

Nutrient loading by anadromous fishes: species-specific contributions and the effects of diversity

Cornelia W. Twining, Eric P. Palkovacs, Maya A. Friedman, Daniel J. Hasselman, and David M. Post

Abstract: Anadromous fishes exhibit diverse life history and functional traits. Spawning anadromous fishes bring nutrients to fresh waters, and their life history and functional traits can influence nutrient loading patterns. We asked how nutrient inputs varied across 12 species of North American anadromous fishes and how these patterns affected river-wide trends in nutrient loading. We used portfolio effect analyses to assess whether diversity stabilized or destabilized nutrient inputs to freshwater ecosystems over time. Recent decreases in body size reduced per individual nutrient loading for several key species, which in turn decreased cumulative loading. Invasion also altered nutrient loading; non-native American shad (*Alosa sapidissima*) now provide nearly half of the annual marine-derived nutrient inputs to the Columbia River. Counter to expectations, species diversity (richness and evenness) did not significantly increase the stability of nutrient inputs to fresh waters. Species loss in the Connecticut River increased stability, while species gain in the Columbia River decreased stability.

Résumé : Les poissons anadromes présentent des cycles biologiques et des caractères fonctionnels variés. Les poissons anadromes reproducteurs apportent des éléments nutritifs dans les milieux d'eau douce, et leur cycle biologique et leurs caractères fonctionnels peuvent influencer la répartition de la charge en éléments nutritifs. Nous avons examiné les variations des apports en éléments nutritifs entre 12 espèces de poissons anadromes nord-américains et l'incidence de ces variations sur l'évolution de la charge en éléments nutritifs à l'échelle de la rivière. Nous avons utilisé des analyses de l'effet de portefeuille pour déterminer si la diversité stabilisait ou déstabilisait les apports en éléments nutritifs dans les écosystèmes d'eau douce au fil du temps. Des diminutions récentes de la taille du corps ont entraîné une baisse de la charge en éléments nutritifs par individu pour plusieurs espèces clés, ce qui s'est traduit par une baisse des charges cumulatives. Les invasions ont également modifié la charge en éléments nutritifs; l'aloise savoureuse (*Alosa sapidissima*), une espèce non indigène, représente aujourd'hui près de la moitié des apports annuels en éléments nutritifs d'origine marine dans le fleuve Columbia. Contrairement aux attentes, la diversité spécifique (richesse et uniformité) n'a pas entraîné une augmentation significative de la stabilité des apports en éléments nutritifs dans les milieux d'eau douce. La disparition d'espèces dans le fleuve Connecticut a accru la stabilité, alors que l'apparition d'espèces dans le fleuve Columbia a réduit la stabilité. [Traduit par la Rédaction]

Introduction

Interest in spatial linkages among ecosystems has expanded over the past two decades with the recognition that migratory animals provide resource subsidies that effect the strength and form of species interactions, food web stability, and local biodiversity (Polis and Hurd 1996; Naiman et al. 2002; Vanni 2002; Schindler et al. 2003). The movement of nutrients by anadromous fishes connects distant food webs and can strongly impact local nutrient dynamics (Donaldson 1967; Durbin et al. 1979; Bilby et al. 1996; Schindler et al. 2003). For example, inputs of marine-derived nutrients to freshwater ecosystems from spawning anadromous fishes have been shown to affect various aspects of ecosystem function in the Pacific Northwest region of North America (Donaldson 1967; Bilby et al. 1996; Naiman et al. 2002; Schindler et al. 2003). Nutrient inputs from anadromous fishes can shape biodiversity and increase primary and secondary production not only in freshwater ecosystems, but also in surrounding riparian zones and terrestrial ecosystems (Ben-David et al. 1998; Naiman et al. 2002; Schindler et al. 2003; Hocking and Reynolds 2011).

Previous research on the movement of nutrients by anadromous fishes between marine and freshwater ecosystems has been dominated by research on Pacific salmon (*Oncorhynchus* spp.), while largely ignoring other anadromous species (Vanni 2002; Flecker et al. 2010). Consequently, the literature on inputs of marine-derived nutrient to freshwater ecosystems reflects the characteristics of Pacific salmon, most of which are semelparous and large-bodied (≥ 2 kg), as well as the ecosystems in which Pacific salmon spawn, which are typically nutrient-poor (Schindler et al. 2003). These characteristics generally result in a large net flow of nutrients from marine into freshwater ecosystems where allochthonous nutrient inputs are often considered beneficial (Schindler et al. 2003; Scheuerell et al. 2005).

In contrast with the extensive research on Pacific salmon, much less is known about the role of other anadromous fishes as vectors for marine-derived nutrients. This is particularly true for species native to the Atlantic Ocean (Nislow et al. 2004; Nislow and Kynard 2009; West et al. 2010). For such species, life histories and local environmental conditions can differ substantially from those of Pacific salmon. For example, most anadromous species in the

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C.W. Twining. Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA.

E.P. Palkovacs, M.A. Friedman, and D.J. Hasselman.* Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95060, USA.

D.M. Post. Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520, USA.

Corresponding author: Cornelia W. Twining (email: cwt52@cornell.edu).

*Present address: Columbia River Inter-Tribal Fish Commission, 3059F National Fish Hatchery Road, Hagerman ID 83332, USA.

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Atlantic Ocean are iteroparous, some are small-bodied (<1 kg), and many move nutrients into freshwater ecosystems that are already nutrient-rich (mesotrophic to eutrophic) because of underlying geochemistry or cultural eutrophication. Research on anadromous alewife (*Alosa pseudoharengus*) in coastal New England rivers and lakes suggests that these fish play a very different ecosystem role than Pacific salmon (Durbine et al. 1979; West et al. 2010; Twining et al. 2013).

Life history traits likely help determine the role of various anadromous fishes as nutrient vectors and drivers of ecosystem function. Semelparous anadromous fishes, such as sockeye salmon (*Oncorhynchus nerka*), which experience 100% postspawning mortality, load nutrients primarily through carcass inputs (Kline et al. 1993; Naiman et al. 2002; Schindler et al. 2003). Iteroparous anadromous fishes, such as alewife, which can live to spawn multiple times over the course of their lives, load nutrients through a combination of carcasses, excretion, and release of gametes (Walters et al. 2009; West et al. 2010). However, iteroparous fishes can also exhibit considerable latitudinal variability in postspawning mortality (Carscadden and Leggett 1975). For example, populations of American shad (*Alosa sapidissima*) typically suffer around 50% postspawning mortality at the center of their range, but approach 100% postspawning mortality at the southern edge of their range (Carscadden and Leggett 1975). Thus, life history variation within and among anadromous species shapes both the form and magnitude of marine-derived nutrients entering fresh waters.

Several key functional traits, including body size, adult residence time, and body stoichiometry, also likely determine the role of anadromous fishes as nutrient vectors. Small-bodied species, such as alewife, have higher mass-specific nutrient excretion rates and therefore load more nutrients per unit biomass through excretion than larger fishes with lower mass-specific nutrient excretion rates (Vanni et al. 2002; Vanni 2002). Within species, recent body size reductions have been observed for a variety of anadromous fishes (Bigler et al. 1996; Morita et al. 2005; Davis and Schultz 2009; Kendall et al. 2011, 2014; Lewis et al. 2015). Such size shifts may have important consequences for nutrient loading. In addition, fishes that spawn at high densities load more nutrients on a per area basis than fishes that spawn at lower densities (Flecker et al. 2010). Thus, a variety of factors influence the nutrient loading potential for any given species, and the diversity of species may influence the nutrient loading potential for any given watershed.

Here, we explore how interspecific diversity, in terms of evenness and richness, influences nutrient transport by anadromous fishes. We estimate nutrient loading for 12 anadromous fish species from three different Orders: Petromyzontiformes (lampreys), Salmoniformes (salmons), and Clupeiformes (herrings). These species include (1) sea lamprey (*Petromyzon marinus*), (2) Pacific lamprey (*Entosphenus tridentatus*), (3) alewife (*A. pseudoharengus*), (4) blueback herring (*Alosa aestivalis*), (5) American shad (*A. sapidissima*), (6) steelhead (*Oncorhynchus mykiss*), (7) sockeye salmon (*O. nerka*), (8) coho salmon (*Oncorhynchus kisutch*), (9) chum salmon (*Oncorhynchus keta*), (10) Chinook salmon (*Oncorhynchus tshawytscha*), (11) pink salmon (*Oncorhynchus gorbuscha*), and (12) Atlantic salmon (*Salmo salar*). We chose these species because they represent some of the best studied and most economically and culturally important anadromous fishes on the Atlantic and Pacific coasts of North America and because they vary in a number of key life history traits (e.g., postspawning mortality rate, and adult and juvenile freshwater residence time), as well as functional traits (e.g., body nutrient content and excretion rates), that we expect to influence the net flux of nutrient into and out of freshwater ecosystems (Moore and Schindler 2004; West et al. 2010; Moore et al. 2011). Further, several of these species have experienced reductions in body size that may contribute to changes in nutrient loading observed through time.

We use data from the Connecticut River on the Atlantic coast and the Columbia River on the Pacific coast of North America to model how the functional and life history traits of a diverse community of anadromous fishes combine to determine ecosystem-wide patterns of nutrient loading. Using fish passage data records from the mid-twentieth century to the present from dams along the Connecticut River and the Columbia River, we converted our modeled per fish phosphorus into estimates of total and species-specific phosphorus fluxes. We focused on the net flux of phosphorus by anadromous fishes because phosphorus has historically been considered to be the limiting nutrient in most freshwater ecosystems (Smith and Schindler 2009), and as a consequence, phosphorus data exists for a much greater number of species.

Anadromous fishes can also provide major fluxes of contaminants and other nutrients, such as nitrogen to fresh waters (e.g., Moore and Schindler 2004). The role of species as nitrogen versus phosphorus fluxes is likely to depend both upon species' stoichiometry as well as their dominant nutrient loading pathway (Flecker et al. 2010). For example, Petromyzontiformes, which lack bones and scales, have low phosphorus to nitrogen ratios and are semelparous and are thus likely to contribute primarily nitrogen through postspawning mortality. In contrast, alosines, which are iteroparous and have higher phosphorus to nitrogen ratios, are likely to contribute more nitrogen through adult excretion, but contribute more phosphorus in their gametes and carcasses (Walters et al. 2009; West et al. 2010).

The period from the mid-twentieth century to present includes many important changes in these rivers, including a major increase in American shad abundance in the Columbia River (Hasselman et al. 2012a, 2012b) and the decline of alosines throughout Atlantic Coast rivers (Limburg and Waldman 2009; Palkovacs et al. 2014). Changes in the species composition of anadromous fishes in these systems may alter the stability of total fish-derived nutrient inputs. We considered these changes in terms of a portfolio effects analysis to compare the temporal stability of phosphorus loading by multispecies assemblages with the stability of loading by individual species. Species diversity is generally thought to stabilize ecosystem processes (Hooper et al. 2005). Here, we test whether species richness increases the stability of nutrient loading to freshwater ecosystems by anadromous fishes.

Methods

Individual species loading rates

In calculating nutrient inputs, we used modifications of previously published anadromous fish nutrient loading models developed by experts on the given species. We used the model developed by West et al. (2010) for alewife, blueback herring, American shad, sea lamprey, Pacific lamprey, and Atlantic salmon and similar models developed by Moore and Schindler (2004) and Moore et al. (2011) for six species of Pacific salmonids: pink, sockeye, chum, Chinook, coho, and steelhead. These previously published models include both the import of nutrients into fresh waters by spawning adults and the export of nutrients by emigrating juveniles. In our final analysis, we choose not to include juvenile export in our models because there were no available data on juvenile outmigration at the river scale for many species from our study systems. As discussed in Scheuerell et al. (2005) and in West et al. (2010), juvenile export only has major effects on loading rates at the population level when adult escapement and biomass are extremely low. For species for which reliable estimates of juvenile escapement are available, we ran models including juvenile export and found a minimal effect on overall loading (e.g., alewife P fluxes with high juvenile survival were 45.76 g per fish, while those without juvenile export were 45.92 g per fish; Atlantic salmon P fluxes with high juvenile survival were 783.84 g per fish, while those without juvenile export were 783.86 g per fish). We

Table 1. Nutrient loading model parameters for the species we considered (NA: not applicable).

	Mean adult mass (g)	Postspawning mortality (fraction)	Adult P content (g P per g adult)	Gamete P contribution (g)	Adult P excretion contribution (g)	Adult residence time (weeks)
River herring (alewife and blueback)	161.5 ^a	0.56 ^b	0.0042 ^c	0.0275 ^{a,c}	0.0518 ^{a,c}	2 ^a
American shad	1543 ^d	0.56 ^b	0.0042 ^{c,d}	0.152 ^{a,c,d}	0.495 ^{a,c}	2 ^k
Pacific lamprey and sea lamprey	650 ^e	1 ^e	0.00077 ^f	NA	NA	NA
Atlantic salmon	2500 ^g	0.5 ^g	0.0047 ^g	1.67 ^{a,g}	0.294 ^{a,g}	2 ^g
Steelhead	1803 ^m	0.38 ⁱ	0.0038 ^h	2.07 ^{a,j}	0.0316 ^k	2 ^h
Sockeye salmon	2240 ^l	1 ^l	0.0038 ^l	NA	NA	NA
Pink salmon	2000 ^m	1 ^l	0.0048 ⁿ	NA	NA	NA
Coho salmon	3600 ^m	1 ^l	0.0038 ^l	NA	NA	NA
Chum salmon	5669 ^m	1 ^l	0.0038 ^l	NA	NA	NA
Chinook salmon	5669 ^m	1 ^l	0.0038 ^l	NA	NA	NA

^aWest et al. 2010.^bKissil 1974.^cWalters et al. 2009.^dD. Hasselman, unpublished data.^eNislow and Kynard 2009.^fC. Twining, unpublished data.^gNislow et al. 2004.^hMoore et al. 2011.ⁱQuinn and Myers 2004.^jBerejikian et al. 2005.^kMunshaw et al. 2013.^lMoore and Schindler 2004.^mWashington Department of Fish and Game: <http://wdfw.wa.gov/fishing/salmon/identification.html>.ⁿGende et al. 2004.

used the following model to calculate individual per fish nutrient inputs:

$$(1) \quad \text{Nutrient loading for anadromous species} \\ = A_{\text{adults}} + A_{\text{gametes}} + A_{\text{excretion}}$$

where A_{adults} is the mass of nutrient loaded into the system by anadromous adult postspawning mortality, A_{gametes} is the mass of nutrients loaded into the system by spawning adults' inputs of eggs and milt, and $A_{\text{excretion}}$ is the mass of nutrient loaded into the system through direct excretion of nutrients by anadromous adults during their residence in the freshwater ecosystem (West et al. 2010). We only included terms for gametes and excretion for iteroparous adults because we assume that semelparous adults contribute all of their nutrients to the system as assumed in the model for sockeye salmon developed by Moore and Schindler (2004). We calculated A_{adults} as the number of adults for a given year and location multiplied by mean adult size, mean adult phosphorus content, and postspawning mortality (Table 1). We calculated A_{gametes} as the number of adults for a given year and location multiplied by gamete phosphorus content and mean gamete mass per adult (summarized in Table 1). We calculated $A_{\text{excretion}}$ as the number of adults for a given year and location multiplied by adult residence time and daily adult phosphorus excretion rates (summarized in Table 1). We obtained species-specific parameters from empirical data, which are summarized in Table 1.

We present nutrient loading rates for all species in terms of both (i) total phosphorus load (g) per individual fish of an average size for each species and (ii) phosphorus load (g) per biomass of fish (g). We calculate phosphorus load per biomass for each species by dividing total phosphorus load by the mean mass of each species.

Multispecies loading rates and portfolio effects

We considered multispecies nutrient loading in two example systems: the upper Connecticut River and the Columbia River. We modeled net phosphorus inputs over time and across the landscape from the current dominant anadromous fish species assemblage in each river system: alewife, blueback herring, American

shad, Atlantic salmon, and sea lamprey in the Connecticut River and Pacific salmon (Chinook, coho, steelhead, sockeye, chum, and pink), American shad, and Pacific lamprey in the Columbia River. We obtained fish count data for the upper Connecticut River from counts at the Holyoke Dam (<http://www.fws.gov/r5crq/Fish/hist.html>) from 1967 to 2013. We obtained fish count data from fish ladders at Bonneville Dam and McNary Dam on the mainstem Columbia River, as well as from Ice Harbor Dam on the Snake River from the Fish Passage Center (<http://www.fpc.org/>). On the Columbia River and Snake River, fish counts started at Bonneville Dam in 1938, McNary Dam in 1957, and Ice Harbor Dam in 1962.

The size of mature adults for several of our selected species has decreased over the time period we considered (ASMFC 2007, 2012; Bigler et al. 1996; Keefer et al. 2012). Sensitivity analyses suggest that adult size is an important parameter to consider in anadromous fish nutrient loading models (West et al. 2010). Therefore, we included in our models changes in adult size for the following species for which clear decreases in adult size over time have been observed: blueback herring, Pacific lamprey, Chinook, coho, chum, pink, and sockeye salmon. We obtained data on blueback herring size from the nearby Hudson River because there were no available data for the Connecticut River (ASMFC 2012) and assumed that blueback herring prior to 1980 were the same size as those in 1980. We obtained data on Pacific lamprey size from Keefer et al. (2012). We obtained data on Pacific salmon sizes from Bigler et al. (1996), which dated back to 1975. We assumed that Pacific salmon prior to 1975 were the same size as those in 1975.

We accounted for the effects of harvesting in the Columbia River by subtracting the number of fish of each species harvested upstream of a given dam from the total number of fish of that species passing that dam. We obtained data prior to 2002 from the Columbia River Fish Runs and Fisheries Status Report (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 2002) and after 2002 from Oregon Department of Fish and Wildlife annual reports (http://www.dfw.state.or.us/fish/oscrp/crm/comm_fishery_updates.asp). We did not include harvesting for the upper Connecticut River because all commercial, and the majority of recreational, American shad fishing on the river occurs below the Holyoke Dam (ASMFC 2007); this was

also the case for the blueback herring and Atlantic salmon fisheries before they closed on the river (ASMFC 2012). Recreational sea lamprey fishing on the Connecticut River is minor and occurs primarily in the lower river below the Holyoke Dam (S. Gephard, personal communication).

We used a portfolio effects analysis to evaluate if a more species-rich community of anadromous fishes increased stability in nutrient subsidies to the upper Connecticut River and the Columbia River. We calculated mean–variance portfolio effects for fish passage at Bonneville Dam in the Columbia River and Holyoke Dam in the Connecticut River using all years of available data. We also calculated portfolio effects at the Bonneville Dam before and after 1976, when major increases in American shad abundance began, and at the Holyoke Dam between 1980 and 1995 when river herring (i.e., alewife and blueback herring) abundances were relatively high and stable and after 1995 when river herring began to decline. We conducted our portfolio effect analyses in R using the package “ecofolio” originally developed by Anderson et al. (2013) for portfolio effect analyses of salmon metapopulation recruitment.

To use this method, we treated phosphorus contributions from each species at a given location as the individual assets within our community portfolio. This approach involves plotting the mean versus variance of species-specific phosphorus contributions on log–log axes and then extrapolating the relationship out to the community mean. The portfolio effect is the ratio between the predicted variability and observed community variability. Portfolio effect values greater than 1 indicate that multispecies nutrient contributions (i.e., those from communities with higher species richness) are more stable than nutrient contributions from a single species (Anderson et al. 2013).

Theoretical studies suggest that portfolio effects should weaken by reduced evenness and (or) increased synchrony in the fluctuations of a community’s constituent populations (Thibaut and Connolly 2013). To understand how these community properties may alter the strength of portfolio effects in our communities, we calculated Shannon’s diversity index as well as Loreau and de Mazencourt (2008) synchrony index. The synchrony index (ϕ) varies between 0 (maximally asynchronous) and 1 (maximally synchronous) and is independent of the number of species (richness).

Results

Individual species loading rates

Lamprey

Sea lamprey and Pacific lamprey had among the lowest phosphorus contributions of any of the species that we considered on both a per individual basis and a per biomass basis (Fig. 1). Phosphorus inputs from lamprey per biomass were lower than for any other species we considered. At the per individual fish level, inputs from lamprey were slightly higher than those from river herring. Although lamprey are semelparous and contribute all body nutrients to fresh waters during their spawning activities, they bring little phosphorus into fresh waters because of their low body phosphorus content, intermediate body size, and relatively small spawning run sizes. Lamprey have extremely low body phosphorus content compared with the other diadromous fishes we considered because they lack scales and ossified bones rich in calcium phosphate (Hendrixson et al. 2007; Table 1).

River herring and shad

Alewife and blueback herring had the smallest phosphorus flux per individual of the species we assessed and the smallest phosphorus flux per gram of adult biomass of the iteroparous species we considered (Fig. 1). American shad contributed slightly more phosphorus per biomass than river herring (Fig. 1a), but contrib-

uted a much larger phosphorus flux per individual than their smaller congeners because of their larger body size (Fig. 1b).

Salmon

Steelhead had the lowest per biomass and per individual phosphorus contributions of any of the salmonids we considered (Fig. 1c). This effect is likely driven by a combination of their iteroparous life history, smaller adult body size, and relatively low body phosphorus content compared with the other salmonids we assessed (Table 1). Atlantic salmon phosphorus fluxes per individual were similar to those of sockeye salmon, while their fluxes per biomass were higher than those of steelhead, but lower than those of the semelparous salmonids we considered (Fig. 1). Sockeye contributed an intermediate flux of phosphorus both per individual and per biomass of adults because of their semelparous life history (Table 1; Figs. 1c–1d). Among the species we considered, pink salmon contributed the greatest net phosphorus flux into fresh waters per biomass (Fig. 1c), which is driven by a combination of 100% postspawning mortality and high body phosphorus content (Table 1). Coho, Chinook, and chum salmon had intermediate per biomass phosphorus contributions (Fig. 1c). Chinook and chum salmon had the highest per individual phosphorus contributions of any of the species we considered (Fig. 1d). Coho, Chinook, and chum had intermediate levels of per biomass phosphorus contributions (Fig. 1c), owing to a combination of their large adult body masses and semelparous life histories (Table 1).

Multispecies loading rates and portfolio effects

In the Columbia River, Chinook salmon and non-native American shad (introduced from the Atlantic coast) generally dominated phosphorus loading, but this varied considerably by year and location (Figs. 2a–2c). Across locations, loading peaked around 1960, 1970, and again around 2000 and 2010. Chinook and Pacific lamprey dominated phosphorus inputs in the Columbia River main stem before the abundance of non-native American shad began to increase markedly after about 1976 (Figs. 3a–3c). The relative nutrient contributions from other salmonids, such as steelhead, increased upstream on the Columbia River main stem while the relative contribution of American shad decreased (Figs. 3a–3c). On the Snake River (Ice Harbor Dam), Chinook and sockeye salmon contributed similar amounts of nutrients while other species contributed relatively little (Fig. 3c). Pacific lamprey contributed little to phosphorus inputs (Figs. 3a–3c).

Over the time period we considered, American shad dominated phosphorus loading in the upper Connecticut River above the Holyoke Dam (Fig. 3d). Total phosphorus loading in the Connecticut River closely tracked loading from this species (Fig. 3d). Over the course of our time series (1967–2013), loading from blueback herring peaked in the 1980s and early 1990s (Fig. 3d). Loading from Atlantic salmon peaked from the 1980s through the late 1990s (Fig. 3d), coinciding with the recent multi-state–federal cooperative Atlantic salmon restoration effort, which has since been discontinued because of low adult return rates. Loading from sea lamprey increased in the late 1990s, but was highly variable throughout the period we considered (Fig. 3d). Alewife spawn in the lower Connecticut River watershed, but rarely ascend all the way to Holyoke Dam, which is why they do not contribute nutrient loading above Holyoke Dam.

Portfolio effects for phosphorus loading by multispecies assemblages in our systems were >1.0, but their 95% confidence intervals still overlapped with 1 at all locations for mean variance portfolio effects (Fig. 2a; also see online Supplementary Fig. 1¹). This result indicates that species richness has the potential to increase the stability of phosphorus loading, but this effect was not significant for the rivers considered. Portfolio effects for the

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0136>.

Fig. 1. Phosphorus loading (*a, c*) per gram of fish and (*b, d*) per fish for key native Connecticut River and key native Columbia River anadromous fishes. Mean adult mass was used to calculate data for panels (*b*) and (*d*): river herring = 161.5 g, American shad = 1543 g, Atlantic salmon = 2500 g, sea lamprey = 650 g, Pacific lamprey = 650 g, steelhead trout = 1803 g, sockeye salmon = 2240 g, pink salmon = 2000 g, coho salmon = 3600 g, Chinook salmon = 5669 g, and chum salmon = 5669 g.

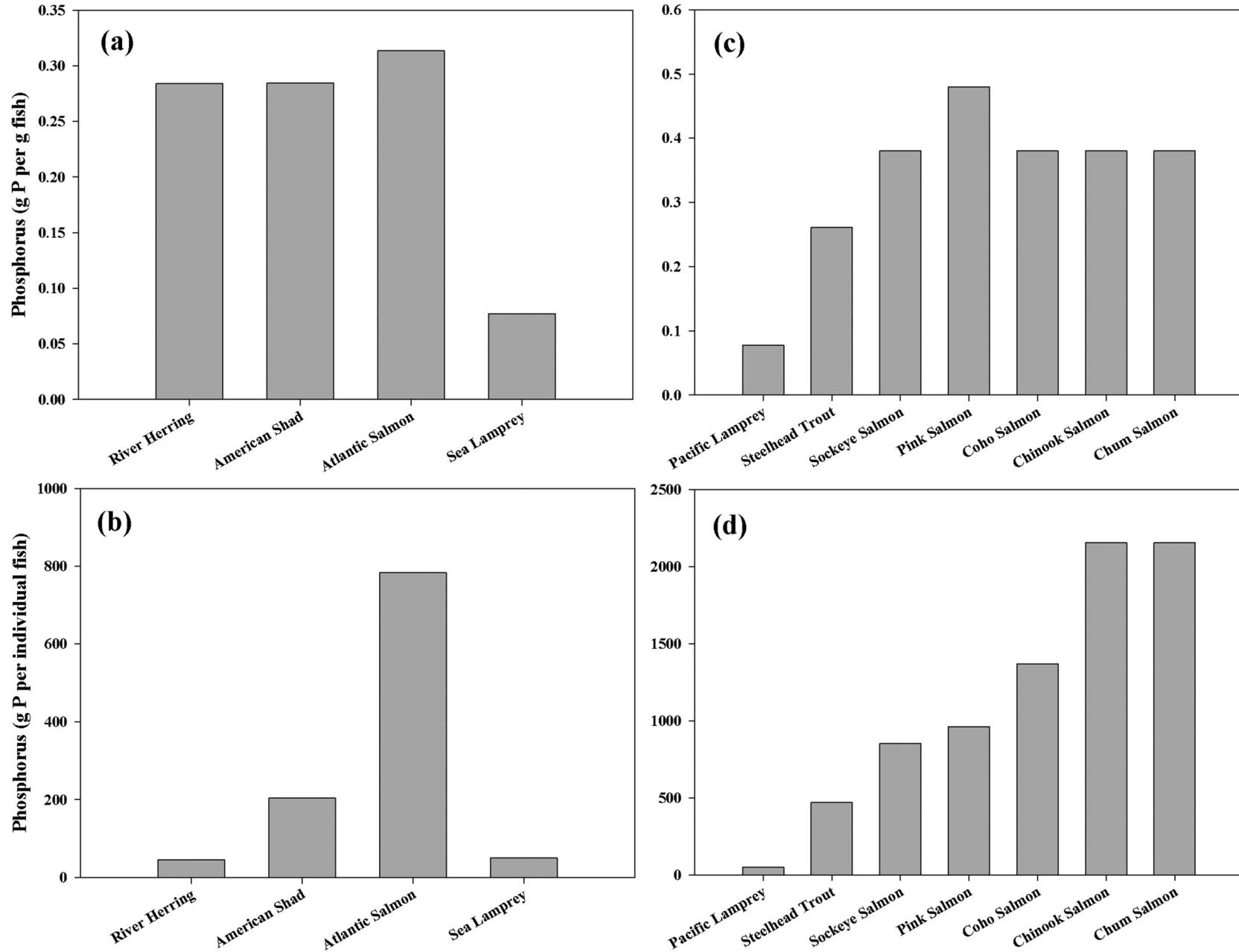
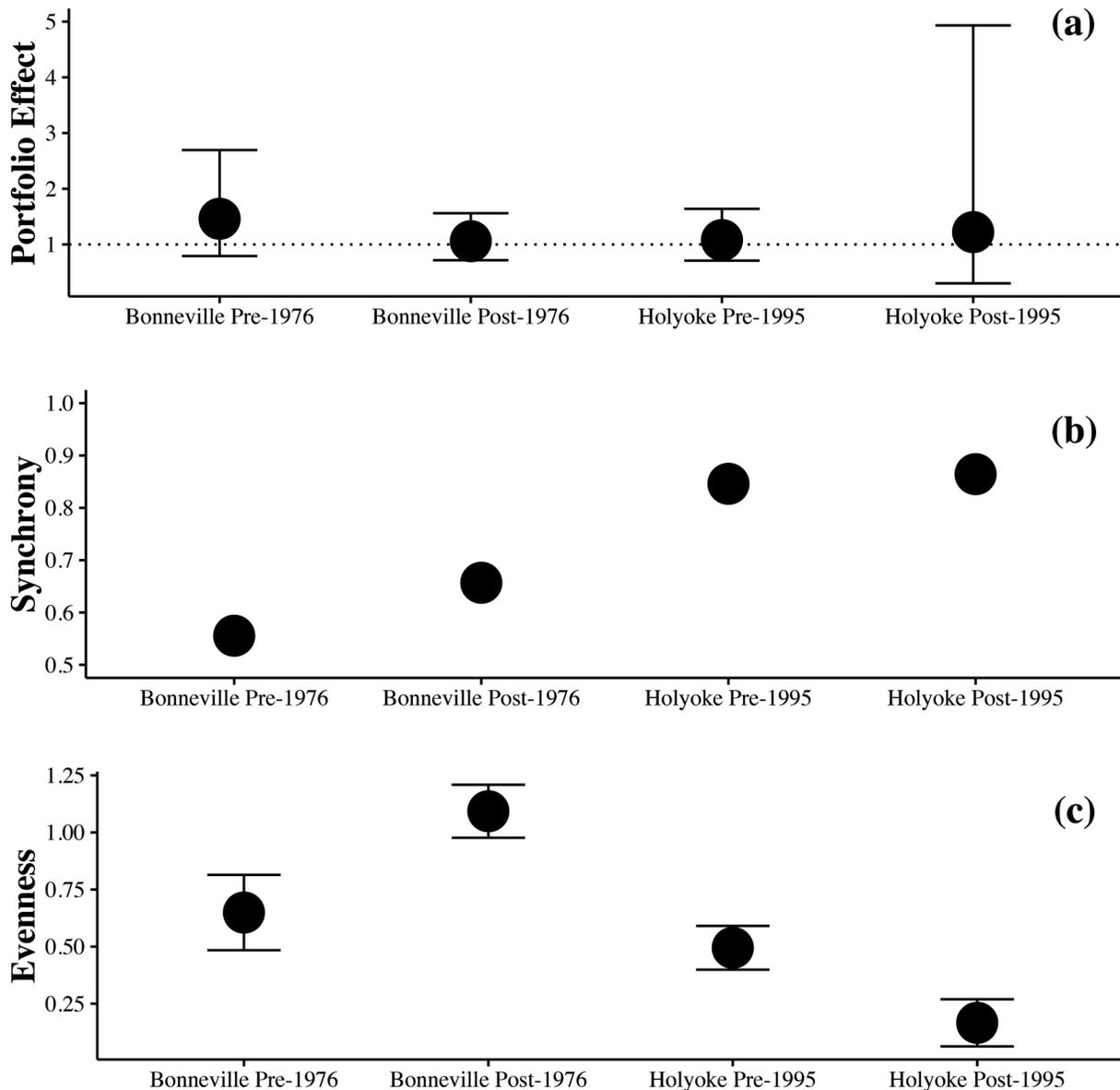


Fig. 2. Portfolio effects (a), synchrony (b), and evenness (c) pre- and post-1976 above Bonneville Dam and pre- and post-1995 above Holyoke Dam. The dotted line at 1 in panel (a) represents the point above which multiple species have greater stability than single species. Error bars represent 95% confidence intervals in panel (a) and standard deviations in panel (c).



Connecticut River were lower (i.e., less stable) prior to the river herring decline beginning in 1995 and had a much narrower confidence interval (Fig. 2b). Contributions of phosphorus loading into the Connecticut River at Holyoke Dam were highly synchronous across the duration of our time series ($\phi = 0.87$). Synchrony did not vary between the periods of relatively high river herring abundance (1980–1995) and after the declines in river herring (>1995; Fig. 2b). Mean evenness in phosphorus loading at Holyoke Dam was relatively low across the time series, peaking when river herring were abundant in the system and decreasing considerably after 1995 (Fig. 2c).

Portfolio effects at the Bonneville Dam decreased substantially following the major increase in American shad beginning in 1976 (Fig. 2a). Before the dramatic increase of American shad in the Columbia River (i.e., pre-1976), synchrony (ϕ) in phosphorus loading at Bonneville Dam was 0.55. Synchrony in phosphorus loading at Bonneville Dam increased to 0.65 after the abundance of American shad increased beginning in 1976 (Fig. 2b). Evenness increased

over the course of our time series after the abundance of American shad began to markedly increase (Fig. 2c).

Effects of decreasing body size

We obtained body size trends through time for seven of the 12 species considered in our analysis. Systematic decreases in body size were observed for Chinook, coho, chum, pink, and sockeye salmon, Pacific lamprey, and blueback herring. We also obtained body size data for American shad, which did not show a consistent decline in body size over the time period we considered. Declines in the size of anadromous adults over time caused portfolio effects to increase slightly (mean variance portfolio effects of 1.16, 1.41, 1.05, and 1.36 with reduced body size versus 1.06, 1.26, 1.05, and 1.25 assuming no size change for Bonneville Dam, McNary Dam, Ice Harbor Dam, and Holyoke Dam, respectively). For Chinook salmon and blueback herring, two of the most important species contributing to nutrient loading, size has declined notably through time. Declines in body size reduced cumulative phosphorus

Fig. 3. Phosphorus loading by anadromous species over time in the Columbia River basin above (a) Bonneville Dam in the Columbia River, (b) the McNary Dam, (c) Ice Harbor Dam (Snake River), and on Connecticut River at (d) Holyoke Dam. The key to Columbia River species is shown in panel (a), and the key to Connecticut River species is shown in panel (d). Note that kilograms of phosphorus are $\times 10^6$ for the Columbia and Snake rivers and $\times 10^5$ for the Connecticut River. [Colour online.]

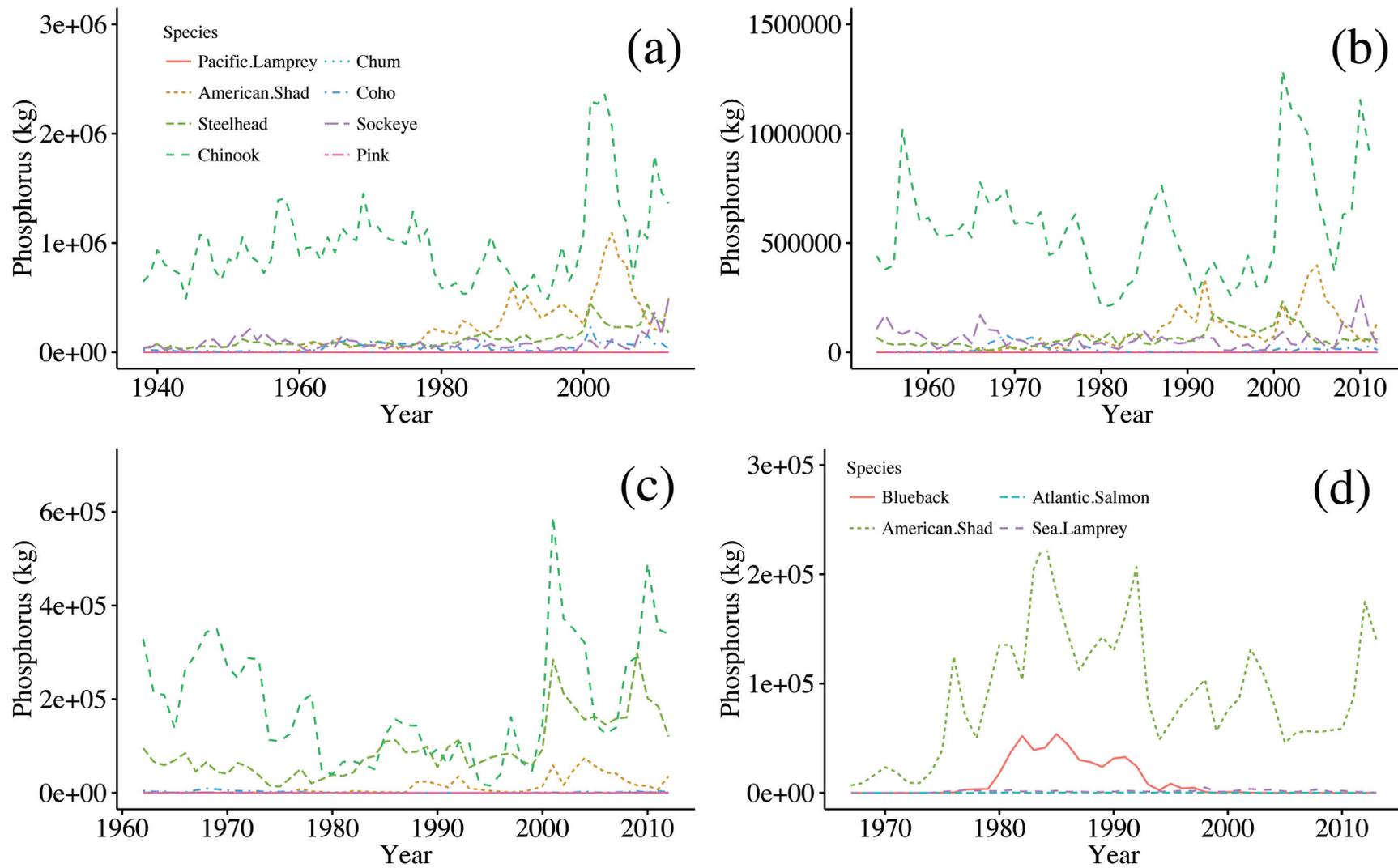
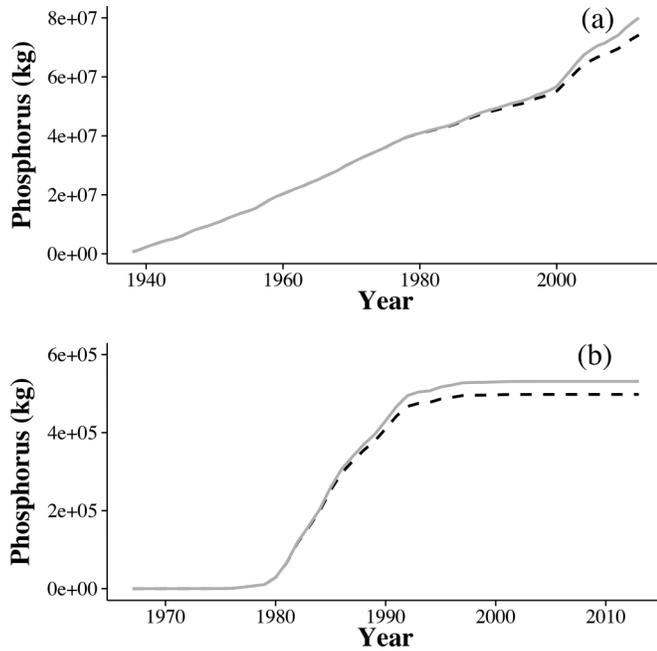


Fig. 4. Cumulative phosphorus loading over time by (a) Chinook salmon in the Columbia River above Bonneville Dam and (b) blueback herring in the Connecticut River above Holyoke Dam accounting for changes in size over time (dashed black line) and assuming constant historical sizes (solid gray line).



loading by Chinook salmon by 5 811 604 kg (7%) and from blueback herring by 33 418 kg (6%) (Figs. 4a–4b). Recent declines in body size across all species reduced cumulative phosphorus loading in the Columbia River by 7 200 857 kg (6%) and in the Connecticut River by 36 958 kg (0.8%). Changes in cumulative loading due to decreases in adult body size were much greater in the Columbia River, where multiple species including Chinook — the most important phosphorus contributor — declined in size compared with the Connecticut River, where only blueback herring, the second most important phosphorus contributor, experienced consistent declines in size over time.

Discussion

In this study, we assessed how nutrient inputs per unit biomass and per individual fish varied across 12 key species of North American anadromous fishes and how these patterns affected river-wide trends in nutrient loading. We employed portfolio effect analyses to assess whether multispecies assemblages of anadromous fishes increased the stability of total fish-derived phosphorus inputs. We found wide variation among the species considered on both per unit biomass and per individual bases. Population abundance, life history strategy (semelparity versus iteroparity), and body size act together to determine the contributions of different species to nutrient loading. Inputs to the Columbia River were historically dominated by large-bodied semelparous taxa, but more recently by iteroparous American shad as well, while inputs to the upper Connecticut River were dominated by small-bodied iteroparous taxa. We found evidence that anadromous fish diversity (richness and evenness) had limited effects on the stability of marine-derived phosphorus inputs to freshwater habitats because the population dynamics of anadromous species were highly synchronous, perhaps due to shared anthropogenic or environmental drivers.

Anadromous lamprey provided some of the lowest phosphorus per fish and per biomass because they are smaller than many of the other species we considered and contain extremely low body

phosphorus content owing to their lack of ossified bones and scales (Table 1). Lamprey had per individual loading rates that were greater than those for river herring, the smallest fish we considered, but their per biomass rates were the lowest of any species examined (Fig. 1). We found that river herring had the second lowest phosphorus per fish of the anadromous fishes considered. American shad contributed a much larger phosphorus flux per individual than river herring (Fig. 1b), driven principally by their larger adult body size (Table 1). Salmonids, especially Chinook and chum salmon, had the highest per fish phosphorus per fish because of their large body size (Fig. 1). Pacific salmonids in general had some of the highest per individual loading rates because of their semelparous life history (Figs. 1a–1b).

Past studies have analyzed the effects of individual parameters on single species nutrient contributions (Scheuerell et al. 2005; West et al. 2010). For example, West et al. (2010) performed sensitivity analyses and found that nutrient loading is most sensitive to adult population size, adult body size, and body nutrient content, parameters for which we have a high degree of confidence based on empirical data. Data for estimating juvenile export are generally lacking. Previous studies have found that anadromous fish nutrient loading models are relatively insensitive to juvenile export (Scheuerell et al. 2005; West et al. 2010). For example, Scheuerell et al. (2005) found that juvenile salmon export was important when adults were at <2% of their historical abundance and only in some of those years. Similarly, West et al. (2010) found that juvenile river herring survival was too low for juvenile export to exceed adult imports unless adult populations were less than 690 adults per hectare and juvenile survival rates were an order of magnitude greater than those typically observed. Therefore, we do not expect that the decision to omit juvenile export from our models had a large effect on our nutrient loading estimates. We used mean parameter values for species traits (except for body size, for which we used system-specific estimates) and are confident that our models across different species captured the most important sources of ecological variation.

In the Columbia River, Chinook salmon and non-native American shad dominated phosphorus loading (Figs. 3a–3c). However, we found that relative inputs from these species varied considerably by year and location. American shad were first observed in the Columbia River in 1876, probably as a result of straying from the Sacramento River, and were purposely introduced to the drainage beginning in 1885 (Smith 1895). The species began to increase dramatically in abundance after about 1976, following the completion of the Dalles Dam (1957) and subsequent inundation of Celilo Falls, which historically blocked upstream migration of this species (Hasselman et al. 2012a; Hinrichsen et al. 2013). Prior to this increase in abundance, total phosphorus loading in the mainstem Columbia River tracked Chinook abundance closely (Figs. 3a–3b). After 1976, Chinook salmon and American shad together became the principal drivers of nutrient loading in the lower Columbia River basin. Declines in adult Chinook body size over time led to a 7% reduction in Chinook cumulative phosphorus loading (Fig. 4a) and an overall 6% reduction in cumulative phosphorus loading across all species. Phosphorus inputs from other salmonids, such as steelhead, were generally minor compared with those of Chinook on the lower Columbia River (Fig. 3a). However, it is believed that American shad largely spawn in the lower Columbia River basin (i.e., the mainstem Columbia River and Snake River; Hasselman et al. 2012a, 2012b), whereas salmonids migrate higher into the watershed and ascend various tributaries to spawn. Thus, the relative nutrient contributions from other species increase upstream on the Columbia River main stem and in the Snake River as American shad inputs decrease (Figs. 3b–3c). On the Snake River, Chinook and sockeye contributed similar amounts of nutrients (Fig. 3c). We found that Pacific lamprey contributed little to phosphorus inputs throughout the time period we considered (Figs. 3a–3c).

As a result of fish propagation, many adult fish entering the Columbia River are of hatchery origin (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 2002) and may be removed from the system as part of ongoing hatchery operations. This scenario raises the concern that hatchery origin fish may be artificially inflating estimates of nutrient loading without actually delivering those nutrients to the Columbia River watershed. A subset (25%–100%) of hatchery origin fish return to hatcheries where their eggs and milt are collected before they are sacrificed (Oregon Department of Fish and Wildlife and Washington Department of Fish and Wildlife 2002; Cascade Columbia Fisheries Enhancement Group 2011). Carcass disposal practices vary among hatcheries and species. Chinook, which are the largest phosphorus contributors (Figs. 3a–3c), are generally frozen and then 100% are returned to tributaries in the Columbia River basin for the purposes of nutrient enhancement (Cascade Columbia Fisheries Enhancement Group 2011). In contrast, hatchery origin steelhead can carry infectious hematopoietic necrosis virus and are often disposed of in landfills to avoid spreading disease to wild stocks, but practices vary across hatcheries and range from 100% landfill disposal to 100% returned to tributaries (Cascade Columbia Fisheries Enhancement Group 2011). The remainder of hatchery origin fish are either caught in commercial fisheries (which we subtracted from our species totals) or are caught in small numbers by recreational or native fishers or suffer natural mortality within the Columbia River basin. We chose to include hatchery origin fish in our nutrient loading models because the majority of nutrients from hatchery origin fish appear to be returned to the Columbia River watershed and because of the high uncertainty associated with attempting to estimate the proportion removed.

At the watershed scale, we found that American shad dominated phosphorus loading in the upper Connecticut River and that total phosphorus loading patterns closely followed American shad abundance (Fig. 3d). Interestingly, patterns in American shad loading in the upper Connecticut River may have been at least partially driven by improvements fish lift operations at the Holyoke Dam in 1975 (Gephard and McMenemy 2004). We found that phosphorus loading from blueback herring was low compared with American shad, even when blueback herring and American shad abundances were similar. We attribute the lower relative inputs from blueback herring primarily to their smaller body size. Declines in adult blueback herring size over time led to a 6% reduction in cumulative blueback phosphorus loading (Fig. 4b) and an overall 0.8% reduction in cumulative loading across all species. We found that phosphorus inputs from both Atlantic salmon and sea lamprey were both minor compared with those of either American shad or blueback herring (Fig. 3d). Although Atlantic salmon had much higher per fish phosphorus contributions than the other species we considered (Fig. 1b), their abundance in the Connecticut River was so low (i.e., on the order of hundreds of fish) that their relative phosphorus inputs at the multispecies level were minor. In contrast, sea lamprey were relatively abundant in the Connecticut River (tens of thousands), but lamprey per fish phosphorus inputs were considerably lower than those of either river herring or American shad (Fig. 1).

Past studies using portfolio effects in fisheries focused on the stability of metapopulations of single species (Anderson et al. 2013). We applied portfolio analyses to assess the stability of multispecies nutrient loading. Our portfolio effects analyses show that anadromous species diversity did not significantly increase the stability of nutrient inputs. In contrast, our results show that increased species richness can destabilize nutrient loading when population dynamics across species are synchronous (Fig. 2a). Counter to expectations, we found evidence for greater stability when a single species within a multispecies community dominated loading patterns (Fig. 2b). Prior to river herring declines in the Connecticut River (beginning in 1995), portfolio effects were

slightly lower and nutrient loading more stable when a single species, American shad, dominated total phosphorus loading (Fig. 2b). However, it is important to note that river herring abundance at the peak of this time interval was likely a small fraction of the historical run size (Limburg and Waldman 2009). Similarly, we found that portfolio effects were stronger in the Columbia River before the population increase in American shad, which decreased the stability of nutrient loading (Fig. 2b). The increase in species richness driven by the initial addition of American shad to the Columbia River and the increase in evenness as American shad populations established and thrived there would both be predicted to increase the strength of the portfolio effect. However, these increases in richness and evenness appear to be offset by a high degree of synchrony between American shad and Chinook population dynamics. Thus, contrary to the general expectation that diversity increases ecosystem stability (Hooper et al. 2005), we found evidence from both the Connecticut and Columbia rivers that time periods of greater richness and evenness were in fact less stable (Fig. 2).

Synchrony in nutrient loading across the anadromous fish community may be driven by shared extrinsic drivers, such as human impacts or ocean conditions, that affected multiple species similarly (Finney et al. 2002; Moore et al. 2010; Carlson and Satterthwaite 2011). In the Connecticut River, blueback herring nutrient inputs closely tracked American shad inputs prior to blueback herring declines ($r = 0.81$; Fig. 3d), while in the Columbia River, American shad inputs closely tracked Chinook inputs after the American shad population increase ($r = 0.53$; Figs. 3a–3c). This result suggests that multispecies assemblages have the potential to destabilize nutrient loading if the dominant taxa have synchronous loading patterns that increase the year-to-year variation in loading, a pattern also observed in studies of portfolio effects across populations of single species (Moore et al. 2010; Carlson and Satterthwaite 2011).

In this study, we considered how life history and species diversity, in terms of richness and evenness, affect the magnitude and stability of nutrients entering fresh waters from anadromous fishes across multiple systems that vary in numerous environmental factors. Factors such as regional climate, geomorphology, phenology, and land use also affect the relative size of marine-derived nutrient inputs and interact with the life history and functional traits of anadromous fishes (Tiegs et al. 2011; Reisinger et al. 2013; Twining et al. 2013). For example, most native anadromous fishes along the Atlantic coast of North America spawn in the spring when discharge is near its highest (Twining et al. 2013), resulting in low nutrient retention, while most native anadromous fishes along the Pacific coast spawn in the late summer and early autumn when discharge is at its lowest (Naiman et al. 2002; Schindler et al. 2003), resulting in high nutrient retention. Non-native American shad are a notable exception to this pattern, returning to the Columbia River in the spring and believed to spawn in the late spring – early summer (Quinn and Adams 1996). As a consequence, American shad have likely altered the phenology of marine-derived nutrient inputs to some West Coast rivers in North America (Hasselmann et al. 2012a, 2012b).

In many systems, anadromous fishes have declined at the same time that human land use has intensified (Gresh et al. 2000; Limburg and Waldman 2009; Moore et al. 2011; Twining et al. 2013). Atlantic and Pacific coast rivers of North America once “ran silver” with migrating anadromous fishes (Waldman 2013). Anadromous fishes perform their ecological role as nutrient vectors when abundant (Redford et al. 2013). When runs are reduced to mere shadows of their former abundances, they become “ghost species”, biologically extant, but ecologically extinct (Hull et al. 2015). For example, Moore et al. (2008) found that high densities of salmon representative of historical abundances produced disproportionately more eggs that were available for other stream fish to consume. Today, human-derived nutrients likely overwhelm the effects of nutrient inputs from anadromous fishes or natural ter-

restrial sources in many systems. For example, both the Columbia River and the Connecticut River have a high degree of human development within their watersheds (Gresh et al. 2000; Twining et al. 2013). Declines in anadromous fish populations on the Columbia River mainly occurred during the past century (Gresh et al. 2000), while those in the Connecticut began hundreds of years ago (Limburg and Waldman 2009; Twining et al. 2013). We suspect that the stability of nutrient inputs may have been greater in both rivers prior to declines in anadromous fish abundance associated with watershed development. Perhaps at that time, species diversity did serve to stabilize nutrient loading. However, we have very limited estimates of anadromous fish populations before Euro-American contact with which to test this idea (but see Selbie et al. 2009 for paleoecological work on nutrient loading by Pacific salmon in lakes).

While we have focused on anadromous species, our approach has relevance for nutrient transport by migratory fishes in general. Catadromous fishes (i.e., those that migrate from fresh waters to the ocean to spawn; e.g., American eel (*Anguilla rostrata*)) may export nutrients from fresh waters when they emigrate as adults on their spawning run. Future studies on nutrient transport via migratory fishes could include the export of nutrients from fresh waters by catadromous fishes as data become available. In addition, recent studies suggest that potamodromous fishes (i.e., those that migrate between bodies of fresh water to spawn), such as *Catostomus* spp., can also serve as important nutrient vectors (Childress et al. 2015). Future studies on nutrient transport by potamodromous freshwater fishes could apply a multispecies portfolio effect approach to understand the effects of various aspects of freshwater migratory fish diversity on the stability of nutrient movement within and between lakes and streams.

We have aimed to broaden the discussion of marine-derived nutrients from a "salmocentric" perspective to encompass a greater diversity of anadromous fishes. The extensive work on Pacific salmon has laid essential groundwork for understanding the importance of anadromous fishes as nutrient vectors (Naiman et al. 2002; Schindler et al. 2003; Compton et al. 2006), but it has also narrowed thinking about migratory fishes and shaped anadromous fish conservation and management efforts across systems (Flecker et al. 2010). Until recently, environmental managers along the Atlantic coast of North America generally assumed that nutrient loading operated as shown in the Pacific Northwest, even though Atlantic salmon are iteroparous and were never as abundant along the Atlantic coast as their Pacific coast counterparts (Carlson 1988, 1992). Only in the recent past have managers on the Atlantic coast begun to focus on smaller but historically more abundant species, such as alewife, blueback herring, and American shad, that can load a substantial amount of nutrients (Durbin et al. 1979; Walters et al. 2009; Twining et al. 2013). We found that non-native American shad provide approximately half of the annual marine-derived nutrient inputs to the Columbia River, which is considered one of the most iconic salmon rivers along the Pacific coast. These results should encourage a broader consideration of the effects of species diversity on nutrient dynamics driven by fish movement.

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