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Source: Journal of the North American Benthological Society, 30(3) : 779-786

Published By: Society for Freshwater Science

URL: <https://doi.org/10.1899/10-133.1>

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Bidirectional delivery of organic matter between freshwater and marine systems: the role of flocculation in Pacific salmon streams

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Abstract. The literature regarding freshwater and marine exchanges of organic matter (OM) focuses predominantly on the unidirectional delivery of allochthonous and autochthonous material from freshwater to the marine environment. Another ecologically significant exchange occurs when anadromous organisms move into coastal and interior watersheds and bring marine-accrued OM and its incorporated marine-derived nutrients (MDN). We use the example of Pacific salmon streams to discuss bidirectional transfers of OM in the upstream and downstream directions with specific reference to the role of flocculation. A fish-floc feedback loop has recently been presented as a mechanism that allows transfer of salmon OM to the gravel-bed matrix in the form of flocs. In the proposed fish-floc feedback loop, the OM source is salmon, but the OM source will change with fish species. Once fish-based flocs enter the gravel bed they can be stored or used by benthic organisms. A salmon disturbance regime that includes redistribution of gravel, fine sediment, and biofilm during redd construction and release of salmon OM to the stream is integral to the fish-floc feedback loop because it provides the inorganic fine sediment and OM required for floc formation. The MDN subsidy provided by returning salmon is important for natal watershed functioning as illustrated by a conceptual OM feedback loop that links these freshwater and marine exchanges. Retention of floc-bound OM in the gravel bed afforded by settling flocs allows slower downstream transfer of nutrients en route to the ocean and a correspondingly increased period for uptake in food webs downstream.

Key words: organic matter, marine derived nutrients, salmon, flocculation, sediment transport, biofilms, ecosystem linkages.

Freshwater and Marine Organic Matter Linkages

Organic matter (OM) transport and particle transformation dynamics in freshwater systems are typically discussed as processes that proceed unidirectionally with stream flow. Energy and OM inputs and their

storage and use by stream biota are largely regulated by the downstream flow of water (Vannote et al. 1980). OM sources include autochthonous material generated within the stream, such as periphyton, and allochthonous material generated outside the stream, such as leaf litter and terrestrial invertebrates from the riparian zone (Bilby and Bisson 1992). Allochthonous OM contributions also can originate from outside the watershed as in the case of anadromous fish returning from the marine environment to spawn. Anadromous

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fish species, such as Pacific salmon (*Oncorhynchus* spp.), alewives (*Alosa pseudoharengus*), and Atlantic salmon (*Salmo salar*) link marine and freshwater systems by upstream transfers of OM during migration. These fishes can deliver substantial quantities of marine-accrued OM and associated marine-derived nutrients (MDN) through metabolic waste while they are spawning and from their post-spawning carcasses if they die and remain in the stream (Naiman et al. 2002, Jonsson and Jonsson 2003, Walters et al. 2009). Bidirectional transport of OM between marine and freshwater systems is presented here using the example of Pacific salmon, but a more general OM transfer framework that emphasizes the role of flocculation is also discussed and can reasonably be expected to occur in other watersheds receiving other types of marine OM inputs (e.g., Atlantic alewife-bearing watersheds).

Transport and Storage of OM in Aquatic Ecosystems

OM in freshwater systems can be characterized as coarse particulate, fine particulate, or dissolved (Cummins 1974). The flux of these OM forms through rivers has been identified (Lamberti and Gregory 1996, Wallace and Grubaugh 1996), quantified (e.g., Minshall 1996, Wipfli and Baxter 2010), and evaluated in the context of the productivity and energetics of aquatic food webs (Power and Dietrich 2002) attesting to their importance in normal river functioning. Shifts between forms of OM have received considerable attention, but relatively little attention has been paid to the interaction of OM with inorganic fine sediments ($<63\ \mu\text{m}$) (Wotton 2007). Particulate OM can move independently as individual particles or flocculate (aggregate) with inorganic sediments to form composite particles called *flocs*.

Flocs make up a significant portion of the suspended sediment load of most rivers and vary in their composition because the quantity of inorganic and the quantity and quality of OM inputs to the channel change over the seasons (Droppo et al. 1997, McConnachie and Petticrew 2006). As such, they play an integral role in the delivery and storage of inorganic and organic matter through a watershed (Droppo 2001). OM-based flocs form in the water column when particles collide with adequate frequency and force under favorable chemical and biological conditions (Kranck and Milligan 1988, Kiorboe 2001, McConnachie and Petticrew 2006). Strong evidence exists that biological processes are the major influence for floc formation in freshwater systems (Droppo 2001, Petticrew and Arocena 2003, Wotton 2007).

In freshwater systems, extracellular polymeric substances (EPS) exuded by microbial organisms are instrumental in floc formation because EPS can bind OM and inorganic sediment together (Wotton 2004, 2005, 2011). The organic microstructures of EPS produced by bacterial and algal cells provide protection, attachment, flotation, and aid their locomotion (Wotton 2004) and are thought to control floc formation and dissociation processes. EPS appears to assist in regulating the shape, size, and internal complexity of flocs by acting as bridges between inorganic particles and other components that make up floc structure (Droppo 2001). All of these morphometric characteristics influence floc density and settling velocity, which in turn, influence the nature of suspended sediment transport because they regulate floc deposition on the stream bed and retention within the stream bed.

Influence of Floc Generation on OM Transport and Storage

Flocs can be generated by in-stream biophysical processes, or they can be delivered to the channel by terrestrial runoff. Flocs are larger than their component parts and, therefore, are more likely to be retained on the river's floodplain during high-water events because settling increases in low water velocities. Along the stream bed, sedimentation can be enhanced by reduced water flow in the streambed matrix that allows particle settling and interception at the sediment-water interface and trapping in intergravel pores.

Particle settling is regulated by ambient hydrologic conditions, such as stream discharge and fluid viscosity, and by the structure (size and shape), composition, and density of the suspended sediment. If shear velocities above the streambed surface exceed the settling velocity of the particle, it will be advected with the flow, but if the shear is less than the settling velocity of the particle, it will sink through the water column and be deposited on the stream bed. Localized velocity reductions can occur as a result of an increase in the hydraulic radius of a channel or a decrease in slope at transition locations, such as between riffle/run areas and pools or where braided channels widen (Knighton 1998). Streambed topography and porosity also play a role in floc retention because elevated bedforms, such as dunes, enhance surface-water movement through porous materials (gravels or sands) (Bjornn and Reiser 1991, Tonina and Buffington 2009). Water can be influent at the crest of these dune-like features and effluent in the trough, where the water pressure is higher. These morphologically modified flow patterns, which include

increased velocity across elevated streambed areas and decreased intergravel velocities (Tonina and Buffington 2007) enhance the opportunity for particle capture and retention.

Flocs moving in the vicinity of the stream bed can be captured by benthic organisms and ingested, processed, and released as waste materials ranging from dissolved OM to fecal pellets (Wotton 2007). The dissolved OM fraction is readily available for heterotrophic use (bacteria, fungi), whereas the fecal pellets are organic–inorganic aggregates that exhibit longer-term release of soluble nutrients or are subject to transport further downstream. Local flow conditions will regulate the entrainment of these pellets and other flocculated particles settled on the stream bed or retained within the gravel pores. Entrainment velocities generally are both lower and less variable within the gravel matrix, but high-energy events, such as floods and localized bioturbation (in this case salmon spawning) can mobilize the bed and resuspend these particles for transport downstream (Petticrew and Albers 2010). OM flocs or aggregates that have settled on the surface of the channel are more easily mobilized because flow environments are more variable at the gravel–water interface than within the gravel. Therefore, entrainment velocities are more often exceeded at the sediment–water interface. If the flocs become laminated or cohesive, the energy required to resuspend them increases and in-stream retention times become longer (Morales et al. 2007).

The retention time of flocs on or in the stream bed will affect their dissociation rate and, thereby, the availability of floc-based OM and nutrients to stream biota (Rex and Petticrew 2008). Microbial digestion of floc-bound OM will release nutrients back to the interstitial and surface water as dissolved OM available for further foodweb use (Rex and Petticrew 2010). At the same time, the breakdown of coarse particulate OM to fine particulate OM will proceed along the stream length and provide more source material for water-column flocculation. As more EPS is created by decomposing microbes, more flocs can be generated, leading to the increased likelihood of settling or capture further downstream. This floc formation, degradation, and formation process retards the downstream transport of nutrients, enhances biotic uptake, and influences the patch dynamics and nutrient spiraling in streams. Nutrient spiraling and patch dynamics have been identified in the literature (Newbold et al. 1982, Winemiller et al. 2010), but the role of flocculation in modifying the spatial and temporal transport of OM and nutrients downstream has not been clarified or incorporated into that conceptual framework.

Ecosystem Linkages and Effects of Upstream MDN Delivery

Each year, millions of anadromous Pacific salmon return from the ocean to their natal freshwater streams to spawn and die (Quinn 2005). Salmon biomass accumulated at sea is transported to upstream freshwater spawning grounds (Naiman et al. 2002). Out-migration of juvenile salmon subsequently exports nutrients back to the marine environment. In some years, this export exceeds what was returned (Scheuerell et al. 2005). Marine-to-freshwater nutrient fluxes and linkages such as this one are increasingly being seen as a crucial component of ecosystem health (Vanni 2002, Lamberti et al. 2010) because they can represent a significant nutrient subsidy to receiving watersheds (Wipfli and Baxter 2010). In other environments, such as the Canadian Arctic, transfers of nutrients to lakes via bird droppings (Michelutti et al. 2009) and historical harvesting of whales (Douglas et al. 2004) have been identified as pathways for freshwater nutrient subsidies.

Spawning salmon enrich aquatic systems through direct consumption pathways (Wipfli et al. 1998) and indirect trophic pathways (Bilby et al. 1996). Nowlin et al. (2008) reported that nutrient pulses travel more quickly through aquatic systems than through terrestrial systems. This result suggests that yearly variability in salmon numbers can strongly affect MDN retention in salmon-spawning stream ecosystems. Large gaps remain in our understanding of the mechanisms by which MDN cycle through their natal streams (Janetski et al. 2009) and of how to quantify their overall effect on aquatic productivity. For example, out-migrating salmon smolts, which export nutrients from freshwater systems on their way to the ocean, may overestimate the positive ecological effect of returning salmon in the MDN cycle (Moore and Schindler 2004). Characterizing the biophysical components (e.g., floc formation, OM retention) of the spawning life stage is a crucial step toward resolving these knowledge gaps. In Fig. 1, we present a conceptual diagram incorporating some of the important biological and biophysical factors regulating the movement of OM and nutrients between marine and freshwater systems in the context of Pacific salmon streams. The importance of the salmon disturbance regime in moderating the transfers of MDN in freshwater systems is emphasized.

Although generally beneficial to stream ecosystems, OM and MDN subsidies to freshwater systems also can provide a vector for marine-derived contaminants. For example, returning salmon were the dominant source of PCB contamination in lakes of some Alaskan and British Columbian watersheds (Krummel et al. 2005).

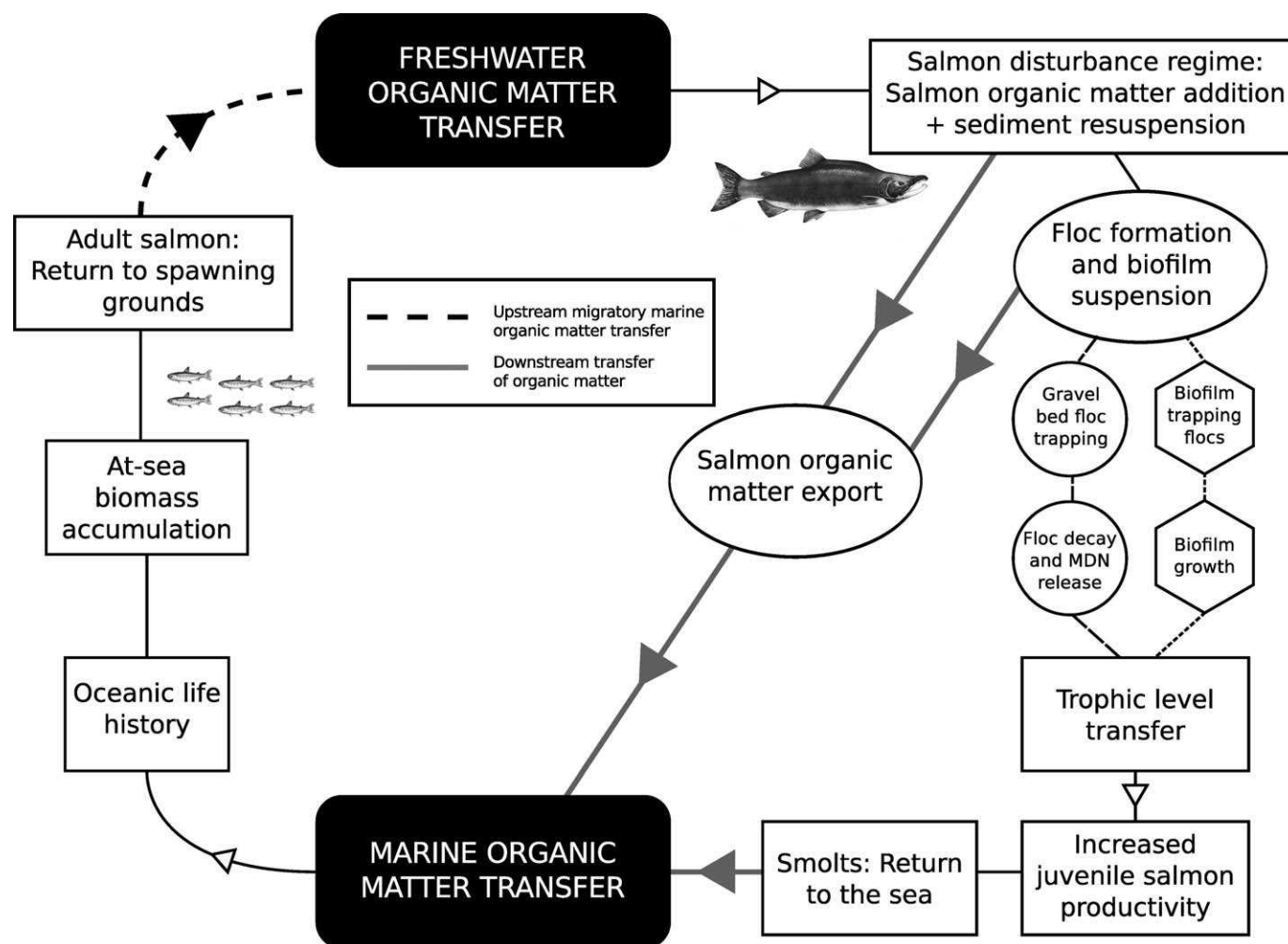


FIG. 1. The bidirectional transfer of nutrients from freshwater to marine systems using the example of Pacific salmon. Factors influencing downstream transport of organic matter (OM) are presented as a series of feedback loops structured by the salmon life cycle. Circles and hexagons refer to freshwater gravel-bed and biofilm processes, respectively.

Furthermore, Blais et al. (2007) stressed that biovectors, such as migratory salmon and sea birds, can focus the delivery of toxins accumulated at sea to discrete locations during their migration. This targeted delivery can have significant environmental implications even though the quantity delivered is small in comparison to contaminants delivered by physical processes, such as oceanic currents or wind. Once these contaminants are in-stream, flocculation will play a significant role in their transport and retention because flocs are prominent sites of contaminant adsorption and transformation (Droppo et al. 1997).

Pathways and Implications of Downstream Transfers of MDN

The temporal overlap of sediment disturbance (via redd construction) and stream fertilization (via

carcass decay) from salmon yields a disturbance regime (Moore and Schindler 2008) that structures the biological ability of a stream to process salmon nutrients (Fig. 1). Rex and Petticrew (2008) observed delivery and retention of MDN to and within the gravel bed in a flume study that simulated the conditions of this temporal overlap of bed disturbance and stream fertilization, here termed the *salmon disturbance regime* (Albers 2010). Flocs formed in the water column in the presence of salmon OM and fine suspended inorganic sediment concentrations that were similar to those of a field-monitored salmon disturbance regime (McConnachie and Petticrew 2006). Once formed, flocs settled on the flume's gravel bed within 30 m of the site of formation and enriched it with bound MDNs. An elevated N signal was observed in the gravels 7–14 d after floc sequestration to the bed (Rex and Petticrew 2010). This delivery

process was termed the *salmon-floc feedback loop* because it relies on the return of adult salmon, subsequent redd construction related to the suspension of fine sediment, and carcass decay products to generate flocs, which are then stored in the gravels (Fig. 1) (Rex and Petticrew 2008). Arkinstall (2005) concluded from results of a laboratory study that OM from salmon decay generated significantly larger flocs and more floc biomass than equivalent amounts of OM from allochthonous stream samples. These results indicate that salmon OM is of higher quality for floc generation and thereby suggests that the salmon-floc feedback loop is the dominant mechanism for transfer of high-quality OM to the stream bed.

Epilithic biofilms can influence the effectiveness of MDN transfers to the stream bed from salmon-OM-based flocs. Biofilm EPS interact with floc EPS to enhance deposition and trapping capacity (Romani and Sabater 2000). Consequently, a reduced biofilm layer during redd construction has a diminished capacity to trap flocculated particles, whereas post-spawning increases in biofilm abundance provide ideal conditions for MDN use by benthic organisms (Albers 2010). The net effect of this salmon disturbance regime will ultimately determine the biological effect of MDN transfers because epilithic biofilms are one of the main processors of OM in lotic ecosystems (Romani and Sabater 2000).

Coastal nutrient-limited streams that receive inputs of MDN generally experience an increase in primary and secondary productivity (Bilby et al. 1996, Quinn 2005). This trend also seems to hold true for interior streams, but these watersheds are much less well studied and possess different characteristics (Johnston et al. 2004, Albers 2010). OM in post-spawning salmon carcasses can be consumed directly by aquatic invertebrates and fish (Bilby et al. 1996, Minakawa and Gara 1999), or their MDN can be taken up by benthic biofilms (Yoder et al. 2006, Chaloner et al. 2007) or can enter the stream bed (Rex and Petticrew 2008, 2010). Verspoor et al. (2011) speculated that the MDN pulse delivered through returning salmon may extend over periods of a season to years because of the interaction of ecosystem components (e.g., leaf litter, which then supports invertebrates). Regardless of the initial or final transfer pathway for salmon OM, the annual nutrient pulse spawning salmon provide will be felt at all trophic levels because grazers that consume basal components of the food web (flocs and biofilms) transfer increases in productivity to higher trophic levels (Bilby et al. 1996, Verspoor et al. 2011). These transfers of MDN have a positive effect on juvenile salmon growth and survivorship (Wipfli

et al. 1999, 2003, Wipfli and Baxter 2010), which suggests a positive feedback loop such that fewer salmon returning to their natal streams will result in a downward spiral of declining salmon populations in a process known as cultural oligotrophication (Fig. 1) (Stockner et al. 2000, Scheuerell et al. 2005). Because of the reliance of aquatic and terrestrial biota on returning salmon nutrients in these watersheds, a decline in spawning salmon populations will have a serious negative effect on the health of these systems.

Conclusion

The temporal and spatial patterns of OM transfers associated with in-stream flocculation play a role in regulating the OM flux from freshwater to the marine environment. At the same time, the magnitude and period of in-stream OM retention and, therefore, uptake within the food web ultimately influence the future abundance of salmon (and thus, MDNs) returning to the watershed. These bidirectional transfers of anadromous fish nutrients, such as that of migrating Pacific salmon, illustrate the importance of sediment-mediated feedback loops within freshwater systems. Biophysical processes, such as flocculation, sedimentation, biofilm-mediated transfer, or storage in and on the stream bed, and the subsequent potential for hyporheic transport and storage influence OM transfers in freshwater systems whether the OM is from anadromous sources or other subsidies. Sediment acts as the inorganic component for floc formation while floc retention retards the downstream transfer of nutrients, at least temporarily, and allows benthic processing. Biofilms serve as a significant storage and processing point of OM within the aquatic ecosystem. These contributions to freshwater productivity play a crucial role in the spatial and temporal distribution and the regulation of future magnitudes of OM transfers between the marine and freshwater environments. We have highlighted the contribution of flocculation to bidirectional salmon OM transfers. However, longer-term processes, such as the decay of large woody debris (LWD), also are important sources of in-stream OM contributions in rivers. In addition, floc capture and retention in LWD-created pools and debris dams can lead to longer riverine retention times for sediment-associated nutrients and contaminants.

We illustrated the significance of OM exchanges between marine and freshwater ecosystems with examples of species transfer that were focused specifically on salmon but also referred to other fish, birds, and whales. These examples of freshwater-marine transfers of nutrients underscore the need to

consider both upstream-freshwater and open-ocean processes and their linkages. However, investigations of these transfers have been focused most often on interactions at the marine-freshwater interface in the estuarine environment, thereby spatially limiting the area of interest. Only the case of salmon streams was presented here in detail, but evaluating OM transfers by other species that link marine and freshwater systems will provide valuable information on ecosystem functioning that can be used to enhance both watershed and marine management.

Acknowledgements

We acknowledge the staff of the QRRRC including Rick Holmes, Bill Best, and Laszlo Enyedy, field assistants who have worked on the salmon-based projects over the years and Fisheries and Oceans Canada. Funding for this work was provided by the Canadian Natural Science and Engineering Research Council, Forest Renewal British Columbia (ELP) and Peace-Williston Aquatic Research Award to JFR and SJA. This is contribution number 11 in the Quesnel River Research Centre publication series.

Literature Cited

- ALBERS, S. J. 2010. The salmon disturbance regime: effects of biofilm, sediment and water. MSc Thesis, University of Northern British Columbia, Prince George, British Columbia.
- ARKINSTALL, D. J. 2005. The influence of dissolved organic carbon on aggregation and aggregate characteristics. MSc Thesis, University of Northern British Columbia, Prince George, British Columbia.
- BILBY, R. E., AND P. A. BISSON. 1992. Allochthonous versus autochthonous organic matter contributions to the trophic support of fish populations in clear-cut and old-growth forested streams. *Canadian Journal of Fisheries and Aquatic Sciences* 49:540–551.
- BILBY, R. E., B. R. FRANSEN, AND P. A. BISSON. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Canadian Journal of Fisheries and Aquatic Sciences* 53:164–173.
- BJORNN, T. C., AND D. W. REISER. 1991. Habitat requirements of salmonids in streams. Pages 83–138 in W. Meehan (editor). *Influences of forestry and rangeland management on salmonid fishes and their habitats*. American Fisheries Society, Bethesda, Maryland.
- BLAIS, J. M., R. W. MACDONALD, D. MACKAY, E. WEBSTER, C. HARVEY, AND J. P. SMOL. 2007. Biologically mediated transport of contaminants in aquatic systems. *Environmental Science and Technology* 41:1075–1084.
- CHALONER, D. T., G. A. LAMBERTI, A. D. CAK, N. L. BLAIR, AND R. T. EDWARDS. 2007. Interannual variation in responses of water chemistry and epilithon to Pacific salmon spawners in an Alaskan stream. *Freshwater Biology* 52:478–490.
- CUMMINS, K. W. 1974. Structure and function of stream ecosystems. *BioScience* 24:631–641.
- DOUGLAS, M. S. V., J. P. SMOL, J. M. SAVELLE, AND J. M. BLAIS. 2004. Prehistoric Inuit whalers affected Arctic freshwater ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* 101:1613–1617.
- DROPPA, I. G. 2001. Rethinking what constitutes suspended sediment. *Hydrological Processes* 15:1551–1564.
- DROPPA, I. G., G. G. LEPPARD, D. T. FLANNIGAN, AND S. N. LISS. 1997. The freshwater floc: a functional relationship of water and organic and inorganic floc constituents affecting suspended sediment properties. *Water, Air, and Soil Pollution* 99:43–53.
- JANETSKI, D. J., D. T. CHALONER, S. D. TIEGS, AND G. A. LAMBERTI. 2009. Pacific salmon effects on stream ecosystems: a quantitative synthesis. *Oecologia (Berlin)* 159:583–595.
- JOHNSTON, N. T., E. A. MACISAAC, P. J. TSCHAPLINSKI, AND K. J. HALL. 2004. Effects of the abundance of spawning sockeye salmon (*Oncorhynchus nerka*) on nutrients and algal biomass in forested streams. *Canadian Journal of Fisheries and Aquatic Sciences* 61:384–403.
- JONSSON, B., AND N. JONSSON. 2003. Migratory Atlantic salmon as vectors for the transfer of energy and nutrients between freshwater and marine environments. *Freshwater Biology* 8:21–27.
- KJORBOE, T. 2001. Formation and fate of marine snow: small-scale processes with large-scale implications. *Scientia Marina* 65:57–71.
- KNIGHTON, D. 1998. *Fluvial forms and processes*. Oxford University Press, Oxford, UK.
- KRANCK, K., AND T. G. MILLIGAN. 1988. Macrobios from diatoms: in situ photography of particles in Bedford Basin, Nova Scotia. *Marine Ecology* 44:183–189.
- KRUMMEL, E. M., I. GREGORY-EAVES, R. W. MACDONALD, L. E. KIMPE, M. J. DEMERS, J. P. SMOL, B. FINNEY, AND J. M. BLAIS. 2005. Concentrations and fluxes of salmon-derived polychlorinated biphenyls (PCBs) in lake sediments. *Environmental Science and Technology* 39:7020–7026.
- LAMBERTI, G. A., D. T. CHALONER, AND A. E. HERSHEY. 2010. Linkages among aquatic ecosystems. *Journal of the North American Benthological Society* 29:245–263.
- LAMBERTI, G. A., AND S. V. GREGORY. 1996. Transport and retention of CPOM. Pages 217–229 in F. R. Hauer and G. A. Lamberti (editors). *Methods in stream ecology*. Academic Press, San Diego, California.
- MCCONNACHIE, J. L., AND E. L. PETTICREW. 2006. Tracing organic matter sources in riverine suspended sediment: implications for fine sediment transfers. *Geomorphology* 79:13–26.
- MICHELUTTI, N., B. E. KEATLEY, S. BRIMBLE, J. M. BLAIS, H. LIU, M. S. V. DOUGLAS, M. L. MALLORY, R. W. MACDONALD, AND J. P. SMOL. 2009. Seabird-driven shifts in Arctic pond ecosystems. *Proceedings of the Royal Society of London Series B: Biological Sciences* 276:591–596.

- MINAKAWA, N., AND R. I. GARA. 2003. Effects of chum salmon redd excavation on benthic communities in a stream in the Pacific northwest. *Transactions of the American Fisheries Society* 132:598–604.
- MINSHALL, G. W. 1996. Organic matter budgets. Pages 591–605 in F. R. Hauer and G. A. Lamberti (editors). *Methods in stream ecology*. Academic Press, San Diego, California.
- MOORE, J. W., AND D. E. SCHINDLER. 2004. Nutrient export from freshwater ecosystems by anadromous sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences* 61:1582–1589.
- MOORE, J. W., AND D. E. SCHINDLER. 2008. Biotic disturbance and benthic community dynamics in salmon-bearing streams. *Journal of Animal Ecology* 77:275–284.
- MORALES, C. F. L., M. STRATHMANN, AND H. FLEMMING. 2007. Role of biofilms on sediment transport – investigations with artificial sediment columns. Pages 358–368 in B. Westrich and U. Forstner (editors). *Sediment dynamics and pollutant mobility in rivers: an interdisciplinary approach*. Springer-Verlag, Berlin, Germany.
- NAIMAN, R. J., R. E. BILBY, D. E. SCHINDLER, AND J. M. HELFIELD. 2002. Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* 5:399–417.
- NEWBOLD, J. D., P. J. MULHOLLAND, J. W. ELWOOD, AND R. V. O'NEILL. 1982. Organic carbon spiralling in stream ecosystems. *Oikos* 38:266–272.
- NOWLIN, W. H., M. J. VANNI, AND L. H. YANG. 2008. Comparing resource pulses in aquatic and terrestrial ecosystems. *Ecology* 89:647–659.
- PETTICREW, E. L., AND S. J. ALBERS. 2010. Salmon as biogeomorphic agents: temporal and spatial effects on sediment quantity and quality in a northern British Columbia spawning channel. *International Association of Hydrological Sciences Publication* 337:251–257.
- PETTICREW, E. L., AND J. M. AROCENA. 2003. Organic matter composition of gravel-stored sediments from salmon-bearing streams. *Hydrobiologia* 494:17–24.
- POWER, M. E., AND W. E. DIETRICH. 2002. Food webs in river networks. *Ecological Research* 17:451–471.
- QUINN, T. P. 2005. *The behavior and ecology of Pacific salmon and trout*. American Fisheries Society, Bethesda, Maryland.
- REX, J. F., AND E. L. PETTICREW. 2008. Delivery of marine-derived nutrients to streambeds by Pacific salmon. *Nature Geoscience* 1:840–843.
- REX, J. F., AND E. L. PETTICREW. 2010. Salmon-derived nitrogen delivery and storage within a gravel bed: sediment and water interactions. *Ecological Engineering* 36:1167–1173.
- ROMANI, A., AND S. SABATER. 2000. Influence of algal biomass on extracellular enzyme activity in river biofilms. *Microbial Ecology* 40:16–24.
- SCHEUERRELL, M. D., P. S. LEVIN, R. W. ZABEL, J. G. WILLIAMS, AND B. L. SANDERSON. 2005. A new perspective on the importance of marine derived nutrients to threatened stocks of Pacific salmon (*Oncorhynchus* spp.). *Canadian Journal of Fisheries and Aquatic Sciences* 62:961–964.
- STOCKNER, J. G., E. RYDIN, AND P. HYENSTRAND. 2000. Cultural oligotrophication: causes and consequences for fisheries resources. *Fisheries* 25(5):7–14.
- TONINA, D., AND J. M. BUFFINGTON. 2007. Hyporheic exchange in gravel bed rivers with pool-riffle morphology: laboratory experiments and three-dimensional modeling. *Water Resources Research* 43:W01421.
- TONINA, D., AND J. M. BUFFINGTON. 2009. Hyporheic exchange in mountain rivers I: mechanics and environmental effects. *Geography Compass* 3:1063–1086.
- VANNI, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* 33:341–370.
- VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130–137.
- VERSPOR, J. J., C. DOUGLAS, D. C. BRAUN, M. M. STUBBS, AND J. D. REYNOLDS. 2011. Persistent ecological effects on a salmon-derived nutrient pulse on stream invertebrate communities. *Ecosphere* 22:1–17.
- WALLACE, J. B., AND J. W. GRUBAUGH. 1996. Transport and storage of FPOM. Pages 191–216 in F. R. Hauer and G. A. Lamberti (editors). *Methods in stream ecology*. Academic Press, San Diego, California.
- WALTERS, A. W., R. T. BARNES, AND D. M. POST. 2009. Anadromous alewives (*Alosa pseudoharengus*) contribute marine-derived nutrients to coastal stream food webs. *Canadian Journal of Fisheries and Aquatic Sciences* 66:439–448.
- WINEMILLER, K. O., A. S. FLECKER, AND D. J. HOEINGHAUS. 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. *Journal of the North American Benthological Society* 29:84–99.
- WIPFLI, M. S., AND C. V. BAXTER. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmon watersheds. *Fisheries* 35:373–387.
- WIPFLI, M. S., J. HUDSON, AND J. CAQUETTE. 1998. Influence of salmon carcasses on stream productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska, USA. *Canadian Journal of Fisheries and Aquatic Sciences* 55:1503–1511.
- WIPFLI, M. S., J. P. HUDSON, J. P. CAQUETTE, AND D. T. CHALONER. 2003. Marine subsidies in freshwater ecosystems: salmon carcasses increase the growth rates of stream-resident salmonids. *Transactions of the American Fisheries Society* 132:371–381.
- WIPFLI, M. S., J. P. HUDSON, D. T. CHALONER, AND J. P. CAQUETTE. 1999. Influence of salmon spawner densities on stream productivity in southeast Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* 56:1600–1611.
- WOTTON, R. S. 2004. The ubiquity and many roles of exopolymers (EPS) in aquatic systems. *Scientia Marina* 68:13–21.
- WOTTON, R. S. 2005. The essential role of exopolymers (EPS) in aquatic systems. *Oceanography and Marine Biology: an Annual Review* 42:57–94.
- WOTTON, R. S. 2007. Do benthic biologists pay enough attention to aggregates formed in the water column of

- streams and rivers? *Journal of North American Benthological Society* 26:1–11.
- WOTTON, R. S. 2011. EPS (Extracellular Polymeric Substances), silk, and chitin: vitally important exudates in aquatic ecosystems. *Journal of the North American Benthological Society* 30:762–769.
- YODER, D. M., A. VIRAMONTES, L. L. KIRK, AND L. F. HANNE. 2006. Impact of salmon spawning on microbial communities in a northern California river. *Journal of Freshwater Ecology* 21:147–155.

Received: 3 October 2010

Accepted: 2 May 2011