Effects of the abundance of spawning sockeye salmon (Oncorhynchus nerka) on nutrients and algal biomass in forested streams

N.T. Johnston, E.A. MacIsaac, P.J. Tschaplinski, and K.J. Hall

Abstract: We used natural variation in sockeye salmon (Oncorhynchus nerka) spawner biomass among sites and years in three undisturbed, forested watersheds in interior British Columbia to test the hypotheses that salmon were a major source of particulate organic matter inputs to the streams and that carcass biomass determined stream-water nutrient concentrations and epilithic algal production. Sockeye carcasses were retained at the spawning sites, primarily (75–80%) by large woody debris (LWD) or pools formed by LWD. The abundance and distribution of sockeye salmon determined stream-water nutrient concentrations and epilithic chlorophyll a concentrations during late summer and early fall when most primary production occurred in the oligotrophic streams. Periphyton accrual rates were elevated at sites with high salmon biomass. Peak chlorophyll a concentration increased with increasing carcass biomass per unit discharge above a threshold value to reach maxima 10-fold greater than ambient levels. Epilithic algae were dominated by a few common, large diatom taxa. Salmon carcasses were the dominant source of particulate organic carbon in low gradient stream reaches. Nutrient budget modeling indicated that most of the salmon-origin nutrients were exported from the spawning streams or removed to the terrestrial ecosystem; diffuse impacts may extend over a much larger area than simply the sites used for spawning.

Résumé : L’étude de la variation naturelle d’un site à l’autre et d’une année à l’autre de la biomasse des reproducteurs chez le saumon rouge (Oncorhynchus nerka) dans trois petits bassins versants boisés et non perturbés de la région intérieure de la Colombie-Britannique nous a servi à vérifier les hypothèses selon lesquelles les saumons constituent un apport substantiel de matière organique partielle dans les cours d’eau et la biomasse des carcasses est responsable des concentrations de nutriments dans l’eau et de la production des algues épilithiques. Les carcasses de saumons rouges sont retenues dans les frayères principalement (75–80 %) par la présence de débris de bois de grande taille (LWD) ou dans les cuvettes formées par les LWD. L’abondance et la répartition des saumons rouges expliquent les concentrations de nutriments dans l’eau et les concentrations de chlorophylle a à la fin de l’été et au début de l’automne au moment où la plus grande partie de la production primaire se fait dans ces cours d’eau oligotrophes. Les taux d’accumulation du périphyton sont élevés au sites de forte biomasse de saumons. Les concentrations maximales de chlorophylle a augmentent en fonction de la biomasse des carcasses par unité de débit au-dessus d’un seuil, pour atteindre des maximums 10 fois plus élevés que les concentrations ambiantes. Les algues épilithiques sont dominées par quelques espèces communes de diatomées de grande taille. Les carcasses de saumons constituent la source principale de carbone organique partielle dans les cours d’eau à pente faible. Des modèles de bilans de nutriments indiquent que les substances nutritives qui proviennent des saumons sont en majorité exportées en aval des cours d’eau de fraye ou incorporées dans les écosystèmes terrestres; il peut y avoir des impacts diffus sur une surface beaucoup plus étendue que celle des seuls sites de fraye.

[Traduit par la Rédaction]

Introduction

The spawning and death of adult anadromous Pacific salmon (Oncorhynchus spp.) may influence the productivity of oligotrophic freshwaters (Cederholm et al. 1999; Gresh et al. 2000; Gende et al. 2002). Spawning salmon impose two types of ecological impacts on freshwater ecosystems. First, redd construction induces bed-load transport and alters substrate characteristics in spawning areas (Kondolf et al. 1993; Gottesfeld 1998). The bioturbation and displacement of sediments during spawning may reduce the standing crop of benthic algae and invertebrates (Peterson and Foote 2000;
Minakawa and Gara 2003). Second, spawners return large amounts of high-quality organic matter to freshwaters (Gresh et al. 2000). This material is available to the biota through direct feeding on carcasses and eggs (Bilby et al. 1998) or decomposition and uptake by bacteria and algae (Richey et al. 1975; Wipfli et al. 1998, 1999). Comparisons between sites with and without salmon spawners in natural streams generally show higher levels of inorganic nutrients (Brickell and Goering 1972; Richey et al. 1975; Sugai and Burrell 1984), periphyton biomass (Richey et al. 1975; Schuld and Hershey 1995), and benthic insect abundance (Schuld and Hershey 1995) at salmon sites. Carcass additions to mesocosms and streams also usually produce higher biomass of periphyton, insects, and fish at sites receiving carcasses (Schuld and Hershey 1995; Wipfli et al. 1998; Bilby et al. 1998). The incremental effects of salmon abundance on productivity are uncertain, however (Gende et al. 2002). Increases in productivity may cease at moderate salmon abundance. In carcass loading experiments in mesocosms, Wipfli et al. (1999) observed that biofilm biomass and macroinvertebrate densities did not increase above the lowest loading rate. Understanding how the productivity of natural ecosystems varies with salmon abundance may aid in establishing escapement goals that maintain ecosystem productivity (Gende et al. 2002).

The importance of spawning salmon in determining the productivity of freshwaters will vary with factors such as the magnitude, timing, and distribution of spawning runs, carcass retention capacity, nutrient storage capacity, water temperature and discharge, background inputs of nutrients and allochthonous organic matter, and the composition of the biological community (Wipfli et al. 1999). Few studies document directly the effects of variations in spawning abundance on natural freshwater ecosystems or provide quantitative information on the processes that govern the effects. We used natural variation in the abundance of sockeye (O. nerka) spawners among sites and among years in three adjacent streams in north-central British Columbia to determine the effects of spawning abundance on stream productivity. We hypothesized that water concentrations of inorganic nutrients and the biomass of epilithic algae would increase with increasing spawning abundance. We also hypothesized that increased nutrient concentrations or altered nutrient ratios might change the composition of the algal community (Borchardt 1996). To assess the relative importance of salmon as a particular carbon source in undisturbed forested stream ecosystems, we measured inputs of salmon and leaf litter and estimated epilithon gross primary productivity. We summarized the effects of salmon abundance on stream nutrient concentrations in a simple empirical process model from which we inferred the fate of salmon-derived nutrients.

**Methods**

**Study sites**

The study sites were forested fourth-order streams (Bivouac, Gluskie, and Forfar creeks) that flow into Takla Lake or Middle River (Fraser River drainage) near 55°02'N by 125°30'W, about 1100 km upstream from the ocean (Fig. 1). Descriptions of the streams, their catchments, and the adjoining riparian forest of mature subalpine fir (Abies lasio-carpa) and hybrid white spruce (Picea glauca × engelmannii) are given in Macdonald et al. (1992) and Hogan et al. (1997). The catchments are physically similar (Hogan et al. 1997) and largely undisturbed, with areas of 43.1, 38.4, and 52.2 km² and main channel lengths of 17.1, 15.3, and 26.2 km for Bivouac, Forfar, and Gluskie creeks, respectively. Sockeye salmon spawn in the alluvial lower 2–5 km of the streams, beginning in early August.

We measured responses to salmon abundance in two or three reaches within each stream (Fig. 1). Reaches were about 10 bankfull channel widths in length and were stratified by channel morphology and planimetric form (Hogan et al. 1997); all reaches within a stratum (i.e., B1, F1, G1; B2, G2, F2; G3, F3) had similar channel morphology, gradient, width, sediment texture, and pool–riffle characteristics (Table 1). All reaches contained large quantities of large woody debris (LWD). Within a stream, relative densities of spawners were greatest at the lowermost reaches and declined upstream (Fig. 2).

**Organic matter inputs**

**Salmon inputs**

We determined inputs of salmon carcasses to the study reaches in 1996, 1997, and 1998. The numbers, timing, and sex ratios of sockeye entering Forfar and Gluskie creeks were obtained by complete enumeration at counting fences operated near the stream mouth by stock assessment personnel from Fisheries and Oceans Canada between late July and the end of August. The duration of life of spawners was measured by tagging individuals at the fences and recovering carcasses in foot surveys done at 3-day intervals. The escapement to Bivouac Creek was estimated from foot surveys at 3-day intervals over the spawning period as the sum of the peak live count plus the cumulative dead count to that date, scaled by the average of carcass recovery rates from similar surveys on Forfar and Gluskie creeks; the sex ratio was determined from the total carcass count.

We determined the instream distribution of spawners by counting live fish and accumulated carcasses in 30 m segments along the stream at about 5-day intervals (Tschaplinski 1994) throughout the spawning period. We determined the number of carcasses on the study reaches from the last of the instream distribution surveys, when few adults remained alive, or from additional counts of carcasses on the reaches shortly after the spawning period. We estimated the average wet weight of carcasses in 1996 and 1997 by weighing and measuring 20–30 fresh carcasses per stream and applying the pooled, sex-specific length–weight regressions for the year to larger samples of fish lengths that were measured at the fences. In 1998, we used the overall regression from the preceding years to estimate average carcass weights from measured lengths. We measured the average percent dry weight (% DW) and proximate composition of subsamples (see below) of 11 fresh carcasses, which were weighed and frozen in the field and later dried to constant weight at 60 °C. To express carcass inputs as areal values, we determined the bankfull and wetted channel areas at each reach from annual measurements at monumented cross sections (Hogan et al. 1997). Areal inputs were adjusted for the measured observer efficiency, the ratio of carcasses recovered to the known escapement for the stream. Carcass recoveries
ranged between 28.4% and 56.7% of known spawner numbers.

On Gluskie Creek, carcasses recovered by stock assessment personnel were “dead-pitched”, i.e., removed to the top of the bank or high, lateral gravel bars to avoid double counting. On Bivouac Creek, carcasses were removed to low, mid-channel bars within the wetted channel. Carcasses were not dead-pitched at Forfar Creek.

**Riparian inputs**

We used litter traps to measure inputs of leaf litter and small coarse particulate organic matter from the riparian vegetation to each reach between mid-July and late October 1996 and 1997. At each reach, we placed 5–8 plastic tubs (0.10 m² each) within the bankfull channel at known distances from the bank. Litter traps were emptied biweekly or monthly, depending on inputs. Material was frozen and then later sorted, dried at 60 °C, and weighed. Ash-free dry weights were determined as the weight loss upon combustion at 500 °C for 4 h. We assumed that carbon (C) comprised 50% of the ash-free dry weight (Webster and Meyers 1997). Because litter inputs varied with distance from the bank, we fitted the measured inputs to a common declining exponential function of bank distance and estimated average inputs to each reach by integrating this function across the channel width (Johnston et al. 2003).

**Algal inputs**

We estimated gross primary production by epilithic algae between mid-July and the end of October from periodic
measurements of chlorophyll $a$ (Chl $a$), using an empirical regression model (Morin et al. 1999). We took duplicate samples of epilithic algae at monthly intervals by scrubbing the biofilm from the upper surfaces of natural gravel or cobble from riffle–glide areas of each reach. We used linear interpolation to estimate Chl $a$ standing crop between sampling dates. Each sample comprised 48 cm$^2$ and was pooled from six separate stones collected from randomly chosen sites along the reach. Stones were collected at similar water depths and flows at each reach. Known volumes of scrubate were vacuum-filtered through 0.47-µm pore size cellulose acetate filters, placed in opaque containers, and frozen. Chl $a$ was measured spectrophotometrically after acetone extraction.

Carcass retention, processing, and decomposition

In 1997, we determined carcass retention elements and measured the processing rate of carcasses on the F1, F2, and B1 reaches by enumerating carcasses at approximately 10-day intervals from the end of spawning onward. “Processing” rates here represent the combined effect of decomposition, fragmentation, transport, and removal by scavengers. We categorized retention elements as LWD, pools, other channel features, and riparian vegetation. LWD included both individual pieces and debris jams. Pools were deep scour pools formed adjacent to or under debris jams. Other channel features were shallow channel margins, bar tops and edges, riffle crests, and stone lines. Riparian vegetation comprised live branches, roots, and small woody debris. We estimated carcass processing rates from an exponential loss model:

\[ \text{Carcasses}_t = A e^{-k_p t} \]

where \( \text{Carcasses}_t \) is the number of carcasses remaining on the reach, \( A \) is the initial number of carcasses, \( k_p \) is the daily loss rate, and \( t \) is the elapsed time in days. Parameters were estimated directly by nonlinear least squares with SYSTAT 10 (SPSS Inc., Chicago, Ill.). We measured nutrient release from decomposing carcasses in 1997 by placing 20 fresh carcasses in individual coarse-mesh bags in a shallow glide area of Gluskie Creek and removing groups of 2–3 fish at known time intervals between 3 and 65 days. We sampled 11 fresh carcasses to establish the initial proximate composition. On retrieval, we weighed the carcass and removed a representative cross-sectional slice (Minshall et al. 1991) comprising the central third of the body. The section was weighed and frozen in the field and then later dried to constant weight at 60 °C and pulverized and the carbon, nitrogen (N), and phosphorus (P) contents were determined. Total C and total N were measured with a CEC 240XA elemental analyzer (Control Equipment Corp., Cazenovia, N.Y.) on known-volume subsamples after homogenizing the sample in deionized distilled water. Total P was determined on known-volume subsamples by the ascorbic acid–molybdate blue method (Stainton et al. 1977) after a 24-h extraction in 1:1 by volume sulphuric acid and nitric acid at 90 °C. We fit single-pool (see above) or two-pool exponential loss models to the percentage of the initial nutrient content that remained after a given time \( t \). For the two-pool model, the nutrient in the carcass was partitioned into labile (e.g., tissue) and refractory (e.g., bone) pools with different release rates, \( k_1 \) and \( k_2 \):

\[ \text{Percent Remaining} = (\text{Percent Labile}) e^{-k_1 t} + (100 - \text{Percent Labile}) e^{-k_2 t} \]

We did not use data from day 65 in the estimation of the P loss rate because many bones were missing from these samples. Loss models for carbon, nitrogen, and dry weight were unaffected by the omission of the day 65 data, but the P loss model was altered because bones contain much of the carcass P.
Water chemistry, temperature, and discharge

Water samples were taken from each reach at varying times between July and late October each year. Grab samples were collected in acid-cleaned glass bottles (for nutrients) or polyethylene bottles (for other solutes) from mid-column at well-mixed areas at the lower boundary of a reach, held on ice in opaque coolers, and frozen. They were later analyzed at Environment Canada’s Pacific Environmental Science Centre laboratory following American Public Health Association (APHA 1989) methods. Soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), and total phosphorus (TP) were determined by the automated ascorbic acid method. Nitrite plus nitrate nitrogen (NO$_3$-N) was measured by the automated cadmium reduction method. Total ammonia (NH$_4$-N) was determined by the automated phenate method. Dissolved inorganic nitrogen (DIN) was calculated as NO$_3$-N plus NH$_4$-N. Total Kjeldahl nitrogen was measured by colorimetric determination following digestion, and total nitrogen (TN) was calculated. Detection limits for SRP, TDP, and TP were 1, 2, and 2 µg P·L$^{-1}$, respectively; those for NH$_4$-N and NO$_3$-N were 5 µg N·L$^{-1}$ and 2 µg N·L$^{-1}$, respectively.

Water temperature and discharge were recorded continuously near the lower boundary of the middle reaches (Cheong et al. 1995; Andersen and Macdonald 1997).

Epilithon

Known volume subsamples of epilithon from our Chl $a$ determinations were preserved in Lugol’s solution. The algae were later identified, enumerated, and measured at 500x phase-contrast magnification. A minimum of 100 cells of the dominant taxon and 300 cells in total were counted for each sample. We calculated algal biovolumes from simple geometric shapes using the dimensions measured from 10 cells of each taxon at each site and date.

We determined the effects of salmon abundance on periphyton accrual in 1997 by monitoring the postspawning Chl $a$ concentration on groups of unglazed ceramic tiles (25 cm$^2$ each) attached to concrete bricks placed in shallow riffle–pool areas at the lower boundary of a reach, held on ice in opaque coolers, and frozen. They were later analyzed at Environment Canada’s Pacific Environmental Science Centre laboratory following American Public Health Association (APHA 1989) methods. Soluble reactive phosphorus (SRP), total dissolved phosphorus (TDP), and total phosphorus (TP) were determined by the automated ascorbic acid method. Nitrite plus nitrate nitrogen (NO$_3$-N) was measured by the automated cadmium reduction method. Total ammonia (NH$_4$-N) was determined by the automated phenate method. Dissolved inorganic nitrogen (DIN) was calculated as NO$_3$-N plus NH$_4$-N. Total Kjeldahl nitrogen was measured by colorimetric determination following digestion, and total nitrogen (TN) was calculated. Detection limits for SRP, TDP, and TP were 1, 2, and 2 µg P·L$^{-1}$, respectively; those for NH$_4$-N and NO$_3$-N were 5 µg N·L$^{-1}$ and 2 µg N·L$^{-1}$, respectively.

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Fate of salmon-origin nutrients

We inferred the fate of salmon-derived nutrients (TN and TP) using a mass balance model, which partitioned salmon-origin nutrient inputs into three components: waterborne export, removal to the terrestrial ecosystem, or retention within the spawning stream. We discuss later why a simple input–output model is appropriate to characterize nutrient dynamics in these streams. We used maximum likelihood (ML) to estimate model parameters that best fitted the observed time series of stream-water nutrient concentrations under a specified error structure. We used the Akaike information criterion (Hilborn and Mangel 1997) to select a removal model.

The stream-water concentration of a nutrient at a given time originated from several sources: a “background” concentration from the catchment, excretion by live spawners, nutrient release from decomposing carcasses, and nutrient release from live or dead reproductive products (eggs or sperm). Salmon-derived inputs depended on the current biomass of live spawners and carcasses, which were reduced by the removal of salmon from the stream by scavengers or predators or through consumption by stream biota. A portion of the salmon-derived material was refractory and thus unavailable for release. Labile nutrients released into the water by the remaining spawners or carcasses may be sequestered by instream retention processes such as uptake by benthic algae, adsorption to sediments, or storage in hyporheic nutrient pools. The model tracked these processes at daily time steps throughout the period of spawning and decomposition to estimate a stream-water concentration as the sum of the current background concentration plus the net daily release of salmon-derived nutrient divided by the daily discharge. The quantity of salmon-origin nutrients accumulated in the various nutrient pools over the period for the maximum-likelihood model defined the fate of salmon-origin nutrients in these streams. Export was the sum of the daily nutrient concentration × daily discharge, removal was the sum of the model-estimated daily removals, and retention at the end of the period was the sum of remaining carcass and egg inputs plus the nutrient content of the epilithon.

We modeled the expected nutrient concentration at any point as the superposition of net releases from all spawners and carcasses upstream of the point. Because of their physical structure, these streams were well mixed over very short spatial and temporal scales. The riffle–pool morphology with short recurrence intervals and large quantities of LWD produced many zones of turbulent mixing, and the relatively high average water velocities resulted in short transit times over which nutrient releases could be considered constant. Longitudinal dispersion during transit was expected to be high, and nutrient dynamics could be approximated by that of a well-mixed reactor, with no explicit consideration of spatial structure.

We calculated nutrient budgets at the lowest point in the catchment for which we had measured nutrient concentrations through time, usually the F1 or G1 reaches, which were just upstream of the counting fences. We did not use data from Bivouac Creek where salmon inputs were estimated rather than enumerated. We could not apply the model to the TN time series at the Gluskie Creek G1 site in 1998 because there was only a single observation during the period of carcass decomposition. We ignored certain retention processes (consumption by instream biota, adsorption to sediments, hyporheic storage) because we obtained good estimates of known exports and removals (i.e., the known dead pitch) for Gluskie Creek without including them.

We assumed an observation model with a lognormal error structure. If Conc$_i$ is a predicted stream-water concentration and $x_i$ is the corresponding observation, then the observation model is

$$x_i = \text{Conc}_i e^{\varepsilon_i}$$

where $\varepsilon_i$ is the observation error, and the $\varepsilon_i$ are normally distributed with a mean of 0 and a standard deviation of $\sigma$. The likelihood of the data, given the parameters, is
\[ L(x|\text{Conc}) = \prod_{i} \frac{1}{\sigma \sqrt{2\pi}} \frac{1}{x_i} e^{-\frac{(\ln(x_i) - \ln(\text{Conc}_i))^2}{2\sigma^2}} \]

The best-fit parameters were estimated by minimizing the negative log-likelihood:

\[ -\ln(L) = \sum \frac{(\ln(x_i) - \ln(\text{Conc}_i))^2}{2\sigma^2} + \text{Constant} \]

The predicted nutrient concentration is

\[ \text{Conc}_i = \frac{\text{Excret}_i + \text{RCarc}_i + \text{REgg}_i + \text{RS}_i - \text{EP}_i}{D_i} + B_i \]

where \( \text{Excret}_i \) is nutrient excretion by live spawners on the date of the \( i \)th observation, \( \text{RCarc}_i \) is the release of labile nutrient from carcasses, \( \text{REgg}_i \) is the release from dead eggs, \( \text{RS}_i \) is the release in sperm, \( \text{EP}_i \) is uptake by epilithon, \( D_i \) is daily discharge, and \( B_i \) is the non-salmon-origin background concentration. Because baseflow discharge varied little over the period of interest (Fig. 3), \( B_i \) was estimated by linear interpolation between measurements before and after the period of salmon spawning and decomposition.

Let \( N_{sp} \) be the total number of spawners that pass upstream of the counting fence, and let \( A(t) \) be the proportion of the spawners that pass upstream on day \( t \). Let \( pd(j) \) be the proportion of spawners that die \( j \) days after passing the fence. Note that \( A(t) \) and \( pd(j) \) were measured directly for the fenced streams. Then the number of spawners alive on day \( t \) from all previous arrivals is

\[ \text{Live}(t) = \sum_{i=t_0}^{t} N_{sp} A(i) \left\{ 1 - \sum_{\lambda=1}^{i} pd(\lambda - i) \right\} \]

where \( t_0 \) is the first day that spawners enter. Excretion by live spawners will be

\[ \text{Excret}(t) = \xi WT \sum_{i=t_0}^{t} N_{sp} A(i) \left\{ 1 - \sum_{\lambda=1}^{i} pd(\lambda - i) \right\} \]

where \( \xi \) is the excretion rate per unit weight per unit time, and WT is the average wet weight of a spawner:

\[ \text{WT} = P_{\text{male}} WT_{\text{male}} + P_{\text{female}} WT_{\text{female}} \]

where \( P_{\text{male}} \) is the proportion of males, \( WT_{\text{male}} \) is the average wet weight of a male spawner, etc. The excretion rate of N by non-feeding sockeye is 221 mg N·day\(^{-1}\)·kg\(^{-1}\) (Brett and Zala 1975). We could not find data on P excretion by spawning sockeye, but starved rainbow trout (Oncorhynchus mykiss) do not release P (Sugiura et al. 2000). We assumed a P excretion rate of zero.

The number of new deaths on day \( t \) from all previous arrival groups is

\[ \text{Carc}(t) = \sum_{i=t_0}^{t} N_{sp} A(i) pd(t - i) \]

Let the quantity of labile nutrient remaining on day \( t \) in a carcass that died on a prior day \( i \) be described (see Results) by

\[ \gamma e^{-k(t-i)} \]

where \( \gamma \) is the average labile nutrient content of a fresh carcass, and \( k \) is a constant. If we ignore the removal of carcasses for the moment, the quantity of labile nutrients, \( \text{Nutr}(t) \), remaining in carcasses on day \( t \) from all deaths before that date is

\[ \text{Nutr}(t) = \gamma N_{sp} \sum_{i=t_0}^{t} e^{-k(t-i)} \left\{ \sum_{\lambda=1}^{i} A(\lambda) pd(\lambda - i) \right\} \]

and nutrient release from the carcasses will be

\[ \text{RCarc}(t) = (1 - e^{-k}) \gamma N_{sp} \sum_{i=t_0}^{t} e^{-k(t-i)} \left\{ \sum_{\lambda=1}^{i} A(\lambda) pd(\lambda - i) \right\} \]

Decaying reproductive products (dead eggs, sperm) will release nutrients that may enter the stream-water pool. Nutrients in sperm will enter the stream-water nutrient pool immediately after males spawn. Eggs that are laid in the gravel and subsequently die will release nutrients at some loss rate, which we assume is the same as \( k \), the loss rate from carcasses. We assumed that eggs are laid on the same day that female spawners die. Because we know the mortality rate for eggs in the gravel in these streams (Cope and Macdonald 1998), we can calculate the quantities of nutrients stored in live eggs and dead eggs at time \( t \) and estimate the release of nutrients from the pool of nutrients in dead eggs on that date. We used recursion to obtain a general relation for the release of labile nutrients from dead eggs on a given date \( t \). Let \( \psi \) be the average quantity of nutrients laid by a spawner:

\[ \psi = P_{\text{female}} WT_{\text{female}} GSI_{\text{female}} P_{\text{effective}} \Phi \]

where \( P_{\text{female}} \) is the proportion of females in the escapement, \( WT_{\text{female}} \) is the average total weight of a female sockeye before spawning, \( GSI_{\text{female}} \) is the average ratio of ovary weight to total weight, \( P_{\text{effective}} \) is the average proportion of eggs that are successfully laid, and \( \Phi \) is the average quantity of nutrient per unit weight of eggs. Then the release of labile nutrients from dead eggs on day \( t \) is

\[ \text{REgg}(t) = (1 - e^{-m})(1 - e^{-m})\psi \sum_{\lambda=0}^{t-t_0} e^{-m}\sum_{i=t_0}^{t-\lambda} \text{Carc}(i)e^{-m(t-\lambda-i)} \]

where \( t_0 \) is here used as the first date of carcass inputs and \( m \) is the egg death rate defined by

\[ \text{Egg}(t + j) = \text{Egg}(t)e^{-mj} \]

where \( \text{Egg}(t + j) \) is the number of eggs alive on day \( t + j \) that were laid on day \( t \). The contribution of sperm to the water-borne nutrient pool is

\[ \text{RS}(t) = \omega \sum_{i=t_0}^{t} N_{sp} A(i) pd(t - i) \]

where

\[ \omega = P_{\text{male}} WT_{\text{male}} GSI_{\text{male}} P_{\text{effective}} \Phi \]

and \( GSI_{\text{male}} \) is the average ratio of unspawned testes weight to total weight, \( P_{\text{effective}} \) is the average proportion of the testes weight that is lost through spawning (i.e., sperm release), and \( \Phi \) is the nutrient content per unit weight of testes.
GSI_{female} was 0.147 and GSI_{male} was 0.0322 for the Forfar Creek stock (Idler and Clemens 1959). The average proportion of eggs laid (about 0.80) was measured separately for each stock for each year (T. Cone, Stock Assessment, Fisheries and Oceans Canada, 100 Annacis Parkway, Delta, BC V3M 2P3, personal communication); retained eggs are already included in the measured weights of spent fish. The proportion of N in eggs was estimated as 1/6.25 of the measured protein content (0.23 by wet weight; D. Patterson, Fisheries and Oceans Canada, School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC V5A 1S6, personal communication). The proportion of P in eggs was that measured for rainbow trout (O. mykiss) by Craik and Harvey (1984a, 1984b): 0.831% DW. The eggs laid on day $t$ died according to an exponential mortality model that produced 67% mortality by the end of September, this being the average of the mortalities measured for these stocks in 1993 and 1994 (Cope and Macdonald 1998).

The dead eggs present on any day released N and P at the rates measured for the labile pools in carcasses, and we assumed that this material moved into the bulk stream water. The N or P remaining in the dead eggs was carried forward to the next day. We ignored any excretion of N or P by live eggs. We assumed that the proportion of the testes wet weight that was lost between newly entered and spent males (0.68, calculated from Idler and Clemens 1959) represented sperm release, all of which entered the waterborne TN pool. We estimated the proportion of N in sperm from the proportion of protein in testes (0.20, from D. Patterson). We assumed that the ratio of P to N in sperm was the same as that in somatic tissue.

We estimated the net uptake of N and P by epilithic algae from the periodic measurements of Chl $a$ on the reaches and measurements of the nutrient content of epilithon. Changes in average epilithon biomass between days resulted in uptake or release of nutrients. We used linear interpolation be-

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**Fig. 3.** Mean daily discharge and temperature in (a and d) Bivouac Creek, (b and e) Forfar Creek, and (c and f) Gluskie Creek during the period of spawning and carcass decomposition in 1996 (dotted lines), 1997 (shaded lines), and 1998 (solid lines).
between measurement sites and between times to estimate an average epilithon concentration. We then estimated epilithon biomass from measurements of wetted widths and intersite distances. Concentrations of $N$ and $P$ per unit Chl $a$ were measured on scrubate from the surface of all gravel and cobble in triplicate 240-cm$^2$ circular plots, collected monthly between mid-July and mid-September 1998 at four sites (N:Chl $a$ = 42.2 by weight; P:Chl $a$ = 3.3, E.A. MacIsaac, unpublished data). Although the scrubate could contain non-algal organic matter, stable isotope data (N.T. Johnston, unpublished data) suggest that this was not the case.

Nutrient release from carcasses will differ from that predicted by eq. 13 because carcasses were removed from the stream to the terrestrial ecosystem by predators and scavengers. At our streams, black bears ($Ursus americanus$) and ravens ($Corvus corax$) were the most common large scavengers. Dead pitch by stock assessment personnel also removed carcasses from Gluskie Creek. We modelled the carcass removal process with two density-dependent functional relationships for bear predation on sockeye salmon, both of which have empirical support (Quinn et al. 2003). The first model removed a constant proportion $\rho$ of the carcasses each day:

$$\text{CRemoval}(t) = \rho \text{Carc}(t) = (1 - e^{-\rho t}) \text{Carc}(t)$$

where $\rho$ is an instantaneous carcass removal rate defined by

$$\rho = \frac{-\ln(\text{Carc}(t,i)/\text{Carc}(t))}{(i-t)}$$

where Carc($t$, $i$) is the number of carcasses remaining on day $i$ from those present on a previous day $t$. Under this model, the release of labile nutrients from carcasses on day $t$ becomes

$$\text{RCarc}(t) = (1 - e^{-\rho t}) \gamma N_{sp} \sum_{k=0}^{i-1} e^{-(\lambda + \rho)(t-i)} \left\{ \sum_{\lambda=0}^{i-1} A(\lambda) p d(i-\lambda) \right\}$$

The second carcass removal model was a curvilinear asymptotic function of carcass abundance:

$$\text{CRemoval}(t) = \frac{\alpha \text{Carc}(t)}{1 + \frac{\alpha \text{Carc}(t)}{\beta}}$$

where $\alpha$ was the rate of removal as carcass abundance approached zero, and $\beta$ was the asymptotic maximum number of carcasses removed daily. This model does not lead to a convenient analytical expression for nutrient release from remaining carcasses but is easily modeled numerically.

The parameter(s) of the removal model were estimated for each nutrient time series using ML methods. We used the Akaike information criterion to select the most parsimonious model. We estimated model parameters separately for the TN and TP time series at each site during the period from immediately before the first passage of spawners above the fence to the end of the period of carcass decomposition, roughly between days 200 and 275. Only the parameters of the removal model were estimated; all other relationships were determined empirically by direct measurement or from published data. We used the likelihood ratio method (Hilborn and Mangel 1997) to determine 95% confidence limits on the estimated carcass removal rates for the “best” model. We examined the effect of time-series bias on our estimates by simulation. We created 1000 nutrient data sets by using the ML parameter estimates as true values, adding lognormally distributed random error with the estimated standard deviation to the observations and then using the model to estimate the parameter values for each simulated data set. We then compared the median value of the distributions of parameter estimates with the known values to assess bias.

The proportions of salmon-origin nutrients that were exported, removed, or retained in the study streams were determined for the best-fit models by accumulating the daily losses to these processes. Approximate confidence limits for these proportions were obtained from the distributions obtained from the simulated data sets.

**Statistical analysis**

Our purpose was to determine the effects of sockeye spawner biomass on measures of productivity for the spawning streams. We expected stream-water nutrient concentrations at a site to vary directly with carcass biomass per unit discharge. By analogy with other nutrient-productivity relationships, we expected Chl $a$ to vary in a log–log relationship with carcass biomass per unit discharge. We assessed carcass effects on nutrient concentrations and productivity measures with Spearman rank correlation coefficients. We used the maxima of response variables over the post-spawning period of carcass decomposition as efficient summary statistics (Senn et al. 2000) for the temporal response to the pulse perturbation. We used the end-of-spawning carcass biomass upstream of the point divided by the average discharge over the period of spawning and decomposition as the independent variable. To account for the possible effects of spatial autocorrelation, we adjusted the degrees of freedom using the method of Dutilleul (1993) as implemented by Legendre (2000). We used the Euclidean distance between reaches as the spatial metric because we expected reaches at similar upstream locations in adjacent streams to be correlated. We used the sequential Bonferroni method (Rice 1989) to maintain a type-I error rate of $\alpha = 0.05$ in multiple comparisons of nutrient concentrations or algal biomass against salmon abundance, although this results in very conservative assessments of effects (Perneger 1998). We used the results of the process model to argue that significant correlations between salmon biomass and nutrient concentrations or Chl $a$ indicated causal relationships. We used piecewise linear regression on log-transformed data to describe the relationship between postspawning Chl $a$ maxima and salmon biomass per unit discharge.

We used a one-way repeated-measures analysis of variance (ANOVA) on log-transformed data to assess the effect of carcass biomass level on periphyton accrual on ceramic tiles.

**Results**

**Carbon inputs**

Live sockeye salmon were present in the streams from approximately day 210 to day 240 each year. They spawned
Table 2. Areal inputs of particulate organic carbon (g C·m\(^{-2}\)) to the study reaches, by source, between mid-July and the end of October, 1996–1998.

<table>
<thead>
<tr>
<th>Source</th>
<th>Bivouac Creek</th>
<th>Forfar Creek</th>
<th>Gluskie Creek</th>
</tr>
</thead>
<tbody>
<tr>
<td>Salmon carcasses</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1996 B1*</td>
<td>53.6</td>
<td>82.7</td>
<td>104.2</td>
</tr>
<tr>
<td>1996 B2</td>
<td>16.6</td>
<td>67.4</td>
<td>101.2</td>
</tr>
<tr>
<td>1997 F1</td>
<td>273.0</td>
<td>164.8</td>
<td>166.1</td>
</tr>
<tr>
<td>1997 F2</td>
<td>14.8</td>
<td>25.2</td>
<td>134.3</td>
</tr>
<tr>
<td>1997 F3</td>
<td>0.0</td>
<td>1.1</td>
<td>20.3</td>
</tr>
<tr>
<td>1998 G1</td>
<td>0.0</td>
<td>1.1</td>
<td>31.1</td>
</tr>
<tr>
<td>1998 G2</td>
<td>0.0</td>
<td>1.1</td>
<td>17.0</td>
</tr>
<tr>
<td>1998 G3</td>
<td>0.0</td>
<td>1.1</td>
<td>0.4</td>
</tr>
<tr>
<td>Riparian litter</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Deciduous leaves</td>
<td>45.7</td>
<td>21.5</td>
<td>20.7</td>
</tr>
<tr>
<td>Conifer needles</td>
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<td>3.8</td>
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<tr>
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<tr>
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<td>18.6</td>
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<tr>
<td>1998 G3</td>
<td>11.5</td>
<td>3.3</td>
<td>5.8</td>
</tr>
</tbody>
</table>

*Note: Salmon inputs are adjusted for measured observer efficiency. Litterfall inputs are averaged over 1996 and 1997 (see text). SOD, small organic debris.

under conditions of stable low discharge and seasonal high temperatures (Fig. 3). Mean daily discharge remained quite constant from the time of spawning until freeze-up but varied about threefold among years during the spawning period. Daily mean temperatures were stable throughout the period of spawning and initial carcass decomposition but declined rapidly after early September. Mean temperatures during August were about 8–11 °C in the 3 years.

Both the total number of spawners and their spatial distributions within the streams varied from year to year (Fig. 2). Spawning escapements in 1996, 1997, and 1998 were 1678, 2055, and 1325, respectively, for Bivouac Creek. The numbers of spawners upstream of the counting fences in 1996, 1997, and 1998 were 8381, 10270, and 956, respectively, for Forfar Creek and 8582, 11257, and 812, respectively, for Gluskie Creek. Even at similar overall abundances, there was considerable among-year variation in spawner abundance at specific locations within a stream (Fig. 2). Maximum salmon densities on the study reaches (unadjusted for observer efficiency) were about 0.8 fish·m\(^{-2}\) of bankfull channel or 1.3 fish·m\(^{-2}\) of wetted channel. Mean fish size also varied among years. Carcass wet weights for males were 2.705 kg (±0.037, N = 112) in 1996, 2.127 kg (±0.025, N = 94), and 2.705 kg (±0.037, N = 124) in 1997, whereas female weights were 2.009 kg (±0.025, N = 124), 1.824 kg (±0.030, N = 94), and 2.256 kg (±0.043, N = 79), respectively. Consequently, inputs of salmon carcass carbon to the reaches varied widely (Table 2).

Inputs of organic matter from the riparian vegetation varied much less among reaches within a stream (Table 2), although there was considerable smaller scale variation arising from site differences in riparian vegetation and from distance from the bank edge. Salmon carcass carbon inputs to the heavily used lowermost reaches were often several times greater than inputs of leaf litter from the riparian vegetation, but riparian litterfall dominated inputs of allochthonous particulate organic matter at upstream reaches. Periphyton gross primary production in these oligotrophic, forested streams was generally lower than both riparian litterfall or salmon carcass inputs (Table 2). Although regression estimates of primary production have wide prediction limits (roughly ×÷1.9; Morin et al. 1999), this would not greatly alter the relative contribution of algal carbon at most sites.

The timing and synchrony of carcass inputs also varied among years because of differences in the timing of stream entry and the duration of stream life. The median dates of stream entry at the Forfar Creek fence were days of year 216, 223, and 215 for 1996–1998, respectively; those for Gluskie Creek were quite similar (days 215, 222, and 211, respectively). Run duration, measured as the central 90% of the cumulative fence count, was 10 days in 1996, 18 days in 1997, and 16 days in 1998 for both Forfar and Gluskie Creeks. Stream life did not differ for sockeye in Forfar and Gluskie creeks in any year (t test, p > 0.06), but stream life differed considerably among years. Mean stream life was 11.5 days (SE = 0.36, N = 80) in 1996, 5.6 days (±0.23, N = 130) in 1997, and 6.9 days (±1.7, N = 7) in 1998.

Carcass processing and decomposition

Identifiable salmon carcasses were present in the streams for 6–7 weeks after spawning (Fig. 4). The carcass processing rate averaged –0.0338 day\(^{-1}\) (SE = 0.0032) for three reaches. “Processing” included decomposition, fragmentation, downstream transport, and consumption by scavengers. Carcasses did not accumulate in the lower reaches, which suggests that little transport occurred under the low discharge conditions of late summer and early fall. LWD, especially debris jams, retained 50–60% of the carcasses initially (Fig. 4). Deep pools associated with debris jams retained another 15–20%, and bed features such as bars, channel margins, and riffles trapped 15–20% of the carcasses that were present initially. Carcass processing rates varied among retention elements (Fig. 4). For the undisturbed Forfar Creek reaches, the rank ordering of disappearance rates was chan-
Fig. 4. Temporal changes in the abundance of carcasses by retention element at (a) F1, (b) F2, and (c) B1 reaches in 1997. Retention elements are (bottom to top): channel bed features (open bars), large woody debris (hatched bars), pools (solid bars), and riparian vegetation and small organic debris (shaded bars). The initial distribution is the number of live salmon and carcasses present near the end of the spawning period.

The proximate composition of the carcasses changed throughout the period of decomposition. The dry weight of fresh carcasses was 15.6% (SE = 0.6, N = 11) of their wet weight. Newly dead carcasses were 42.8% C (SE = 2.9), 13.5% N (±1.0), and 1.67% P (±0.37) by DW and thus had a molar C-to-N ratio of 3.7:1 and a N-to-P ratio of 17.7:1. The N content of carcass tissue declined continuously to a final value of 5.9% DW (SE = 0.7, N = 2) at day 65, whereas P content increased to 5.5% DW (±0.2) as bone became a larger proportion of the remaining material.

Water chemistry

In the absence of spawners, water concentrations of nutrients were low, TP being about 5 µg P·L⁻¹ and TN being 60 to 100 µg N·L⁻¹ (Figs. 6 and 7). Following the spawning period, short-duration pulses of P and N occurred at reaches with abundant spawners (Figs. 6 and 7). Nutrient concentrations varied little at sites with few or no spawners. Observed peak nutrient concentrations at a given reach varied among years, being higher in years of high spawner abundance (compare 1997 and 1998). Note that the monthly sampling frequency in 1996 largely missed the postspawning nutrient pulses. Much of the waterborne N and P occurred as organic compounds (Figs. 6 and 7). Inorganic P (measured as SRP) increased greatly at sites with high spawner abundance, from concentrations near the detection limit to maxima of 30 to 40 µg P·L⁻¹ (Fig. 6). Both NO₃-N and NH₄-N also increased during the period of carcass decomposition (Fig. 7). Nitrate-N was about 10 µg N·L⁻¹ before spawning and increased to maxima of 70 to 100 µg N·L⁻¹ after spawning. Nitrate-N concentrations were influenced by factors other than carcass decomposition, however. NO₃-N increased again in the autumn after leaf-fall (Fig. 7). Also, NO₂-N concentrations in Bivouac Creek were high during a low discharge year (1998), although salmon did not enter the stream. In contrast, NH₄-N concentrations were consistently near the detection limit except during the decomposition period when maxima of up to 200 µg N·L⁻¹ occurred. Peak NH₄-N concentrations greatly exceeded peak NO₂-N concentrations in 1997 (high salmon abundance), but the reverse was true during 1998 (low salmon abundance).
SRP ($r_{\text{Spearman}} = 0.65$, $df = 13.58$, $F = 9.83$, $p = 0.0075 < p_{\text{critical}} = 0.010$), TDP ($r_{\text{Spearman}} = 0.78$, $df = 14.48$, $F = 22.11$, $p = 0.0031 < p_{\text{critical}} = 0.0083$), TP ($r_{\text{Spearman}} = 0.74$, $df = 14.96$, $F = 18.05$, $p = 0.0007 < p_{\text{critical}} = 0.0063$), and NH$_4$-N ($r_{\text{Spearman}} = 0.93$, $df = 13.66$, $F = 101.4$, $p < 0.0001 < p_{\text{critical}} = 0.0056$) were significantly correlated with the carcass biomass per unit discharge upstream of the point of measurement. However, neither NO$_3$-N ($r_{\text{Spearman}} = 0.35$, $df = 10.02$, $F = 1.44$, $p = 0.25$) nor TN ($r_{\text{Spearman}} = 0.38$, $df = 10.10$, $F = 1.71$, $p = 0.22$) were correlated with salmon biomass per unit discharge.

Epilithon

Periphyton accrual on unglazed ceramic tiles differed between the low and high carcass biomass reaches: the time × carcass biomass level interaction was significant ($p < 0.0001$; Fig. 8). The exponential growth rate was about 40% higher initially at the high carcass biomass sites ($0.37 ± 0.021$ day$^{-1}$) than at the low carcass biomass sites ($0.26 ± 0.026$ day$^{-1}$). Periphyton growth rates declined after day 250 to $0.056 ± 0.0011$ day$^{-1}$ at the high biomass sites and to zero ($−0.0072 ± 0.0017$ day$^{-1}$) at the low sites; nutrient concentrations at the low sites had returned to prespawning values by this date. Final Chl $a$ concentrations were very similar to those observed on natural substrates at the sites (Fig. 9).

Epilithic Chl $a$ increased during the period of carcass decomposition, with maximum values occurring in late September samples (Fig. 9). Sites with no or few spawners showed little change in Chl $a$ values over the period. At low spawner abundance, peak Chl $a$ concentrations during the postspawning period were independent of carcass biomass and averaged about 0.5 $\mu$g·cm$^{-2}$ (Fig. 10). Peak Chl $a$ increased with increasing salmon carcass biomass per unit discharge above a threshold of about 300 kg DW·m$^{-3}$·s$^{-1}$ ($r_{\text{Spearman}} = 0.85$, $df = 8.91$, $F = 23.54$, $p = 0.0009 < p_{\text{critical}} = 0.0071$). The apparent slope of the log–log relationship above the threshold was 0.76 ($±0.12$).

Epilithic periphyton communities in the spawning streams were dominated by pennate diatoms. Diatoms comprised 34 of the 44 taxa identified and accounted for most of the biovolume in 80% of the samples throughout the June to October period (Table 3). A few common diatom species (a large-celled variety of Cocconeis placentula, Gomphonema olivaceum, Hannaea arcus) generally were the biovolume dominants. Achnanthes minutissima, Cymbella ventricosa, Diatoma hiemale, Fragilaria spp., and Synedra ulna were common minor biovolume components. Filamentous green algae (Cladophora) dominated the biovolume in 13% of the samples, and filamentous blue-green algae (Lyngbya, Oscillatoria, and Phormidium) in 7.5% of the samples. Postspawning maximum diatom biovolume was not significantly correlated with salmon biomass per unit discharge ($r_{\text{Spearman}} = 0.67$, $df = 7.51$, $F = 6.20$, $p = 0.039 > p_{\text{critical}} = 0.0125$), nor was total algal biovolume ($r_{\text{Spearman}} = 0.62$, $df = 7.72$, $F = 4.93$, $p = 0.058 > p_{\text{critical}} = 0.0167$).

Fate of salmon-origin nutrients

In all cases, the Akaike information criterion for the proportional removal model was lower than that for the asymptotic removal model (Table 4). The constant proportion...
removal model resulted in good fits to the observed time series (Fig. 11), with coefficients of determination between 0.70 and 0.95 (Table 4). For Gluskie Creek, where the proportion of carcasses removed by dead-pitching was known, the best-fit models also produced accurate total removal estimates. The known minimum removal of carcasses in 1997 was 56%, whereas those estimated from the TN and TP time series were 50% and 64%, respectively (Table 4). The known removal by dead pitch in 1998 was 45%, whereas the removal estimated from the TP data was 66% (Table 4). We expect the true removals to be somewhat greater than the dead pitch because scavengers also removed carcasses. Because 1998 was a year of low salmon abundance, the removal of small numbers of fish by scavengers would have a proportionately larger effect on the percentage removal estimate. The agreement between minimum known removals and those estimated from the models, as well as the fits to the nutrient concentration time series, suggest that the model structure accurately represented the major processes that determined stream-water nutrient concentrations.

Median estimates of removal rates for simulated data sets were within 0.2% to 2.4% of true values, which suggested that time-series bias was negligible. Removal rates estimated from TN and TP time series showed similar patterns of variation among sites and years, and confidence limits on estimates for the same site each encompassed the estimate derived from the other nutrient (Table 4). Removal rates for both streams were higher in the year of low salmon abundance, but removal rates at Forfar Creek were always much lower than those at Gluskie Creek, which was dead-pitched. Nutrient release from decomposing carcasses accounted for most of the observed changes in stream-water nutrient concentrations (Fig. 11). Excretion of N by spawners and nutrient release from dead eggs and sperm were small com-

Fig. 6. Water concentrations of (a, b, c) soluble reactive phosphorus (SRP), (d, e, f) total dissolved phosphorus (TDP), and (g, h, i) total phosphorus (TP) at the study sites in 1996 to 1998 as the abundance of sockeye (*Oncorhynchus nerka*) spawners varied. Streams: triangles, Bivouac Creek; circles, Forfar Creek; squares, Gluskie Creek. Reach strata: solid symbols, R1; shaded symbols, R2; open symbols, R3. Note the changes in scale.
ponents of the total solute concentrations (Fig. 11). Very little of the salmon-origin nutrients was sequestered in epilithic algae (Table 4). Little (<11%) of the salmon-origin N was predicted to be retained in the spawning streams past the end of September (Table 4). About two-thirds of the N and one-half the P were exported from Forfar Creek, whereas about 20–35% of the P was retained, mostly as refractory P, i.e., bone (Table 4). Less than 5% of the salmon-origin nutrients were retained in Gluskie Creek, which had been dead-pitched. Removal to the terrestrial ecosystem accounted for most of the salmon-derived nutrients, but one-third to one-half of salmon-derived N and P were exported from Gluskie Creek (Table 4).

Discussion

Our results show that the abundance of mass-spawning Pacific salmon can be an important influence on the primary productivity of forested stream ecosystems. The abundance and distribution of mass-spawning sockeye salmon determined stream-water nutrient concentrations and epilithic Chl a concentration during late summer and early fall when most primary production occurred in these oligotrophic streams. Periphyton accrual rates were elevated at sites with high salmon biomass, and peak Chl a concentration increased with increasing carcass biomass per unit discharge to reach maxima 10-fold greater than ambient levels. Nutrient budget calculations indicated that most of the salmon-derived nutrients were exported from the spawning streams or removed to the terrestrial ecosystem; thus, diffuse impacts may extend over a much larger area than simply the streams used for spawning. These conclusions agree with inferences from more-limited mensurative experiments that compared sites with and without salmon and from point additions of salmon carcases to ponds, streams, and mesocosms (Richey et al. 1975; Schuldt and Hershey 1995; Wipfli et al. 1998). The
stimulatory effects of salmon-derived nutrients on primary productivity extended to the highest salmon densities observed in the streams, but the incremental effect of an additional carcass decreased with increasing biomass because the apparent slope (0.76 ± 0.12) of the log–log relationship between Chl \textsubscript{a} and salmon biomass per unit discharge was less than one.

Decomposition and mineralization of carcass material by microbes and the subsequent utilization of solutes by benthic algae appeared to be an important path through which salmon carcasses altered productivity in these streams. Elsewhere direct feeding on carcass tissue and eggs by insects and fish (Bilby et al. 1998; Chaloner et al. 2002) has been important. Salmon carcasses were the dominant source of particulate organic carbon in the heavily used lower reaches of these streams, with inputs that were up to fivefold greater than riparian leaf litter and many times greater than algal production. Carcasses were also a high quality, if ephemeral, source of organic matter, with a C-to-N ratio of 3.7:1. Nevertheless, few stream invertebrates were found colonizing carcasses, and direct consumption by macroinvertebrates did not appear to be an important component of carcass processing within these streams. Carcasses on bar edges or other sites that were accessible to blowflies (Calliphoridae) were, however, quickly colonized by maggots and consumed; observed processing rates were highest for such sites. Carcass placements elsewhere have resulted in large numbers of benthic macroinvertebrates colonizing carcasses (Chaloner et al. 2002). The disturbance of the substrate at sites with high spawner densities (Gottesfeld 1998) may have inhibited invertebrate colonization of carcasses by temporarily reducing invertebrate abundance, as seen elsewhere (Peterson and Foote 2000; Minakawa and Gara 2003), but it is also likely that the direct consumption of carcass tissue by stream macroinvertebrates will depend on the composition, abundance, and phenology of the community. The relative importance of direct consumption and decomposition as mechanisms by which salmon-derived materials enter stream food webs will likely vary among locations.

Sockeye carcasses were retained at the spawning sites, primarily (75–80%) by LWD or pools formed by LWD.

These results for natural spawners are similar to observations on experimentally placed coho salmon \textit{(O. kisutch)} carcasses in small coastal streams (Cederholm et al. 1989). Thus, LWD seems to be an important carcass-retention element in both interior and coastal streams. Carcasses subsequently disappeared both by instream processing and by removal. The measured disappearance rate of carcasses in Forfar Creek (about 0.034·day\textsuperscript{−1}) was similar to
the rate at which carcasses lost mass (0.036·day$^{-1}$) and suggested that in-stream carcass processing rather than the removal of carcasses from the stream accounted for their disappearance. The low removal rates estimated for Forfar Creek sites in 1997 were consistent with this view. In-stream carcass processing may include carcass fragmentation and downstream transport as decomposition proceeds, especially for carcasses in LWD jams and other areas of high water velocity. Carcasses in deep pools persisted as intact entities for longer periods. Because carcasses were not uniquely identified, our processing rates could be biased if significant transport occurred between reaches, but this seems unlikely under the prevailing low flow conditions.

The decomposition of carcasses within the stream produced transient pulses of waterborne N and P, the magnitudes of which varied with carcass loadings upstream of the point of measurement and with discharge. As in other streams with abundant mass spawning salmon, stream-water concentrations of SRP and DIN increased greatly during carcass decomposition, with NH$_4$-N comprising most of the DIN (Juday et al. 1932; Brickell and Goering 1972; Sugai and Burrell 1984). The increases in NH$_4$-N observed during carcass decomposition and the large proportion of peak TN comprised by NH$_4$-N strongly suggested that microbial processing was an important pathway for the cycling of salmon-derived N in these streams. Relatively small amounts of the NH$_4$-N were derived from excretion by live spawners. Concomitant increases in NO$_3$-N indicated the rapid uptake and nitrification of excess NH$_4$-N, as noted elsewhere (Peterson et al. 1993). The relative constancy of peak NO$_3$-N during years of high and low salmon abundance, while peak NH$_4$-N varied 5- to 10-fold, suggested a fixed capacity for instream nitrification that was low relative to potential loadings of salmon-origin N. Sediment interstitial waters were well oxygenated (Cope and Macdonald 1998), so denitrification should not be significant. The high proportion of organic or particulate N (> 40% of waterborne TN) at high salmon abundance further suggested that the capacity of these streams to mineralize and sequester salmon-derived N may be exceeded frequently.

P loss from sockeye carcasses was well described by a two-compartment exponential loss model with labile (59%) and completely refractory (41%) pools. Other decomposition studies have also noted that 40–50% of fish P was bound in refractory bone or scales (Kitchell et al. 1975; Parmenter and Lamarra 1991). P loss from the labile pool occurred at 1.65 times the N loss rate, similar to the 1.5 ratio for rainbow trout decomposition over a 53-day period at 10–15 °C ($k_p = -0.142$·day$^{-1}$, $k_N = -0.097$·day$^{-1}$, calculated from table 1 of Parmenter and Lamarra 1991). The subsampling method that we used might underestimate the P content of carcasses because the heavily ossified head was not sampled, but our carcass composition data were similar to those of rainbow trout (N, 10.1% DW; P, 1.8% DW; Parmenter and Lamarra 1991). Carcasses from Takla tributaries contained less P than spent Alaskan sockeye (C, 42.6% DW; N, 13.2% DW; P, 2.5% DW; Mathisen et al. 1988), but the Takla fish also migrated a much longer distance upriver (1100 km), so a lower P content might be expected. Thus, the parameter values for P content and loss from carcasses that were used to predict water TP concentrations seemed reasonable.

Simple process models correctly predicted the observed temporal patterns of stream-water nutrient concentrations from known inputs of salmon. Calculated nutrient budgets indicated that most of the N and P entering the spawning streams in salmon were exported to Takla Lake or Middle River before freeze-up. The proportion of salmon-origin P that was retained in-stream was larger than that of N, but much of the retained P was in bone, which was refractory over the 65-day measurement interval. Our data do not suggest other long-term instream storage sites for salmon N or P: a conservative model in which all nutrients released from carcasses went into transport produced good fits to observed concentrations without any explicit provision for instream storage mechanisms other than algal uptake. Although the absence of instream storage mechanisms may seem unrealistic, Newbold et al. (1983) noted that water concentrations of NH$_4$-N converged to a theoretical no-uptake curve within a few hours when ammonium was added to a small stream at a concentration of 100 µg N·L$^{-1}$. Thus, at least some streams have a limited capacity to retain greatly increased N loadings. Although biomass accrual by the epilithon retained small amounts of N and P, and some may be sorbed to sediments (Bilby et al. 1996), stored in the hyporheic zone (Wipfli et al. 1999), or incorporated into insects and fish (Bilby et al. 1998), the proportion of salmon-origin nutrients retained past September by these mechanisms appeared to be small in our streams. The extensive reworking of bottom sediments by spawning salmon (Gottesfeld 1998), which increases sediment permeability, would reduce hydraulic residence times within sediments and thus reduce hyporheic storage. Short-term uptake, storage, and release of nutrients may occur but would only be detectable as systematic differences in the observed and predicted temporal patterns of nutrient concentration (e.g., Triska et al. 1989), which differences are not evident in our data. It is possible that some of the nutrients that our calculations assigned to the physical removal of carcass tissue from the stream may have been se-
questered in the stream. Because carcass removal rates were estimated from observed concentrations, any mechanism that quickly immobilized salmon-origin nutrients and retained them throughout the monitoring period would cause carcass removal, and thus transfers of salmon nutrients to the terrestrial ecosystem, to be slightly overestimated. However, the agreement between model-estimated and known removal rates for Gluskie Creek suggest that such mechanisms were relatively unimportant.

Carcass removal rates were low for Forfar Creek, where carcasses were not dead-pitched, and suggested that little scavenging occurred. Casual observations supported the estimates: few carcasses were noted on land near the stream. Removal rates for both streams were greater in the year of low salmon abundance than during the high abundance year. The estimated rates for Forfar Creek implied peak removals of 24–63 fish·day–1 in 1997 but only 11–12 fish·day–1 in 1998 and suggested that scavengers altered their utilization of salmon in response to variations in abundance. Nevertheless, total removals were 10–35%. Black bears and ravens were the most obvious scavengers, but bear abundance was low on the streams: in 1997, we saw two adults and two

### Table 3

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### Table 4

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cubs. Higher rates of predation and scavenging on salmon carcasses have been noted in coastal streams where bears were abundant (Cederholm et al. 1989; Quinn et al. 2003). In some coastal watersheds, the movement of salmon-derived material to the terrestrial ecosystem by predators and scavengers provides a nutrient subsidy to riparian vegetation (Hilderbrand et al. 1999). The consequences of carcass removals in these interior watersheds cannot be assessed solely from the removal estimates, but the rates suggest that 10% to 35% of salmon N or P may be transferred to the terrestrial ecosystem.

The fate and longer-term effects of the small amounts of salmon-derived material that remained in the spawning streams after freeze-up is wholly unknown. Much of the retained material was refractory P in bone. Weathering processes may eventually make the P available in soluble form, or algae and microorganisms colonizing the bone surface may be able to extract some of the nutrient. Alternatively,
the large, snowmelt-driven spring freshets seen in these streams may bury the bones or transport them downstream to Takla Lake or Middle River.

In the oligotrophic stream ecosystems characteristic of the Pacific Northwest, additions of even small quantities of readily assimilated SRP and NH$_4$-N at near-optimal stoichiometry for algal nutrition will increase autotrophic production. At SRP concentrations greater than 1–2 µg P·L$^{-1}$, we expect peak areal periphyton biomass to be limited by the diffusion of nutrients through the algal mat and to vary directly with PO$_4$-P concentration (Bothwell 1989). Because peak areal periphyton biomass saturates above 30–50 µg P·L$^{-1}$ (Bothwell 1989), increases in algal production may be reduced or cease at very high salmon carcass loadings (e.g., Bothwell 1989), increases in algal production may be re-

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Acknowledgements

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References


Legendre, P. 2000. Program Mod_t.test. Département des Sciences Biologiques, Université de Montréal (http://www.fas.umontreal.ca/BIO/Legendre/).


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