Nutrient fluxes and the recent collapse of coastal California salmon populations

Jonathan W. Moore, Sean A. Hayes, Walter Duffy, Sean Gallagher, Cyril J. Michel, and David Wright

Abstract: Migratory salmon move nutrients both in and out of fresh waters during the different parts of their life cycle. We used a mass-balance approach to quantify recent changes in phosphorus (P) fluxes in six coastal California, USA, watersheds that have recently experienced dramatic decreases in salmon populations. As adults, semelparous Chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon imported 8.3 and 10.4 times more P from the ocean, respectively, than they exported as smolts, while iteroparous steelhead (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) imported only 1.6 times more than they exported as kelts and smolts. Semelparous species whose life histories led them to import more nutrients were also the species whose populations decreased the most dramatically in California in recent years. In addition, the relationship between import and export was nonlinear, with export being proportionally more important at lower levels of import. This pattern was driven by two density-dependent processes — smolts were larger and disproportionately more abundant at lower spawner abundances. In fact, in four of our six streams we found evidence that salmon can drive net export of P at low abundance, evidence for the reversal of the “conveyor belt” of nutrients.

Résumé : Les saumons migrateurs déplacent des nutriments tant vers les eaux douces qu'hors des eaux douces durant les différentes étapes de leur cycle biologique. Nous utilisons une méthode de bilan massique pour mesurer les changements récents dans les flux de phosphore (P) dans six bassins versants côtiers de Californie, É.-U., qui ont connu des déclins spectaculaires de leurs populations de saumons. Au stade adulte, les saumons chinook (*Oncorhynchus tshawytscha* et coho (*Oncorhynchus kisutch*) sémelpares importent respectivement 8,3 et 10,4 fois plus de P de l'océan qu'ils n'en exportent au stade saumoneau; en revanche, les truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) itéropares importent seulement 1,6 fois plus qu'ils en exportent comme bécards et saumoneaux. Les espèces sémelpares dont le cycle biologique les amène à importer plus de nutriments sont aussi les espèces dont les populations ont décru de façon la plus spectaculaire en Californie ces dernières années. De plus, la relation entre l'importation et l'exportation n'est pas linéaire et l'exportation est proportionnellement plus importante aux faibles niveaux d'importation. Ce patron s'explique par deux processus dépendants de la densité — les saumoneaux sont de plus grande taille et de façon disproportionnée plus abondants aux faibles abondances de reproducteurs. En fait, dans quatre des six cours d'eau, nous trouvons des preuves que les saumons peuvent contrôler l'exportation nette de P aux faibles abondances; ce sont des indications du renversement de la « courroie de transmission » des nutriments.

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Introduction

Species can control fluxes of nutrients and energy across ecosystem boundaries through their own movements (Lundberg and Moberg 2003; Polis et al. 2004). Nutrients can be liberated in the recipient ecosystem when individuals of the species die or excrete there. For example, nesting seabirds import marine-derived nutrients to roosting and nesting islands, where their guano fuels terrestrial communities (Sánchez-Piñero and Polis 2000). It follows that the loss of these species that link ecosystems may have profound consequences; for example, seabird population declines have led to dramatic changes in the community composition and productivity of island ecosystems (Croll et al. 2005; Young et al. 2010).

Pacific salmon (*Oncorhynchus* spp.) represent one of the most well-known examples of biotic control of ecosystem fluxes. These anadromous species grow large in the ocean and subsequently migrate to coastal fresh waters where they spawn, often at high abundance. Through this migration,

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anadromous salmon can act as a "conveyor belt" of nutrients and energy, moving the nutrients and energy that make up their bodies from marine to coastal freshwater ecosystems (Larkin and Slaney 1997; Gresh et al. 2000; Naiman et al. 2002). In spawning habitats with high densities of salmon, salmon-derived nutrients such as nitrogen (N) and phosphorus (P) can comprise a large component of ecosystem nutrient budgets (Naiman et al. 2002; Schindler et al. 2003). N and P are commonly limiting nutrients in coastal fresh waters (Elser et al. 2007; Sanderson et al. 2009). Studies in regions with high abundances of salmon have found that their nutrients directly and indirectly subsidize a variety of aquatic and riparian species, ranging from bears to insects to plants (e.g., Cederholm et al. 1999; Wipfli and Baxter 2010). Even in highly altered river systems such as those that flow through agricultural areas in central California, salmon-derived resources are heavily used by a variety of riparian scavengers (Merz and Moyle 2006).

Anadromous salmon also export nutrients from fresh waters as outmigrating juvenile salmon, not only acting as importers of nutrients to fresh waters when adults migrate in from the ocean to spawn (Moore and Schindler 2004). Juvenile salmon spend up to several years feeding and growing in fresh waters prior to outmigration. This outmigration of juvenile salmon, or smolts, represents the movement of nutrients and energy from freshwater coastal ecosystems to marine ecosystems. Few studies have calculated both nutrient import and export due to salmon migrations. For semelparous species, the net flux of salmon nutrients can be calculated as the import by spawners minus the export by smolts. Studies on these anadromous and semelparous species have found that spawners generally import more nutrients than smolts export but that these patterns are influenced by density-dependent feedbacks (Moore and Schindler 2004; Scheuerell et al. 2005). Specifically, Moore and Schindler (2004) found that P import is approximately six times greater than export for Alaskan sockeye (*Oncorhynchus nerka*) populations, and Scheuerell et al. (2005) found import is approximately five times greater than export for Chinook salmon (*Oncorhynchus tshawytscha*) in the Snake River basin.

Many salmon populations have declined over the last century because of a suite of human impacts, especially towards the southern extent of their range, such as in California (Gustafson et al. 2007). These salmon declines have raised concerns about the loss of salmon-derived nutrients and corresponding potential declines in coastal freshwater productivity (e.g., Stockner et al. 2000). How do patterns of import and export change at low salmon abundance? Moore and Schindler (2004) proposed that export would be proportionally more important at lower population sizes because of density dependence, and Scheuerell et al. (2005) found evidence of this relationship for Snake River Chinook. Thus, net import of nutrients may decline faster than anticipated as salmon populations decline. It is even possible that at low abundances salmon become net exporters of nutrients — reversing the direction of the conveyor belt of marine-derived nutrients, stripping nutrients out of freshwater systems at low abundances. Thus, there remains great uncertainty into how these patterns of flux might change as salmon populations decline.

For iteroparous species with more complicated life histories, there is potential for a lower import–export ratio, as adults can survive spawning to migrate back out to the ocean. While fluxes have never before been quantified for iteroparous Pacific salmonids (i.e., steelhead (or sea-run rainbow trout), *Oncorhynchus mykiss*), previous research on iteroparous Atlantic salmon (*Salmo salar*) found that they can either act as a net importer (Lyle and Elliott 1998; Jonsson and Jonsson 2003) or net exporter of nutrients (Nislow et al. 2004). Thus, different species with different life histories may exhibit fundamentally different patterns of nutrient import and export.

Our goal was to quantify annual nutrient fluxes by multiple salmon species over recent decreases in salmon population abundances. In coastal California, where streams contain coho salmon (*Oncorhynchus kisutch*), steelhead trout (*O. mykiss*), and to a lesser extent, Chinook salmon (*O. tshawytscha*), populations have been declining. Of great conservation concern are coho salmon in the California coastal region, listed as federally Threatened or Endangered depending on the location (Federal Register 2005), which have rapidly declined in abundance over 2008–2010 (Miller 2010). Central California represents the southern extent of coho salmon in North America. For some spawning populations, there is concern that these populations will go extinct in the near future without human intervention (Miller 2010). It is thought that this recent decline is due to the combination of the legacy of past human degradation of freshwater habitats coupled with poor ocean conditions (Miller 2010). Using salmon abundance data from this period of population declines, we used a mass-balance approach to examine recent changes in nutrient fluxes in six coastal California streams. We asked the question, how did patterns of nutrient fluxes change over the recent collapse of California salmon populations? In particular, we examined the possibility that density-dependent processes could drive disproportionately rapid loss of net nutrient import. We also examined the role of multiple salmon species in contributing to nutrient fluxes during this period.

Materials and methods

Study systems

We compiled data on coho salmon (six streams), steelhead (five streams), and Chinook salmon (one stream) from six study streams (Table 1); five of these streams (the exception being Little River) represent all of the life-cycle monitoring stations (adult and smolt abundance) of the developing California Coastal Salmon Monitoring Plan (Adams et al. 2011). These stations consist of both adult upstream traps and downstream smolt traps. Adult escapement in Little River is based on redd counts (Gallagher et al. 2010). Adult traps are monitored from mid-November through late March. Downstream smolt traps are operated from early March until early June (Gallagher and Wright 2009). These streams are dominated by coniferous redwood forests (*Sequoia sempervirens*); stream lengths accessible to anadromous fishes range from 6 to 117 km, flow directly into the ocean, and are groundwater-fed with peak flows in winter following heavy rains (Table 1).

Annual abundances of smolts and adults (spawners) of each species were obtained using standard population estimation techniques (Johnson et al. 2007). Each of the life-cycle monitoring stations consists of a downstream smolt trap and

Table 1. Study streams, ordered from north (top) to south (bottom).

Stream	Flow ($m^3 \cdot s^{-1}$)[a]	Size (km)[b]	Diadromous salmonids	Years
Prairie Creek	0.05–8.80	21	Chinook, coho, steelhead[c]	2001–2008
Pudding Creek	0.01–7.65	18	Coho, steelhead	2006–2009
Noyo River	0.16–33.41	117	Coho, steelhead	2001–2009
Caspar Creek	0.01–5.92	14	Coho, steelhead	2002–2009
Little River	0.01–3.35	6	Coho, steelhead	2002–2009
Scott Creek	0.013–17	23	Coho, steelhead	2006–2009

[a] Range of observed stream flow.

[b] River kilometres accessible to spawning salmon.

[c] We did not include steelhead in our calculations of nutrient fluxes in Prairie Creek because monitoring only occurred during a subset of the available years. Steelhead were also not as abundant as Chinook and coho and thus did not contribute as much to nutrient fluxes.

an upstream migrant trap to catch emigrating adults. Smolt traps were generally monitored daily during the outmigration season. Trap efficiency tests were performed by experimental releases of marked smolts. Annual estimates of smolt abundance were obtained by extrapolating observed numbers based on these trap efficiency estimates. Annual adult estimates were generally obtained by combining observed numbers of upstream migrants with estimates based on mark and recapture techniques (Szerlong and Rundio 2008). More information on these life-cycle monitoring stations and these study streams can be found in Hayes et al. (2008), Gallagher and Wright (2009), Gallagher et al. (2010), and Campbell Timberland Management (2008).

Quantifying nutrient fluxes

We calculated the nutrient fluxes due to the migrations of salmon, following Moore and Schindler (2004) and Scheuerell et al. (2005). Similarly, we focused our analyses on P as a key limiting nutrient (Elser et al. 2007; Sanderson et al. 2009). In six northern California streams the N:P ratio was extremely high (total P and total N averaged 9.05 and 305.00 $\mu g \cdot L^{-1}$, respectively; Wilzbach et al. 2005), suggestive of P limitation in these streams. For each species, we estimated annual import (I) of P during year t as the product of the number of adults (A), their average mass (m_A), and the proportion of P in their bodies (p_A)

$$(1)\qquad I_t = A_t m_A p_A$$

For semelparous species, export of P during the year (E_t) is also the product of the number of outmigrating smolts (S), their average mass (m_S), and the proportion of P in their bodies (p_S).

$$(2)\qquad E_t = S_t m_S p_S$$

For iteroparous steelhead that can survive spawning, export was calculated as

$$(3)\qquad E_t = S_t m_S p_S + A_t m_A p_A k b$$

with the second half of the equation representing export from outmigrating, postspawning adults, or kelts, given their P concentration (p_A), the probability of surviving spawning (k), and the proportional change in mass during the spawning process (b). We estimate net annual flux as the difference between import (I_t) and export (E_t). These calculations of P flux could easily be translated to nitrogen flux by using N:P ratios.

We used previously published information as well as our own data to estimate parameters. Through comparing masses of individually marked steelhead before and after spawning (S.A. Hayes, unpublished data), we estimated the mass of postspawning steelhead to be 73% of prespawning fish (value of parameter b). We estimated the proportion of steelhead surviving spawning (k) at 0.62 through using mark–recapture estimates of adult steelhead from Scott Creek. Specifically, using the program MARK (White and Burnham 1999), we used a spatially explicit form of the Cormack–Jolly–Seber (CJS) model (Cormack 1964; Jolly 1965) for species that express an obligate migratory behavior, where recaptures are structured spatially along a migratory corridor (Burnham 1987). The model incorporates upstream and downstream migrating steelhead that were known to be missed by the weir, thus enabling maximum-likelihood estimates for the capture efficiency of the weir. Finally, correcting actual upstream and downstream steelhead counts at the weir with their respective capture efficiencies allows the estimate of total escapement and total kelt outmigration, the difference of which is the total steelhead carcasses remaining in the watershed. Through communications with other steelhead biologists, this estimate of spawning survival meshes well with other estimates that range from 0.5–0.85 (T. Seamons, University of Washington, School of Aquatic and Fishery Sciences, Seattle, Washington, personal communication, 2010; Mayer et al. 2008; S. Gallagher, unpublished data). We assumed that P concentrations for adults (p_A) and smolts (p_S) were 0.38% and 0.43% of mass, respectively, following Moore and Schindler (2004) and Scheuerell et al. (2005).

Although in some cases individual fish mass was directly measured, lengths were more often collected on a subset of individuals. Owing to the nonlinearity of length–mass relationships, we used a bootstrapping algorithm for this conversion. We drew iteratively from the observed mean and standard deviation of length and converted those draws to masses using length–mass regressions. We used an average of 5000 draws as the average mass. Fish sizes were not collected for some species in some years; for these we used the average size and standard deviation for that species based on other years from the same system. We restricted our analyses of fluxes to the years when we possessed full information on adult and smolt abundance for all major species (Table 1).

Quantifying dynamics in nutrient flux

We calculated patterns of P flux based on both an annual basis and on a brood-year basis. On an annual basis, net P flux is simply equal to I_t minus E_t. We used "salmon year" as the appropriate period; for example, fish that returned to spawn in December 2008 were considered part the 2009 salmon year. We also compared import and export on a brood-year basis; we compared parental nutrients (I_t) to the nutrients that their offspring would export (E_{t+1} for coho and E_{t+2} for steelhead; these lags reflect the dominant life histories). We did not lag nutrient export by steelhead kelts because they migrate back to the ocean in the same year they migrate to fresh water to spawn. The calculation of brood-year P fluxes allowed us to investigate potential density dependence in patterns of nutrient flux. To quantify patterns of density dependence, we fit Beverton–Holt functions where instead of recruits as a function of spawners, export was a function of import (Moore and Schindler 2004). We fit this function using the nls (nonlinear least-squares) procedure in R (R Development Core Team 2010). We restricted this function-fitting to systems with at least 7 years of data (excluding Scott and Pudding creeks). The Beverton–Holt model did not converge for Prairie Creek, so these results are not included.

To compare patterns of fluxes across species and streams, we compared total import versus total export summed across the whole time series for a given species and a given stream. As an index of change in abundance and nutrients, we calculated the proportional decrease in abundance and nutrients of each time series, comparing the average of the oldest two time points with the average of the two most recent time points.

We acknowledge that these calculations have some uncertainty associated with them. All parameter estimates have some uncertainty. Furthermore, population estimates of smolts and spawners were made using the best available salmon population estimation techniques, which do have uncertainty. While variation in these parameters and inputs may change some of the detailed output, we believe that these would not systematically change the results.

Results

Across the six focal stream systems in coastal California, there were substantial decreases in annual nutrient import associated with migratory salmonids over the last decade. With the exception of the most northern of the study streams (Prairie Creek), all streams had annual import of thousands of grams of P that declined by at least one order of magnitude between 2001 and 2009 (Fig. 1). For example, in Caspar Creek from 2002 to 2005, salmon migrations led to the net annual import of 1346 to 7115 g P. In contrast, in 2009 salmon only led to the net import of 36.1 g P in Caspar Creek. Salmon actually acted as net exporters of nutrients in two of the six streams (Scott and Pudding creeks) in 2009. Specifically, we estimate that salmon migration led to the net export of 110 and 18 g P in Scott and Pudding creeks, respectively.

Changes in annual nutrient import were driven by dynamics within and across species. For example, in Little River, a declining trend in import by steelhead populations through time is masked somewhat by variability in abundance (Fig. 2*a*). However, in a given year, steelhead smolts and kelts exported most (68% if import and export are summed across years) of the P that was imported by spawning adults, and steelhead export exceeded import in 2009 (Fig. 2*a*). In contrast, in the early half of the decade, coho salmon imported much more P than steelhead did, primarily because of the higher abundance of coho (Fig. 2*b*). During earlier years with higher adult abundances, coho smolts exported little P relative to that imported. However, coho adult spawners declined by 95% over the time series, decreasing import. Furthermore, smolts exported relatively more P as populations declined. As a result, there was a decrease in net salmon import of P from over 1000 g P per year during the first half of the decade to less than 40 g P per year during the last 3 years of data (Fig. 1*c*).

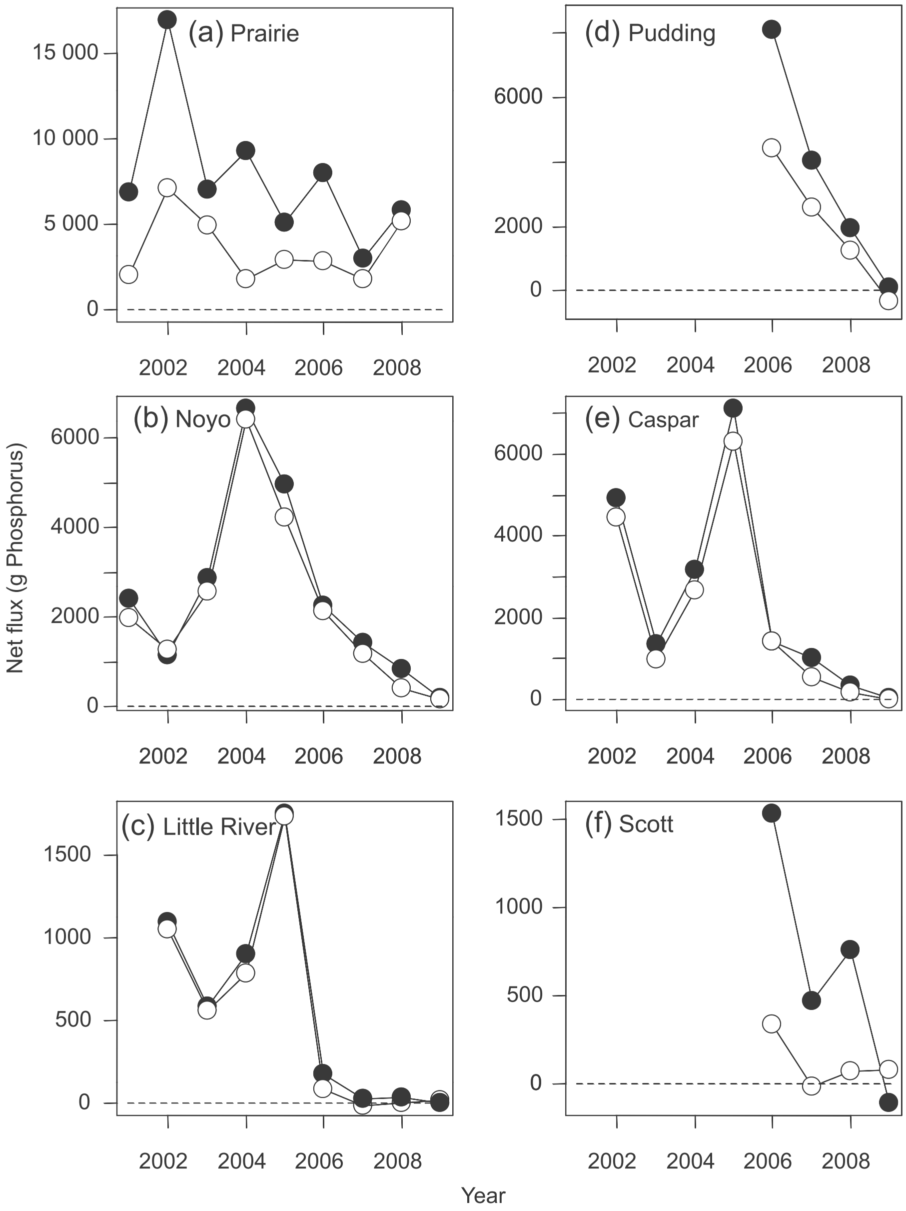
Density-dependent processes led to nonlinear relationships between brood-year import and export. For example, for coho salmon in Little River, smolts exported a higher fraction of the nutrients that were imported by their parents at low spawning population sizes (Fig. 3*a*). This relationship was strongly nonlinear, approximated by a power function (slope = 9.17, exponent = –0.85, R^2 = 0.87). Specifically, smolts exported less than 5% of parental nutrients, except at low spawner abundance, when they were observed to export up to 97% of the amount of parental P. This is likely driven by the combination of two density-dependent processes. First, there was strong density dependence in the relationship between the number of spawners and the number of smolts produced — few spawners produced disproportionately many smolts, following a Beverton–Holt relationship (Fig. 3*b*). Second, there was a negative relationship between the number of smolts and their size in a given year, presumably driven by density-dependent growth (Fig. 3*c*; $F_{[1,8]} = 11.58$, $R^2 = 0.59$, $p = 0.009$).

Patterns of density dependence in nutrient import vs. export varied across streams and species (Fig. 4). We analyzed three streams for each species; the other streams either had insufficient data to try to parameterize these relationships or models did not converge. According to model fits, coho export saturated quickly in two of the three systems (Fig. 4*a*), while steelhead export showed less nonlinearity (Fig. 4*b*). For steelhead, model fits predicted that one of the three streams (Noyo River) will enter the net export parameter space at low abundances (at approximately 47 adult steelhead; Fig. 4*b*). Coho are also predicted to become a net exporter in a second system (Little River), but only at an exceedingly low abundance threshold (of approximately two spawners; Fig. 4*a*). Thus, at lower spawner abundances, density dependence drives a relative increase in export compared with import, thereby contributing to nonlinearity in the relationship between spawner abundance and net import.

The three species of salmonids had different relationships between import vs. export (Fig. 5*a*). Spawning adults of the two semelparous species imported much more than their smolts exported; export represented 12% of import for Chinook and 9.6% ± 10.8% for coho (mean ± 1 standard deviation). In contrast, steelhead, which export nutrients both as outmigrating smolts as well as adults that have survived spawning (kelts), exported 63.7% ± 9.8% of the P that is imported by spawning adults. In other words, steelhead export the equivalent of the majority of the nutrients that they import.

In the last decade, across the different species and study streams, there were large decreases in spawner abundances (Fig. 5*b*). The two semelparous species decreased more than

Fig. 1. Annual phosphorus flux due to migration of Pacific salmon in six coastal California streams. Filled circles show total annual net P flux, while the open circles show the total flux due to coho salmon. The dotted line through flux = 0 is where import is equal to export; points above this line indicate net import, points below this line indicate net export. Note the different *y* axis scale on different panels.



iteroparous steelhead. Specifically, Chinook decreased by 85% in the only stream in which they were present, and coho populations decreased by an average of 68% ± 28% across all streams. When the northernmost site was excluded (Prairie Creek), the average coho decline was 77%. In contrast, steelhead populations decreased by 46% ± 29%. We also note that the shorter time series did not show as large a decrease because of data truncation of the population decline.

Discussion

Over the last decade, populations of anadromous salmonids, especially coho (Miller 2010), have decreased precipitously in coastal California streams. Using a mass-balance approach to estimate P import and export, we found that these decreases in adult returns have driven a corresponding decrease in nutrient import to these coastal fresh waters. Depending on the stream, annual net P import has declined by roughly an order of magnitude over the last decade. Historical records of salmon populations from these watersheds are sparse, which makes it difficult to put these contemporary population decreases into context. We can gain some perspective into historic steelhead and salmon populations and nutrient import in one of our study streams (Scott Creek) from a century ago. This stream was historically used as a location to collect coho and steelhead eggs to jumpstart a hatchery operation. California Fish and Game Commission kept archives of the number of eggs collected from this watershed. For example, in 1909, personnel collected eggs from an estimated 437 female steelhead and 518 female coho from Scott Creek (California Fish and Game Commission 1910), assuming that steelhead average 5000 eggs and

Fig. 2. Phosphorus flux due to migrations of salmon in Little River. Filled circles show import of phosphorus via spawners, and the open circles show the export due to outmigrating smolts or kelts for steelhead (*a*) and coho (*b*).

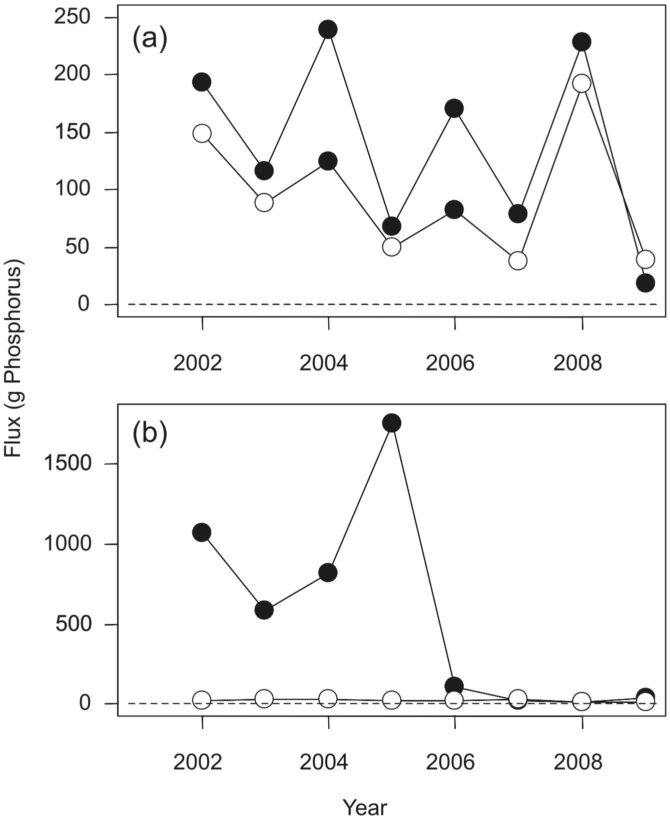
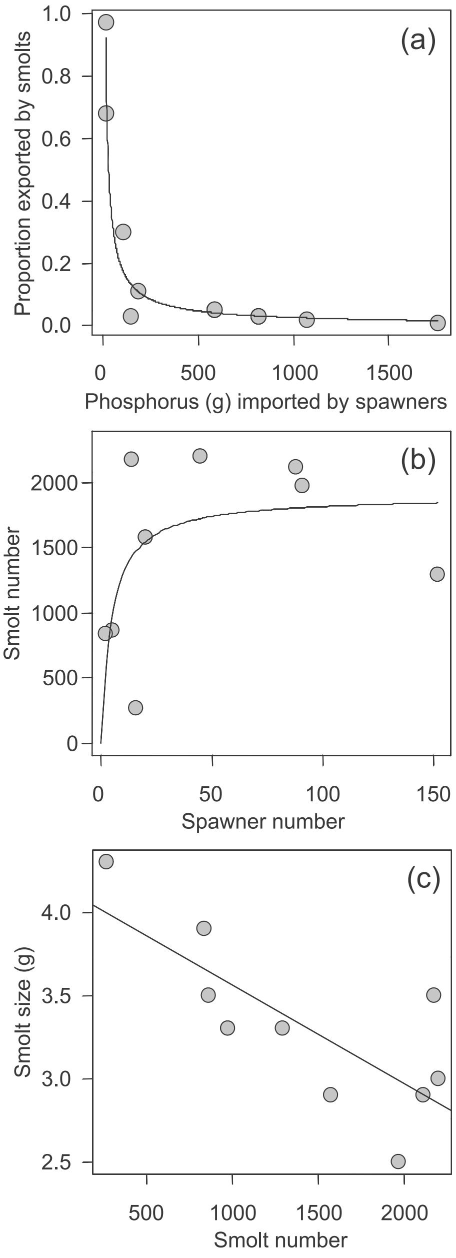


Fig. 3. Density dependence in nutrient import and export of coho salmon in Little River. Each point represents a different brood year. (*a*) The relationship between import by spawners for a given brood year and the proportion of that amount of nutrients that were exported by the resultant smolts. The line represents the best-fit exponential relationship. (*b*) The relationship between the number of spawning adults and the number of outmigrating smolts in the subsequent year. The line represents the best-fit Beverton–Holt relationship. (*c*) Average smolt size as a function of the number of smolts in that year. Also shown is the best-fit line.



coho average 2700 eggs (D. Streig, Monterey Bay Salmon and Trout Project, 825 Big Creek Road, Davenport, CA 95017, USA, unpublished data). If we conservatively assume a 50:50 sex ratio and that every single female fish was harvested, this equates to an annual import of 16 246 g P. The highest annual import observed in this study in Scott Creek was 2964 g P during 2006, representing 18% of 1909 import. Since 2006, import has decreased even further; most recently in 2009 salmon imported only 372 g P, 6% of historic import. To put these fluxes in context of a previous experiment, Wipfli et al. (2004) found that the addition of 22.2 g P·m^{-2} in Alaskan systems drove a significant increase in juvenile salmon body condition. Thus, 16 246 g P could “fertilize” at least 732 m^2 of Scott Creek at this concentration. We note that these numbers are for import only and do not consider export dynamics; these patterns of flux would be accentuated if export were considered. Thus, the recent decrease in salmon-derived nutrients is likely only the tail end of a century-long process of declines (Gustafson et al. 2007).

As salmon populations decrease, density-dependent processes can shift the patterns of nutrient fluxes. Specifically, salmon exported relatively more nutrients at low spawner densities, as proposed by Moore and Schindler (2004) and documented by Scheuerell et al. (2005) for Snake River Chinook. In addition, density dependence in survival and growth of alewife (*Alosa pseudoharengus*) may drive a similar nonlinear relationship between import and export for these anadromous fish (West et al. 2010). We found that for both coho salmon and steelhead, export became relatively more important in a strongly nonlinear relationship as spawner populations decreased. These patterns were driven by the combination of two density-dependent relationships; juvenile fish were disproportionately more abundant as well as larger at low spawner densities. While this density dependence in

Fig. 4. Density dependence in salmon nutrient import and export across streams and species for coho (*a*) and steelhead (*b*). Shown are the fitted Beverton–Holt relationships of phosphorus import and phosphorus export for that brood year, assuming outmigrating fish are 1 and 2 years old for coho and steelhead, respectively. Solid line is for Caspar Creek, dashed line is Noyo River, and dotted line is Little River. The region where export is greater than import (net export) is portrayed with the gray polygon. Note the different *x* and *y* axes on the two panels.

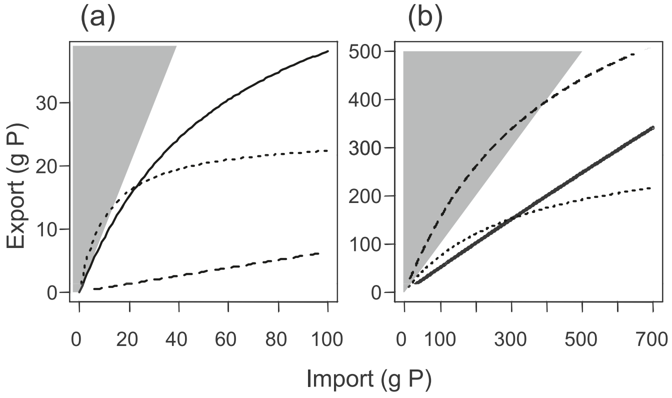


Fig. 5. Box and whisker plots of species-specific patterns of nutrient flux and population dynamics. Box plots show the distribution of observed values across the different stream systems. Only one stream had a Chinook population. (*a*) The proportion of imported nutrients that were exported, averaged across the time series for the different stream systems. (*b*) The proportional decrease in abundance of the different species over the course of the time series. The dotted line at 0 indicates the value where there was no change in abundance over the time series; dotted line at 1.0 indicates complete extirpation.

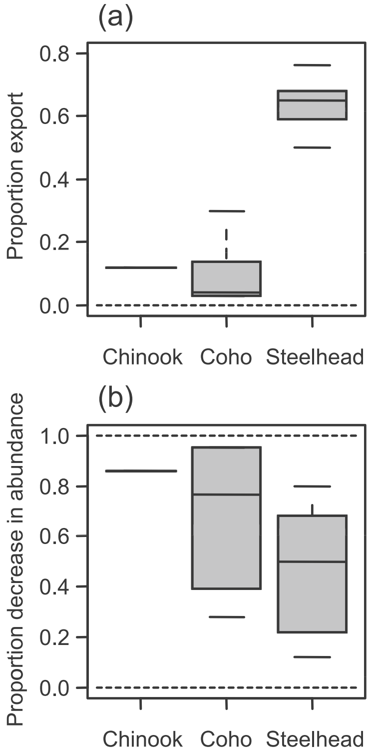
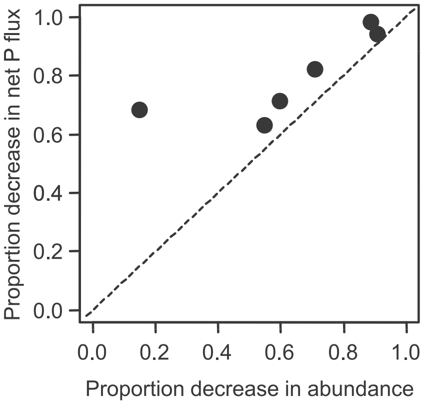


Fig. 6. Scatterplot showing the proportional decrease in abundance and the proportional decrease in net P flux, with each point representing a different stream. The dotted line at 1:1 indicates the predicted change in net P flux, if it was a linear relationship with abundance. Thus, points above this line indicate greater than predicted decrease in nutrients.



growth and survival can help salmon populations recover quickly from low abundances, these density-dependent processes also can increase nutrient export relative to import at low salmon abundance. Not surprisingly, as different streams and species have different patterns of density dependence, different streams and species also exhibited different nonlinear patterns of import and export. As we observed for two streams in 2009 (Scott and Pudding creeks) and predicted for another two streams based on model fits (Noyo and Little rivers), salmon can change from being net importers to net exporters of nutrients at low abundances. In other words, at low abundances, salmon can reverse their ecological function, stripping nutrients out of coastal fresh waters.

We found that even though nutrient import and export by the different species were driven by their abundance and body size, patterns of net flux that also incorporated export were more complicated. Semelparous Chinook and coho salmon imported 8.3 and 10.4 times, respectively, more than they exported, while the iteroparous steelhead exported the majority of the amount that they imported (importing only 1.6 times more than exporting). Thus, different species with different life histories exhibit different patterns of nutrient transport. The semelparous species also decreased more in abundance over the time series. Regardless of the mechanism driving different apparent vulnerability, the species that import more nutrients were also the species that decreased the most dramatically. Thus, this study represents an example of how species vulnerability may be positively related to their potential ecosystem impact, which can exacerbate the ecosystem consequences of biodiversity loss (Zavaleta et al. 2009).

Net import of nutrients declines more rapidly than salmon population abundance, driven by the combination of density-dependent processes (growth and survival in juveniles) and differential species vulnerability (Fig. 6). Total adult anadromous salmon abundance declined by 15%–91% (mean = 64%), depending on stream, but net P import declined even more, a decrease ranging from 63% to 98% (mean = 80%) (Fig. 6). This is now the second documented pathway by which the loss of the function performed by migratory salmon decreases disproportionately rapidly as populations decrease. Previously, Moore et al. (2008) found that subsidies of salmon eggs to resident fishes were also a positive nonlinear function of salmon density due to habitat saturation. Thus, if salmon populations decline, their subsidies to fresh waters decline even faster than would be predicted based on a simple linear function (Fig. 6). As a result, previous estimates of nutrient loss due to salmon declines (e.g., Gresh et al. 2000) are likely underestimates of the relative change in net nutrient flux.

There is still great uncertainty regarding the ecosystem consequences of salmon subsidies (Schindler et al. 2003; Janetski et al. 2009). Salmon-derived nutrients such as P can directly and indirectly fuel coastal food webs (Stockner et al. 2000; Naiman et al. 2002; Schindler et al. 2003). Alternatively, salmon nest-digging can be a substantial disturbance of benthic communities in spawning habitats (e.g., Peterson and Foote 2000; Moore and Schindler 2008). Thus, migratory salmonids not only deliver material subsidies (e.g., nutrients in carcasses) but also can modify key processes in coastal ecosystems (sensu Flecker et al. 2010). The mass-balance approach we used is a basic “ecosystem” ecology approach, calculating what comes in and what comes out, but does not examine the ecological consequences of those nutrient fluxes. The full ecological consequences of population declines of salmon will depend on the response variable and be driven by nonlinear dynamics such as those documented here and the potentially complex propagation of direct and indirect pathways, all likely modified by the environmental context (Tiegs et al. 2008; Janetski et al. 2009; Holtgrieve et al. 2010). Thus, management actions that attempt to replace the lost function of salmon, such as artificial nutrient additions, are not replicating the real complexity of the impacts of salmon (Compton et al. 2006). For example, nutrient enhancement programs often use the past salmon escapement to estimate the appropriate nutrient load (Washington Department of Fish and Wildlife 2004), but these calculations ignore the potentially important export of nutrients by outmigrating smolts.

The salmon densities and thus nutrient fluxes in these California systems that we observed are much lower than those observed in regions with more abundant salmon populations, such as Alaska. However, salmon nutrient fluxes still likely represent a major contribution to P budgets of these small streams. While we lack the data to create complete nutrient budgets, we can estimate the daily flux of P in streams during low flow periods as the product of the P concentration and the minimum observed discharge. If we use published P concentration data from nearby California streams (Wilzbach et al. 2005) and low summer discharge data from all streams, we can estimate the daily flux of P to be between 17.8 and 285.5 g P·day^{-1} for the different streams, scaling to stream discharge. The maximum annual net flux from salmonids for each stream thereby represents around between 23 and 473 days of watershed P flux during the low water period. However, it is important to note that this region is dominated by a Mediterranean climate, with discharges during irregular winter storms that can exceed 200 times that of low summer flows; watershed loading of P is going to be dominated by high discharges in winter. For example, maximum annual net P flux from salmonids for the streams represents between 0.1 and 1.1 days of watershed P flux during peak discharge. Thus, the degree to which salmon nutrient fluxes influence these California freshwater and riparian systems remains unknown. For example, Wilzbach et al. (2005) did not observe substantial impacts of experimental salmon carcass addition and suggested northern California streams may be light-limited. Even if the ecological consequences of the nutrient fluxes that we describe here are small, it is still important to understand that anadromous salmon populations at low abundances may switch their ecological function and reverse the direction of the conveyor belt of nutrients.

Human activities are altering global nutrient cycling through direct inputs (e.g., fertilizers) as well as by altering abundances of the organisms that control those cycles (Vitousek et al. 1997; McIntyre et al. 2007; Maranger et al. 2008). By linking ecosystems, migratory species can perform key roles in nutrient cycling (Lundberg and Moberg 2003; Willson et al. 2004; Flecker et al. 2010). There is increasing appreciation that a diverse set of migratory species can contribute to nutrient cycling in coastal fresh waters, including salmon, alewife (Durbin et al. 1979; Walters et al. 2009; West et al. 2010), Arctic charr (*Salvelinus alpinus*) (Swanson et al. 2010), and shrimp (Greathouse et al. 2006). Populations of many migratory fishes are declining (Limburg and Waldman 2009; Humphries and Winemiller 2009). It is easy to imagine that a migratory life cycle, which exposes the species to barriers as well as potential degradation in multiple habitats, would increase their vulnerability to population decline (Wilcove and Wikelski 2008). Decreases in migratory fish populations can alter nutrient fluxes in a nonlinear manner with relatively unknown consequences for coastal ecosystems.

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