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Richard A. Hinrichsen [a] , Daniel J. Hasselman [b e] , Curtis C. Ebbesmeyer [c] & Barbara A. Shields [d]

[a] Hinrichsen Environmental Services , 9034 45th Avenue Northeast, Seattle , Washington , 98115-3845 , USA

[b] School of Aquatic and Fishery Sciences , University of Washington, Post Office Box 355020 , Seattle , Washington , 98195-5020 , USA

[c] Beachcombers' Alert , 6306 21st Avenue Northeast, Seattle , Washington , 98115-9616 , USA

[d] Bonneville Power Administration , 905 Northeast 11th Avenue, Portland , Oregon , 97232-4169 , USA

[e] Department of Ecology and Evolutionary Biology , University of California Santa Cruz, Long Marine Laboratory , 100 Shaffer Road, Santa Cruz , California , 95060-5730 , USA

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ARTICLE

The Role of Impoundments, Temperature, and Discharge on Colonization of the Columbia River Basin, USA, by Nonindigenous American Shad

Richard A. Hinrichsen*
Hinrichsen Environmental Services, 9034 45th Avenue Northeast, Seattle, Washington 98115-3845, USA

Daniel J. Hasselman[1]
School of Aquatic and Fishery Sciences, University of Washington, Post Office Box 355020, Seattle, Washington 98195-5020, USA

Curtis C. Ebbesmeyer
Beachcombers' Alert, 6306 21st Avenue Northeast, Seattle, Washington 98115-9616, USA

Barbara A. Shields
Bonneville Power Administration, 905 Northeast 11th Avenue, Portland, Oregon 97232-4169, USA

Abstract

Ecologists have become increasingly aware of the combined effects of habitat disturbance and climate change on the establishment and proliferation of invasive species. Long-term data on the population of the invasive American Shad *Alosa sapidissima* in the U.S. portion of the Columbia River basin provide an opportunity to examine how habitat disturbances affect the abundance and spatial distribution of an invasive species in a heavily modified environment. After the establishment of American Shad in the Columbia River in the late 1800s, the drainage was transformed from its natural lotic state to a series of reservoirs, with concomitant changes to discharge and temperature regimes, which are confounded by climate change. As the Columbia River was dammed, American Shad extended its range and increased in abundance. A large and rapid increase in spawning population abundance (recruits per spawner = 63) followed completion of The Dalles Dam in 1957, which inundated Celilo Falls, a natural barrier to upriver American Shad migration. Regressions revealed that the annual percentage of American Shad migrating upstream from McNary Dam varied with water temperature and discharge ($R^2 = 0.72$), but not population density. When Atlantic coast rivers were dammed, however, American Shad lost spawning habitat and declined in abundance. Understanding the rapid colonization of the Columbia River by American Shad may reveal ways to help American Shad recolonize rivers where they are native. Understanding the roles of water temperature and discharge may allow us to project effects of climate change on the future distribution and abundance of American Shad in the Columbia River basin. Our results suggest that dam construction and alterations to the temperature and discharge regimes of the Columbia River have contributed to the increase in abundance and spatial distribution of American Shad. These changes might have improved the reproductive success of American Shad by providing access to additional spawning grounds and creating suitable juvenile rearing conditions.

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*Corresponding author: rich@hinrichsenenvironmental.com

[1] Present address: Department of Ecology and Evolutionary Biology, University of California Santa Cruz, Long Marine Laboratory, 100 Shaffer Road, Santa Cruz, California 95060-5730, USA.

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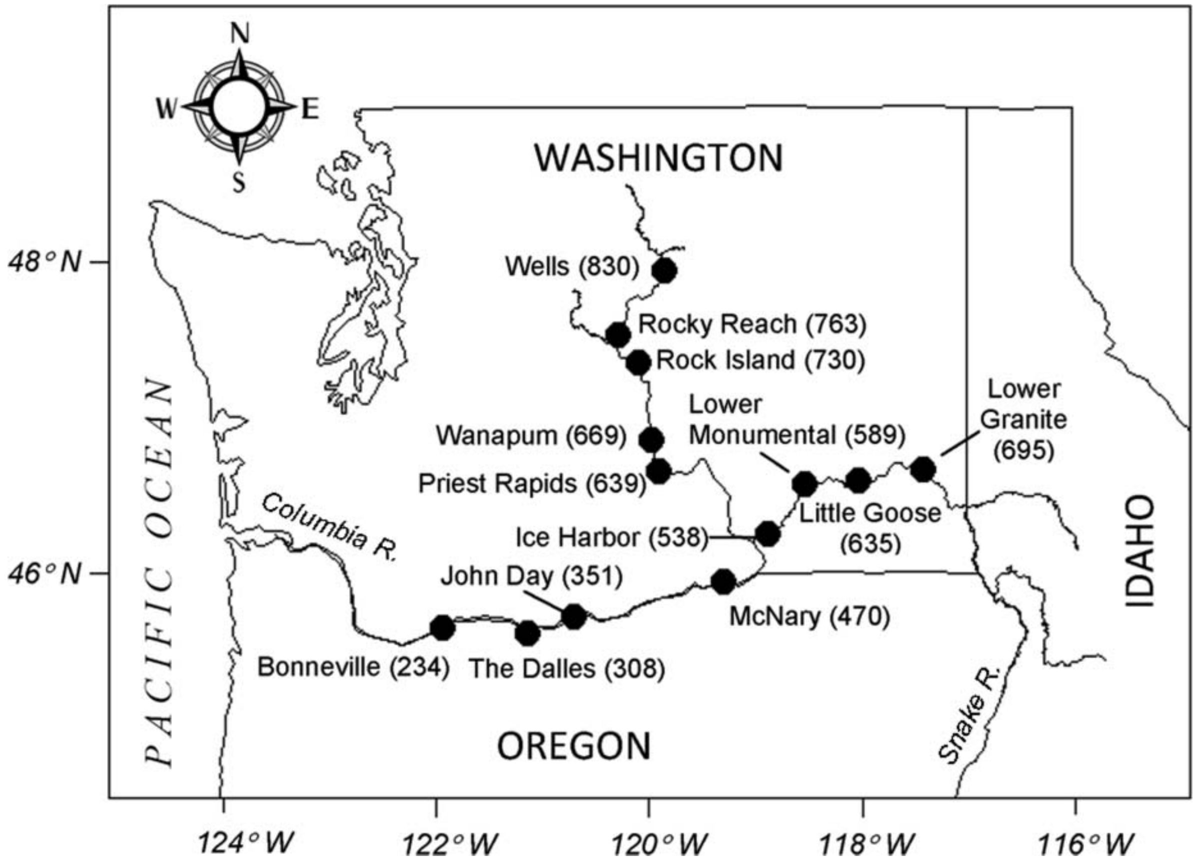

FIGURE 1. Locations of run-of-the-river dams on the main-stem Columbia River within the USA and Snake River, and distances from the Columbia River mouth (km).

Biological invasions result from a sequence of stages including introduction, establishment, dispersal, and impact (Williamson 1996; Kolar and Lodge 2001; Sakai et al. 2001). The spread of nonindigenous species constitutes a serious threat to global biodiversity (Vitousek et al. 1996; Simberloff et al. 2005; García-Berthou 2007), second only to the effects of habitat loss in the endangerment of native species (Wilcove et al. 1998). Initially, populations of nonindigenous species may be small, but once established, they may increase in abundance and distribution to dominate ecosystems (Waldeck et al. 2003), disrupt community trophic structure (Deegan and Buchsbaum 2005), alter species compositions of ecosystems (Chapin et al. 1997), and threaten the persistence of indigenous taxa (Wilcove et al. 1998). Ecologists are becoming increasingly aware of the effects that anthropogenic habitat disturbances and climate change can exert on the proliferation of invasive species (Hierro et al. 2005; Davis 2009; Walther et al. 2009). Although, to become established, nonindigenous species must respond rapidly to changes in the selective regimes imposed by the colonized system (Hänfling 2007), alterations to the environment that reflect conditions in their native range may aid this process. Therefore, identifying the abiotic factors responsible for the increased abundance and spatial distribution of invasive species is crucial for mitigating threats posed to native biota.

The Columbia River basin (Figure 1) is home to more than 350 nonindigenous species (Sanderson et al. 2009). Because the river has been extensively altered by anthropogenic influences, it provides an opportunity to study the effects of habitat disturbance on the proliferation of nonindigenous species. Dam construction in support of hydroelectric power development, irrigation needs, flood control, and navigation has transformed the once free-flowing Columbia River into hundreds of reservoirs, with concomitant changes to water temperature and discharge regimes (Pradeep and Jay 2005; Waples et al. 2007). These changes, confounded by regional climate change (Pradeep and Jay 2005; Battin et al. 2007), bear ecological consequences for other migratory fishes (Dauble et al. 2003; Waples et al. 2007).

The Columbia River basin contains approximately 30 nonnative fish species (Waldeck et al. 2003; Sanderson et al. 2009), but the effects of these species on the ecosystem remain largely unknown (see also Levin et al. 2002). The most abundant nonnative fish is the anadromous American Shad *Alosa sapidissima* (Waples et al. 2007). Though native to the Atlantic coast of North America—ranging from southern Labrador to northern

Florida—American Shad rapidly dispersed after their introduction to the Sacramento River, California, in 1871 (Green 1874). The species was first observed in the Columbia River in 1876 (Smith 1896, but see Jordan 1916; reviewed in Hasselman et al. 2012a). Since then, American Shad in the Columbia River basin have dramatically increased in abundance, raising concern because of their potential impacts on native fishes and ecosystem function (Hasselman et al. 2012b). More than 4 million adult American Shad were annually counted passing upstream of Bonneville Dam (river kilometer [rkm] 234) from 2003 to 2006, and from 1977 to 2008 adult American Shad outnumbered all adult native salmonids (hatchery and wild combined). Adult American Shad are counted at fishways installed at Bonneville Dam and other dams on the lower main stems of the Columbia and Snake rivers. All of these fishways, with the exception of that at Priest Rapids Dam in the mid-Columbia River (Figure 1), allow American Shad to successfully pass upstream.

Specific information on the conditions suitable for American Shad spawning and juvenile survival in the Columbia River basin is lacking. However, in their native range, American Shad spawning is associated with moderate water temperature (13–26°C) and current velocity (30–90 cm/s), shallow waters (<5 m water depth), and adequate dissolved oxygen (>5 mg/L) (Klauda et al. 1991; Beasley and Hightower 2000; Harris and Hightower 2011). American Shad spawn over a variety of substrates (Stier and Crance 1985; Beasley and Hightower 2000). Although survival of juvenile American Shad in their native range has been associated with the distance that adults migrate and the availability of suitable prey in upstream reaches (Limburg 1996a, 1996b, 2001), variations in river discharge and temperature during early larval development are usually considered important regulators of year-class strength and recruitment to the spawning stock (Marcy 1976; Leggett 1977; Shoubridge and Leggett 1978; Crecco and Savoy 1987).

Given the dominant influences of water temperature and discharge on American Shad recruitment in their native range, we sought to understand how dam construction and associated changes to water temperature and discharge regimes (confounded by climate change) might have influenced the proliferation and spatial distribution of American Shad in the Columbia River basin. By understanding the factors contributing to the rapid colonization of the Columbia River by American Shad, we may discover ways to aid American Shad on the East Coast of the United States to recolonize rivers where they are native and of increasing conservation concern (Limburg and Waldman 2009; Hasselman and Limburg 2012). Furthermore, understanding the roles of water temperature and discharge may allow us to project how climate change, which is expected to cause further alterations to temperature and discharge regimes, may influence the future abundance and spread of American Shad on the Columbia River. In this study, we (1) characterize the growth of the American Shad spawning population in response to increases in available contiguous reservoir habitat as a result of dam construction, and (2) demonstrate how the spatial distribution of the spawning run within the Columbia River basin varies with alterations to discharge patterns and water temperature regimes. We then discuss possible factors responsible for the patterns we observed, and discuss future research needs and management implications.

METHODS

Study Area

The study area included the main-stem Columbia River upstream of Bonneville Dam (rkm 234) and main-stem Snake River. American Shad return to the Columbia River to spawn in locations that extend to Priest Rapids Dam (rkm 639) on the mid-Columbia River and Lower Granite Dam (rkm 173) on the Snake River (Figure 1). The study area is contained within the Columbia River basin, which drains a watershed of 671,000 km^2 (Ebel et al. 1989) and extends into seven U.S. states and one Canadian province (Waples et al. 2007). The drainage is regulated by more than 200 dams (Ebbesmeyer and Tangborn 1992).

Adult American Shad Data

We retrieved annual adult American Shad passage data from the U.S. Army Corps of Engineers (USACE) database for Bonneville Dam (1938–2012), The Dalles Dam (1957–2012), John Day Dam (1968–2012), McNary Dam (1954–2012), Ice Harbor Dam (1962–2012), Lower Monumental Dam (1969–2012), Little Goose Dam (1970–2012), and Lower Granite Dam (1975–2012) (available from www.nwp.usace.army.mil/Missions/Environment/Fishdata.aspx [September 2012]).

River Data

Columbia River data.—To examine the effects of environmental conditions on American Shad abundance and distribution in the Columbia River basin, we obtained the following habitat data from the USACE: (1) available contiguous reservoir surface area (km^2) from Bonneville Dam through McNary Reservoir (i.e., Lake Wallula) on the upper Columbia River and through Lower Granite Reservoir on the Snake River (Figure 1); (2) daily water temperature measured at Bonneville Dam as reported in annual USACE fish passage reports from 1949 to 2012 (available from www.nwp.usace.army.mil/Missions/Environment/fishdata.aspx [September 2012]); (3) change in cumulative active storage capacity (CRWMG 2002). We also obtained summer discharge data from the U.S. Geological Survey (USGS) at The Dalles USGS gauge station 14105700 (available from waterdata.usgs.gov/nwis [September 2012]). Contiguous reservoir surface area is used as a measure of areal habitat of American Shad in the Columbia River, and it consists of flowing water because the dams that create the reservoirs that American Shad inhabit are “run of the river.” In this study, “available contiguous reservoir habitat” refers to the available contiguous reservoir surface area (km^2).

Delaware River temperature.—To show how Columbia River water temperatures differ from those experienced by American Shad in their native range, we compared Columbia River water temperature to Delaware River temperature. We used the Delaware River because it is the only remaining undammed river in the eastern United States that American Shad inhabit, it is near the center of the species' native range, and it provides a baseline of more natural hydrological conditions to compare with Columbia River conditions. This analysis does not attempt to infer what the water temperature regime of the Columbia River would be in the absence of dams, but provides insight into whether the altered temperature regime of the Columbia River is approaching that of a river in the species' native range. We used daily temperature data (1954–2012) for the Delaware River at the Trenton, New Jersey, USGS gauge station 01463500 (available from waterdata.usgs.gov/usa/nwis/uv?site_no=01463500 [September 2012]). The Delaware River is 674 km long and its mouth is located at latitude 39.47°N, whereas the mouth of the Columbia River is at 46.24°N (approximately 750 km farther north of the Delaware River mouth).

Data Analysis

Adult population abundance.—To illustrate the trend of abundances of adult American Shad, we plotted the times series of adult American Shad passing Bonneville Dam. Because American Shad counts at Bonneville Dam were often lower than the counts at The Dalles Dam after 1971 (possibly due to American Shad passing undetected through the Bonneville Dam navigation lock), the number of American Shad passing Bonneville Dam was estimated as the maximum of The Dalles and Bonneville dams adult American Shad counts (adjusted count; ADJ). To show the effect of adjusting the American Shad counts, we compared the ADJ counts with the actual counts (unadjusted count; UNADJ) at the Bonneville Dam fish ladders. Assuming that the adult shad passing The Dalles Dam must have also passed Bonneville Dam, the ADJ count was a more accurate estimate of the true spawning population passing Bonneville Dam. The ADJ and UNADJ time series of counts were strongly correlated over the years 1938–2012 ($r = 0.98$, SE = 0.02) and over 1970–2012 ($r = 0.97$, SE = 0.04). We calculated correlation separately for 1970–2012 because, after 1970, The Dalles Dam American Shad count exceeded the Bonneville Dam count in most years, and thus this period was one of maximum difference between the ADJ and UNADJ counts.

Recruits per spawner.—As an index of population growth, we developed crude estimates of yearly recruits per spawner. We estimated spawners as the count of adult American Shad passing Bonneville Dam, and estimated recruits as the average estimated count of adult American Shad passing Bonneville Dam 3–6 years later. We chose a 3–6 year time frame because this covered the age range of the bulk of spawning adults reported in previous studies (Wendler 1967; Petersen et al. 2003). We used an unweighted average for recruits instead of weighting by the age-specific percentages reported in Wendler (1967) or Petersen et al. (2003), because age structure is likely to vary widely among samples and return years. As an alternative to equal weighting, we estimated recruits by weighting the number of subsequent spawners according to the Petersen et al. (2003) age structure data, but we found that it produced minute differences in the estimated series of recruits per spawner (data not shown). A more refined estimate of recruitment would only be possible with yearly age structure data for Columbia River American Shad since adult counts began in 1938; however, such data do not exist. We calculated recruits per spawner using both the ADJ and UNADJ counts at Bonneville Dam. The two resulting $\log_e$(recruits per spawner) series were strongly correlated over brood years (BYs) 1938–2006 ($r = 0.98$, SE = 0.02) and over BYs 1970–2006 ($r = 0.92$, SE = 0.06).

To determine the effect of increasing available contiguous reservoir habitat on adult American Shad abundance, we plotted the time series of $\log_e$(recruits per spawner) and compared it with the time series of available contiguous reservoir surface area (km^2) upstream from Bonneville Dam. To test whether the recent (i.e., 2005–2011) decline in American Shad abundance was unusual, we compared recent recruits per spawner observations to the frequency distribution of recruits per spawner over the entire data series beginning in 1938.

Adult upriver distribution.—To characterize the upriver distribution of adult American Shad on the Columbia and Snake rivers, we used American Shad counts at Bonneville, The Dalles, John Day, and McNary dams on the Columbia River, and Ice Harbor, Lower Monumental, Little Goose, and Lower Granite dams on the Snake River. Using the yearly American Shad counts retrieved from the USACE database, we calculated the average number of American Shad passing each dam from 1980 to 2012. We used this time period because Lower Granite Dam was not completed until 1975, and beginning in 1980 allowed invasion upstream from the dam to proceed for about a generation before the average upstream distribution was calculated. For greatest accuracy, we used the ADJ Bonneville count for this analysis.

Adult upriver distribution versus river covariates.—To test for a linear relationship between upriver adult American Shad distribution and water temperature, we regressed the percentage of American Shad migrating to points above McNary Dam (y_t), against the average May–August water temperature at Bonneville Dam (x_{1t}) from 1970 to 2012, using least-squares regression. We used May–August data because Bonneville Dam counts show that most of the American Shad (99.99%) pass Bonneville Dam during this period (USACE 2010). Although water temperature was measured at the Bonneville Dam, water temperature fluctuations at Bonneville Dam reflected fluctuations at other locations in the main-stem Columbia River (Yearsley et al. 2001). Acknowledging that water temperature is related to discharge, we also regressed upriver distribution against average May–August discharge at The Dalles USGS gauge station (x_{2t}) from 1970 to 2012. Lastly, we regressed y_t against both x_{1t} (water temperature) and x_{2t} (discharge), using multiple linear regression. The number of American Shad passing Bonneville Dam was excluded as a covariate in these regressions because its correlation with upriver adult American Shad distribution was not significantly different from zero ($r = 0.12$, SE = 0.16).

To compare the fits of alternative models, we calculated the Akaike information criterion (AIC) of each model. Models with lower AIC values indicated a better fit to the data (Akaike 1973). We tested for lag-1 autocorrelation in residuals by using an autoregressive process of order 1 (Box et al. 1994). To determine whether multicollinearity might be an issue in the multiple linear regression (Belsley 1991), we calculated the Pearson correlation coefficient for the covariates water temperature and discharge. We used the ADJ Bonneville count for this analysis.

River covariate trends.—To illustrate the change in Columbia River discharge as storage capacity increased, we plotted time series of discharge measured at The Dalles USGS gauge station and storage capacity (1880–2012) on the same graph. We also demonstrated the change in the temperature distribution at Bonneville Dam during 1954–1963 and 2003–2012 by plotting daily averages for these periods. To illustrate how temperature during these periods differed for a river in the American Shad's native range, we also plotted mean daily temperature of the Delaware River, measured at Trenton, New Jersey, during these same time periods. In addition, to show diverging trends, we plotted time series of annual average May–August temperatures for the Columbia River (1949–2012) and Delaware River (1954–2012). For each temperature data set, we tested for a trend using a Mann–Kendall test (Mann 1945). Because the Columbia River temperature data set exhibited serial dependence, we applied the Mann–Kendall test with a block bootstrap approach using 10,000 bootstrap replications and a block size of 5 years (Lahiri 2003).

RESULTS

Data Analysis

Adult population abundance.—The number of American Shad at Bonneville Dam peaked at 6 million in 2005 (Figure 2). In 2010, American Shad passing Bonneville Dam declined to approximately 1.2 million fish (ADJ); a lower count (ADJ) has not been observed since 1982.

Adult population growth.—After completion of The Dalles Dam (rkm 308) in 1957, the estimated number of adult American Shad passing Bonneville Dam increased dramatically (Figure 2). After construction of The Dalles Dam, recruits per spawner peaked at 63 (ADJ and UNADJ) [$\log_e$(recruits per spawner) = 4.14] in BY 1959 (Figure 3). The geometric mean number of recruits per spawner during BYs 1956–1962 was 9.77 (ADJ and UNADJ) [average $\log_e$(recruits per spawner) = 2.5]. The available contiguous reservoir habitat increased by 38 km^2 after The Dalles Dam was constructed. A larger increase of 383.1 km^2 in available contiguous reservoir habitat occurred with the completion of John Day Dam in 1968, and the number of recruits per spawner peaked at 2.79 (ADJ) [$\log_e$(recruits per spawner) = 1.03] in BY 1971. The geometric mean of recruits per spawner over BYs 1968–1974 was 1.95 (ADJ) [average $\log_e$(recruits per spawner) = 0.67], considerably less than the geometric mean recruits per spawner corresponding to the completion of The Dalles Dam (Figure 3). The recent decline in shad numbers yielding recruits per spawner (ADJ) of 0.246 [$\log_e$(recruits per spawner) = −1.40] in BY 2005 was rare in the entire data set; only one previous observation of recruits per spawner was less than or equal to 0.246, and that was in BY 1945 (Figure 3).

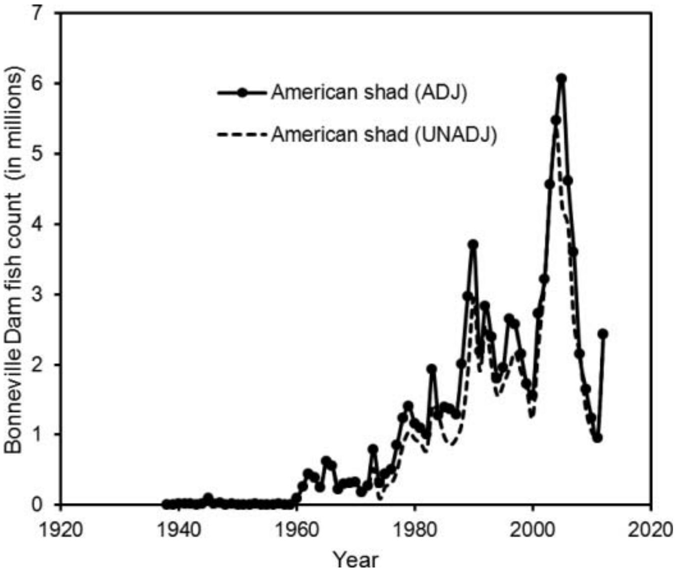

FIGURE 2. Estimated adjusted (ADJ) and unadusted (UNADJ) numbers of adult American Shad passing Bonneville Dam, 1938–2012.

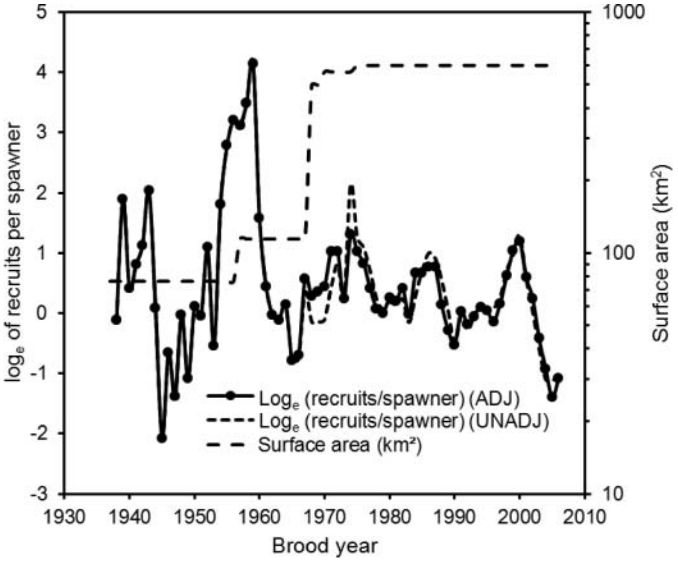

FIGURE 3. Natural log of recruits per spawner of American Shad counted at Bonneville Dam and available contiguous reservoir habitat (measured in surface area) extending from Bonneville Dam and to Priest Rapids Reservoir on the mid-Columbia River and to Lower Granite Reservoir on the Snake River.

TABLE 1. Average number of American Shad passing main-stem dams on the Columbia and Snake rivers (1980–2012); rkm = river kilometer, *n* = number of observations, Mean = sample mean, SE = standard error of sample mean.

Dam	rkm	*n*	Mean	SE
Columbia River				
Bonneville	234	33	2,413,782	224,102
The Dalles[a]	308	31	2,435,378	232,583
John Day	351	24	1,114,825	116,280
McNary	470	33	665,279	79,748
Snake River				
Ice Harbor	538	33	91,617	17,107
Lower Monumental	589	24	39,658	11,393
Little Goose	635	15	17,265	6,491
Lower Granite	695	33	5,364	1,443

[a] The Dalles Dam has a larger mean count than Bonneville Dam because shad counts at The Dalles Dam were halted after 2010 and Bonneville Dam counts were relatively low during 2011–2012.

Adult upriver distribution.—Declines in passage counts of adult American Shad with upstream distance were apparent in both the lower Columbia and the Snake rivers (Table 1). On average, 28% of the adult American Shad passing Bonneville Dam traveled an additional 236 km to pass McNary Dam, while 6% of the adult American Shad that passed Ice Harbor Dam traveled an additional 157 km upstream to pass Lower Granite Dam.

Adult upriver distribution versus river covariates.—The results of the regression analyses using percent adult American Shad penetrating upstream of McNary Dam as the response variable and mean May–August discharge and mean May–August water temperature as the explanatory variables are summarized in Tables 2 and 3. The regression containing both water temperature and discharge and their interaction had the lowest AIC value and highest coefficient of determination (R^2). The overall fit for each regression was significant ($P < 0.001$). Mean May–August water temperature was a significant predictor of upriver American Shad distribution ($P < 0.001$) (Figures 4a, 5a). The slope of the regression was 8.79 (SE = 1.48) and indicated that when average May–August water temperature rose by 1°C, approximately 9% more of the American Shad counted at Bonneville Dam migrated to points upstream from McNary Dam. Mean May–August discharge was also a significant predictor of upriver distribution of American Shad ($P < 0.001$) (Figures 4b, 5b) and explained 12% more of the variation in the percent American Shad passing McNary Dam than did the mean May–August temperature. The slope of the regression was −4.09 (SE = 0.59) and indicated that lower proportions of the American Shad spawning population migrated to spawning areas upstream from McNary Dam in years with higher mean May–August discharge. In the multiple linear regression, which contained both mean May–August river temperature and mean May–August discharge, the slopes of mean May–August river temperature, mean May–August discharge, and their interaction were each significant ($P < 0.001$). Thus, despite the correlation between the two predictor variables, mean May–August water temperature and mean May–August discharge, in the multiple linear regression ($r = -0.65$, SE = 0.12), regression coefficient estimates were all significant. Correlation

TABLE 2. Regression results for percentage of American Shad penetrating upstream from McNary Dam (rkm 470). The number of observations was *n* = 43 (1970–2012). The Null model includes an intercept parameter only and no autocorrelation in the residuals. All regressions include an intercept term. The models "Temperature" and "Discharge" used first-order autocorrelation in the residuals, while the others assumed independent residuals; df = degrees of freedom of the residuals, R^2 = coefficient of determination, AIC = Akaike information criterion.

Model	df	R^2	AIC
Null	42	0.00	321.2
Temperature	40	0.42	301.6
Discharge	40	0.54	291.5
Temperature + Discharge + (Temperature × Discharge)	39	0.72	272.2

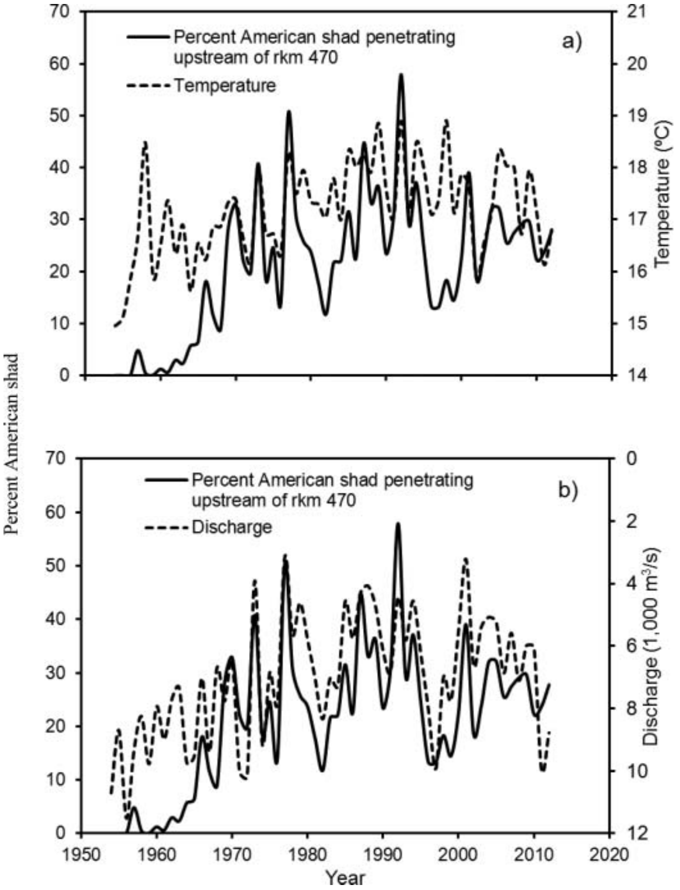

FIGURE 4. Time series of the percent of American Shad penetrating upstream from rkm 470 plotted with times series of (**a**) mean May–August water temperature measured at Bonneville Dam and (**b**) mean May–August discharge.

TABLE 3. Regression coefficient estimates for alternative models. Temperature is mean May–August river temperature, and Discharge is mean May–August discharge. In the regression, temperature is in units of °C and discharge is in units of 1,000 m^3/s; SE = standard error, t = standardized regression coefficient estimates, P = probability of obtaining a test statistic at least as extreme as the one observed, Phi = autocorrelation coefficient, Temperature × Discharge = regression coefficient of the product of mean May–August water temperature and mean May–August discharge.

Model	Coefficient	Estimate	SE	t	P
Null	Intercept	26.98	1.49	18.07	<0.0001
Temperature	Intercept	−126.28	25.94	−4.87	<0.0001
	Temperature	8.79	1.48	5.93	<0.0001
	Phi	0.44	0.14	3.02	0.0044
Discharge	Intercept	53.26	4.03	13.20	<0.0001
	Discharge	−4.09	0.59	−6.94	<0.0001
	Phi	0.27	0.16	1.70	0.0975
Temperature + Discharge	Intercept	−368.36	77.91	−4.73	<0.0001
	Temperature	23.93	4.43	5.41	<0.0001
	Discharge	56.99	11.53	4.94	<0.0001
	Temperature × Discharge	−3.49	0.67	−5.24	<0.0001

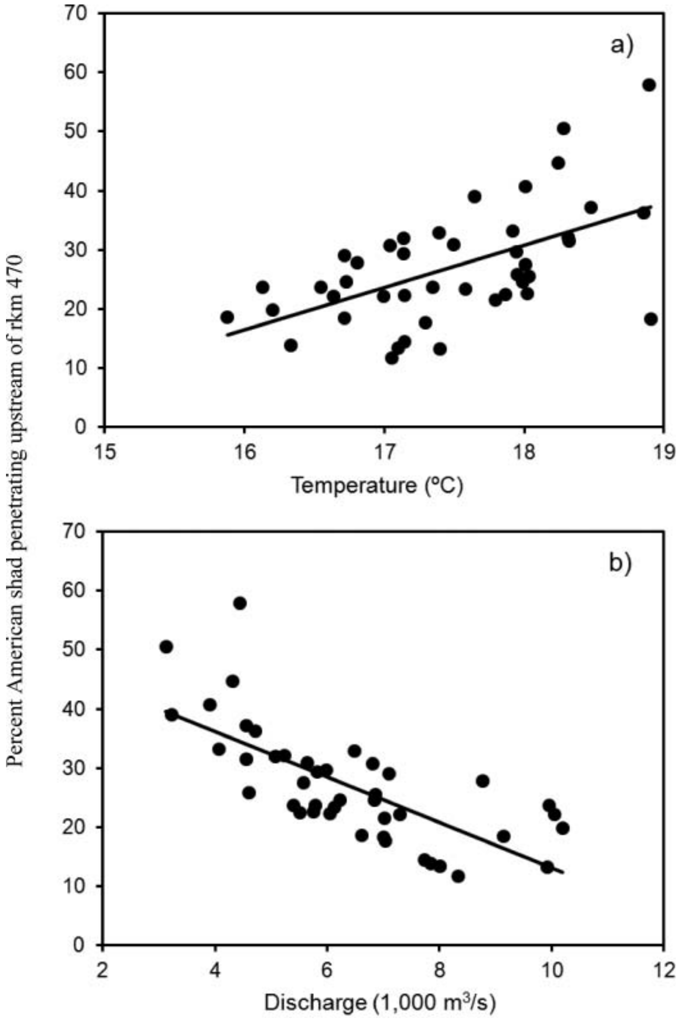

FIGURE 5. Least-squares line fits of the percent of American Shad penetrating upstream from rkm 470 versus (**a**) mean May–August water temperature or (**b**) mean May–August discharge, 1970–2010.

between predictor variables (or multicollinearity) can produce nonsignificant regression coefficients when predictor variables are important (Belsley 1991). The negative estimate of the interaction coefficient indicates that as average May–August temperature increases, the effect of discharge on upriver distribution of American Shad becomes stronger. At higher temperatures, the temperature contours bunch closer together (Figure 6), increasing the effect of an increment in mean May–August discharge on upriver distribution of American Shad.

When all the time series used in the regressions were detrended using a least squares fit to year (Shumway and Stoffer

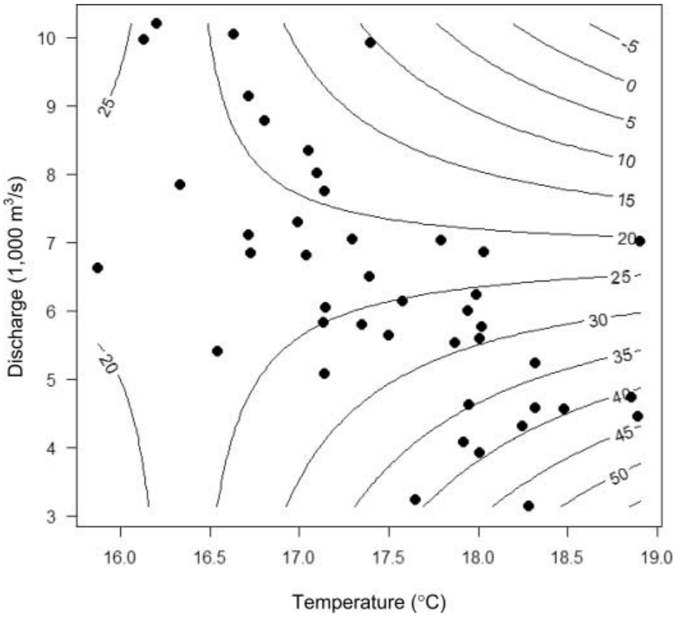

FIGURE 6. Contours of the predicted percentage of American Shad penetrating upstream from rkm 470 from the multiple linear regression model. Solid dots represent observed values of mean May–August river temperature and mean May–August discharge.

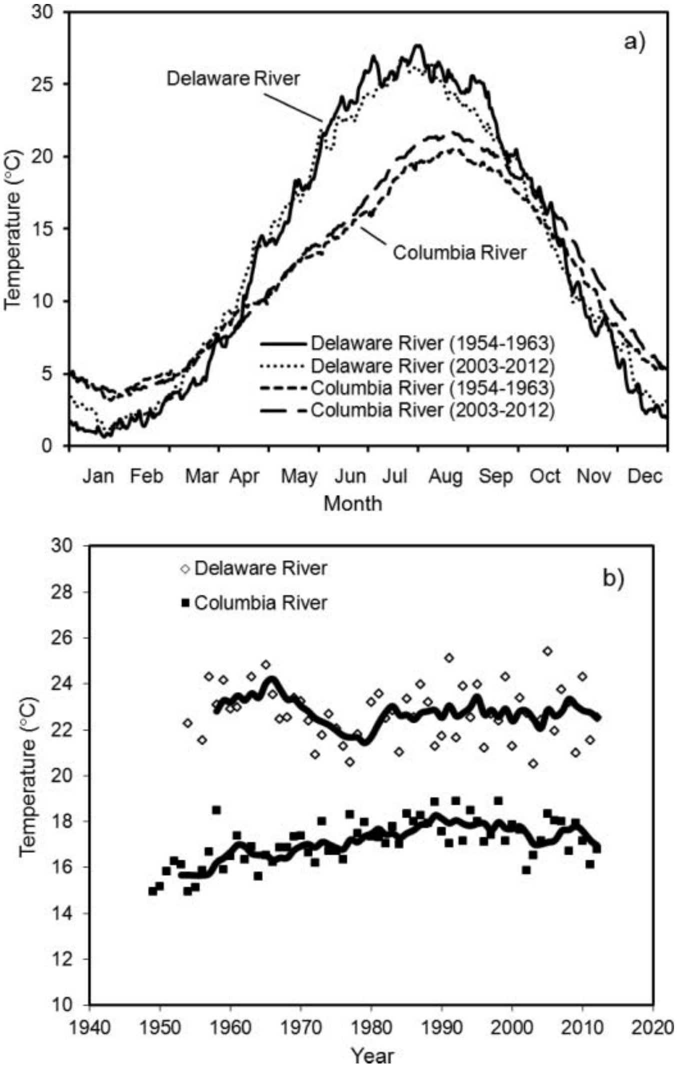

FIGURE 7. (**a**) Daily water temperatures on the Columbia River over the past 60 years compared with those of the Delaware River. (**b**) Time series of average May–August water temperatures on the Columbia River and Delaware River. Solid lines represent 5-year running averages.

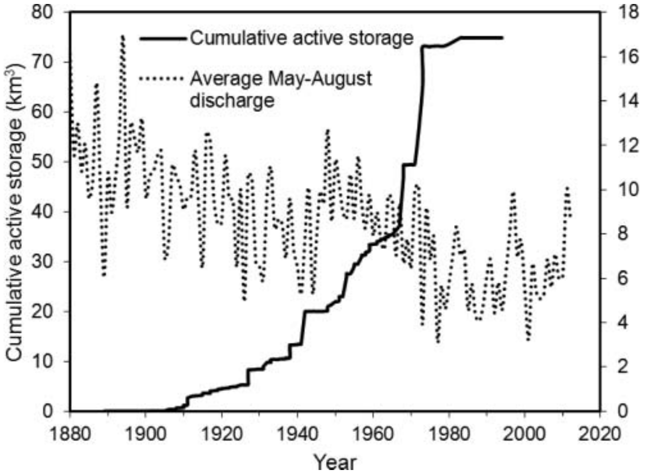

FIGURE 8. Columbia River basin active storage capacity and average May–August discharge since the 1880s.

2000), the overall model fits continued to be significant ($P <$ 0.001). Thus, trends in the data series do not drive the statistical relationships between upriver American Shad distribution and the river covariates of mean May–August temperature and mean May–August discharge (see Figure 4).

River covariate trends.—Annual average May–August water temperatures at Bonneville Dam have increased over the last 64 years, approaching those of the Delaware River (Figure 7). The Mann–Kendall tests for trend showed that the upward trend in the Columbia River annual average May–August water temperature data was statistically significant ($P = 0.004$), but no statistically significant trend existed in the Delaware River annual average May–August water temperature ($P = 0.482$). In the Columbia River, the 5-year running average of annual average May–August water temperature increased by 1.3°C between the periods 1949–1953 and 2008–2012. This increase in average May–August water temperature coincided with the rapid increase in active storage in the Columbia River basin and decrease in average May–August discharge (Figure 8).

DISCUSSION

A central tenet of invasive species ecology is that habitat disturbance can facilitate the establishment and proliferation of nonindigenous species (Gray 1879; Hierro et al. 2005). An example is the transformation of a naturally lotic system into a series of reservoirs, which act as stepping stones for dispersal of nonindigenous species (Havel et al. 2005). Our study demonstrates that the growth of the Columbia River American Shad spawning population upriver from Bonneville Dam coincides with dam construction. Furthermore, the upriver spatial extent of the adult American Shad spawning population is strongly related to alterations of discharge and water temperature regimes.

The spawner–recruit data developed in this study helped determine the effect of opening new habitat on population growth of adult American Shad, and places the recent decline of Columbia River American Shad in context. The greatest increase in the adult American Shad count at Bonneville Dam (63 recruits per spawner) occurred after the completion of The Dalles Dam, which inundated Celilo Falls, a natural barrier to American Shad migration (Wendler 1967; Gregory et al. 2002; Hasselman et al. 2012a). Inundation of Celilo Falls allowed adult American Shad to migrate farther up the Columbia River. Note that a much smaller increase in the adult American Shad count at Bonneville Dam (three recruits per spawner) occurred after the completion of John Day Dam, even though this dam created more available contiguous reservoir habitat than did The Dalles Dam. We suspect that there are two important reasons for this. First, construction of John Day Dam did not remove a natural barrier to American Shad upstream migration, while construction of The Dalles Dam did. We would expect that the construction of a dam that removed a natural barrier upstream would have a larger effect on American Shad abundance than would the construction of a dam that did not remove a barrier. Second, American Shad abundance decreased sharply, by about 70% between Bonneville Dam and McNary Dam (Table 1), with upstream river migration distance. Thus, we expect that an increase in habitat upstream of John Day Dam would have less net effect on American Shad abundance than an increase in habitat downstream of John Day Dam, which includes the habitat created by the construction of The Dalles Dam.

Inundation of Celilo Falls allowed access to not only main-stem Columbia River habitat, but also to large upstream tributaries such as the Deschutes and Umatilla rivers. Although American Shad use upriver main-stem habitat in the Columbia River, the extent to which American Shad use upstream Columbia River basin tributaries, perhaps for spawning, is unknown. Downstream from Bonneville Dam, American Shad are known to use the following tributaries: Willamette River (Foster and Boatner 2002); Sandy River (Wendler 1967); John Day River near Astoria, Oregon, in the Columbia River estuary; and tributary streams to Youngs Bay (Robinson 1974). Wendler (1967) noted that with the exception of these rivers and the Snake River, few American Shad have been observed in Columbia River basin tributaries.

Studies that map the spawning and rearing habitat suitability of the Columbia River basin are lacking. Such studies may help us understand the rapid population growth of American Shad that occurred after they were able to access to new upstream spawning and rearing habitat. Atlantic coast American Shad studies show that spawning locations are related to substrate, depth, water velocity, and dissolved oxygen (Klauda et al. 1991; Beasley and Hightower 2000; Harris and Hightower 2011). These studies show that American Shad spawn in shallow areas (<5 m depth) in which water flows over coarse substrates. Shallow, flowing areas are available in the reservoirs of the lower Columbia and lower Snake rivers, where dams are run of the river. On the Columbia River, systematic studies of substrate, water temperature, water velocity, pH, and dissolved oxygen, which are all factors used to define habitat requirements for American Shad (Klauda et al. 1991), are not available. However, we were able to identify a few habitat studies of the John Day Reservoir that, when taken together, allowed us to identify ranges for these habitat factors (Gilbreath et al. 2000; Cross and Twichell 2004; Tiffan et al. 2006). Mapping of substrate in the John Day Reservoir showed that 10% of the total reservoir floor consisted of gravel beds free of fine sediment (Cross and Twichell 2004), which would be suitable for American Shad. Measurements by Gilbreath et al. (2000) in John Day Reservoir demonstrated that dissolved oxygen ranged from 8.4 to 12.8 mg/L, which is greater than the value of 5 mg/L known to be suitable for survival of American Shad at the egg, juvenile, and migrating adult stages (Klauda et al. 1991). Gilbreath et al. (2000) found that temperatures in the John Day Reservoir ranged from 10°C to 22°C during June–August, which lies within the temperature range of 13–26°C known to be suitable for development and survival of American Shad eggs (Klauda et al. 1991). Tiffan et al. (2006) found that water velocities at two stations within the John Day Reservoir varied by discharge and distance from shore, and ranged from 0 to 30 cm/s, which is lower than velocities thought to be optimal for American Shad spawning and egg incubation (30–90 cm/s), but within the range optimal for larvae (6–30 cm/s) and juveniles (6–75 cm/s). However, these stations were not located near the tailrace of McNary Dam (located at the upstream end of John Day Reservoir), where water velocities from the shore to midchannel can range from 0 to 100 cm/s (Faler et al. 1988). This suggests that there are areas within the McNary Dam tailrace that contain water velocities optimal for American Shad spawning and egg incubation. Measurements of pH levels in the John Day Reservoir (7.7–8.6) by Gilbreath et al. (2000) meet the criteria for egg (>6.0) and larval stages (>6.7) (Klauda et al. 1991) of American Shad in their native range.

The recent large decline in American Shad counts at Bonneville Dam (Figure 2) is not unprecedented. Similar low values of recruits per spawner occurred during the 1940s (Figure 3). The decline, however, is rare and not understood (Pearcy and Fisher 2011). Pearcy and Fisher (2011) showed that fish counts at Bonneville Dam are correlated with abundance estimated by sampling over the continental shelf. This suggests there was an actual decline in population abundance of American Shad in the Columbia River, not simply a redistribution to areas downstream from Bonneville Dam. In 2012, over 2 million adult shad were observed passing Bonneville Dam, suggesting a resurgence in the spawning population. Our lack of understanding of the recent dramatic decline of American Shad abundance from 6 million in 2005 to 1 million in 2011 in the Columbia River basin reveals two critical needs: (1) statistical tests relating the time series of number of recruits per spawner to important biotic and abiotic factors and (2) information on cause and effect. Statistical and causative relationships will help fisheries managers understand not only the recent population decline, but also population variations throughout the entire record of counts. Statistical tests for relationships would include important abiotic factors (e.g., Pacific Decadal Oscillation [PDO], coastal upwelling index, temperature), as well as biotic factors (e.g., zooplankton abundance in reservoirs, estuary, ocean). Changes in temperature, discharge, and available habitat have probably influenced recruits per spawner of American Shad, but other factors that influence recruits per spawner are also possible, including oceanic factors. Examples include the Oregon Production Index, which was found to be negatively correlated with American Shad counts, and the PDO, which recently has switched to a cool–wet phase (Pearcy and Fisher 2011). Causal information might include surveys of prey abundance in reservoirs and stomach contents of rearing juveniles (Haskell et al. 2006), as well as parasite loads and associated mortality rates of American Shad (Shields et al. 2002; Hershberger et al. 2010).

We found that adult American Shad abundance declines with upriver distance above Bonneville Dam (Table 1), and the decline is greater with lower water temperature and higher discharge (Figure 4). The cause for the decline in abundance with upriver distance is unknown. Both energy costs and prey abundance (for juvenile American Shad) may be important factors in determining migration distance. Selection may favor American Shad that spawn in reservoirs with sufficient prey for their young. Energy used by adults to migrate a greater distance upstream is not available for reproduction and decreases the energy reserve necessary for iteroparity (Leggett et al. 2004; Castro-Santos and Letcher 2010). Petersen et al. (2003) estimated that 32% of American Shad in the Columbia River basin are repeat spawners. Energy costs could also be increased by migration delays at dams (Castro-Santos and Letcher 2010). If energy cost of migration explains variation in upriver distribution, higher discharge would increase energy costs of migration, discouraging longer migrations, especially at high temperatures when energetic costs of locomotion are greatest (Glebe and Leggett 1981). Indeed, by focusing on the region of the contour plot where the average May–August temperature and discharge observations are concentrated, we found that a higher fraction of American Shad migrated beyond McNary Dam when average May–August discharge was low, and the effect of average May–August discharge was greatest at high average May–August water temperatures (Figure 6).

The availability of prey resources for juvenile shad in different reservoirs also could play an important role in the upstream distribution of adults. Although adults feed little during their spawning migration in freshwater, prey sources for larval and juvenile shad are important for survival (Stier and Crance 1985; Limburg 1996b). American Shad may choose spawning locations that increase opportunities for their young to find suitable prey, which are unevenly distributed in the Columbia River. Haskell et al. (2006) found that prey abundance for juvenile American Shad was greater in the John Day Reservoir than in the McNary Reservoir (upriver from John Day Reservoir) largely because John Day Reservoir had twice the mean retention time of McNary Reservoir, with conditions more favorable for zooplankton abundance. Therefore, if American Shad spawned in the McNary Reservoir instead of the John Day Reservoir (downstream of McNary Dam), there would be less suitable prey available to their young.

The decline of American Shad with upriver distance may also be related to fish ladder design and the hydraulic conditions experienced by adults. American Shad migration depends upon appropriately designed fishways to pass migration barriers (Moffitt et al. 1982; Quinn 1994). When a fishway at John Day Dam went into operation in 1968, American Shad were reluctant or unable to pass through the submerged orifices in the ladders (Monk et al. 1989). The resultant “traffic jam” of American Shad became problematic because it delayed passage of Pacific salmon. It was discovered that American Shad used surface weirs but not submerged orifices to move upstream and downstream (Haro and Kynard 1997). Modifications of John Day Dam ladders in 1972 reduced water velocity and created surface passage weirs (“slot-type” weirs); fish ladders at Bonneville Dam were similarly modified in 1973 (Perkins and Smith 1973). The American Shad population grew when these ladder modifications were made in the early 1970s, reaching a maximum of 3.7 recruits per spawner (ADJ) in BY 1974 (Figure 3). The fisheries agencies used the inability of American Shad to migrate through the submerged orifices of Priest Rapids Dam fishways as a strategy to block further invasion of upstream habitat by this species (FERC 2006).

Why focus on water temperature and discharge? Our results suggest that average May–August water temperature and discharge affect the extent of the upriver spawning migration. In turn, upriver extent of the spawning migration may have consequences for juvenile American Shad growth and survival (Limburg 1996a, 1996b), recruitment, and, ultimately, fitness. From Atlantic coast studies, we know that water temperature and discharge affect year-class strength of American Shad populations (e.g., Crecco and Savoy 1984). Therefore, to understand the spread and increase in abundance as well as possible future population increases, it is important to understand how and why Columbia River water temperature and discharge have changed and how they are expected to change in the future.

Construction of dams has altered the Columbia River food web to support increases in abundance of American Shad. The Columbia and Snake rivers have been converted from lotic to lentic ecosystems (ISAB 2011), with the exception of the Hanford Reach in the mid-Columbia River. This alteration has shifted food sources from benthic or terrestrial in origin (e.g., caddisflies, mayflies, stoneflies) to planktonic (e.g., copepods, cladocerans) (ISAB 2011). This change in prey base might have favored juvenile American Shad, which are planktivorous (Haskell et al. 2006). Haskell et al. (2006) found that zooplankton made up 99% of the juvenile American Shad diet during their out-migration (August–November). Yearly zooplankton abundances fluctuate with water temperature and discharge in both the John Day and McNary reservoirs (Haskell et al. 2006). These fluctuations in prey abundance probably influence juvenile American Shad survival (Crecco and Savoy 1985) and consequently population growth. Therefore, an important area for future research is to test whether prey abundance is a significant predictor of number of recruits per spawner, which is a measure of population growth.

The shift from free-flowing to reservoir habitats in the Columbia River basin may hold evolutionary implications for American Shad. It is unlikely American Shad in their native range have experienced lentic conditions similar to those of the Columbia River basin during their evolutionary history (Baxter 1977). The lentic condition of the Columbia River basin might have presented the species with altered selection pressures, which may become manifest as altered phenotypes (Haas et al. 2010; Franssen 2011), life histories (Hammann 1982; Wetzel et al. 2011), and demography (Rottiers et al. 1992).

Impoundments like those of the Columbia River basin may be an important evolutionary driver acting on aquatic biodiversity (Haas et al. 2010). Because evolutionary adaptations may facilitate future establishment and spread of invasive taxa (Allendorf and Lundquist 2003), understanding the life history variation exhibited by American Shad is important for effective management of their population in the Columbia River basin.

To understand the true impact of American Shad on native taxa in the Columbia River basin, it is essential to know the species' distribution throughout the entire Columbia and Snake rivers, not just in the main-stem Columbia River upstream from Bonneville Dam. If the observed pattern of decreasing adult American Shad abundance with upriver distance applies to areas downriver from Bonneville Dam, then the American Shad passing Bonneville Dam could represent a small fraction of the entire spawning population. Furthermore, yearly counts of shad in tributaries downstream (and upstream) from Bonneville Dam do not exist. An important area of future research is mark–recapture experiments to estimate the abundance of the adult American Shad population spawning downstream from Bonneville Dam.

The status of American Shad in the Columbia River versus the Atlantic coast of the United States reveals an irony (Hinrichsen and Ebbemeyer 1998; Gregory et al. 2002). As the Columbia River was dammed, American Shad extended their in-river range and increased in abundance. As rivers on the Atlantic coast were dammed, American Shad lost spawning habitat and declined in abundance (e.g., St. Pierre 1994, 2003). Several factors other than dam construction have contributed to declines in American Shad populations on the Atlantic coast, including overfishing, pollution, and land development (Rulifson 1994; Bilkovic et al. 2002; Limburg et al. 2003). As a result, catch levels on the Atlantic coast dropped from 30,000 metric tons at the turn of the 20th century to 600 metric tons by 1996 (Greene et al. 2009). Several measures have been used in an attempt to restore Atlantic coast American Shad populations, including use of American Shad hatcheries (Hendricks 2003). To aid recovery of American Shad populations in their native range, the development of effective fishways is needed (Moffitt et al. 1982; Quinn 1994; Weaver et al. 2003; Katopodis 2005). Perhaps there are lessons from fishway designs and operations used to successfully pass American Shad on the Columbia River that can assist in this effort. American Shad on the Columbia River have demonstrated that spawning populations can increase in abundance without hatchery inputs when fishways are effective and other sources of mortality are held in check.

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