Phosphorus flux due to Atlantic salmon (*Salmo salar*) in an oligotrophic upland stream: effects of management and demography[1]

Keith H. Nislow, John D. Armstrong, and Simon McKelvey

Abstract: Little is known concerning the role of Atlantic salmon (*Salmo salar*) in the transport of nutrients to and from river systems. We used demographic data from the River Bran, an oligotrophic river in Scotland, UK, to construct a budget for the transport of phosphorus (P) and applied it to investigate the effects of management strategies and demographic rates on potential transport. At present, because few adults return to their spawning grounds, salmon export 0.2–0.5 kg P·year^{-1}. In contrast, increasing passage rates to a level sufficient to maintain a population without stocking would likely result in a gain of up to several kilograms per year. However, this effect depended on the retention of adult-derived P, which varies across systems and is poorly known at present. Egg-derived P exceeded that from adults at low (<25%) retention rates but was insufficient on its own to balance losses. Increased marine survival rates also increased the potential for positive P flux, while reduction in egg–smolt survival reduced the magnitude of transport. These results indicate the importance of considering within-river movements of individuals and nutrients and the need to fill critical data gaps in assessing the role of Atlantic salmon in nutrient transport.

Résumé : On connaît mal le rôle du saumon atlantique (*Salmo salar*) dans l'importation et l'exportation de nutriments dans les rivières. Des données démographiques dans la Bran, une rivière oligotrophe d'Écosse, nous ont servi à construire un bilan du transport du phosphore (P) que nous avons utilisé pour évaluer les effets des stratégies d'aménagement et des taux démographiques sur le transport potentiel. À l'heure actuelle, parce que peu de saumons retournent à leur site de fraye, les saumons exportent 0,2–0,5 kg P·an^{-1}. En revanche, l'augmentation des taux de passage à un niveau suffisant pour maintenir la population sans empoisonnement entraînerait vraisemblablement un gain pouvant atteindre plusieurs kilogrammes par année. Cependant, un tel effet suppose la rétention du P dérivé des adultes, un phénomène qui varie d'un système à l'autre et qui est actuellement mal connu. Le P dérivé des oeufs est plus important que celui dérivé des adultes aux taux faibles (<25 %) de rétention, mais ne suffit pas seul à compenser les pertes. Une augmentation des taux de survie en mer accroît la probabilité d'un flux positif de P, alors que la réduction de la survie de l'oeuf jusqu'au stade saumoneau diminue l'importance du transport. Nos résultats démontrent l'importance de tenir compte des déplacements des individus et des nutriments au sein du cours d'eau et soulignent la nécessité d'obtenir les données critiques manquantes nécessaires afin d'évaluer le rôle du saumon atlantique dans le transport des nutriments.

[Traduit par la Rédaction]

Introduction

Anadromous salmonids can be significant importers of marine-derived nutrients to temperate, upland stream systems and riparian forests and wildlife. Removing this source of nutrients, via barriers to upstream migration and fisheries exploitation, can reduce overall ecosystem productivity and diversity and threaten the sustainability of populations (Stockner et al. 2000; Stockner and Ashley 2003). The role of Pacific salmon (*Onchorhynchus* spp.) in nutrient dynamics and fish production in northwestern United States has been well documented and is an area of active research (Bilby et al. 1996; Wipfli et al. 2003). Several studies have shown increases in periphyton, invertebrate, and juvenile salmonid production (Chaloner et al. 2002; Chaloner and Wipfli 2002; Wipfli et al. 2003) in response to addition of salmon carcasses and higher production in streams with salmon spawning runs compared with streams without

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salmon (Bilby et al. 1996; Cederholm et al. 2000). These results have led to explicit recommendations to managers, emphasizing the role of Pacific salmon as importers of marine-derived nutrients in maintaining ecosystem function and fisheries productivity (Bilby et al. 2001; Michaels 2003; Lackey 2003). In contrast with this large body of information on Pacific salmon, it is unclear whether anadromous Atlantic salmon (*Salmo salar*), their counterparts in the Atlantic basin, may function similarly as net importers of nutrients. Given major changes in the abundance and distribution of migratory Atlantic salmon (Parrish et al. 1998), understanding this role may be critical both for salmon conservation and management and for gaging the impacts of changes in population status and management strategies on river ecosystems.

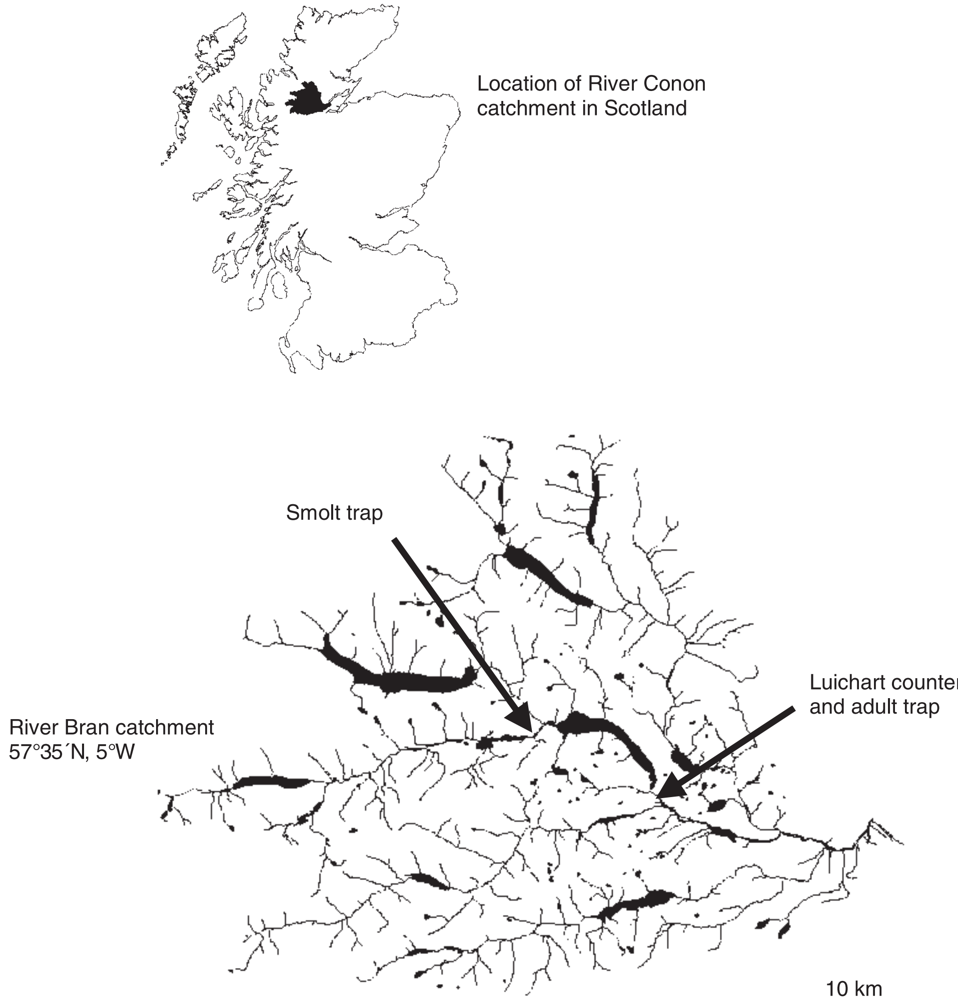
Owing to key life history differences, it is unlikely that Atlantic salmon translocate nutrients to the same extent as Pacific salmon. Pacific salmon (with the exception of steelhead (*Onchorhynchus mykiss*)) are semelparous, with all individuals dying in rearing streams after spawning, whereas Atlantic salmon may migrate or wash out from spawning streams before dying downstream or leaving the river. In addition, the extended freshwater rearing period of Atlantic salmon results in fewer smolts (the life stage that migrates from fresh water to sea) and returning adults produced per unit area of rearing habitat compared with species such as pink salmon (*Onchorhynchus gorbuscha*) and chum salmon (*Onchorhynchus keta*) that migrate from rivers within a few months of emergence. However, under some circumstances, Atlantic salmon may have important impacts on nutrient fluxes. Survival of anadromous Atlantic salmon after spawning varies considerably among years and river systems, and many adults die and provide sources of marine-derived nutrients in some streams (Fleming 1998). However, there is almost no information on the extent to which Atlantic salmon carcasses are retained in rearing streams. Marine-derived nutrients may also be imported by routes other than carcasses. Spawned salmon eggs, which can compose 20% of the body weight of female spawners, are essentially all retained in rearing streams and might be a source of marine-derived nutrients even when spawners survive and outmigrate. Breakdown of muscle tissue for spawning and nest defense may also release marine-derived nutrients to streams (Jonsson et al. 1997). Previous studies on other species indicate that iteroparity and long freshwater rearing duration do not preclude a role for migratory fish in nutrient import. Durbin et al. (1979) found that the migration of the alewife (*Alosa pseudoharengus*), an iteroparous clupeid, resulted in a net import of marine-derived nitrogen (N) and phosphorus (P) and enhancement of plankton production in small spawning ponds in a coastal New England watershed. Schuldt and Hershey (1995) found that introduced chinook salmon (*Oncorhynchus tshawytscha*) resulted in a significant import of nutrients to a Lake Superior, US, stream in spite of extended freshwater rearing and small run size.

The importance of nutrient transport via salmon is not solely a function of total amounts transported. In systems that are characteristically low in nutrients (oligotrophic), relatively small chronic losses or gains can have major consequences. Many salmon streams, particularly in the uplands of larger river systems, are underlain by old, crystalline bedrock and are naturally poor in nutrients, with consequently low levels of primary productivity (Elliott et al. 1998). Compounding the intrinsically low productivity is a suite of anthropogenic influences that have acted to remove nutrients from upland systems, a phenomenon referred to as cultural oligotrophication (Stockner et al. 2000). Owing to their long history of intensive settlement (compared with Pacific basin systems), Atlantic salmon rivers may be particularly affected by cultural oligotrophication. As an example, in the New England region of the United States, >70% of the original forest (a major source of long-term nutrient storage; Foster 1992), practically all anadromous fish (a potential source of marine-derived nutrients), and most of the original population of the North American beaver (*Castor canadensis*) (whose activities store and make available large quantities of N and P; Cirmo and Driscoll 1993; Naiman et al. 1994) were lost from the northern forest ecosystem. More recently, acidification associated with atmospheric emissions has compounded losses of productivity (Driscoll et al. 2001). As this suite of anthropogenic effects (logging and land clearance, elimination of keystone species, and loss of stream buffering capacity) is common to salmon rivers to different degrees, loss of productivity may be of widespread concern.

Few studies have addressed nutrient transfer by Atlantic salmon. Lyle and Elliott (1998) presented a mass-balance assessment of several major salmon and sea trout rivers in the United Kingdom by estimating the flux of dissolved nutrients and salmonids (Atlantic salmon and sea trout) at the mouths of large rivers. They found that nutrients imported by adults exceeded nutrients exported by smolts, but that fish represented a very small fraction (<1%) of total nutrient flux through the system. However, the authors cautioned that nutrient export from the river mouth is likely to be dominated by anthropogenic sources (agricultural and municipal) on the mainstem that may not constitute important rearing or spawning habitat. They also suggest that transport by salmonids may be a much more significant component of fluxes to upland rearing streams. This suggestion was supported by a more recent mass-balance assessment of salmon nutrient transport in the River Imsa in Norway (Jonsson and Jonsson 2003). In this small (~1 km from the ocean) coastal river, as in the United Kingdom rivers studied by Lyle and Elliott (1998), migratory salmon accounted for a net import of nutrients to the river system. In the River Imsa, an oligotrophic river that largely consists of suitable spawning and rearing habitat, the proportion of total carbon (C), N, and P budgets accounted for by migratory salmon was generally an order of magnitude higher than that found by Lyle and Elliott (1998), encompassing as much as 17% of the total P budget in some years, in spite of low mortality and low carcass availability.

Assessing the role of Atlantic salmon in the nutrient dynamics of upland oligotrophic systems is of particular importance for fisheries and ecosystem management in the context of extensive human alteration of river environments. Relatively high gradient upland areas may provide the best physical spawning and rearing habitat for salmon. However, passage of salmon to and from these upland systems is impeded by the large in-river migration distance, during which mortality can occur, and a greater number of natural and artificial obstructions relative to lowland reaches. Atlantic

Fig. 1. Map of the River Bran system (Scotland, UK), showing locations of fish counter, fish passes, and smolt trap.



salmon are in decline throughout their range. In Scotland, the rate of decline is highest in those sectors of stocks within rivers that tend to return early in the year and spawn in upland areas. In Scotland, as well as in other regions (Parrish et al. 1998), populations impacted heavily by anthropogenic reductions in river connectivity and high marine mortality are supplemented or sustained by restoration and enhancement stocking of eggs and fry, resulting in a situation where considerable numbers of smolts are produced, but essentially no adults are able to access spawning areas. Understanding the potential effects of these management strategies on nutrient dynamics is critical for maintenance of productive, self-sustaining upland fisheries and ecosystems.

Our goal was to determine how variation in management strategies and population dynamics affect the role of Atlantic salmon in the transport of P. Phosphorus is the most frequently limiting nutrient in upland oligotrophic watersheds (Meyer and Likens 1979; Newbold et al. 1983; Bradford and Peters 1987), and several major field studies have demonstrated increased salmonid production in response to experimental P addition (Johnston et al. 1990; Deegan and Peterson 1992; Griswold et al. 2003). In anadromous species, P addition has resulted in decreased freshwater rearing times, larger outmigrant smolts, and higher smolt–adult survival rates (Slaney et al. 2003). For detailed study, we chose a Scottish upland system from which good data have been obtained on outputs of smolts, returns of adults, and the impact of obstructions to upstream migrations. The stock on the system is supported by a combination of enhancement stocking and natural spawning. Using these data, we compiled a P budget to assess the current P flux, explored the consequences of a number of management scenarios, and predicted the effects of variations in marine and in-river return migration mortality on Atlantic salmon. Though centered on a case study, our goal was to provide a framework for assessing salmon-associated nutrient transport applicable to a wide range of situations.

Materials and methods

The study site

The River Bran (57°35′N, 5°W) is a tributary of the River Conon in North Scotland, with a catchment of 191 km^2 (Mills 1964) (Fig. 1). Dissolved P on the Bran system is below the detection limit of 5 $\mu g \cdot L^{-1}$ (R. Harriman, Fisheries Research Services Freshwater Laboratory, Faskally, Pitlo-

Table 1. Calculations and values for salmon transport of P budget in the River Bran.

Parameter	Equation	Values	Source
No. of stocked eggs		x = 629 000	River Bran stocking statistics
Mass per egg (g)		x = 0.058 g dry weight	Mills 1984
[P] eggs		0.002 841	Poston and Ketola 1989
Smolt number		x = 11 175	River Bran smolt trap
Mass per smolt (g)		x = 16 g	River Bran smolt trap
[P] smolts		0.0045 g wet weight	Lyle and Elliott 1998
No. of returning adults		x = 338.3	Fish counter on the Luichart Dam, supported by survival to returning fish of tagged smolts
No. of adults to spawning grounds	Returning adults × in-river passage proportion	In-river passage set at a range of rates from 0 to 1.0; current rate = 0.075	Current rate from Gowans et al. 2003
Mass per adult (g)		2500 $g \cdot adult^{-1}$	River Bran adult trap
No. of carcasses	Adults × carcass retention via mortality	Carcass retention set at range of rates from 0 to 1.0	
Mass of carcasses (g)	($Mass \cdot adult^{-1}$ × no. of carcasses) – mass of females as eggs	Proportion of females = 0.6	River Bran adult trap
		Proportion of female mass as eggs = 0.2	Mills 1984
$P_{carcass}$		0.0047 g wet weight	
Adult biomass (g)	Male biomass + female biomass		
P_{adults}	Adult biomass × $P \cdot g^{-1}$ adult	$P \cdot g^{-1}$ adult = 0.0047	Lyle and Elliott 1998
P_{eggs}	Proportion biomass as eggs × female biomass	$P \cdot g^{-1}$ egg = 0.002841	Poston and Ketola 1989
Net P	$(P_{adults} + P_{eggs}) - P_{smolts}$		

chrie, Perthshire PH16 5LB, UK, personal communication). As part of a plan to mitigate losses of salmon stocks associated with the generation of hydroelectricity, a salmon population has been established in the River Bran by stocking (1953–1970 and 1992–2002) progeny of fish from a neighboring tributary, the River Blackwater. Of an estimated wetted area of 0.661 km^2, an area of approximately 0.287 km^2 is stocked annually. The upstream passage of returning fish has been facilitated by a fish pass at the Conon Falls, which previously was a complete barrier. Fish moving to the headwaters negotiate a series of fish passes and lochs (Gowans et al. 2003).

A trap collected all adult salmon returning to the River Blackwater. The fish were then stripped, and the eggs were fertilized and held at the Contin hatchery. They were distributed widely throughout suitable rearing habitat in the River Bran, generally as eyed ova introduced into specially constructed artificial redds and occasionally as first-feeding fry. Fish leaving the system as smolts were collected each spring in a Wolf trap at Achanalt, examined, and then trucked and released downstream below Torachilty Dam. Stocking levels were increased over time, and the output of smolts from the River Bran reached a plateau level in 1998, suggesting that full productive capacity of the system had been reached. The stocking levels were determined from a combination of habitat surveys to identify total areas of suitable habitat and estimates of egg and fry densities needed to saturate the productive capacity (S. McKelvey, unpublished data). Current stocking levels are $3 \cdot m^{-2}$ and compromise between a target of $5 \cdot m^{-2}$ and maximizing the area stocked. Data collected from egg deposition and the resulting smolts and anadromous adults from 1995 to 2001 are considered in this study.

The total numbers of eggs and fry stocked were recorded. Smolts leaving the system were trapped throughout April–June and counted, and subsamples of 1000–2000 individuals were weighed and measured. Records from the resistivity counter, which used a wheatstone bridge circuit to detect differences in the conductivity of fish and water, in the Borland Lift fish pass at Luichart (Fig. 1) were taken as estimates of salmon returning to the system. A visual check in 1999 suggested that this counter is highly accurate, and counts tallied well with estimates of predicted returns based on the survival of a subsample of smolts tagged with passive integrated transponders and recorded automatically on their return migration (S. McKelvey, unpublished data). An estimate of the survival of salmon from Luichart to the spawning areas of the River Bran was taken from the radio-tracking observations of Gowans et al. (2003). Estimates of sex ratio and weights of adult fish were also taken from Gowans et al. (2003).

The P budget

A budget (Table 1) was constructed to estimate the net flux of P due to Atlantic salmon and to quantify the relative importance of constituent pathways under a range of scenarios. Estimates of P output (as smolts) and input were calculated from data collected in the River Bran in 1998–2000 along with parameter values obtained via previous studies.

Our basic budget equation is

$$\text{Net P} = (P_{adults} + P_{eggs}) - P_{smolts}$$

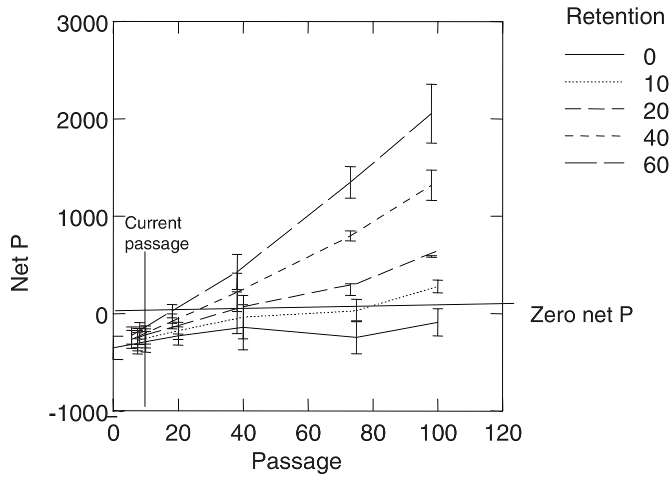
P_{adults} is the P concentration attributable to adults, adult size, return rate of adults, and retention within spawning streams; P_{smolts} is the P concentration attributable to smolt mass and number; and P_{eggs} is the P concentration attributable to egg number.

The annual P input from stocking was calculated as the product of the weight of stocked eggs and fry and their weight-specific P content (assuming no differences between eggs and fry before they have started to feed). The annual P input from returning adults was calculated in two components: the contribution from spawned eggs and from adults. Counts of returning fish at Luichart were adjusted to levels on the spawning grounds using a range (0%–100%) of passage (upstream survival) indices, which included the observed value (7.5%) under conditions pertaining in 1997 (Gowans et al. 2003). At each of the given passage levels, the total number of salmon was adjusted by the sex ratio to give the number of females. P input from their eggs was calculated as a product of the number of females, the fraction of their total biomass composed of eggs, and weight-specific P content of eggs. When female spawner passage was predicted by the budget to provide an equal or greater number of eggs as that from stocking, we no longer considered stocked eggs as an input term, simulating an end to stocking with sufficient spawner returns. Input from adults was calculated as the product of the remaining adult biomass (minus the eggs), the proportion of adult biomass retained (range from 0 to 0.6), and the weight-specific P content of adults.

We used this budget to predict net P flux from alternative management and demographic scenarios. Our basic scenario represents net P at current stocking, smolt production, and adult return levels over a range of passage and adult-derived annual P retention rates. Retention of adult P is a key parameter in the model and represents both P contributed from carcasses of dead spawners and P released by adult metabolism in nest defense and spawning activities. Adult-derived P retention rates ranged from 0 (no P retained) to a maximum of 60, which we felt was close to a maximum conceivable retention rate given outmigration, washout of carcasses, and advective transport of adult-derived particulate and dissolved P. In addition, this value of 60% approximates retention found by Lyle and Elliott (1998) and Jonsson and Jonsson (2003), making this level an appropriate maximum and a useful point of comparison among the three studies. In-river passage levels ranged from 0 (no upstream access; representative of highly regulated, impounded systems supported entirely by stocking) to 100% passage.

Outputs from the budget scenarios were used to assess the effects of changes in river passage, differences in adult P retention, and changes in marine and pre-smolt mortality on the magnitude and direction of P flux in the River Bran. Specifically, we considered the following questions: (*i*) What is the maximum P drain with effectively zero adult return? (*ii*) What is the net P flux under current conditions of in-river passage of returning adults? (*iii*) If upstream passage of fish can be improved to the point that natural spawning replaces stocking, will there be a net gain or drain of P to the system? (*iv*) What is the contribution of P from spawned eggs versus adults? (*v*) How will changes in egg–smolt and marine survival influence the P budget? Output was expressed as the median and range of values across the 3 years of data. We were particularly interested in the relationships of these variables to the threshold of zero net P flux, the point at which salmon become a net gain or drain on the system. To make this assessment, we determined whether the range of P flux for a given scenario was negative (range below and not overlapping the zero threshold), positive (range above and not overlapping the zero threshold), or zero (range overlapping the zero threshold).

Fig. 2. Relationship between adult passage and Net P flux (g·year^{-1}) from 1998 to 2000; egg stocking, smolt outmigration, and adult return levels are at five different adult P retention levels. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.



Results

P transport with low adult passage

Under conditions of zero adult return, as occurs in stocked systems above impassable barriers and has historically occurred in the River Bran, a loss of 316–553 g P·year^{-1} would result (Fig. 2). This deficit is the balance of 290–550 g P introduced as stocked eggs and 706–865 g P lost as smolts. Under current conditions of low (7.5%) passage (Gowans et al. 2003), Atlantic salmon result in a net drain on P from the River Bran (Fig. 2). P contained in outmigrating smolts exceeds that of adult and egg inputs under all scenarios. The magnitude of this loss depends on what proportion of salmon adult P is retained within the system, but this effect was relatively small, ranging from a loss of 284–502 g P·year^{-1} under zero adult P retention to a loss of 140–317 g P·year^{-1},with retention of 60% of adult P. At the upstream passage rates recorded in 1997, a drain of ~100 g P·year^{-1} would result even if all (100%) adult P was retained in the system.

P transport under increased rates of adult passage

Increased passage of adults to spawning grounds strongly influenced predicted net P flux. In contrast with the low-passage scenarios, resultant P fluxes at higher passage rates were greatly affected by differences in adult P retention (Fig. 2). For example, at 20% passage, P input could balance P outputs, but only at the highest level (60%) of adult P retention (Fig. 2). At 75% passage rates, budgets were balanced (zero net flux) at relatively low levels (10% retention rates) and resulted in net positive fluxes of >1 kg P with high (>20%) retention. Given current average sex ratio and fecundity in the River Bran (Table 1), meeting spawning targets for egg deposition would require between 187 and 354 adults returning to the spawning grounds, which corresponds to ~50% passage. These returns resulted in large between-year differences in net P flux (Fig. 3). In general, P losses by smolts were balanced by adult and egg contributions at 10%–20% adult P retention and were predicted to result in high net P imports of up to 2 kg P·year^{-1} at higher retention percentages (Fig. 3).

Contribution of eggs compared with adults

Budget predictions indicated that P associated with spawned eggs could be a major component of total P flux under some scenarios. At current low passage rates (7.5% of returning adults), P from eggs exceeded P from adults at all retention levels. At higher passage rates (>20%), P contribution of eggs exceeded P contributions of adults until retention levels exceeded 20% (Fig. 4), and at high retention and passage levels, adult contributions were two- to four-fold greater than egg P. Importantly, egg contributions alone were not sufficient to balance the P budget even at the highest levels of in-river passage (Fig. 2; zero retention line) under current smolt and marine survival rates.

Effects of changes in marine and freshwater survival

Changes in marine survival had strong effects on P flux via migratory salmon. Increasing survival from current levels of 2% of outmigrating smolts to 7%, which was historically exhibited by many salmon-rearing streams in eastern Scotland, greatly increased the import of P to the system. This high marine survival scenario resulted in a balanced P budget even at current low passage (7.5%), given a high (60%) retention rate (Fig. 5). Increasing passage rates to 75% of returning adults resulted in predicted positive net P flux with retention rates as low as 10% and net P imports of 2–4 kg at high retention levels (Fig. 5). Reducing marine survival to 0.5% resulted in negative P flux at all retention levels, even at high (75%) passage (Fig. 6).

Changes in egg–smolt survival also strongly affected P flux. In general, at current marine survival rates, reduced egg–smolt survival reduced the overall scope of both negative and positive potential transport, as fewer smolts were predicted to transport P from the system, yielding fewer adults to transport it back (Figs. 7 and 8). Reduction in egg–smolt survival from current levels of ~2% to 0.5% reduced the overall scope of P transport and resulted in small (<300 g), positive net P flux under current low passage at all retention levels. In contrast, doubling egg–smolt survival to 4% of deposited eggs strongly increases the scope of P transport, with potential losses (under low passage and retention scenarios) and potential gains (under high passage and retention scenarios) of >1 kg P·year^{-1}.

Discussion

Our analysis provides an effective framework for bracketing the conditions under which salmon may transport nutrients to and from rearing streams. This understanding is an essential element in moving towards an ecosystem-level approach to salmon research, conservation, and management (Naiman et al. 2002). We clearly map out the way in which aspects of Atlantic salmon life history interact to determine the magnitude and direction of nutrient flux. While this study is focused on specific conditions in the River Bran, our approach is amenable to modification and should be widely applicable to a range of systems and situations.

We found that under current conditions of smolt production, marine survival, and in-river passage, which have been relatively stable over the past several years, Atlantic salmon currently are a net drain on the P budget of the River Bran, with smolts consistently exporting more P than is predicted to be returned from eggs and adults. This is in contrast with the findings of both Lyle and Elliott (1998) and Jonsson and Jonsson (2003) of positive net import of nutrients via migratory Atlantic salmon. Our prediction of net export is robust

Fig. 3. Relationship between adult P retention and Net P flux (g·year^{-1}) from 1998–2000; egg stocking, smolt outmigration, and adult return levels are at spawning target adult passage levels. Points represent median values over the 3 data collection years; error bars indicate the range of values.

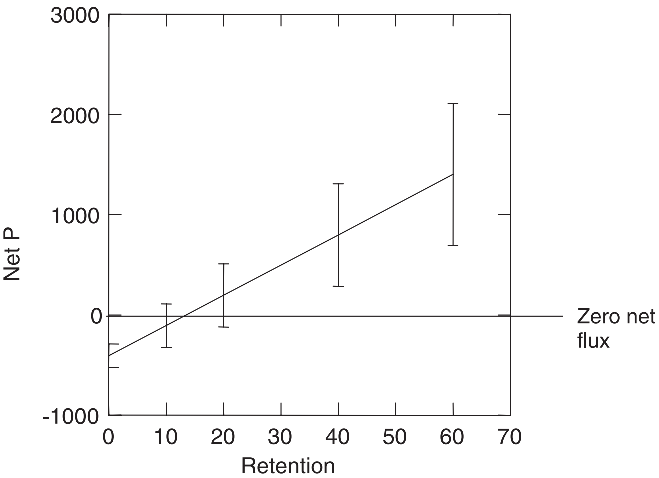


Fig. 4. Relationship between adult passage and the ratio of adult- to egg-derived P from 1998–2000; egg stocking, smolt outmigration, and adult return levels are at four different adult P retention levels. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.

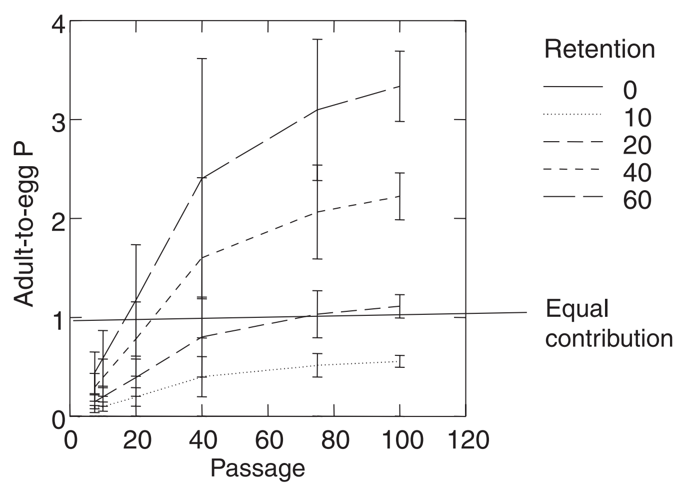


Fig. 5. The effects of marine survival (proportion of outmigrating smolts returning to the river) on net P flux at four different adult P retention levels under the current passage level of 7.5%. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.

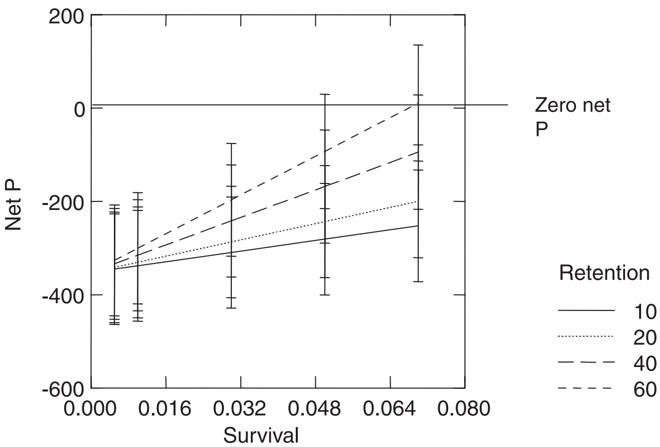


Fig. 6. Effect of marine survival (proportion of outmigrating smolts returning to the river) on net P flux at four different adult P retention levels under an increased passage level of 75%. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.

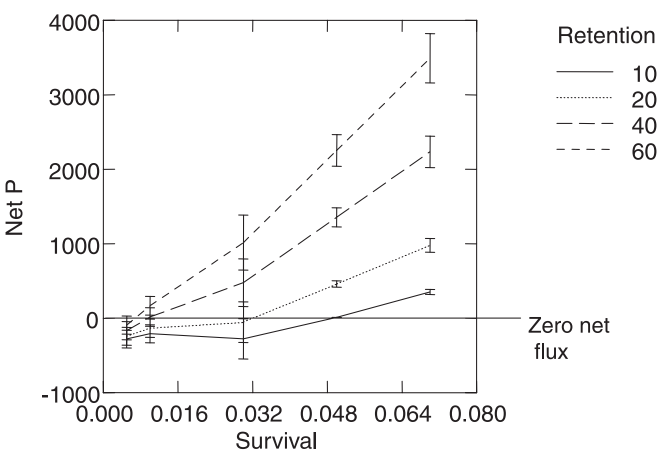


Fig. 7. Effect of smolt survival on net P flux at four different adult P retention levels under the current passage level of 7.5%. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.

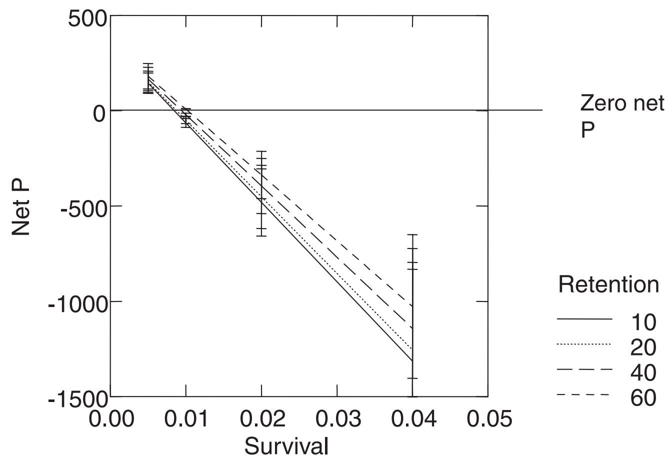
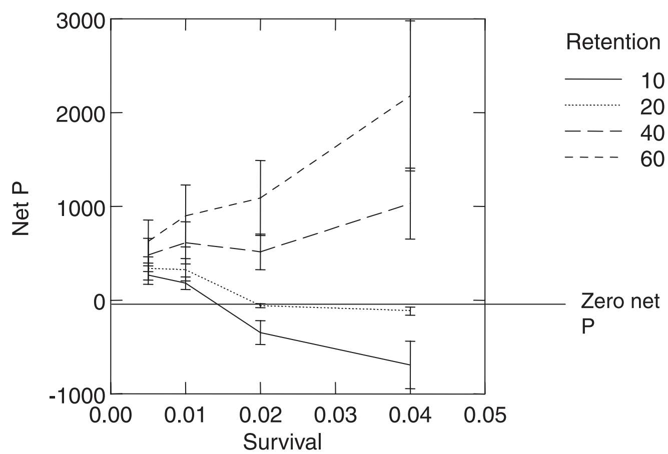


Fig. 8. Effect of smolt survival on net P flux at four different adult P retention levels under an increased passage level of 75%. Adult passage is the percentage of adults returning to the lower River Bran that successfully access spawning grounds in the upper river. Points represent median values over the 3 data collection years; error bars indicate the range of values.



to the major element of budget uncertainty, retention of adult P. As some studies have shown that overyearling salmon parr leave upstream spawning areas a year or more before smolt migration (Meister 1962; Riddell and Leggett 1981; McCormick et al. 1998), net export may be even greater than we predict. For example, in the Girnock Burn in northeastern Scotland, Youngson et al. (1994) found that up to 30% of overyearling parr moved downstream in the autumn.

Our analysis indicates that net loss of P via migratory salmon in the River Bran is primarily the result of constraints on the ability of adults to reach spawning grounds. Increasing access to spawning grounds (e.g., by increasing the effectiveness of bypass lifts on dams, a process that is currently underway on the River Bran) to the levels observed in rivers lacking barriers to passage (in which there is an approximately 81% survival to spawning; A. Gowans, Environment Agency, Ghyll Mount, Gillian Way, Penrith 40 Business Park, Penrith, Cumbria CA11 9BP, UK, personal communication) would likely result in at least a balanced P budget and quite probably a net gain of P to the system. The probability of net import is reinforced by our finding that adult passage at replacement levels (adequate to achieve spawning targets) produced positive P flux under most retention scenarios. Therefore, in conjunction with the two previous studies on wild populations (Lyle and Elliott 1998; Jonsson and Jonsson 2003), our results indicate that self-sustaining populations of migratory Atlantic salmon are net importers of marine-derived nutrients.

Although we predict that improved passage will improve the P budget of the River Bran, retention of adult-derived P has had a very strong effect on the magnitude and direction of P flux. This sensitivity points to a major gap in our understanding of the role of Atlantic salmon in the transport of P to and from rearing areas. While marine-derived P from salmon eggs could equal or exceed adult-derived P under some conditions, it was not sufficient to counter current smolt losses, underscoring the need to accurately assess adult retention. In their analysis of P budgets across several English rivers, Lyle and Elliott (1998) found that on average 60% of the P contained in returning adult salmon was retained in the river system, largely because of in-river mortality of kelts (adult salmon after they have spawned). This high level of retention was an important factor in their finding of a net positive flux of marine-derived nutrients, including P, in their study rivers. However, this level of carcass P retention is almost certainly an overestimate of retention in upland spawning and rearing sections of river systems. Many kelts may not die until they are in the lower sections of rivers, and of those that do die in upstream rearing sections, many of their carcasses, as well as particulate and dissolved material derived from these carcasses, will be transported significant distances downstream of rearing areas. Previous studies on Pacific salmon have shown that retention of carcasses can be significantly influenced by the hydrologic regime and habitat structure of spawning reaches and that mechanisms of retention and movement are complex (Cederholm et al. 2000). In contrast, Jonsson and Jonsson (2003) found that in the River Imsa in-river mortality was low, and carcasses were a relatively minor source of adult-derived P. Instead, most adult-derived P was contributed by metabolic losses from the breakdown of body tissues while adults were on the spawning grounds. While these losses are somewhat straightforward to measure in a small coastal river such as the River Imsa, they are problematic in larger systems, where losses can occur before adults reach the spawning grounds, and processes such as advection can transport nutrients lost on the spawning grounds to lower river reaches. In strongly P-limited systems, however, dissolved P can be rapidly absorbed by benthic biofilms and taken up by streamside vegetation, providing a mechanism for local retention (Naiman et al. 2002). Studies in which outmigration, mortality, metabolism, and carcass retention of Atlantic salmon can be assessed at a finer spatial scale than has been accomplished previously are therefore critical in improving our ability to predict the role of salmon in nutrient dynamics.

At present, smolt and adult production on the River Bran is supported by stocking. We found that stocking strategy has an important influence on potential P flux in the system. Most importantly, continuing to stock and produce smolts from a system where adults lack access to spawning areas ensures a net loss of P from the system via migratory salmon. However, this P drain should be self-regulating to some extent. If smolt production is positively associated with P availability, then P loss should eventually result in lower smolt production and a smaller yearly loss of P from the system, so that overall salmon production and P flux should stabilize at some lower level. For the River Bran, our results indicate that this production “floor” may occur at an egg–smolt survival of ~1%, less than half of current values, representing a major loss of productive capacity.

As we do not have a full P budget for the River Bran, it is difficult to evaluate the importance of P flux via migratory Atlantic salmon relative to total P transport in this system. However, the River Bran is similar in some important respects to the River Imsa, where total P fluxes have been measured (Jonsson and Jonsson 2003). Both systems have similar P concentrations in streamwater ($<5\ \mu g \cdot L^{-1}$) and similar overall fluxes of salmon-derived P (several kg) at “natural” passage and retention levels. While the River Bran is a considerably larger system in total, the salmon-rearing zone of the River Bran has a similar drainage area as that of the River Imsa. If these similarities translate to similar percentage transport, this finding provides support for a potentially significant role of salmon in oligotrophic river systems.

Determining the dynamics and thresholds involved in this process point to knowledge gaps that must be bridged to understand the interaction between migratory salmon and nutrient dynamics more fully. One key factor is the relationship between salmonid production and system trophic status. Plante and Downing (1993), using data from a large number of studies in lake systems, developed a quantitative relationship between P concentration in lakes and salmonine production. While several studies in rivers and streams indicate positive responses to nutrient addition (Johnston et al. 1990; Deegan and Peterson 1992; Griswold et al. 2003), a similar quantitative relationship between nutrient status and salmonid production in riverine systems has not been established. In addition, while we and others (Lyle and Elliott 1998) have investigated the amount of nutrients potentially transported by migratory Atlantic salmon, factors influencing the actual availability of these nutrients may ultimately determine their influence on stream ecosystems and fish production. Investigations on the pathways by which nutrients derived from Pacific salmon enter river and riparian food webs have revealed complex interactions between biological and physical factors occurring on a wide range of temporal and spatial scales (Willson and Halupka 1995; Cederholm et al. 2000). At present, these pathways in Atlantic salmon streams are essentially unknown. Future work should simultaneously apply our budget framework to other systems with appropriate and adequate data and focus on empirical investigations designed to refine parameter estimates and fill knowledge gaps.

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