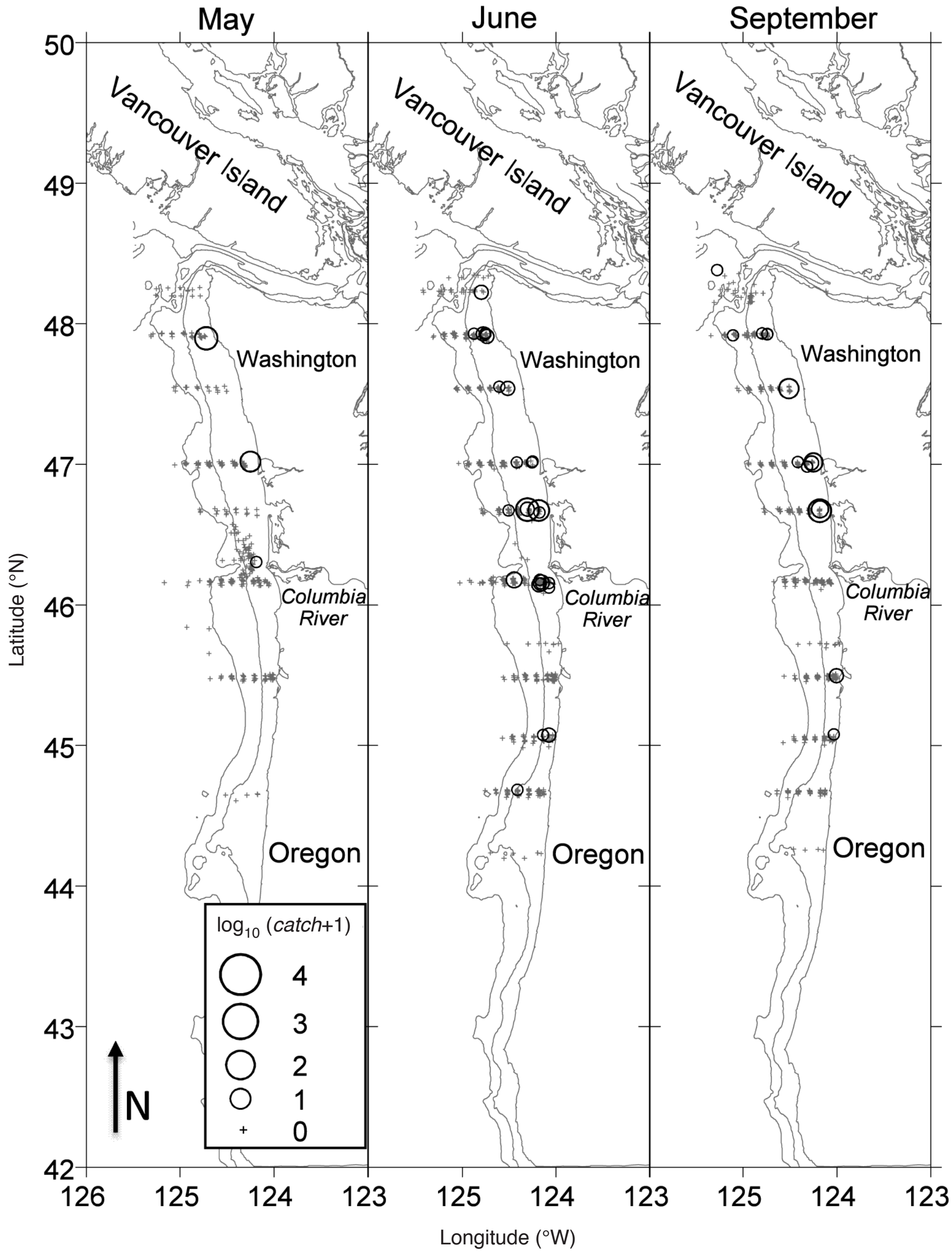


**Figure 4**

Catch of American shad (*Alosa sapidissima*) in Northwest Fisheries Science Center surface trawls (most 30 minutes) by month, for the combined years 1998–2008. Catches are $\log_{10}$-transformed. Isobaths are 100 m and 200 m.

countercurrent to the north during the spring and early summer off Oregon (Huyer et al., 1975) may passively transport shad to the north.

Most commercial landings of shad in Oregon are from gill nets fished in the Columbia River and along the Oregon coast during May and June when fishing effort is high and shad are migrating into the Columbia River (up to 40 to 172 t per month in some years between 1978 and 2009). Shad are also caught and landed in bottom and midwater trawls used to target Pacific whiting (*Merluccius productus*) during the summer, and some are landed in trawls or gill nets during the fall and winter, October–March (Table 3; Karnowski and Hurtado[6]). In northern California, where up to 32 t of shad are landed in some years, more shad were landed in the ocean and inland waters during the “winter” than the “summer” (Table 3; Larinto[7]). Observer data on shad catches in the limited-entry trawl groundfish fishery (Majewski and Bellman[8]; Olson[9]) indicated that the percentage of tows with shad was higher in the "summer" (April–October) than in the "winter" (November–March). Although the average number of shad caught in positive tows was higher in California in the winter, catches were still taken in Oregon and Washington waters in the winter (Table 3). Lower catches per positive tows in the winter may be related to the deeper distribution of shad below 200 m in the winter, as found by Talbot and Sykes (1958).

Moreover, shad were rarely caught in fisheries targeting Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) in southern California during any season of the year (Sweetman[10]), or in pelagic trawling off the central California coast (Brodeur et al., 2003). During eleven years of sampling (1995–2005) with variable mesh gill nets in bays and estuaries of California, Allen et al. (2006) and L. Allen[11] found shad in the Klamath and Eel rivers, but mainly in San Francisco Bay. These are apparently the only bays where shad spawn. In the southern California Bight, only 78 American shad were caught in thirteen years of sampling in shallow, protected embayments from Santa Barbara to Oceanside during the summer and fall. In summary, from all these observations of the geographic distribution of catches of shad, we see little evidence for long-distance seasonal migrations of stocks along the Pacific coast and a massive exodus from northern waters in the fall and large increases in southern California waters below 35°N. These differences are probably driven by the more extreme ranges of seasonal temperatures along the east coast in contrast to the temperature ranges along the west coast of North America.

In our study, most shad were also caught in bottom trawls in shallow water (<150 m depth), which is consistent with ocean catches in the Atlantic (Neves and Depres, 1979), and with the few catches of shad beyond the continental shelf in bottom and midwater trawls off California, Oregon and Washington (Brodeur et al., 2003, 2005; Ralston and MacFarlane[12]). We found no evidence that shad were more abundant offshore or that they avoided cooler nearshore waters along the Pacific coast during the upwelling season by migrating offshore as postulated by Leggett and Whitney (1972).

Shad caught along the Pacific coast were generally larger in deep water along the outer continental shelf where bottom temperatures are cooler and surface temperatures are warmer during spring and summer months than inshore (Table 1). The lower catch number for shad off California (Fig. 2A) may also reflect their preference for cool bottom temperatures to the north. Although shad weight increased with latitude in the AFSC survey (Fig. 6A), it did not in the NWSC

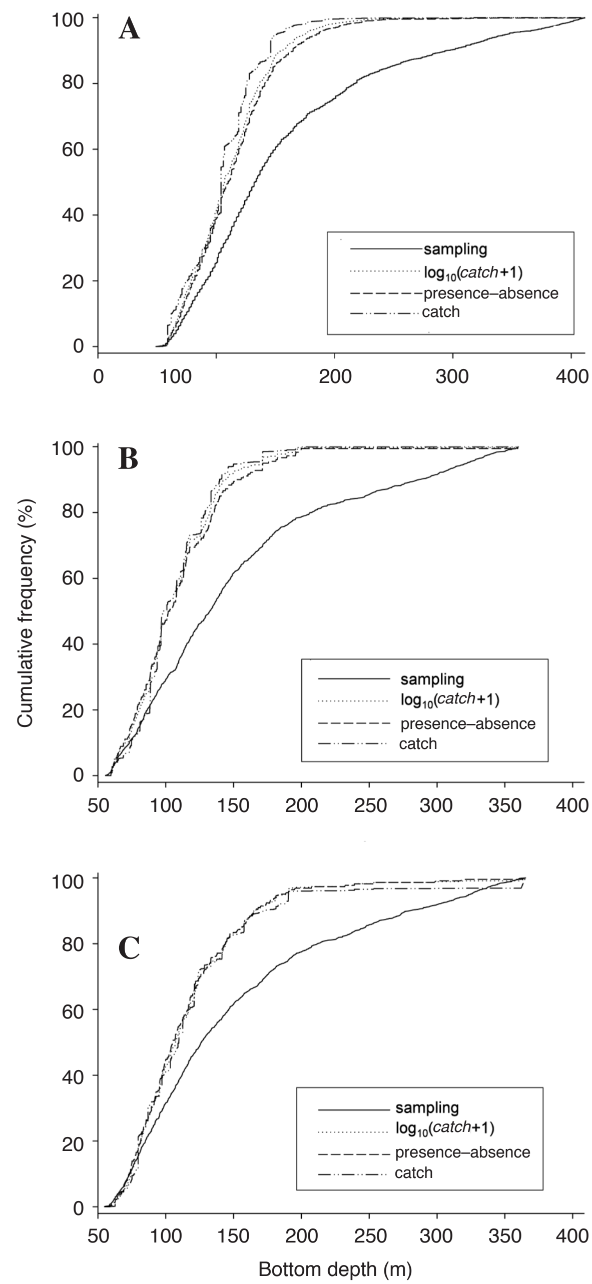


**Figure 5**

Cumulative frequency curves for sampling effort (number of tows), $\log_{10}$-transformed catch, presence–absence (1=present, 0=absent) of fish, and raw catch of American shad (*Alosa sapidissima*) vs. bottom depth out to the greatest depth of American shad catch during (**A**) the 1977–2004 Alaska Fisheries Science Center triennial surveys, and (**B**) the 2003–2008 Northwest Fisheries Science Center early season sampling, and (**C**) late season sampling surveys.

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[10] Sweetman, D. 2010. Personal commun. California Dept. of Fish and Game, 8604 La Jolla Shores Dr., La Jolla, CA 92037.

[11] Allen, L. 2010. Personal commun. Southern California Marine Institute, 820 S. Seaside Ave, Terminal Island, CA 91330.

[12] Ralston, S., and B. MacFarlane. 2010. Personal commun. NOAA Southwest Fisheries Science Center, 110 Shaffer Rd., Santa Cruz, CA 95060.

**Table 1**

Results of forward selection multiple regression models relating the average weight (kg) of American shad (*Alosa sapidissima*) in Alaska Fisheries Science Center (AFSC) and Northwest Fisheries Science Center (NWFSC) sampling surveys in different years to sea-surface temperature (SST), bottom depth, and day of year. Shown for each model are the significant ($P$<0.05) coefficients and $r^2$ (coefficient of determination). SST was not available from the NWFSC sampling.

| | | Regression coefficients for weight on: | | | |
|---|---|---|---|---|---|
| Year | No of hauls | SST (kg/°C) | Depth (kg/m) | Day of year (kg/d) | $r^2$ |
| AFSC | | | | | |
| 1977–2004 | 1168 | ns | 0.0029 | 0.0027 | 0.23 |
| 1977 | 29 | 0.12 | ns | ns | 0.15 |
| 1980 | 26 | ns | 0.0120 | ns | 0.46 |
| 1983 | 133 | ns | 0.0024 | 0.0039 | 0.20 |
| 1986 | 152 | ns | 0.0044 | ns | 0.18 |
| 1989 | 94 | 0.04 | 0.0040 | ns | 0.38 |
| 1992 | 191 | ns | 0.0021 | 0.0057 | 0.36 |
| 1995 | 154 | ns | 0.0018 | 0.0056 | 0.35 |
| 1998 | 163 | —[a] | 0.0026 | 0.0050 | 0.43 |
| 2001 | 95 | ns | 0.0029 | 0.0025 | 0.25 |
| 2004 | 108 | ns | 0.0031 | 0.0025 | 0.23 |
| NWFSC | | | | | |
| 2003–08 | 387 | — | 0.0026 | ns | 0.15 |
| 2003 | 57 | — | 0.0038 | ns | 0.28 |
| 2004 | 76 | — | 0.0041 | 0.0020 | 0.36 |
| 2005 | 106 | — | 0.0025 | ns | 0.16 |
| 2006 | 60 | — | 0.0017 | ns | 0.08 |
| 2007 | 52 | — | 0.0030 | ns | 0.14 |
| 2008 | 36 | — | ns | ns | 0.00 |

[a] SST was removed from model because it was highly correlated ($R$>*0.5*) with the other, stronger variables.

**Table 2**

Total landings of American shad (*Alosa sapidissima*) in known management areas for British Columbia (1997–2010 provided by Department of Fisheries and Oceans), and Oregon, Washington and California (1981–2010 provided by the Pacific Fisheries Information Network database). Data for the United States are summarized for ocean, inland, and unknown areas and for the two seasons: April-October (summer) and November–March (winter).

| Area | Ocean/ Inland | Season | Weight landed (t) | Area | Ocean/ Inland | Season | Weight landed (t) |
|---|---|---|---|---|---|---|---|
| BC | Ocean | Summer | 17 | CA | Ocean | Summer | 13 |
| | Ocean | Winter | 3 | | Inland | Summer | 23 |
| OR and WA | Ocean | Summer | 420 | | Ocean | Winter | 27 |
| | Inland | Summer | 2307 | | Inland | Winter | 51 |
| | Unknown | Summer | 577 | | | | |
| | Unknown | Winter | 3 | | | | |

sampling survey. However, shad landed off Vancouver Island were usually larger (2.0–3.0 kg; Davidson and Fargo[5]) than farther to the south (Figs. 6 and 7), indicating that larger shad may migrate farther to the north and remain in these cooler water longer, as do other pelagic species, such as Pacific whiting (Bailey et al., 1982; Dorn, 1995) and sardine (Emmett et al., 2005). Increased tolerances of cool water by large shad may explain both their extensive inshore–offshore and latitudinal distributions.

We found that shad occurred over a wide range of sea-surface temperatures; largest catches occurred

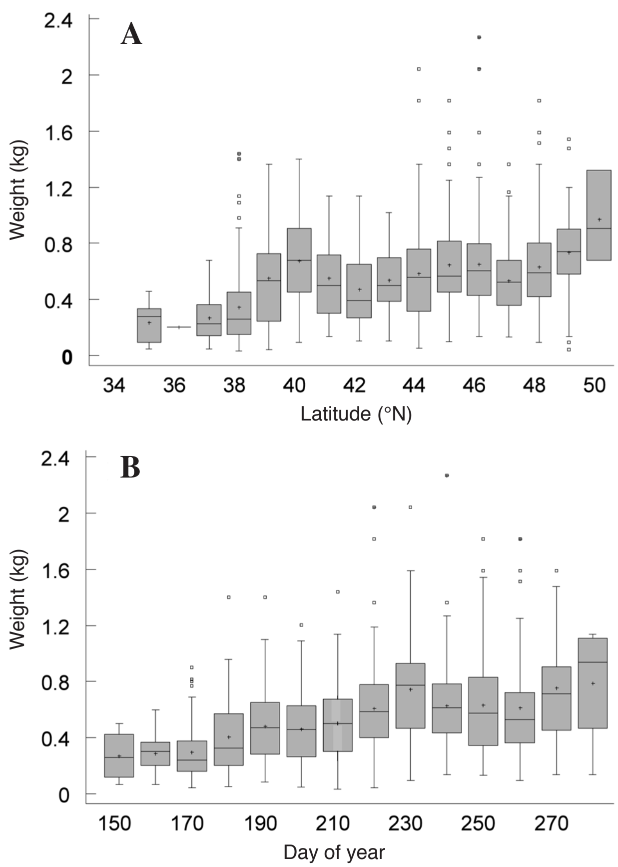


**Figure 6**

Trends in weight of American shad (*Alosa sapidissima*) by (**A**) latitude, and (**B**) day of year during the 1977–2004 Alaska Fisheries Science Center triennial surveys. Boxes span the 25th to 75th percentiles. The line and cross within each box indicate the median and mean weight, respectively. The whiskers indicate the minimum and maximum weights, except when outliers are present at more than 1.5 interquartile ranges (box heights) above or below the box. Small squares indicate outliers and small squares with crosses extreme outliers.

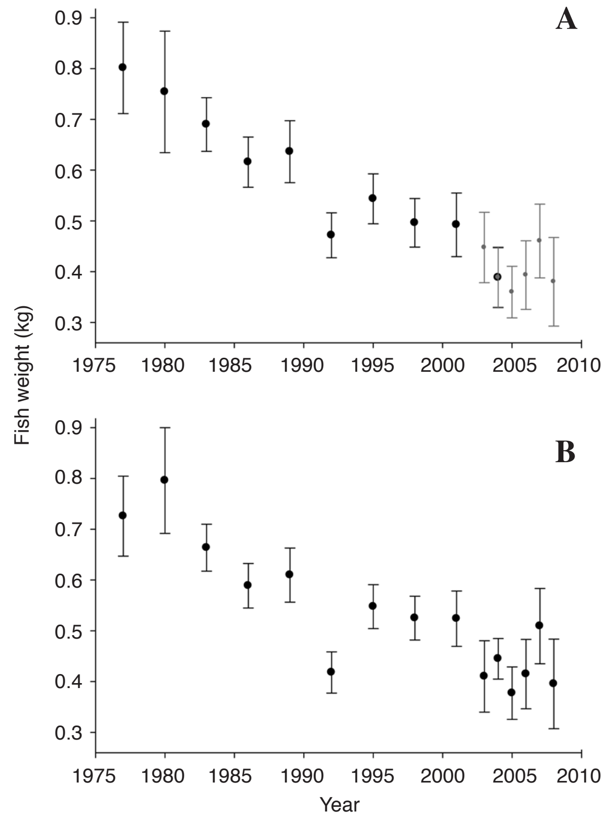


**Figure 7**

Mean weight (±2 standard errors) of American shad (*Alosa sapidissima*) by year during the 1977–2004 Alaska Fisheries Science Center triennial (black) and the 2003–08 Northwest Fisheries Science Center (gray) surveys: (**A**) uncorrected for date or depth of capture, and (**B**) results of a general linear model applied to both surveys combined where weight is the response variable, year is the categorical variable, and depth and day of year are quantitative variables ($r^2$=0.30). In (B) the mean weights are standardized to the average depth of 114 m and the average sample day 219 (August 7). In 2004 weights of shad in both surveys were very similar.

where SSTs were between 13° and 17°C and bottom temperatures were usually between 6.4° and 8°C. Neves and Depres (1979) caught Atlantic shad at SSTs of 2–23°C but concluded that bottom temperatures of 3–15°C provided a better basis for predicting movements of Atlantic shad in the ocean during all seasons of the year.

These differences in distributional and migration patterns of Pacific and Atlantic American shad are consistent with the phenotypic plasticity that has allowed adaptations to the unique environmental conditions along the Pacific coast over the past 100 years (see also Petersen et al., 2003). Rottiers et al. (1992) found that juvenile shad from the Columbia River had higher growth rates than did shad from the Delaware River and that the two stocks differed genetically. Quinn and Adams (1996) concluded that shad in the Columbia River have evolved a migratory pattern that allows greater behavioral response to environmental conditions because they now migrate into the river earlier in the year and at lower temperatures than during the prior 45 years. Future molecular and otolith microchemistry studies are needed to determine possible differences among spawning runs in different rivers, home stream fidelity, and distributional and migratory patterns at sea during their ocean migrations along the Pacific coast.

Counts of shad migrating past Bonneville Dam on the Columbia River provide important data on their abundances and interannual variability. The different indices of shad abundance (% FO, average $\log_{10}(catch+1)$, and average raw catch) during the AFSC and NWFSC demersal sampling on the shelf (≤200 m) between 44°N and 50°N in different years were all strongly and positively correlated with shad counts at Bonneville Dam in the same years (Table 4). These positive correlations indicate that the abundance estimates of shad off northern Oregon and Washington during these surveys were good indicators of the spawning populations of Columbia River shad above Bonneville Dam, despite the fact that shad were not a target species of these demersal surveys. Average weight of shad in ocean surveys was also strongly negatively correlated with shad counts at Bonneville Dam (Table 4), indicating that the proportion of younger year classes in ocean sampling increased as the abundance of spawners increased.

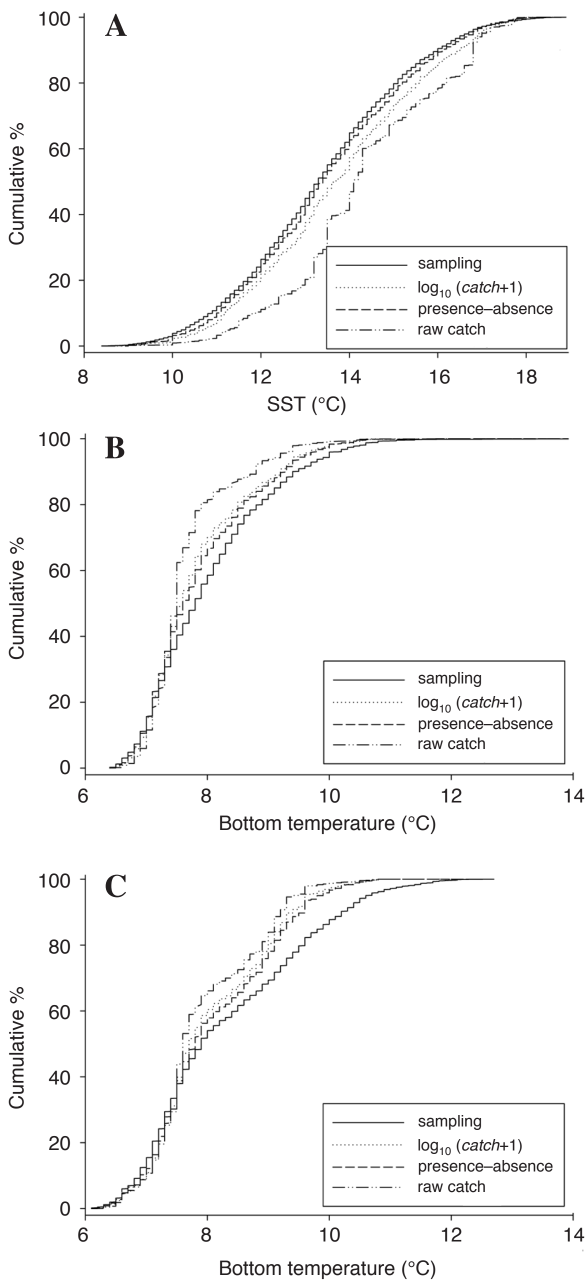


**Figure 8**

Cumulative frequency of sampling effort (number of tows), $\log_{10}$-transformed catch, presence–absence (1=present, 0=absent), and raw catch of American shad (*Alosa sapidissima*) vs. (**A**) sea-surface temperature (SST °C), and (**B**) bottom temperature during the Alaska Fisheries Science Center sampling, and (C) bottom temperature during the Northwest Fisheries Science Center sampling (both early and late season sampling combined).

The numbers of shad counted are related to ocean conditions and the survival of coho salmon as indicated by the Oregon Production Index or OPI (Fig. 9). The OPI is an index of smolt-to-adult survival of coho salmon mainly from Columbia River hatcheries. We assumed that ocean conditions that affect the survival of coho salmon may also affect the survival and return of Columbia River shad. During the cool Pacific Decadal Oscillation (PDO) regime between 1970 and 1976 shad counts were comparatively low. At this time coho salmon survival was high (Fig. 9, A and B). During the relatively warm PDO phase from 1977 to 1998 shad counts increased rapidly, whereas coho salmon survival was generally low, especially during the warm ocean conditions of the late 1990s. After 2000 shad counts increased markedly with warm PDOs, whereas coho salmon survival increased to high levels following several earlier years with cool PDOs and then declined. Shad counts at Bonneville were significantly negatively correlated with the OPI index ($n$=39 years, $R$=−0.45, $P$=0.004). From these trends we conclude that ocean survival of shad and coho salmon off Oregon and Washington are inversely related and that warm ocean conditions favor increased shad abundances and cool, more productive ocean periods favor coho salmon survival. In purse seine sets there was also a positive correlation between $\log_{10}$(*catch*) of shad and SST ($n$=29 sets, $R$=0.43, $P$=0.02, SST from about 12.2° to 16.4°C). The occurrence of shad off Kamchatka in 1935–1939, and again in 1987, all during warm phases of the PDO (jisao.washington.edu/pdo, accessed July 2011), indicate that shad distributions may increase with predicted future climate change and a warmer ocean, just as Pacific hake, Pacific sardine, Pacific mackerel (*Scomber japonicus*), and jack mackerel (*Trachurus symmetricus*) increased off Oregon and Washington after ocean warming increased in 1977 (Ware and McFarlane, 1995; Emmett and Brodeur, 2000; Emmett et al., 2006).

In recent years, numbers of shad counted at Bonneville Dam have decreased dramatically. The run in 2010 was the lowest since 1982 (Columbia Basin Bulletin[13]). Reasons for this decline are unknown, but increased incidence of a protozoan parasite, endemic to the Pacific Ocean has been suspected (Columbia Basin Bulletin[13]).

[13] Columbia Basin Bulletin. 2011. American shad: non-native to Columbia Basin, runs exceed one million fish, peaking at 6.5 million. The Columbia Basin Bulletin, May 13, 2011. [Available at: http://www.cbbulletin.com, accessed July 2011.]

**Table 3**

Data on counts of shad (*Alosa sapidissima*) in limited-entry groundfish catches, summarized for "summer" (April–October) and "winter" (November–March), by state (California, Oregon, and Washington) for as many as eight years, 2002–09. Counts were collected by onboard observers.

| State | Season | Shad count | Years | Tows with shad | All observed tows | % of tows with shad | No. of shad per positive tow |
|---|---|---|---|---|---|---|---|
| CA | Summer | 3224 | 8 | 324 | 4940 | 6.6 | 10 |
| CA | Winter | 1035 | 8 | 37 | 2002 | 1.8 | 28 |
| OR | Summer | 22,068 | 8 | 1056 | 11,147 | 9.5 | 21 |
| OR | Winter | 1853 | 8 | 133 | 4150 | 3.2 | 14 |
| WA | Annual[a] | 9381 | 3 | 96 | 620 | 15.5 | 98 |
| WA | Summer | 14,402 | 5 | 466 | 1969 | 23.7 | 31 |
| WA | Winter | 346 | 5 | 59 | 527 | 11.2 | 6 |

[a] For three of eight years only the annual catch off Washington was available.

**Table 4**

Correlation coefficients ($R$) between counts of American shad (*Alosa sapidissima*) at Bonneville Dam on the Columbia River and frequency of occurrence (FO) and abundance of shad determined from data from the Alaska Fisheries Science Center (AFSC) and Northwest Fisheries Science Center (NWFSC) demersal sampling survey over the continental shelf (≤200 m depth) from 44°N–50°N in different years. Tows that were negative for shad were included when calculating abundance. Shown also is the correlation ($R$) between average corrected weight of shad for the combined AFSC and NWFSC sampling survey in different years (Fig. 7B) and for the count of shad at Bonneville Dam.

| | $n$ | % FO | $\text{Log}_{10}(catch+1)$ | Catch | Weight |
|---|---|---|---|---|---|
| AFSC | 10 years | 0.61, $P$=0.06 | 0.77, $P$=0.01 | 0.73, $P$=0.02 | –0.77, $P$<0.001 |
| NWFSC | 6 years | 0.84, $P$=0.03 | 0.88, $P$=0.02 | 0.89, $P$=0.02 | |

Prolonged infection by this parasite may cause mortality of larger adult fish that spend more years in the ocean and may relate to the decrease in size we observed in later years (Fig. 7, Table 4). Other possible explanations for declining numbers include changes in the temperature and river flows that may affect survival (Leggett and Whitney, 1972; Crecco and Savoy, 1986; Petersen et al., 2003), competition for zooplankton with forage fishes in the ocean that increase during cool ocean conditions (Emmett and Brodeur, 2000), dietary overlap with salmonids in the estuary (McCabe et al., 1983), and increased predation by seabirds in the Columbia River estuary (Petersen et al., 2003).

## Conclusions

In conclusion, American shad along the Pacific coast of North America were mainly confined to the continental shelf and highest catches occurred from Oregon northward into British Columbia and near San Francisco Bay. Shad were bigger in deeper water. No evidence was found for large-scale seasonal migrations as reported along the Atlantic coast. The abundance of shad was highly correlated with the counts of shad passing Bonneville Dam on the Columbia River, and negatively correlated with the survival of coho salmon.

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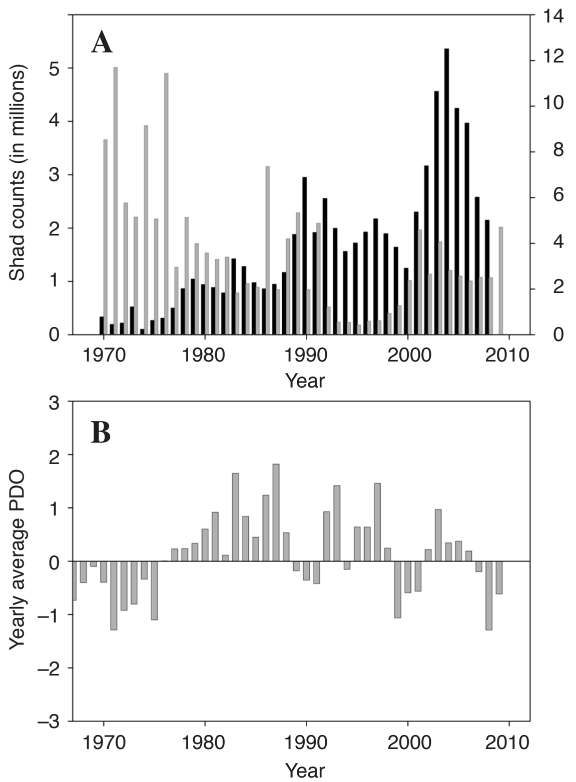


**Figure 9**

(**A**) American shad (*Alosa sapidissima*) counts at Bonneville Dam (black bars) and Oregon Production Index (OPI) coho salmon smolt-to-adult survival rates (SARs) (gray bars) along with (**B**) yearly average deviations of the Pacific Decadal Oscillation (PDO) index for the same years

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