

The response of stream periphyton to Pacific salmon: using a model to understand the role of environmental context

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SUMMARY

1. In stream ecosystems, Pacific salmon deliver subsidies of marine-derived nutrients and disturb the stream bed during spawning. The net effect of this nutrient subsidy and physical disturbance on biological communities can be hard to predict and is likely to be mediated by environmental conditions. For periphyton, empirical studies have revealed that the magnitude and direction of the response to salmon varies from one location to the next. Salmon appear to increase periphyton biomass and/or production in some contexts (a positive response), but decrease them in others (a negative response).
2. To reconcile these seemingly conflicting results, we constructed a system dynamics model that links periphyton biomass and production to salmon spawning. We used this model to explore how environmental conditions influence the periphyton response to salmon.
3. Our simulations suggest that the periphyton response to salmon is strongly mediated by both background nutrient concentrations and the proportion of the stream bed suitable for spawning. Positive periphyton responses occurred when both background nutrient concentrations were low (nutrient limiting conditions) and when little of the stream bed was suitable for spawning (because the substratum is too coarse). In contrast, negative responses occurred when nutrient concentrations were higher or a larger proportion of the bed was suitable for spawning.
4. Although periphyton biomass generally remained above or below background conditions for several months following spawning, periphyton production returned quickly to background values shortly afterwards. As a result, based upon our simulations, salmon did not greatly increase or decrease overall annual periphyton production. This suggests that any increase in production by fish or invertebrates in response to returning salmon is more likely to occur via direct consumption of salmon carcasses and/or eggs, rather than the indirect effects of greater periphyton production.
5. Overall, our simulations suggest that environmental factors need to be taken into account when considering the effects of spawning salmon on aquatic ecosystems. Our model offers researchers a framework for testing periphyton response to salmon across a range of conditions, which can be used to generate hypotheses, plan field experiments and guide data collection.

Keywords: bioturbation, ecological modelling, marine derived nutrients, Pacific salmon, periphyton

Introduction

In stream ecosystems, spawning Pacific salmon both deliver subsidies of marine-derived nutrients and disturb the stream bed during spawning (Gende *et al.*, 2002; Moore, Schindler & Scheuerell, 2004). The net effect of this resource subsidy and physical disturbance

on primary producers at the base of stream food webs is mixed, with empirical studies showing both increases and decreases in periphyton biomass and production (Janetski *et al.*, 2009; Verspoor, Braun & Reynolds, 2010). Here, we asked how environmental conditions could mediate the response of periphyton to salmon spawners. Specifically, under what set of environmental conditions

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might we expect to see increases in periphyton biomass/production or decreases in biomass/production in response to spawning salmon?

It is frequently assumed that returning adult salmon stimulate biological production in the oligotrophic streams in which they spawn (Kline *et al.*, 1990; Bilby, Fransen & Bisson, 1996; Cederholm *et al.*, 1999; Gende *et al.*, 2002). This increased productivity is believed to create additional food resources (e.g. aquatic invertebrates) that feed the progeny of spawning salmon before they migrate to the ocean. The paradigm holds that, because salmon home to their natal streams they create a positive feedback loop, whereby the more adult spawners that return, the more food resources they contribute, thereby sustaining a greater number of juveniles, which in turn yield more returning adults (Cederholm *et al.*, 1999; Stockner, 2003). One of the main trophic pathways thought to fuel this positive feedback occurs from the 'bottom-up'; nutrients excreted or leached out of adult salmon and their carcasses increase the production of periphyton at the base of the food web. This enrichment effect subsequently propagates up from periphyton to invertebrates and from invertebrates to fish (Gende *et al.*, 2002).

Although studies illustrate that salmon spawners can indeed increase the biomass and production of stream periphyton (Johnston *et al.*, 2004; Chaloner *et al.*, 2007), this is not invariably the case; other studies clearly show that salmon spawners can actually decrease periphyton biomass and production (Tiegs *et al.*, 2009; Collins *et al.*, 2011; Holtgrieve & Schindler, 2011). The reason for this is that spawning salmon also mobilise or scour stream bed gravels during nest building (redd construction). In some streams, for example, such disturbance by salmon accounts for half the annual bed load (Hassan *et al.*, 2008). This 'bioturbation' has been shown to dislodge benthic organisms, including periphyton and aquatic invertebrates, reducing both their biomass and production (Moore & Schindler, 2008; Tiegs *et al.*, 2009; Collins *et al.*, 2011; Holtgrieve & Schindler, 2011; Campbell *et al.*, 2012).

Understanding whether, and under what conditions, returning adult salmon might actually have a positive feedback on the next generation via bottom-up processes will require an understanding of how periphyton communities respond to both the nutrients salmon provide and the physical disturbance they create. Although it is evident that the direction and magnitude of the periphyton response to salmon are highly variable (Janetski *et al.*, 2009; Verspoor *et al.*, 2010; Rüegg *et al.*, 2012), a clear understanding of why responses differ from one location to the next is lacking. Conceptual models have helped to highlight the mechanisms that are likely to be involved

in determining the periphyton response; however, they are qualitative and do not explicitly incorporate feedback loops, nonlinear responses and indirect interactions. For instance, although salmon can directly reduce periphyton biomass via bed disturbance, indirectly this disturbance might increase the rate of periphyton turn-over by reducing density dependence (Fisher *et al.*, 1982). Understanding when, where and, most importantly, why we might observe responses in a certain direction will require the development of process-based approaches that explicitly account for not only the magnitude of the salmon run, but also (i) the environmental factors that influence periphyton dynamics (e.g. background nutrient concentrations, substratum grain size and light) and (ii) the critical feedback loops that determine how periphyton responds to changes in both the density of salmon spawners and environmental conditions.

To explore further the influence of salmon on stream periphyton, we formalised the current understanding of periphyton dynamics into a process-based model that explicitly links periphyton to both environmental conditions and salmon spawners. We used the model to simulate how environmental conditions (nutrient concentrations and substratum particle size) mediate the response of periphyton to spawning salmon. Specifically we asked (i) how does the environmental context of the stream affect the periphyton response (biomass and production) to spawning salmon? (ii) what are the implications of spawning for total annual autotrophic production and how might this influence production higher in the web (i.e. secondary production)? and (iii) how do the effects of salmon compare to those of other environmental factors in determining total annual periphyton production (APP)? The goal of was not to make predictions for a specific location, but to explore the more general role of salmon in periphyton dynamics.

Methods

Modelling approach

Our model links periphyton biomass to the positive and negative feedback loops that influence periphyton production and mortality (Fig. 1). The relative strengths of these different feedback loops, and the resulting patterns of periphyton biomass, are set by mechanistic linkages to environmental conditions of the stream, including water temperature, turbidity, discharge, photosynthetically active radiation, stream shading, channel slope, substratum grain size and dissolved nutrient concentrations (nitrogen and phosphorus). The influence of salmon

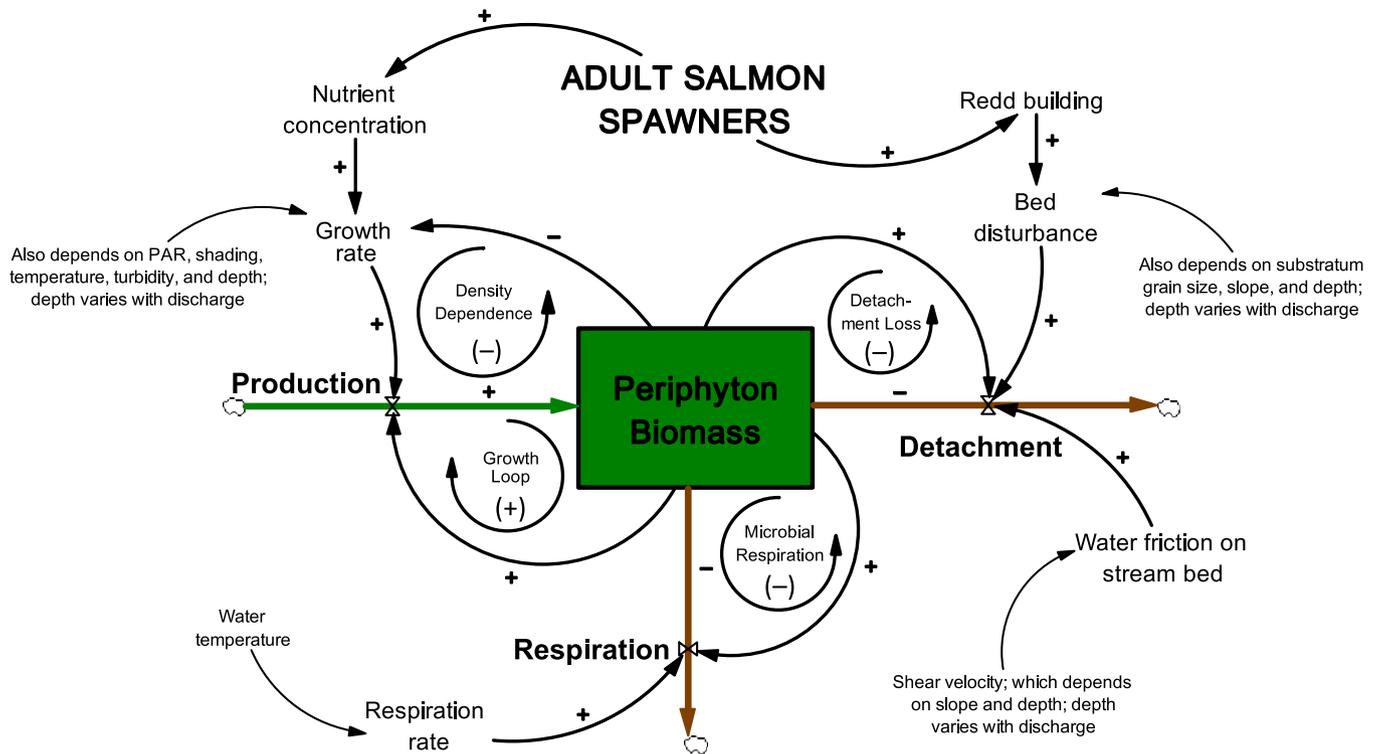


Fig. 1 Causal loop diagram showing the basic structure of the model. Boxes represent stocks of material (periphyton biomass), large arrows attached to the stock indicate the direction of material flux (production, respiration and detachment), circular arrow signs represent positive and negative feedback loops, and plus/minus signs indicate positive and negative causal relationships. Salmon spawners effect periphyton dynamics both by increasing stream nutrient concentrations and disturbing the stream bed during redd construction. PAR = total photosynthetically active radiation with no shading.

spawning was modelled by linking salmon to environmental conditions (Fig. 1). Specifically, we directly linked salmon to (i) periphyton production via the labile nutrients (nitrogen and phosphorus) excreted/leached from salmon and their carcasses and (ii) periphyton mortality via redd building, which detaches periphyton biomass by disturbing the stream bed. Reductions in periphyton biomass caused by disturbance from spawners also indirectly influence periphyton production via positive and negative feedback loops (the ‘growth’ and ‘density-dependent’ loops in Fig. 1). It should be noted that this model is focussed on the autotrophic portion of the periphyton community and does not address potential responses of heterotrophic biofilms. We used STELLA® 9.1.4 (ISEE Systems, Lebanon, NH, U.S.A.) to construct the model and run the simulations.

Periphyton model structure

The general form of our model closely resembles other mechanistic models of periphyton dynamics (McIntire, 1973; Uehlinger, Bühner & Reichert, 1996; Rutherford, Scarsbrook & Broekhuizen, 2000; Boulétreau *et al.*, 2006),

where periphyton is modelled as a single stock of biomass that increases via production of new biomass and decreases via both respiration and detachment. The model is run on a daily time step with units of grams of ash-free dry mass of periphyton per square metre (g AFDM m^{-2}). Periphyton biomass at time (t) is represented by the equation:

$$\text{Biomass}_t = \text{Biomass}_{t-1} + \text{Production}_t - \text{Respiration}_t - \text{Detachment}_t \quad (1)$$

The production term has the form:

$$\text{Production} = B g_{\max} \left(1 - \frac{B}{B + (1 - p_{\text{disturb}}) k_b} \right) \left(\text{MIN} \left(\frac{[N]}{[N] + k_n}, \frac{[\text{SRP}]}{[\text{SRP}] + k_p} \right) \right) \left(\frac{\text{PAR}_{\text{bed}}}{\text{PAR}_{\text{bed}} + k_{\text{par}}} \right) (\theta^{T - T_{\text{ref}}}) \quad (2)$$

where g_{\max} is the maximum rate (day^{-1}) of growth when periphyton biomass (B) is very low and environmental conditions are ideal (McIntire, 1973). Monod equations, and associated half-saturation values (k_b , $k_{n,p}$, k_{par}), serve as limitation terms and represent the

effects on growth rate of (i) periphyton biomass (i.e. density dependence); (ii) the concentration of a single limiting nutrient (mg L^{-1}), either nitrogen (N ; $\text{NO}_2 + \text{NO}_3 + \text{NH}_4$) or soluble reactive phosphorus (SRP); and (iii) photosynthetically active radiation ($\text{mol m}^{-2} \text{day}^{-1}$) reaching the bed of the stream (PAR_{bed}). The half-saturation value for biomass (k_b) is adjusted at each time step to account for the proportion of the stream bed disturbed or mobilised (p_{disturb}) by both salmon redd excavation and high scouring flows. During active bed disturbance, we assume that these surfaces are unsuitable for periphyton growth. The influence of water temperature (T) on growth is determined using a theta model, where θ is the temperature coefficient for growth, T is the mean daily water temperature, and T_{ref} is the reference water temperature ($T_{\text{ref}} = 20 \text{ }^\circ\text{C}$; Chapra, 1997; Abdul-Aziz, Wilson & Gulliver, 2010).

The amount of light reaching the bed of the stream is determined from empirical estimates of above-canopy PAR (PAR_{can}) following Julian, Stanley & Doyle (2008):

$$\text{PAR}_{\text{bed}} = (\text{PAR}_{\text{can}}(1 - p_{\text{shade}})p_{\text{reflect}})e^{-0.17\text{NT}d} \quad (3)$$

where p_{shade} is the proportion of light lost to shading, p_{reflect} is the proportion of PAR that enters the water after reflection, NT is nephelometric turbidity, and d is average water depth in metres.

Respiration is the loss of periphyton biomass to decay and has the form:

$$\text{Respiration} = \text{Br}_{\text{ref}}\left(\theta_2^{T-T_{\text{ref}}}\right) \quad (4)$$

where r_{ref} is the respiration rate at the reference temperature ($T_{\text{ref}} = 20 \text{ }^\circ\text{C}$) and θ_2 is the temperature coefficient for periphyton respiration.

Detachment includes periphyton losses due to both (i) water friction on the stream bed (Uehlinger *et al.*, 1996) and (ii) disturbance or mobilisation of the stream substratum. The detachment equation has the form:

$$\text{Detachment} = (c_{\text{det}}u_* (B_t - B_0)) + (r_{\text{disturb}}(B_t - B_0)) \quad (5)$$

where c_{det} is the detachment coefficient, u_* is friction or shear velocity on the stream bed, r_{disturb} is the rate of periphyton loss from both high scouring flows and salmon redd excavation, and B_0 is the biomass of periphyton that is resistant to detachment, which allows for recolonisation following extreme disturbance events. Friction velocity (u_*) is calculated as follows:

$$u_* = \sqrt{gSd} \quad (6)$$

where g is acceleration due to gravity and S is channel slope. We assume that average water depth (d) is equal

to the hydraulic radius of the channel (Gordon *et al.*, 2004), although this is only true in streams of greater width. Water depth and wetted width are calculated from stream discharge (Q) using hydraulic geometry relationships developed for the Pacific Northwest, U.S.A (Castro & Jackson, 2001). The rate of bed disturbance (r_{disturb}), is set as:

$$r_{\text{scour}} = \begin{cases} \frac{(1-p_{\text{disturb},t-1})-(1-p_{\text{disturb},t})}{(1-p_{\text{disturb},t-1})} & \text{if } p_{\text{disturb},t} > p_{\text{disturb},t-1} \\ \text{else } 0 & \end{cases} \quad (7)$$

This formulation allows for the rate of bed disturbance to be positive only when the proportion of the bed being disturbed increases from one time step to the next. In other words, once the proportion of bed disturbance stabilises (or decreases), no additional periphyton biomass is removed from the system due to disturbance. The proportion of bed disturbance (p_{disturb}) is determined by first calculating the diameter of substratum particles at the threshold of motion (critical substratum grain size, D_{crit}) for a given water depth and slope (Gordon *et al.*, 2004; Schwendel, Death & Fuller, 2010):

$$D_{\text{crit}} = \frac{dS}{(\rho_s - 1)\tau^*} \quad (8)$$

where ρ_s is substratum mass density (i.e. mass per volume), and τ^* is the Shields number, set at 2650 kg m^{-3} and 0.045, respectively, following Henderson (1966, p. 415). Critical substratum grain size (D_{crit}) is then compared against a cumulative substratum particle size distribution for the stream bed (Fig. 2) to calculate the proportion of the stream bed with particles smaller than the critical size; this represents the portion of the stream bed disturbed (p_{disturb}) by hydraulic forces alone. During salmon spawning, additional disturbance of the stream bed occurs via redd building (see below).

Linking salmon to periphyton dynamics

Our model tracks salmon through four stages: (i) arrival of salmon in the modelled stream segment, (ii) spawning, (iii) post-spawn salmon and (iv) mortality and decomposition. We assumed the arrival of salmon to be normally distributed around an average arrival time, after which, salmon remain in the modelled river segment a specified number of days prior to spawning. Once spawning commences, females are assumed to be continuously involved in redd building activities for a set number of days. Post-spawn salmon remain in the modelled river segment until death, after which their

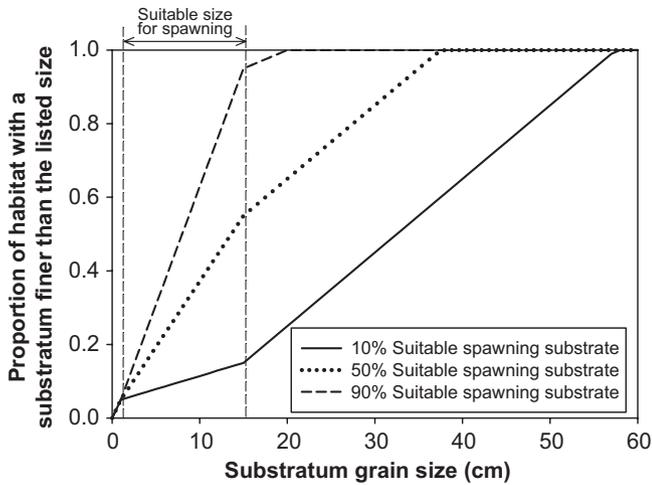


Fig. 2 Cumulative substratum size distributions used in model simulations, which illustrate the proportion of benthic habitat with a substratum finer than a given size. The three lines represent conditions whereby 10, 50 and 90% of all benthic habitat have a substratum of a suitable diameter (1–15 cm) for spawning (redd construction). Vertical lines illustrate the minimum (1 cm) and maximum (15 cm) particle sizes suitable for salmon spawning.

decomposition through time is represented by:

$$\text{Carcass Decomposition} = B_{\text{carcass}} r_{\text{decay}} \quad (9)$$

where B_{carcass} is the total biomass of salmon carcasses (grams of wet mass) in the modelled river segment (individual salmon weight = 5 kg) and r_{decay} is a temperature-dependent decay rate (day^{-1}) developed from empirical data on fish decomposition (Chidami & Amyot, 2008).

The contribution of dissolved nitrogen [N_{salmon}] and phosphorus [$\text{SRP}_{\text{salmon}}$] in the water column from live salmon spawners (in mg L^{-1}) is calculated as:

$$\begin{aligned} [N_{\text{salmon}}] &= \frac{B_{\text{salmon}} N_{\text{excret}}}{Q86400} \\ [\text{SRP}_{\text{salmon}}] &= \frac{B_{\text{salmon}} \text{SRP}_{\text{excret}}}{Q86400} \end{aligned} \quad (10)$$

where B_{salmon} is the total biomass of salmon in the spawning reach, N_{excret} and $\text{SRP}_{\text{excret}}$ are mass-specific daily nutrient excretion rates ($\text{mg g}^{-1} \text{day}^{-1}$) and Q is discharge (L s^{-1}), which is multiplied by the number of seconds in a day, to calculate the total volume of water moving through the spawning segment per day. After mortality, the contribution of nutrients from carcasses is determined by replacing live salmon biomass and nutrient excretion rates, with carcass biomass (B_{carcass}) and associated nutrient leaching rates (N_{leach} , $\text{SRP}_{\text{leach}}$). Leaching rates from carcasses were assumed to be 10% of excretion from live salmon, as studies have illustrated

that live salmon contribute far more nutrients than carcasses (Tiegs *et al.*, 2011). Contributions of nitrogen and phosphorus from both live and dead salmon are added to background nutrient concentrations in the water column to calculate the total nutrient concentrations available to stream periphyton in eqn 2.

Salmon-induced disturbance of benthic substrata is equal to the proportion of the total wetted area excavated by spawning:

$$p_{\text{disturb, salmon}} = \frac{R_{\text{success}} A_{\text{redd}}}{A_{\text{wet}}} \quad (11)$$

where R_{success} is the number of redd sites that are successfully used after accounting for redd superimposition (overlapping redd positioning), A_{redd} is average redd area (m^2), and A_{wet} is the total wetted area of the modelled segment. The effect of redd excavation on periphyton growth and detachment was calculated using eqns 2 and 7, respectively. This level of disturbance was assumed to continue until all salmon completed redd building. The number of successful redds (i.e. redds that are not superimposed) is given by the function (Maunder, 1997):

$$R_{\text{success}} = (K_{\text{redd}}) \left[1 - \exp \left(- \frac{S_{\text{female}}}{K_{\text{redd}}} \right) \right] \quad (12)$$

where K_{redd} is redd carrying capacity and S_{female} is the number of female spawners. K_{redd} was calculated by dividing the area of suitable spawning habitat in the model segment (A_{suitable}) by average redd area (A_{redd}). Using this formulation, superimposition increases if either the numbers of spawners increases or the amount of suitable spawning habitat decreases. Suitable spawning habitat (A_{suitable}) was the proportion of stream bed that contained substratum of an appropriate grain size for redd building (1–15 cm in diameter) that was not being scoured by hydraulic forces at the time of spawning.

Model parameterisation and sensitivity analysis

The goal of model parameterisation was to add realism to the model by representing environmental conditions typical of salmon spawning streams. We parameterised the model using existing environmental data from salmon spawning tributaries of the upper Columbia River in the state of Washington, U.S.A specifically the Entiat, Methow and Okanogan Rivers. These are snowmelt-dominated systems with hydrographs and temperature regimes typical of many salmon bearing streams, although there are numerous other patterns (e.g. rain-dominated, rain-snow mix, spring-fed). Discharge,

temperature, turbidity and PAR regimes used in model simulations are shown in Fig. 3 and represent the median of environmental conditions across numerous long-term monitoring stations in the region. The mean time of salmon arrival, redd building and death were set at 21 July, 1 September and 21 September, respectively, with a standard deviation of 6 days. These values are typical of spring Chinook salmon in the Columbia River basin, but could easily be adjusted to the timing of different salmon species or sub-populations found in other locations. In all our simulations, we assumed a 1 : 1 male to female sex ratio and an average spawner mass of 5 kg. Table 1 shows all of the environmental input variables, along with values, sensitivity ranges (see below) and data sources. Values, sensitivity ranges and literature sources for all other model parameters are reported in Appendix S1.

We performed global sensitivity analyses (GSA) to identify parameters producing the most uncertainty in our model simulations. The GSA ranks parameters by importance, considering both model structure and variability in parameter estimation. We applied the same technique as Harper, Stella and Fremier (2011), who used the Random Forest statistical method to rank parameter importance. We created 4000 random permutations of parameter estimates using the sensitivity ranges reported in Table 1 and Appendix S1 and used these values to

calculate annual primary production (APP). With the matrix of input parameter estimates and modelled annual production values, we applied Random Forest (R package Random Forest 4.6-2; The R Foundation, Vienna, Austria) to calculate the residual sum of squared errors (node impurity metric) for each parameter (Breiman & Cutler, 2011). Node impurity values for each factor were normalised by the sum of the total. An additional GSA was run solely using the environmental input parameter estimates (Table 1) to compare the effect of salmon spawners on periphyton production with that of other environmental factors.

Model simulations

Our simulations present the response of both periphyton biomass and production to four different densities of spawning salmon: (i) no spawners (background conditions), (ii) 0.1 spawners m^{-2} (or 0.5 kg wet mass m^{-2} ; 'low density'), (iii) 0.5 spawners m^{-2} (2.5 kg m^{-2} ; 'medium density') and (iv) 1.0 spawners m^{-2} (5 kg m^{-2} ; 'high density'). Although we could easily run the model for any other spawning density, we selected these values as they are within the range observed in the field. Moreover, we found that these particular densities exposed the general dynamics of the periphyton response to salmon in our model, without the need for additional runs.

Table 1 Environmental input variables used in the model. Variables are separated by those that remain 'set' and those that are manipulated in our simulations. GSA range represents the range of values used in the global sensitivity analysis

Environmental variables	Units	Symbol	Variable type	Values used	GSA range		
					Minimum	Maximum	Source*
Set variables							
Discharge	m^3s^{-1}	Q	Temporally variable	3–42 [†]	1–21	11–169	1
Temperature	°C	T	Temporally variable	0.8–19.0 [†]	0.5–11.4	1.0–24.7	2
Nephelometric turbidity	NTU	NT	Temporally variable	1.1–10.4 [†]	0.4–4.0	4.0–38.0	2
Above-canopy PAR	$\text{mol m}^{-2} \text{d}^{-1}$	PAR_{can}	Temporally variable	7.6–54.6 ^{†,‡,§}	–	–	3
Shading (proportion of PAR lost to shading)	–	P_{shade}	Constant	0.1	0.1	0.9	4
Slope	m m^{-1}	S	Constant	0.004	0.001	0.2	5
Variables manipulated in simulations							
Nitrogen	mg L^{-1}	N	Constant	0.02, 0.1, 0.5	0.02	0.5	2,6
Soluble reactive phosphorus	mg L^{-1}	SRP	Constant	0.002, 0.01, 0.05	0.002	0.05	2,6
Spawner density	spawners m^{-2}	–	Constant	0.0, 0.1, 0.5, 1.0	0	1	4
Substratum particle size distribution	m	–	Cumulative distribution	8, 14, 32 [¶]	8	32	4

*Sources: 1. USGS surface water data; 2. Washington Department of Ecology (2013); 3. USDA, UV-B Monitoring and Research Program, accessed December 2012, http://uvb.nrel.colostate.edu/UVB/da_queryPar.jsf; 4. Assumed or idealised values; 5. Bureau of Reclamation (2008); 6. Environmental Protection Agency (2000).

[†]The value of this environmental input changes through time, see Fig. 3.

[‡] PAR_{can} was not directly included in GSA, because P_{shade} was used to represent changes in light availability.

[§]PAR data obtained from the Washington State University Meteorological Station, Pullman, Washington

[¶]Median substratum particle size (D_{50}) from cumulative substratum particle size distributions, see Fig. 2.

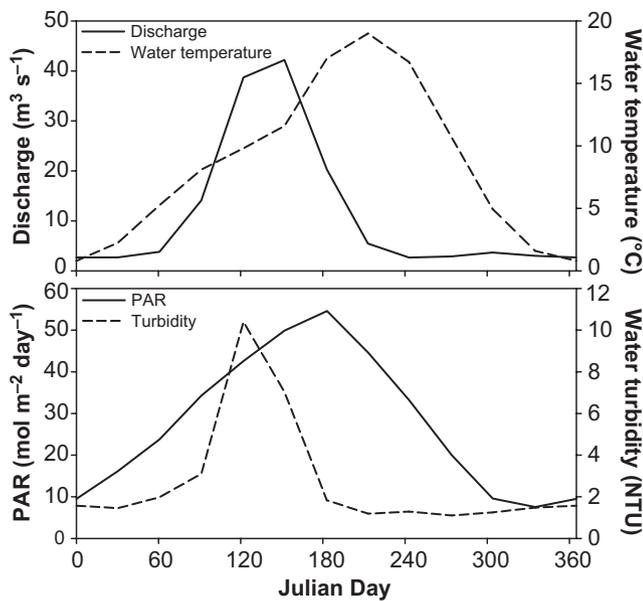


Fig. 3 Annual regimes of discharge and water temperature (top), along with incident photosynthetically active radiation (PAR) and water turbidity (bottom), used in model simulations. Discharge, water temperature and water turbidity values represent the median of conditions found across many long-term monitoring stations in spring Chinook salmon spawning tributaries of the upper Columbia River.

To evaluate how environmental conditions mediate the periphyton response to spawning salmon, we simulated each spawner density category with varying background concentrations of nutrients (N and P) and different amounts of suitable spawning habitat. We simulated three different concentrations for phosphorus [SRP] and nitrogen [$\text{NO}_2 + \text{NO}_3 + \text{NH}_4$]: low nutrients = 0.002 and 0.02, medium nutrients = 0.01 and 0.1 and high nutrients = 0.05 and 0.5, for phosphorus and nitrogen, respectively. These values represent concentrations (mg L^{-1}) at the low, medium and high end of the range found in salmon spawning streams of the Pacific Northwest (Table 1). For suitable spawning habitat, we modified the distribution of substratum grain sizes in the model to create three different categories of habitat available to spawning: 10, 50 and 90% suitable spawning habitat (i.e. percentage of the stream bed containing substratum between 1 and 15 cm in diameter; Fig. 2). The proportion of the bed that contained substratum particles coarser or finer than the suitable diameter was not disturbed by spawners; larger particles cannot be effectively mobilised, whereas salmon frequently avoid smaller particles as they are easily scoured by flows and/or may not allow adequate water circulation through the egg pocket during incubation (Quinn, 2005).

We chose to vary nutrients and substratum suitability in our simulations because we expected they would

strongly mediate the periphyton response to salmon, that is, the degree of nutrient limitation of the periphyton, and the probable strength of the response to spawner-induced bed disturbance. We chose to not vary additional environmental factors (e.g. slope, discharge and shading). Although these other factors could interact to determine the overall magnitude of any observed response, we would not expect them to generate novel dynamics not already revealed by varying spawning density, nutrient concentrations and substratum coarseness (see Appendix S2).

We ran the model for all combinations of spawner density, nutrient concentrations and suitable spawning habitat (36 simulations). All other environmental inputs and model parameters were held constant at their mean value, as this is the most parsimonious assumption given model complexity (Appendix S1). Stochasticity is not built into the model and therefore our model is deterministic. All simulations were run for 517 days, starting on 1 January with an initial periphyton biomass of 50 g AFDM m^{-2} . Simulations began well before salmon entered the system in July to allow the model to equilibrate to this initial condition. Results are reported for a 365-day period from 1 June to 31 May.

An additional set of simulations was run to evaluate the impact of spawners on APP, where annual production is the sum of daily production over the 365-day period from 1 June to 31 May. For each spawner density, we conducted 1000 runs with different combinations of background phosphorus concentration (between 0.002 and 0.05 mg L^{-1}) and suitable spawning habitat (between 0 and 100%). Nitrogen concentration was set at 10 times that of phosphorus in these simulations (similar to the ratio of N to P found in spawning streams in the upper Columbia River; Washington Department of Ecology, 2013) and, as such, phosphorus was the limiting nutrient (molar N : P ratio = 22 : 1). We used these simulations to evaluate the percentage change in APP due to salmon spawning (% change APP = APP with spawners – APP with no spawners) under different concentrations of a limiting nutrient (phosphorus) and different percentages of suitable spawning habitat.

Results

Global sensitivity analysis

Based on our global sensitivity analysis, the half-saturation coefficient for periphyton biomass (k_i) and the maximum periphyton growth rate (g_{max}) produced by far the greatest model uncertainty (Appendix S3). The value of these

two parameters strongly influenced the magnitude of periphyton biomass and production. However, changing the value of these parameters did not measurably alter the response of periphyton to spawning salmon (i.e. results were robust to changes in these two uncertain parameters). Thus, we held experimentally derived parameters constant at their mean value for all other model runs (Appendix S1).

The global sensitivity analysis (GSA) with only the environmental variables showed the importance of physical conditions in determining APP, specifically substratum grain size, stream slope and shading (Fig. 4). The importance of substratum grain size and slope is probably exaggerated because they are cross-correlated. Of lesser importance (in descending order) were phosphorus concentration (SRP), turbidity, temperature, discharge, nitrogen concentration and salmon spawners. These results suggest that the amount of periphyton produced on an annual basis is likely to be more sensitive to changes in local physical factors that control both bed scour (stream slope, substratum grain size, discharge) and the amount of light that reaches the stream bed (shading, turbidity, discharge), rather than to differences in the density of spawning salmon.

Simulation results

Spawning salmon changed the temporal pattern of periphyton biomass in all simulations (Fig. 5). The magnitude and direction of change varied with background nutrient concentrations, percentage of the habitat suitable for spawning and spawner density (Figs 5 & 6). Three distinct patterns emerged from the simulations: (i) only under low nutrient conditions was there a positive

periphyton response (Figs 5a–c & 6a–c), (ii) spawners generated significant removal of periphyton, particularly when much of the bed was suitable for spawning (Figs 5c,f,i & 6c,f,i), and (iii) on an annual time scale, the overall net effect of spawners on periphyton production was relatively small (Fig. 7).

At low background concentrations of nutrients, salmon initially increased periphyton biomass above background conditions (no spawners; Fig. 5a–c). After spawning began, however, the response depended on the proportion of the habitat suitable for spawning. When 10% of the habitat was suitable (Fig. 5a), periphyton biomass generally remained above background throughout the simulation. In contrast, spawning disturbance overwhelmed nutrient enrichment effects when larger percentages of the bed were suitable for spawning (50 and 90%), resulting in sharp decreases in periphyton biomass (Fig. 5b,c).

At medium nutrient concentrations, spawning salmon slightly increased periphyton biomass prior to spawning (Fig. 5d–f). After spawning began, periphyton biomass decreased for all values of habitat suitability. The magnitude of the decrease was mediated by the proportion of the habitat suitable for spawning, with greater values of suitability resulting in greater disturbance. Simulations with high concentrations of nutrients were similar to those with medium concentrations, except that we no longer observed an increase in periphyton biomass prior to spawning (Fig. 5g–i). In other words, the response of periphyton biomass to salmon spawners was always negative when background nutrient concentrations were high.

In general, higher densities of spawning salmon resulted in greater positive and negative periphyton responses (Figs 5 & 6). There were exceptions to this pattern, however, which highlight nonlinear relationships and interactions between spawner density, suitable spawning habitat and nutrient concentration. For example, when 50% of the bed was suitable for spawning (Fig. 5b,e,h), increasing spawner density from 0.5 to 1.0 m^{-2} did not result in any further decreases in periphyton biomass (Fig. 5b,e,h) and actually increased biomass when nutrient concentrations were low (Fig. 5b). In these simulations, additional spawners did not result in further biomass decreases because suitable spawning habitat had already been saturated with redds at the medium spawning density (0.5 m^{-2}). In other words, adding more spawners resulted in greater redd superimposition and not a larger proportion of the stream bed disturbed by redd construction. These additional spawners did provide more nutrients, however, which dampened the effects of bed disturbance when nutrients were limiting (Fig. 5b).

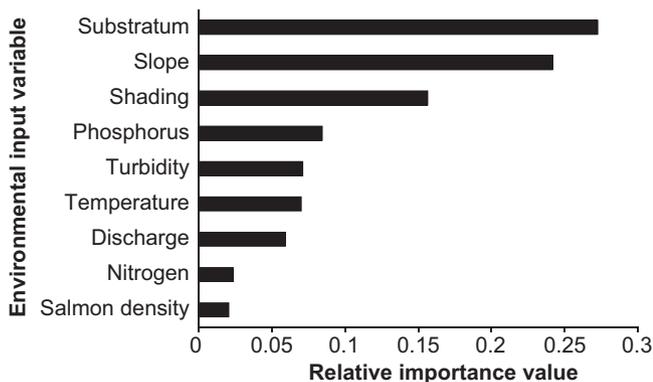


Fig. 4 Normalised Random Forest importance values (node impurity) for each environmental input parameter in a 4000 simulation global sensitivity analysis. Values indicate the relative importance of each parameter and its interactions with all other parameters in determining annual periphyton production.

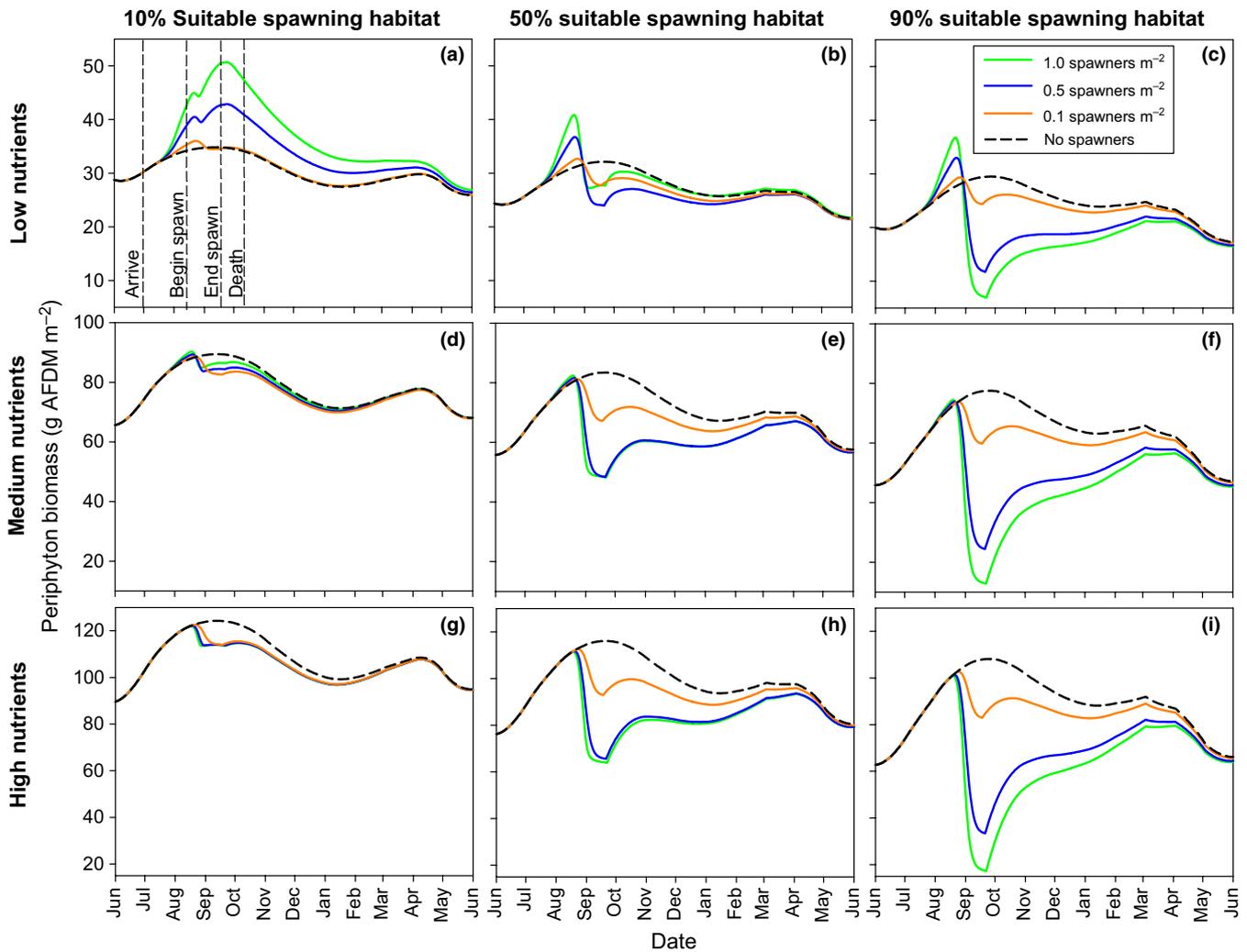


Fig. 5 Model simulations of periphyton biomass dynamics with different combinations of (i) salmon spawners (within each panel), (ii) suitable spawning habitat (columns) and (iii) nutrient concentrations (rows). Nutrient concentrations (in mg L^{-1}) were low nutrients = 0.002 and 0.02, medium nutrients = 0.01 and 0.1 and high nutrients = 0.05 and 0.5, for phosphorus (SRP) and nitrogen ($\text{NO}_2 + \text{NO}_3 + \text{NH}_4$), respectively. Dotted vertical lines in the top left panel represent key times in the sequence of salmon spawning, including arrival of the first spawner ('arrive'), beginning of spawning ('begin spawn'), end of spawning ('end spawn') and death of the last spawner ('death').

Salmon spawners also changed the temporal dynamics of daily periphyton production (Fig. 6). These changes largely displayed the same patterns as periphyton biomass (Fig. 5). Unlike biomass, however, the temporal dynamics of production were more closely linked to the timing of salmon arrival, death and redd building. For example, whereas periphyton biomass often stayed far below (or above) background conditions long after spawning salmon had died, periphyton production generally returned rapidly to background following the end of spawning activity.

The percentage change in APP due to salmon spawners was generally negative (Fig. 7). Three-dimensional response surfaces of low, medium and high spawning densities revealed that positive APP responses were

exhibited only when either or both nutrient concentrations and/or the proportion of suitable spawning habitat was low. These figures also illustrate that if the proportion of suitable spawning habitat was high (>80%), nutrient concentrations had to be extremely low [$\text{SRP} < 0.005$] to generate a positive response in APP to spawning salmon, and *vice versa*. Regardless of the direction of the response of APP to salmon spawners, the overall magnitude of change was generally <10% (and almost always < 15%).

Discussion

Understanding the response of freshwater communities to spawning Pacific salmon requires accounting for both

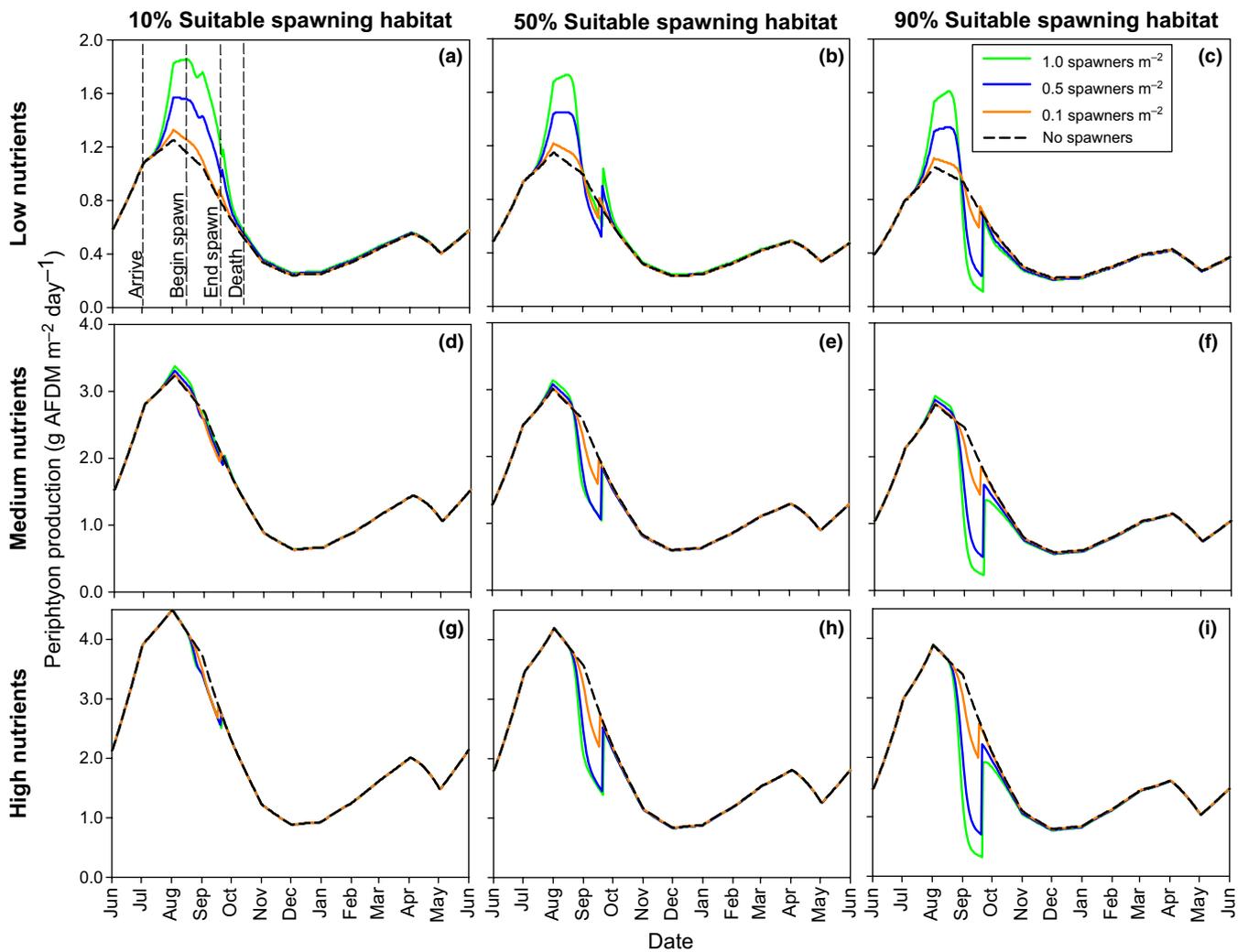


Fig. 6 Model simulations of the temporal dynamics of periphyton production with different combinations of (i) salmon spawners (within each panel), (ii) suitable spawning habitat (columns) and (iii) nutrient concentrations (rows). Nutrient concentrations (in mg L^{-1}) were low nutrients = 0.002 and 0.02, medium nutrients = 0.01 and 0.1, and high nutrients = 0.05 and 0.5, for phosphorus (SRP) and nitrogen ($\text{NO}_2 + \text{NO}_3 + \text{NH}_4$), respectively. Dotted vertical lines in the top left panel represent key times in the sequence of salmon spawning, including: arrival of the first spawner ('arrive'), beginning of spawning ('begin spawn'), end of spawning ('end spawn') and death of the last spawner ('death').

the subsidies salmon provide (nutrients and organic matter; Gende *et al.*, 2002) and the disturbance they create (bioturbation during redd building; Moore *et al.*, 2004). By incorporating both processes into a model, we showed that environmental conditions mediated the response of periphyton to salmon spawners by altering the strengths of nutrient enrichment and physical disturbance. Only when background nutrient concentrations were low, and little of the bed was suitable for spawning, did we find that salmon increased periphyton biomass and production. When nutrient concentrations were higher and/or a larger proportion of the bed was suitable for spawning, salmon reduced periphytic biomass and production. These simulations provide a mechanistic understanding

of why periphyton might respond differently to salmon in different situations, as illustrated by empirical studies (Janetski *et al.*, 2009; Verspoor *et al.*, 2010; Rüegg *et al.*, 2012). When periphyton responses to salmon were integrated over the whole year, however, salmon spawners did not greatly increase or decrease periphyton production, indicating that periphyton responses observed during spawning, and shortly thereafter, may have little effect on the total amount of periphyton produced annually. If so, this would suggest that responses of organisms higher in the food web (i.e. invertebrates and fish) to spawning salmon are more likely to occur via direct consumption of salmon carcasses and eggs (Bilby *et al.*, 1996; Kiernan, Harvey & Johnson, 2010).

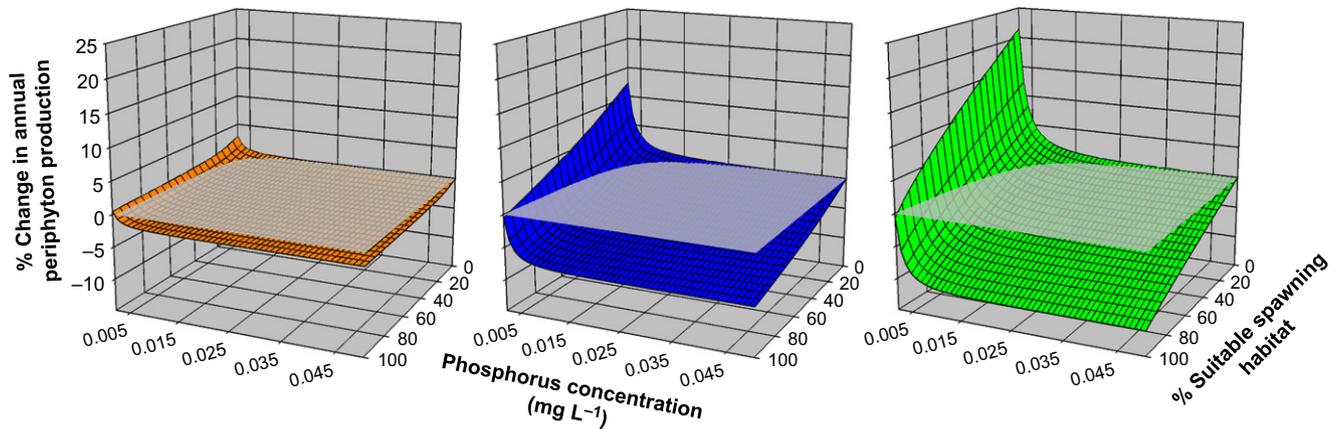


Fig. 7 Percentage change in annual periphyton production due to salmon spawning under different concentrations of a limiting nutrient (phosphorus), and different percentages of habitat suitable for salmon spawning. The areas of the three-dimensional surfaces above the transparent grey layer represent a net positive response of annual periphyton production to salmon spawners, whereas areas below the grey layer represent a net negative response. Left = 0.1 spawner m^{-2} , middle = 0.5 spawner m^{-2} , and right = 1.0 spawner m^{-2} .

Environmental conditions mediated periphyton response to salmon in our model by altering the strengths of the positive and negative feedbacks associated with periphyton growth and detachment. In simulations with low background concentrations of nutrients, periphyton production was perhaps not surprisingly strongly limited by nutrients. Consequently, even modest nutrient additions from salmon increased periphyton growth rate and strengthened the positive growth loop, resulting in greater periphyton production and biomass. In contrast, when stream nutrient concentrations were already high, the periphyton was much less nutrient limited and nutrients contributed by salmon had little influence. The strength of the negative detachment loop was controlled by the proportion of habitat suitable for spawning (substratum grain size). In simulations with large proportions of suitable spawning habitat (50 and 90%), salmon were able to disturb a significant percentage of the stream bed (particularly at high densities). Alternatively, when little (10%) of the bed was suitable for spawning, the same amount of salmon spawned in a smaller area, superimposing their redds and disturbing far less of the stream bed. Simply by altering the amount of suitable spawning habitat and background nutrient concentrations, we observed that the periphyton response to salmon ranged from entirely positive, to a positive response followed by a negative response, to an entirely negative response.

Of course, many other environmental conditions, such as discharge, channel slope and light availability, vary across the range of habitats used by spawning salmon and are also likely to mediate the strength of the

responses observed here. We did not vary these additional factors in our simulations because, in a separate set of analyses, we found that altering these conditions did not produce any novel dynamics not already exhibited by varying nutrient concentrations and substratum sizes alone (see Appendix S3). In the context of understanding the magnitude of the periphyton response to salmon at a particular location, however, these other factors (i.e. discharge, slope and light) should be considered, as they can strongly mediate the strength of both positive and negative periphyton responses (Appendix S2).

Although our model has yet to be validated in the field, results of empirical studies conducted in real salmon spawning streams are consistent with our simulations. These studies illustrate that variation in environmental conditions can mediate the periphyton response to salmon (Janetski *et al.*, 2009; Verspoor *et al.*, 2010; Rüegg *et al.*, 2012). For instance, several studies have found that streams with a finer substratum are more disturbed by spawning salmon than streams with coarser substratum less suitable for spawning (Tiegs *et al.*, 2008; Janetski *et al.*, 2009; Holtgrieve *et al.*, 2010; Collins *et al.*, 2011). This relationship is not restricted to periphyton; Campbell *et al.* (2012) found that benthic sediment grain size mediated the responses of aquatic invertebrates to spawning salmon. Although we have yet to include invertebrates into our modelling framework, changes in the benthos may be another pathway by which salmon spawners could influence periphyton dynamics – by altering the species composition and abundance of grazers.

Fewer studies have illustrated the extent to which spatial variation in background nutrient concentration medi-

ates periphyton responses to salmon (perhaps because most studies have been conducted in nutrient-poor streams). However, studies suggest that this mechanism exists; Levi *et al.* (2012) found that higher background nutrient concentrations in Michigan streams were generally associated with weaker responses of gross primary production to salmon compared with those of more oligotrophic streams in Alaska. Similarly, the results of a nutrient limitation experiment conducted by Rüegg *et al.* (2011) suggest that the importance of the nutrient subsidy from salmon spawners for periphyton may depend on the background concentration of nutrients.

A recognised weakness of these empirical studies is that they are often limited (Janetski *et al.*, 2009) to the period shortly before salmon spawning to shortly after the spawners have died. Although our simulations suggest that the greatest response to spawners does indeed occur during this period, they also illustrate that such short-term studies potentially exaggerate or, depending on the exact timing of the study, misrepresent the overall periphyton response to salmon. For example, we show that the salmon effect on periphyton can switch from an initial positive response before spawning, to a negative response shortly after the onset of spawning (Figs 5b,c & 6b,c); this suggests that the exact timing of periphyton measurements relative to these switches could lead to incorrect conclusions about overall net response. Moreover, without a broader temporal context, these short-term studies may inflate the perceived magnitude of the periphyton response to salmon, as they do not show how long the effect on periphyton dynamics persists. In our simulations, changes in periphyton production caused by spawning salmon returned quickly to background values almost immediately after spawning (Fig. 6). Nevertheless, periphyton biomass frequently remained discernibly higher or lower than background for several months, a finding which highlights that the perceived 'recovery' time may depend on the metric being measured. In sum, our model results suggest that a greater understanding of both the direction and magnitude of the periphyton response to salmon would be gained from longer-term (year-round) studies incorporating measurements of both biomass (chlorophyll *a* and AFDM) and production (stream metabolism estimates).

By running our simulations for an entire year, we found that even though the magnitude of the periphyton response could be substantial during the salmon run, overall effects on total annual production were much less pronounced. Even at extremely high salmon densities, the strongest positive response to spawners represented only a 20% increase in annual production.

Applying a simple trophic efficiency model, in which we assume that 10% of production is transferred to the next trophic level (Odum & Barrett, 2005; Mcgarvey & Johnston, 2011) and that fish are two trophic levels above periphyton, a 20% increase in periphyton production would translate into only a 0.2% increase in annual fish production. This simple thought experiment casts doubt on the notion that salmon fuel greater fish production via bottom-up pathways and indicates that direct consumption of carcasses by invertebrates and fish may be necessary for marine derived materials to increase fish production substantially (Kiernan *et al.*, 2010). Moreover, our model sensitivity analyses suggested that salmon were far less important, relative to environmental factors such as channel slope and available light, in determining overall periphyton production. This suggests that spatial variation in periphyton production within catchments may be driven more by local environmental factors (substratum grain size, stream slope and shading), rather than differences in the density of spawning salmon. Nevertheless, the temporal pattern of periphyton biomass and production may be just as important for higher trophic levels as the absolute magnitude of periphytic production. If, for example, salmon stimulate periphyton growth at times when the availability of attached algae is low and/or demand for food by grazers is high, then this could have a disproportionate effect on secondary production.

There are several reasons why the simulations presented here may not accurately represent the connection between periphyton and salmon. First, as with all models, ours is a simplification of a complex system. Our model, for instance, omits both aquatic invertebrate grazers, which can exert strong top-down control on periphyton (Hillebrand, 2002), and the heterotrophic portion of the biofilm community. However, additional model complexity is not always needed to represent system dynamics (Ford, 2010). The general structure of our periphyton model is simple, but has provided reasonable representations of periphyton dynamics in a number of different contexts (Uehlinger *et al.*, 1996; D'Angelo *et al.*, 1997; Boulêtreau *et al.*, 2006; Labiod, Godillot & Caussade, 2007; Fovet *et al.*, 2010). A second reason why our model may be inaccurate is that it includes several highly uncertain parameters (see Appendix S1). Obtaining more accurate estimates for these parameters would probably increase the predictive capacity of the model; however, doing so may not significantly alter the general dynamics of the system, as our simulations were relatively robust to changes in the most highly sensitive parameters identified via the global sensitivity analysis.

Third, the structure of our model might miss key parameters or the right mathematical formulations, which would indicate an incomplete understanding of the mechanistic linkages between salmon and periphyton; yet, this is true of all models, including statistical models derived from empirical data sets. Finally, the length of our simulations may be inadequate to represent the effects of salmon on periphyton. It could require several years or decades of high salmon returns to adequately 'prime' the system, that is, increase the nutrient concentrations enough to substantially increase periphyton productivity. Although our model is capable of running these simulations, that was not the goal of this particular exercise. Moreover, isotopic studies suggest little carry-over of salmon nutrients in periphytic biomass from one season to the next (Holtgrieve *et al.*, 2010), suggesting that in some streams, the response of periphyton to spawning salmon may reset each year.

For the reasons listed above, the results from this model should not be interpreted as predictions, but rather as hypotheses of how environmental factors might mediate the periphyton response to salmon. We embrace the adage that 'all models are wrong, but some useful'. Our model is useful in that it provides a quantitative framework for deductive reasoning and hypothesis generation that can be used to guide empirical studies. In turn, data from these empirical studies can be used to refine either parameter values in the model and/or the structure of the model itself. This feedback between process-based models and empirical data creates a structured framework for learning and hypothesis generation (Power, Dietrich & Sullivan, 1998; Ford, 2010).

In conclusion, our model illustrates that the response of periphyton to salmon is likely to be just as dependent on local environmental conditions as it is on the absolute number of spawners returning. By changing just two environmental factors (background nutrient concentrations and substratum grain size), we strongly altered the strengths of salmon-induced nutrient enrichment and physical disturbance, generating periphyton responses to salmon that ranged from entirely positive to entirely negative. These simulations suggest that spatial heterogeneity in environmental conditions that occur within and across catchments could result in a patchwork of periphyton responses to salmon that vary from one location to the next. For example, spatial heterogeneity in channel morphology, which controls stream power and substratum coarseness (Montgomery & Buffington, 1997), might mediate periphyton responses to salmon at the segment scale, whereas differences in lithology and climate, which control dissolved nutrient

concentrations, might mediate responses at the catchment scale.

For the management community, our model emphasizes that environment context (both abiotic and biotic) needs to be considered prior to nutrient supplementation efforts, such as the addition of salmon carcasses. Our simulations suggest that such efforts may only minimally increase basal level periphyton production, particularly if the system is not nutrient limited. Nevertheless, marine-derived materials can enter aquatic food webs via several pathways (Gende *et al.*, 2002), and invertebrates and fish could potentially respond to this subsidy even if the primary production response is small (Kiernan *et al.*, 2010). In the future, we plan to expand our model to include the direct consumption of salmon carcasses and eggs by both invertebrates and fish, which would provide a better understanding of how salmon might influence aquatic ecosystem structure and processes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Values, sensitivity ranges and literature sources for all model parameters (excluding environmental input variables).

Appendix S2. Effects of stream discharge, channel slope and percent shading on the periphyton response to salmon spawners.

Appendix S3. Normalised Random Forest importance values (node impurity) for each model parameter and environmental input in a 4000 simulation global sensitivity analysis.

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