Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*)

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Abstract: Anadromous and semelparous salmon transport nutrients from the ocean to fresh waters when they return to spawn and die, a process inspiring a large body of research on the role of salmon-derived nutrients in coastal ecosystems. However, salmon also transport nutrients out of fresh waters when they migrate to the ocean as smolts. Using a total of 76 years of age-specific smolt-migration and adult-escapement data, we calculated the amounts of nitrogen and phosphorus that sockeye salmon (*Oncorhynchus nerka*) imported and exported from four major systems in Bristol Bay, Alaska. Smolts removed an average of 16% of the phosphorus and 12% of the nitrogen that their parents transported into fresh waters. The percentage of parental nutrients that smolts exported varied through time and among sites, ranging from 1% to 65% of the phosphorus and from less than 1% to 47% of the nitrogen. In systems where smolts were larger, they exported a higher percentage of nutrients. Depending on the strength of density-dependence, smolts could theoretically export more nutrients than their parents import to freshwater ecosystems at low spawning densities. Ignoring nutrient export by outgoing smolts will consistently lead to overestimation of nutrient import by Pacific salmon to freshwater ecosystems.

Résumé : Les saumons anadromes et sémelpares transportent des nutriments de l'océan vers les eaux douces lorsqu'ils retournent pour frayer et mourir; c'est un phénomène qui a suscité un nombre important de recherches sur le rôle des nutriments provenant des saumons dans les écosystèmes côtiers. Cependant, les saumons exportent aussi des nutriments lorsque les saumoneaux émigrent vers l'océan. Des données réparties sur 76 années sur la migration des saumoneaux en fonction de l'âge et sur l'échappement des adultes nous ont servi à calculer les quantités d'azote et de phosphore que les saumons rouges (*Oncorhynchus nerka*) importent et exportent dans quatre systèmes hydrographiques majeurs dans la baie de Bristol, Alaska. Les saumoneaux retirent en moyenne 16 % du phosphore et 12 % de l'azote que leurs parents ont apportés dans les eaux douces. Les pourcentages des nutriments parentaux que les saumoneaux exportent varient dans le temps et d'un site à un autre, allant de 1 % à 65 % du phosphore et de moins de 1 % à 47 % de l'azote. Les saumoneaux exportent un pourcentage plus grand de nutriments dans les systèmes qui ont des saumoneaux de plus grande taille. Selon l'intensité de la dépendance de la densité, les saumoneaux pourraient en théorie exporter plus de nutriments que leurs parents en importent dans les écosystèmes d'eau douce lorsque les densités de reproducteurs sont faibles. Si l'on néglige de considérer l'exportation par les saumoneaux qui émigrent, on surestime systématiquement l'importation de nutriments vers les eaux douces par les saumons du Pacifique.

[Traduit par la Rédaction]

Introduction

Migrating adult anadromous and semelparous salmon transport massive quantities of nutrients from oceans to the fresh waters where they spawn and die (Larkin and Slaney 1997; Schmidt et al. 1998; Gresh et al. 2000). For example, adult Pacific salmon historically contributed over 3 million kg of nitrogen and 0.36 million kg of phosphorus each year to the Columbia River ecosystem (Gresh et al. 2000). This ecosystem resource subsidy (Polis et al. 1997) directly and indirectly fuels numerous species of flora and fauna of coastal ecosystems (Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003). Declines in salmon populations have raised concerns about how reductions of this subsidy will impact specific species as well as the overall productivity and biodiversity of coastal ecosystems (Willson and Halupka 1995; Naiman et al. 2002; Schindler et al. 2003).

However, salmon do not transport nutrients unidirectionally from oceans to fresh waters as adults returning to spawn. The migration of salmon smolts from fresh waters to the ocean represents a flow of nutrients from fresh waters to the ocean. The term smolt refers to juvenile salmon that have undergone the physiological and behavioral changes that occur prior to migration to marine or estuarine ecosystems (Groot and Margolis 1991). Juveniles of some species and populations of salmon migrate out of fresh waters immediately after emerging (especially *Oncorhynchus gorbuscha* and *Oncorhynchus*

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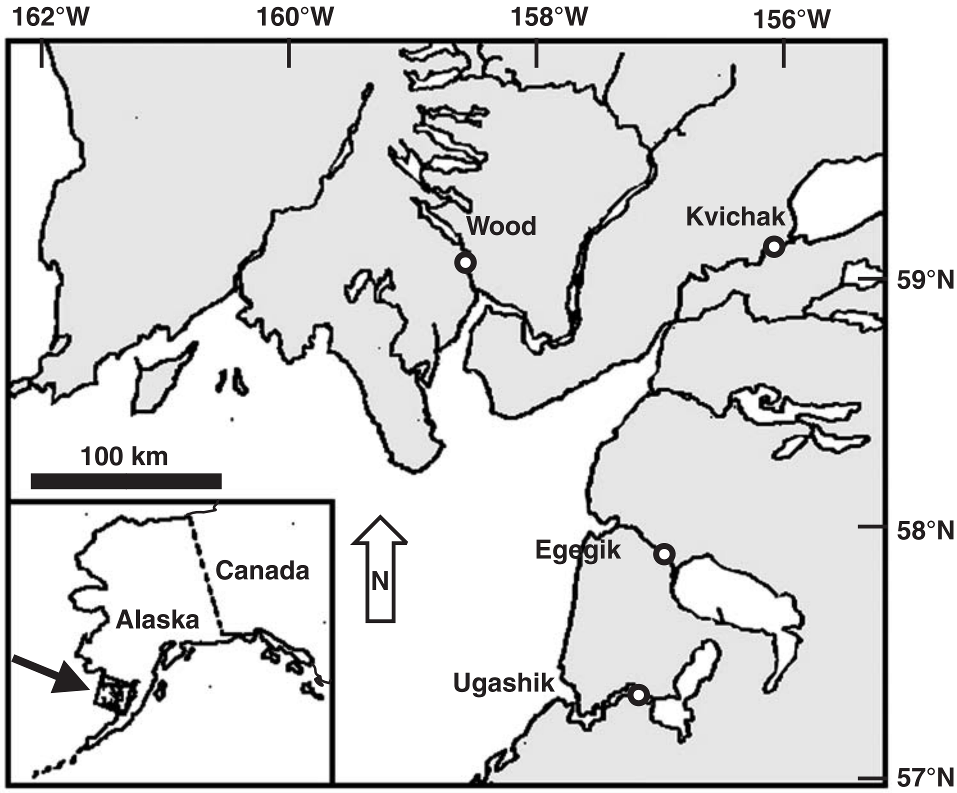
Fig. 1. Map of Bristol Bay, Alaska, USA, showing the four systems where data used in our analyses were obtained for analyzing nutrient transport by sockeye salmon (*Oncorhynchus nerka*) (modified from Hilborn et al. 2003). The locations of smolt sampling sites are indicated by circles.



keta), while other species and populations spend up to several years in fresh waters prior to migration (Groot and Margolis 1991).

This aspect of nutrient transport by anadromous salmon is usually ignored (e.g., Larkin and Slaney 1997; Gresh et al. 2000), or dismissed by citing that from 95% to over 99% of the mass of anadromous salmon is acquired in the ocean, implying that smolt nutrient export from fresh waters is inconsequential. However, this assumes that the number of smolts leaving fresh waters is equal to the number of adults returning to fresh waters, even though ocean mortality of smolts is often substantial (e.g., >80%; Burgner 1991). To the best of our knowledge, no study has systematically analyzed the export of nutrients from freshwater systems by smolts across systems and years. However, in previous studies of a specific system it has been estimated that smolts export from 6.7% to 24.2% of the nutrients that their parents imported (Donaldson 1967; Naiman et al. 2002). Thus, how much of the nutrients imported to fresh waters by returning adults is exported by out-migrating smolts remains unknown. In other words, while previous studies have quantified the nutrients that adult salmon transport to fresh waters (Larkin and Slaney 1997; Schmidt et al. 1998; Gresh et al. 2000), we do not know how salmon impact net nutrient transport. For these reasons we quantified the relative magnitudes of nutrient transport by out-migrating smolts and returning adult sockeye salmon (*Oncorhynchus nerka*).

Using historical smolt and adult escapement data from four major sockeye salmon nursery systems in Alaska, we calculated the amounts of nitrogen and phosphorus that anadromous sockeye salmon import to and export from fresh waters, using a total of 76 years of data from four different systems. Based on these calculations, we found that sockeye salmon are consistent net importers of nutrients to fresh waters, but that out-migrating smolts often export a substantial fraction of the nutrients that their parents imported, and that the percentage exported varies considerably across space and time.

Materials and methods

We analyzed smolt and escapement data from four systems (Fig. 1) that comprise a large percentage of the sockeye fishery of Bristol Bay, Alaska (Hilborn et al. 2003). The Egegik system consists of the King Salmon River and the Egegik River and all of their tributaries. The Kvichak system consists of the Kvichak River, which drains Iliamna Lake and Lake Clark. The Wood River system consists of the Wood River, draining all of the Wood River lakes. The Ugashik system is located on the Alaska Peninsula and is dominated by flows from the Upper and Lower Ugashik lakes. These systems are located around 158°W and 58°N. The vegetation of these watersheds is a mix of spruce, alder, and tundra. Sockeye salmon is the most common species of Pacific salmon in these systems, although other species do spawn in these watersheds. Over the last 40 years, the total annual run to these systems has averaged 24 million sockeye. Over this period a total of 0.8 billion kg of sockeye

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Table 1. Description and source of constants considered for calculations.

Description	Value used	Source
Spawners		
Phosphorus content ($C_{\mathrm{P,adult}}$)	0.36% wet weight	Larkin and Slaney 1997
	0.38% wet weight*	Donaldson 1967
	0.48% wet weight	Mathisen et al. 1998
Nitrogen content ($C_{\mathrm{N,adult}}$)	2.67% wet weight	Mathisen et al. 1998
	3.04% wet weight*	Larkin and Slaney 1997
	3.30% wet weight	Ramseyer 2002
Smolts		
Phosphorus content ($C_{\mathrm{P,smolt}}$)	0.43% wet weight*	Donaldson 1967
Nitrogen content ($C_{\mathrm{N,smolt}}$)	2.49% wet weight*	Kline and Willette 2002
	2.49% wet weight	Ramseyer 2002†

*Value was used in the analyses presented.
†Values from Ramseyer (2002) were calculated from a regression ($r^2 > 0.99$) of sockeye salmon (*Oncorhynchus nerka*) body mass and nitrogen content for the average-sized smolt or spawning sockeye.

have spawned in these systems, while the fishery has harvested an additional 1.6 billion kg of sockeye. The dynamics of the last century of fisheries in the Bristol Bay are further described by Hilborn et al. (2003).

We reconstructed gross nutrient transport using smolt-migration and adult-escapement data from the Egegik, Wood, Kvichak, and Ugashik systems and published nutrient contents of sockeye. We analyzed a total of 76 years of data where age- and size-specific data on escapement of adult sockeye overlapped with age- and size-specific smolt data: 17 years from Egegik, 29 from Kvichak, 13 from Wood, and 17 from Ugashik.

Data used in these analyses were collected by the Alaska Department of Fish and Game (Hilborn et al. 2003; Weiland et al. 2003). Escapement data were collected via visual counting towers located on the major rivers that lead into these lake systems. Thus, these counting towers provide estimates of escapements of sockeye after they have passed the fisheries at the mouths of these systems (Weiland et al. 2003). Age composition and weight-at-age of the escapement for each system in each year were calculated by sampling scales and masses of large numbers of returning adults to determine the percent composition of the different age classes in relation to the overall salmon return.

Data on out-migrating smolts were collected with the aid of fyke nets and hydroacoustic equipment near the mouths of the rivers flowing out of each system, prior to smolts entering the estuarine habitats (Crawford 2001). The size and age composition of the out-migrating smolt population was estimated using samples collected from fyke nets. Smolt mass and freshwater age based on scale annuli were taken from a large sample (around 400 individuals) of smolts every day during migration, which typically lasts 3 weeks (Crawford 2001). Thus, these data not only give the number of out-migrating smolts from each system, but also the age composition of the population and the average mass of each age class for each year.

For each brood year, t, we calculated the gross import of a nutrient, n, as

$$\mathrm{Import}_{n,t} = \sum_{\mathrm{age}} (E_{\mathrm{age},t} \cdot \mathrm{AM}_{\mathrm{age},t} \cdot C_{n,\mathrm{adult}})$$

where $E_{\mathrm{age},t}$ is the age-specific escapement (in numbers of returning adults) in year t, $\mathrm{AM}_{\mathrm{age},t}$ is the average mass of that age class of spawners in year t, $C_{n,\mathrm{adult}}$ is the percent wet weight content of the nutrient of interest (phosphorus or nitrogen) in spawning sockeye bodies summed across all age classes in the escapement in year t. Because sockeye achieve >99% of their lifetime growth in the marine ecosystem and because of tissue turnover (Burgner 1991), we are assuming that nutrients from returning adult sockeye are completely of marine origin.

We calculated the gross export of nutrients by smolts produced from brood year t of spawners as

$$\mathrm{Export}_{n,t} = \sum_{\mathrm{age}} (S_{\mathrm{age},t} \cdot \mathrm{SM}_{\mathrm{age},t} \cdot C_{n,\mathrm{smolt}})$$

Thus, for a given brood year t, gross nutrient export by smolts equals the number of outgoing smolts of a given age class ($S_{\mathrm{age},t}$) times the average mass of those smolts (SM_t) times their nutrient content by weight ($C_{n,\mathrm{smolt}}$). We calculated import and export on a brood-year basis; in other words, these smolts did not all leave in the same year, but they were sired by the same population of spawners. We are assuming that out-migrating smolts are completely of freshwater origin, and this is supported by the observation that juvenile salmon quickly lose the isotopic signature of their parents (Kline et al. 1993).

We used previously published values or relationships for the phosphorus and nitrogen nutrient content of sockeye carcasses and smolts (Table 1). Although previous estimations of nutrient concentrations are relatively consistent, there are slight differences due to either measurement error or variability among sockeye populations (Table 1). Therefore, for constants where there were multiple estimates, we used the intermediate estimate for our calculation.

To explore the possible effect of density-dependent juvenile growth and survival on the balance between nutrient import and export by sockeye, we fit Beverton–Holt stock–recruit relationships to nutrient fluxes calculated above for each system (Beverton and Holt 1993). The Beverton–Holt function is often used to characterize density-dependence in salmon populations (e.g., Liermann and Hilborn 1997). Salmon populations often exhibit density-dependence; for example, higher numbers of spawning salmon often produce

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smolts that are characterized by a lower freshwater survival rate (Koenings and Burkett 1987) or smaller size (Eggers and Rogers 1987). In nutrient currency, the Beverton–Holt stock–recruit function is expressed as

$$\text{Export} = \frac{a \cdot \text{import}}{b + \text{import}}$$

where the export of nutrients in brood year t is a function of the import of nutrients for that brood year. We fit the unknown parameters a and b to observed data by minimizing the negative log-likelihood of the model (Hilborn and Mangel 1997) using brood-year-specific export and import (in kilograms of phosphorus) and assuming log-normally distributed errors. We focused on phosphorus because it is a limiting nutrient for these fresh waters (Goldman 1960; D.E. Schindler, unpublished data). However, because the nitrogen to phosphorus (N:P) ratio of smolt was 73% of the N:P ratio of adult salmon, the percentage of adult nitrogen that smolt export was 73% of the percentage of phosphorus exported. We also used hypothetical stock–recruit relationships of systems with intermediate (a = 10 000, b = 30 000) and strong (a = 10 000, b = 3000) density-dependence to illustrate that nutrient export by smolts could theoretically be larger than import by adults at low spawner densities. These values for the Beverton–Holt relationship are arbitrary, and are chosen to illustrate the potential impacts of density-dependence on the percentage of parental nutrients that smolt export. Based on the predicted relationship between import and export, we calculated the predicted percentage of parental nutrients that smolts export across a gradient of escapements (import).

Results

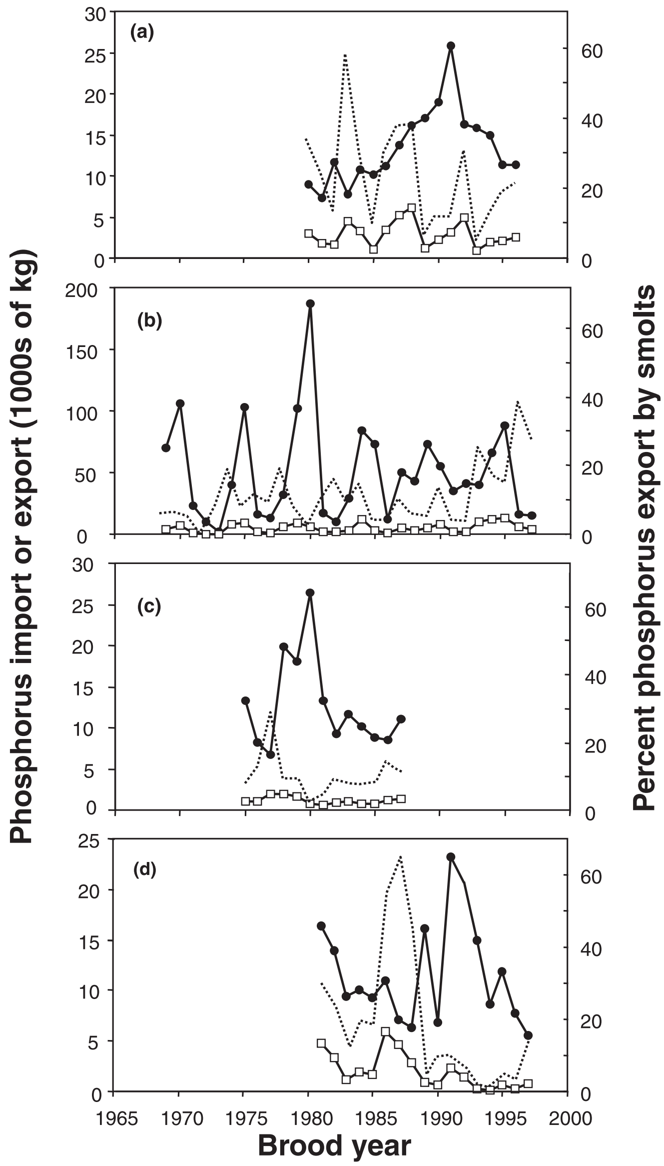
Anadromous sockeye transported large quantities of nitrogen and phosphorus both as adults and as smolts. However, sockeye consistently acted as net importers of nutrients (Fig. 2). Averaged across systems and years, smolt exported 16% of the phosphorus and 12% of the nitrogen that their parents imported. Because the N:P ratio of adult sockeye (7.92) was higher than that of smolts (5.76), smolt consistently exported a smaller fraction (73%) of parental nitrogen than phosphorus.

In the Egegik system, adult salmon transported 13 500 ± 4600 kg (mean ± 1 standard deviation) of phosphorus and 106 000 ± 36 000 kg of nitrogen into freshwater nursery ecosystems each year. Smolts transported 23.3 ± 13.9% of phosphorus and 17.0 ± 10.1% of nitrogen back to the ocean, corresponding to 2900 ± 1500 and 16 530 ± 8943 kg of phosphorus and nitrogen, respectively, each year.

The Kvichak system was characterized by higher levels of nutrient transport that were highly variable through time: adult salmon transported 50 200 ± 40 800 kg of phosphorus and 397 000 ± 324 000 kg of nitrogen each year. Smolts transported 5000 ± 3800 kg of phosphorus and 29 054 ± 21 961 kg of nitrogen, which translates to 11.8 ± 8.4% of the phosphorus and 8.6 ± 7.0% of the nitrogen that their parents transported from the ocean.

The Wood River system had more consistent nutrient transport by sockeye: adults transported 12 700 ± 5600 kg of phosphorus and 101 000 ± 44 400 kg of nitrogen each year.

Fig. 2. Phosphorus import by adult sockeye salmon (*Oncorhynchus nerka*) (●) and export by sockeye smolts (□) by brood year in the Egegik (*a*), Kvichak (*b*), Wood (*c*), and Ugashik (*d*) river systems in Bristol Bay, Alaska. Note the different scales on the left-hand *y* axis. The import and export of nitrogen can be envisioned by multiplying the values for phosphorus by 7.9 for adults and 5.7 for smolts, their respective N:P ratios. The dotted line shows the percentage of parental nutrients that smolts export, corresponding to the right-hand *y* axis.



Smolts transported 10.5 ± 6.2% of this phosphorus and 7.6 ± 2.6% of this nitrogen each year, i.e., 1150 ± 441 kg of phosphorus and 6645 ± 2544 kg of nitrogen per year.

Returning sockeye transported 11 700 ± 5140 kg of phosphorus and 92 300 ± 40 600 kg of nitrogen each year to the Ugashik system. Smolts transported 19.2 ± 18.9% of this phosphorus and 14.0 ± 13.8% of this nitrogen each year from fresh waters to the ocean, i.e., 1980 ± 1760 kg of phosphorus and 11 428 ± 10 133 kg of nitrogen.

The percentage of parental nutrients that smolts exported, averaged across years for each system, was highly correlated

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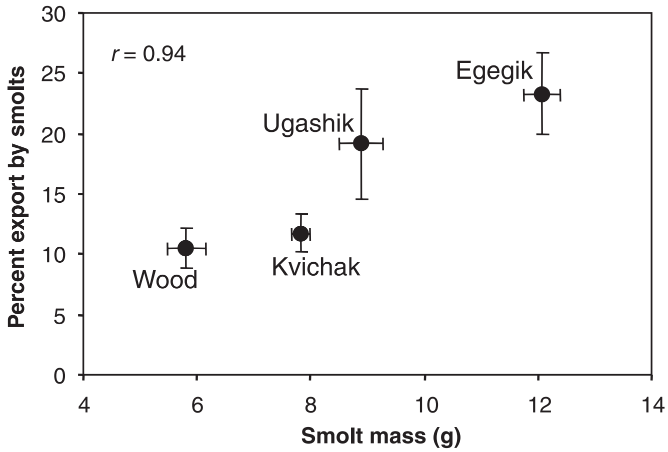
Fig. 3. Relationship between smolt body mass and the percentage of nutrients imported by spawners that smolts subsequently exported, averaged across all years of data (●). Error bars (±1 standard error) are shown for both smolt size and percentage exported to represent differences across years.

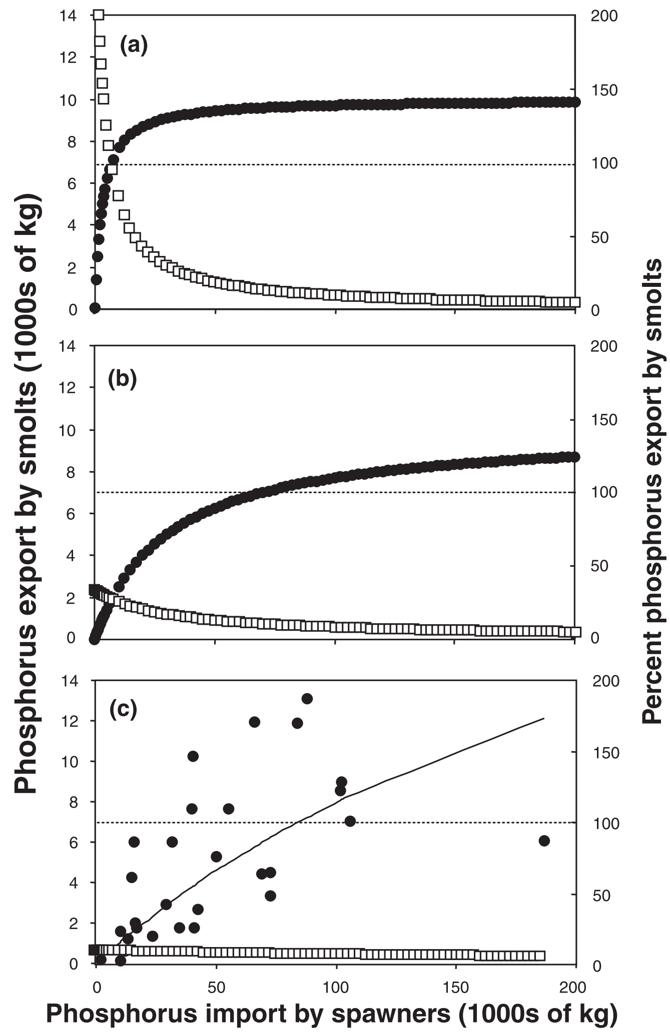


with the average smolt body size for that system (for phosphorus: Pearson's correlation, N = 4, r = 0.94, P = 0.07; Fig. 3), but was not significantly correlated with the average number of smolts per spawner (for phosphorus: Pearson's correlation, N = 4, r = 0.625, P = 0.39). The results for nitrogen were similar.

The percentage of the adult nutrients that smolts transported to the ocean varied not only from site to site but even more substantially through time (Fig. 2). In Egegik, smolts transported from 5.6% to 57% of the phosphorus and from 4.1% to 41.8% of the nitrogen their parents translocated from the ocean, while in Kvichak it ranged from 1.0% to 38.6% of the phosphorus and from 0.7% to 28.1% of the nitrogen. In Wood River, smolt transport ranged from 2.9% to 28.4% of the phosphorus and from 2.1% to 20.7% of the nitrogen, while in Ugashik it ranged from 1.3% to 64.7% of the phosphorus and from 0.9% to 47.1% of the nitrogen.

The percentage of parental nutrients that smolts export could also be influenced by the number of spawners and the degree of density-dependence that is characteristic of the system (Fig. 4). The two hypothetical stock–recruit (import–export) relationships that represented systems with intermediate and strong levels of density-dependence revealed that the lower the escapement (import), the higher the percentage of nutrients exported by out-migrating smolts (Figs. 4*a* and 4*b*). For example, with intermediate density-dependence, when spawners import less than 1000 kg of phosphorus to the system, smolts export 32% of the phosporus when they out-migrate. However, at large escapements, when spawners import, for example, 170 000 kg of phosphorus to the system, smolts subsequently export less than 5% of these nutrients. These differences are magnified even more in the case of strong density-dependence (Fig. 4*a*), where smolts export 8% of the phosporus imported by their parents when their parents imported 120 000 kg of phosphorus. However, when spawners import less than 7000 kg of phosphorus, smolts export more phosporus than their parents imported, and sockeye are acting as net exporters of nutrients from fresh waters rather than importers. The Beverton–Holt stock–recruit function described the Kvichak system reasonably well (negative log-likelihood = 31.8, a = 30 551, b = 283 800; Fig. 4*c*), but the relationships for the other three systems were poorly defined and thus are not presented. Using these parameters for Kvichak to predict nutrient export for a given level of import, smolts exported a relatively constant and low percentage of the nutrients their parents brought in (Fig. 4*c*). However, at lower escapements (lower import), smolts export a slightly higher percentage of the nutrients that their parents imported.

Fig. 4. Import–export (stock–recruit) relationships of phosphorus transport by sockeye for theoretical systems with strong (*a*) and intermediate (*b*) density-dependence. (*c*) Best-fitting import–export relationship for the Kvichak system (solid line) and the resulting percentage exported by smolts. Export by smolts for a given import by spawners is shown (●, corresponding to the left-hand *y* axis). The percentage of parental nutrients that smolts export is also shown (□, corresponding to the right-hand *y* axis). The broken line through 100% indicates when smolts export as much as spawners import.



Discussion

Sockeye transport large quantities of nitrogen and phosphorus from the ocean to freshwater ecosystems throughout Bristol Bay, Alaska. For example, in the Kvichak system, es-

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capement of sockeye transported, on average, 49 000 kg of phosphorus and 395 000 kg of nitrogen per year. Out-migrating smolts also transport large quantities of nitrogen and phosphorus. Smolts exported, on average, 16.2% of the phosphorus their parents exported. However, this average varied from 10.4% to 23.3% depending on the system, and varied from less than 1% to 64.3% depending on the year. From an alternative perspective, sockeye consistently act as net importers of nutrients to freshwater ecosystems, and, on average, spawners import over 6 times the phosphorus that their offspring export back to the ocean. Because the N:P ratio of adult sockeye was 73% higher than that of smolts, smolt consistently exported a smaller fraction of parental nitrogen than phosphorus.

To the best of our knowledge, there have been few studies in which nutrient transport by both smolts and adult salmon has been explicitly calculated. In his thesis on the phosphorus budget for Lake Iliamna (in the Kvichak system), Donaldson (1967) estimated that smolts removed 24.2% and 19.3% of the phosphorus that their parents brought in for the 2 years that he analyzed. These values are around twice as high as the average percent removal that we calculated for the Kvichak system. In addition, Naiman et al. (2002) calculated that smolts exported 6.7% of the cumulative nutrients that their parents had imported to Lake Iliamna, Alaska, over the last 40 years. This percent export is less than ours primarily because we calculated it on a brood-year basis and they averaged percent export of the nutrients that accumulated across all years. In addition, Stockner (1987) summarized the phosphorus budgets of five sockeye nursery lakes in Russia and the Pacific coast of North America, including quantifying phosphorus transport by adult and smolt sockeye. Using these phosphorus budgets, we calculated that smolt transport an average of 14.1% of the nutrients that their parents imported in these five lakes, and the percentage varied from 6.2% to 24.3%. Thus, in sockeye systems across the Pacific Basin, smolts consistently export from 5% to 25% of the nutrients that their parents import.

The percentage of parental phosphorus that out-migrating smolts export varies substantially among the four systems, from 10.4% for Wood River to 23.3% in Egegik. These differences between systems in the percentage of nutrients that smolts transport could be due to different numbers of recruits (smolts) per spawner, different sizes of out-migrating smolts, or the interaction between these factors. Although our statistical power was limited because we had data for only four systems, systems with larger smolts tended to have higher percentages of nutrient transport. For example, Egegik smolts export 23.3% of the phosphorus that their parents imported, around twice that exported by Wood River smolts (10.4%), and the Egegik smolts were around twice as heavy as the Wood River smolts (12.1 vs. 5.9 g). However, systems with higher numbers of outgoing smolts per spawner did not have significantly higher percentages of nutrient transport, perhaps because of strong density-dependence in smolt size at out-migration (e.g., Eggers and Rogers 1987).

There are several potential sources of error in our estimations of nutrient transport by smolt and adult sockeye. First, there is the potential for both human and instrumental errors in determining the numbers of returning adults and especially out-migrating smolts. Second, prior estimations of the nutrient content of salmon varied slightly. Any errors in the nutrient content or abundance of smolt and adult sockeye salmon would be linearly transferred to calculations of nutrient import and export. For example, changing a nutrient-content estimate by 1% of its value would lead to a 1% change in our calculation of net nutrient transport.

In the four sockeye systems in Bristol Bay, Alaska, that we examined, smolts exported an average of 16.1% of the nutrients that their parents imported. However, it is unclear how these calculations would compare with those from different systems with different species of salmon, different-sized smolts, different recruits-per-spawner relationships, and different ocean mortality rates. We predict that smolts will export a higher percentage of the nutrients their parents imported in systems with larger smolts, higher ocean mortality rates, and higher smolt production.

We investigated how nutrient export varies across different escapements with both our data and with hypothetical stock–recruit (import–export) relationships. The Kvichak system stock–recruit relationship was best defined by a Beverton–Holt relationship with a = 30 551 and b = 283 800, which produces very weak density-dependence in smolt production. However, if systems are characterized by stronger density-dependence, the percentage of parental nutrients that smolts export is often much higher at low spawner levels. Hypothetically, in systems that are characterized by extreme density-dependence, at low levels of escapement or nutrient import, smolts could actually export more nutrients than their parents import from the ocean. For example, if a pair of sockeye each weighing 2 kg produced 4000 eggs, and 15% of those survive to become smolts that averaged 10 g each, this pair of sockeye will have produced 6 kg of smolts. This pair of sockeye would have imported 15.4 g of phosphorus and 121.6 g of nitrogen while siring smolts that exported 25.9 g of phosphorus and 149.4 g of nitrogen. These size and egg-production values are within observed ranges (Burgner 1991).

Insight into the relationship between net import and net export can be gained by examining the parameters of the Beverton–Holt function in more algebraic detail (Fig. 5). By solving for import as a function of a and b, we can calculate the combinations of a, b, and import that will produce net import, net export, and a net balance of nutrient flux from fresh waters. If import is equal to export (smolts export 100% of the nutrients that their parents imported), then import is equal to parameter a minus parameter b. However, if import is greater than a minus b, then spawners import more than smolts export (net import) in systems with strong density-dependence in smolt production. Alternatively, if import is less than a minus b, then smolts export more than their parents imported (net export). Therefore, human activities such as fisheries that reduce escapement levels (import) could shift systems from a state where salmon act as net importers of nutrients to an alternative state where salmon act as net exporters of nutrients. Alternatively, human activities that cause decreases in smolt production could temporarily decrease the percentage of parental nutrients that smolts export from fresh waters, but this pattern would only be maintained if spawner numbers are not subsequently reduced.

This study quantifies gross fluxes of nutrients transported by sockeye between freshwater and marine ecosystems, but

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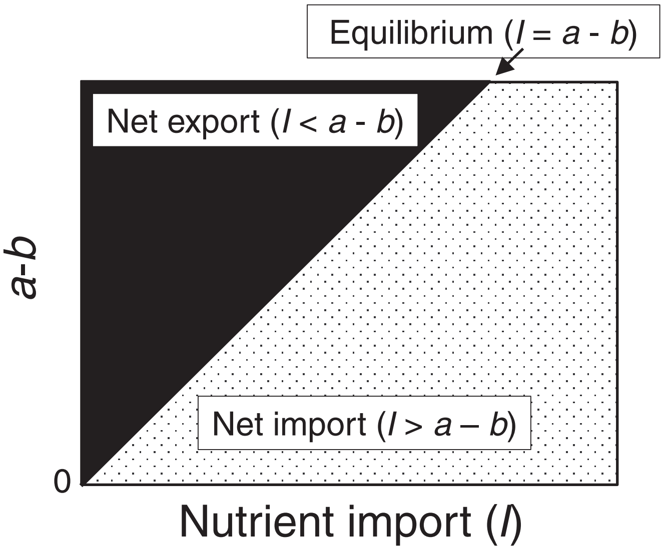
Fig. 5. Relationship between the Beverton–Holt parameters *a* and *b* fit to data in nutrient currency and net nutrient flux by salmon (*Oncorhynchus* spp.). The black region corresponds to situations where import (*I*) by spawners is less than the difference between parameters *a* and *b*, when salmon act as net exporters of nutrients. The stippled region corresponds to situations where import by spawners is greater than the difference between parameters *a* and *b*, when salmon act as net importers of nutrients.



does not attempt to track the pathways that these nutrients take or the impacts of the nutrients on the ecosystem. There is widespread evidence from analyses of stable isotopes that marine-derived nutrients accumulate in fresh waters (reviewed by Gende et al. 2002; Naiman et al. 2002; Schindler et al. 2003). In previous studies it has been observed that when adult salmon migrate to fresh waters and die, the nutrients from their bodies are incorporated into a variety of ecosystem components: nutrients are incorporated directly via consumption by predators and scavengers such as grizzly bears (e.g., Hilderbrand et al. 1996) or juvenile coho salmon (e.g., Bilby et al. 1998), deposited into lake sediments (e.g., Donaldson 1967; Finney et al. 2000), or exported back into the ocean by hydrologic flows (e.g., Sugai and Burrell 1984) or smolts, or soluble fractions are taken up by periphyton or riparian vegetation (e.g., Helfield and Naiman 2001).

Returning salmon are only one of many sources of the nitrogen and phosphorus in fresh waters. Therefore, export of nutrients by out-migrating smolts, while composing a large fraction of the nutrients imported by adult salmon, comprises a smaller fraction of the total nutrient budget. However, returning adult salmon can be the dominant source of phosphorus in freshwater systems (Donaldson 1967) and a substantial source of nitrogen (Naiman et al. 2002). For example, according to Donaldson's (1967) phosphorus budget for Lake Iliamna, each year out-migrating smolts remove, on average, the equivalent of 6.6% of the phosphorus in the plankton, 1.7 times the phosphorus that is lost to sediments, and 29% of the phosphorus that leaves in the river outflow. It is likely that nitrogen export by out-migrating smolts is less ecologically important than phosphorus export, for two reasons: first, smolts export a smaller proportion of the nitrogen imported by their parents than of the phosphorus; second, these systems are generally phosphorus-limited, especially given the prevalence of nitrogen-fixing alder trees in these watersheds.

The pathways and impacts of the nutrients smolts transport from fresh waters to oceans are less well studied for smolts than for their parents. Juvenile salmon probably accumulate the majority of their nutrients from pelagic food webs in lakes, where they feed primarily on zooplankton (Burgner 1991). Thus, out-migrating smolts transport nutrients from the freshwater pelagic food web to marine ecosystems. Nutrients exported by smolts are probably incorporated into the marine food web as ocean-going salmon are eaten by birds, fishes, and marine mammals (reviewed by Burgner 1991).

In most previous studies of salmon-derived nutrients, nutrient transport by out-migrating smolts has been ignored (e.g., Larkin and Slaney 1997; Gresh et al. 2000) or assumed to be a small, constant fraction of the adult body mass. Our study has three important messages. First, out-migrating smolts can transport thousands of kilograms of nitrogen and phosphorus; in some years, a substantial portion of the nutrients that their parents brought in are taken back out to the ocean. Second, the percentage of adult nutrients that smolts transport to the ocean varies enormously across time and space, ranging from less than 1% to as high as 65%. Third, in systems characterized by strongly density-dependent stock–recruit relationships, smolts export a higher percentage of nutrients at lower escapements and in some circumstances could export more than adults. Therefore, human activities that reduce spawner numbers will not only reduce the raw import of nutrients (Larkin and Slaney 1997; Gresh et al. 2000), but also may increase the percentage of these nutrients that salmon smolts subsequently export back to the ocean, additionally decreasing net nutrient import to fresh waters by salmon. Furthermore, systems that are stocked with juvenile salmon but do not have naturally spawning adults may represent a case where anadromous salmon are acting as net exporters of nutrients from fresh waters. In the management of salmon-rearing systems, consideration should be given not only to the nutrients that adult salmon return to fresh waters, but also to the nutrients that smolts take away from fresh waters. Failure to do so will lead to consistent overestimation of the net amount of nutrients that anadromous salmon transport to fresh waters.

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References

Beverton, R.J.H., and Holt, S.J. 1993. On the dynamics of exploited fish populations. Chapman and Hall, London.

Bilby, R.E., Fransen, B.R., Bisson, P.A., and Walter J.K. 1998. Response of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead (*Oncorhynchus mykiss*) to the addition of salmon carcasses to two streams in southwestern Washington, U.S.A. Can. J. Fish. Aquat. Sci. **55**: 1909–1918.

Burgner, R.L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). *In* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. University of British Columbia Press, Vancouver. pp. 1–117.

Crawford, D.L. 2001. Bristol Bay sockeye smolt studies for 2001. Regional Information Rep. No. 2A01-27, Alaska Department of Fish and Game, Anchorage.

Donaldson, J.R. 1967. The phosphorus budget of Iliamna Lake, Alaska, as related to the cyclic abundance of sockeye salmon. Dissertation, University of Washington, Seattle, Wash.

Eggers, D.M., and Rogers, D.E. 1987. The cycle of runs of sockeye salmon (*Oncorhynchus nerka*) to the Kvichak River, Bristol Bay, Alaska: cyclic dominance or depensatory fishing? Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 343–366.

Finney, B.P., Gregory-Eaves, I., Sweetman, J., Douglas, M.S.V., and Smol, J.P. 2000. Impacts of climatic change and fishing on Pacific salmon abundance over the past 300 yeas. Science (Wash., D.C.), **290**: 795–799.

Gende, S.M., Edwards, R.T., Willson, M.F., and Wipfli, M.S. 2002. Pacific salmon in aquatic and terrestrial ecosystems. Bioscience, **52**: 917–928.

Goldman, C.R. 1960. Primary productivity and limiting factors in three lakes of the Alaska peninsula. Ecol. Monogr. **30**: 207–230.

Gresh, T., Lichatowich, J., and Schoonmaker, P. 2000. An estimation of historic and current levels of salmon production in the Northeast Pacific ecosystem: evidence of a nutrient deficit in the freshwater systems of the Pacific Northwest. Fisheries, **25**: 15–21.

Groot, C., and Margolis, L. (*Editors*). 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Helfield, J.M., and Naiman, R.J. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology, **82**: 2403–2409.

Hilborn, R., and Mangel, M. 1997. The ecological detective: confronting models with data. Princeton University Press, Princeton, N.J.

Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. Proc. Natl. Acad. Sci. U.S.A. **100**: 6564–6568.

Hilderbrand, G.V., Farely, S.D., Robbins, C.T., Handley, T.A., Titus, K., and Servheen, C. 1996. Use of stable isotopes to determine the diets of living and extinct bears. Can. J. Zool. **74**: 2080–2088.

Kline, T.C., and Willette, T.M. 2002. Pacific salmon (*Oncorhynchus* spp.) early marine feeding patterns based on $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Prince William Sound, Alaska. Can. J. Fish. Aquat. Sci. **59**: 1626–1638.

Kline, T.C., Goering, J.J., Mathisen, O.A., Poe, P.H., Parker, P.L., and Scalan, R.S. 1993. Recycling of elements transported upstream by runs of Pacific salmon. II. ^{15}N and ^{13}C evidence in the Kvichak River watershed, Bristol Bay, southwestern Alaska. Can. J. Fish. Aquat. Sci. **50**: 2350–2365.

Koenings, J.P, and Burkett, R.D. 1987. Population characteristics of sockeye salmon (*Oncorhynchus nerka*) smolts relative to temperature regimes, euphotic volume, fry density, and forage base within Alaska lakes. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 216–234.

Larkin, G.A., and Slaney, P.A. 1997. Implications of trends in marine-derived nutrient influx to south coastal British Columbia salmonid production. Fisheries, **22**: 16–24.

Liermann, M., and Hilborn, R. 1997. Depensation in fish stocks: a hierarchic Bayesian meta-analysis. Can. J. Fish. Aquat. Sci. **54**: 1976–1984.

Mathisen, O.A., Parker, P.L., Goering, J.J., Kline, T.C., Poe, P.H., and Scalan, R.S. 1988. Recycling of marine elements transported into freshwater systems by anadromous salmon. Verh. Int. Ver. Limnol. **23**: 2249–2258.

Naiman, R.J., Bilby, R.E., Schindler, D.E., and Helfield, J.M. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. Ecosystems, **5**: 399–417.

Polis, G.A., Anderson, W.B., and Holt, R.D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu. Rev. Ecol. Syst. **28**: 289–316.

Ramseyer, L.J. 2002. Predicting whole-fish nitrogen content from fish wet weight using regression analysis. N. Am. J. Aquacult. **64**: 195–204.

Schindler, D.E., Scheuerell, M.D., Moore, J.W., Gende, S.M., Francis, T.B., and Palen, W.J. 2003. Pacific salmon and the ecology of coastal ecosystems. Front. Ecol. Environ. **1**: 31–37.

Schmidt, D.C., Carlson, S.R., Kyle, G.B., and Finney, B.P. 1998. Influence of carcass-derived nutrients on sockeye salmon productivity of Karluk Lake, Alaska: importance in the assessment of an escapement goal. N. Am. J. Fish. Manag. **18**: 743–763.

Stockner, J.G. 1987. Lake fertilization: the enrichment cycle and lake sockeye salmon (*Oncorhynchus nerka*) production. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 198–215.

Sugai, S.F., and Burrell, D.C. 1984. Transport of dissolved organic carbon, nutrients, and trace metals from the Wilson and Blossom rivers to Smeaton Bay, southeast Alaska. Can. J. Fish. Aquat. Sci. **41**: 180–190.

Weiland, K.A., Morstad, S., Sands, T., Fair, L., Crawford, D., West, F., and McKinley, L. 2003. Annual management report: Bristol Bay. Alaska Department of Fish and Game, Regional Information Rep. No. 2A03-18.

Willson, M.F., and Halupka, K.C. 1995. Anadromous fish as keystone species in vertebrate communities. Conserv. Biol. **9**: 489–497.

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