

Salmon subsidize an escape from a size spectrum

Morgan D. Hocking, Nicholas K. Dulvy, John D. Reynolds, Richard A. Ring and Thomas E. Reimchen

Proc. R. Soc. B 2013 **280**, 20122433

Supplementary data

["Data Supplement"](#)

<http://rsjb.royalsocietypublishing.org/content/suppl/2012/12/28/rsjb.2012.2433.DC1.html>

References

[This article cites 52 articles, 9 of which can be accessed free](#)

<http://rsjb.royalsocietypublishing.org/content/280/1753/20122433.full.html#ref-list-1>

Subject collections

Articles on similar topics can be found in the following collections

[ecology](#) (1234 articles)

Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)



Research

Cite this article: Hocking MD, Dulvy NK, Reynolds JD, Ring RA, Reimchen TE. 2013 Salmon subsidize an escape from a size spectrum. *Proc R Soc B* 280: 20122433. <http://dx.doi.org/10.1098/rspb.2012.2433>

Received: 13 October 2012

Accepted: 6 December 2012

Subject Areas:

ecology

Keywords:

abundance, body size, food webs, Pacific salmon, resource subsidies, terrestrial size spectra

Author for correspondence:

Morgan D. Hocking
e-mail: mhocking@sfu.ca

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2012.2433> or via <http://rspb.royalsocietypublishing.org>.

Salmon subsidize an escape from a size spectrum

Morgan D. Hocking^{1,2,3}, Nicholas K. Dulvy¹, John D. Reynolds^{1,2}, Richard A. Ring^{3,4} and Thomas E. Reimchen³

¹Earth to Ocean Research Group, Department of Biological Sciences, and ²Hakai Network for Coastal People, Ecosystems and Management, Faculty of Environment, Simon Fraser University, 8888 University Drive, Burnaby, British Columbia, Canada V5A 1S6

³Department of Biology, University of Victoria, PO Box 3020, STN CSC, Victoria, British Columbia, Canada V8W 3N5

⁴Royal BC Museum, 675 Belleville Street, Victoria, British Columbia, Canada V8W 9W2

A general rule in ecology is that the abundance of species or individuals in communities sharing a common energy source decreases with increasing body size. However, external energy inputs in the form of resource subsidies can modify this size spectrum relationship. Here, we provide the first test of how a marine resource subsidy can affect size spectra of terrestrial communities, based on energy derived from Pacific salmon carcasses affecting a forest soil community beside streams in western Canada. Using both species-based and individual approaches, we found size structuring in this forest soil community, and transient community-wide doubling of standing biomass in response to energy pulses from Pacific salmon carcasses. One group of species were clear outliers in the middle of the size spectrum relationship: larval calliphorid and dryomyzid flies, which specialize on salmon carcasses, and which showed a tenfold increase in biomass in their size class when salmon were available. Thus, salmon subsidize their escape from the size spectrum. These results suggest that using a size-based perspective of resource subsidies can provide new insights into the structure and functioning of food webs.

1. Introduction

The availability and use of energy provide a fundamental limit to the abundance of species within communities [1–2]. These limits are determined not only by local abiotic and ecological factors such as primary production, temperature and species interactions, but also by an individual's energy use, which is determined by its metabolic rate and body size [3–7]. This is largely because metabolic rate scales positively with body size (M) as $\sim M^{0.75}$ within a trophic level, constraining abundance (N) to scale negatively with body size as $\sim M^{-0.75}$ such that energy use is equivalent across size classes [8,9]. The resulting negative relationship between body size and abundance is arguably one of the best-known patterns in ecology.

Body size–abundance relationships are used in two main ways to understand community-wide patterns of energy use. The classical approach is to make comparisons among species. These show that smaller-bodied species can either be rare or abundant, while larger species can only be rare; hence species abundances tend to be constrained beneath an upper bound of energy limitation defined by the negative scaling of abundance with body size [10–12]. The second approach is to ignore species distinctions and make comparisons among all individuals pooled together. The resulting size distributions, called size spectra, are now commonly used in aquatic communities that are dominated by indeterminate growing organisms, and in terrestrial soil communities, where size may matter more than species identity [13–16]. As with the classical species-based approach, the size spectrum approach shows that summed individual abundances (N) scale negatively across log body size categories (M), as $M^{-0.75}$ or steeper. This yields community $N \sim M$ scaling patterns that can parallel the

upper-bound slope defined by the species-level $N \sim M$ relationship [12]. These $N \sim M$ scaling relationships provide an important framework for understanding community structure and energy flow. However, little is known about how external subsidies of nutrients and energy may shape the $N \sim M$ relationship.

External resource subsidies may break the rules upon which body size–abundance relationships are founded, because multiple energy sources mean that even though individuals in communities may live together in space and time, their abundances will not be constrained solely by local productivity and the ecological interactions occurring within their community. For example, cross-system flows of nutrients and detritus can increase productivity across trophic levels, as shown by terrestrial carbon inputs to streams and lakes [17–19]. Furthermore, external energy subsidies may bypass the scaling rules if they enter food webs at higher trophic levels. For example, the migration of animals commonly subsidizes higher trophic levels such as the populations of local scavengers and predators [20,21]. Studies of resource subsidy effects generally show shifts in local species abundance that can alter community structure, but none have tested how subsidies may affect the size spectrum relationship. Taking a size-based approach, the intercept and/or slope of $N \sim M$ in communities can shift owing to changes in local resource availability, or through the coupling of benthic and pelagic food web compartments [22–24]. Large but transient outliers in abundance that depart from the linearity of the $N \sim M$ size spectrum have also been observed, which can cause trophic cascades and benefits for other species and size fractions [25,26].

Here, we provide a novel test for shifts in both the species-level and individual-level body size–abundance relationship of a forest soil community subsidized by the carcasses of Pacific salmon (*Oncorhynchus* spp.). Salmon return to spawn in thousands of streams throughout the Pacific Rim, which causes predator aggregations and can increase the productivity of nutrient-limited coastal watersheds [27,28]. Salmon-bearing ecosystems provide a unique opportunity to test the effects of resource subsidies on size spectra for two reasons: salmon spawning densities (here 20–30 tonnes ha^{-1}) are some of the highest biomass densities observed on Earth, and the availability of non-spawning areas plus the seasonality of salmon presence allows for good controls for understanding community-wide subsidy effects. Salmon subsidize adjacent forest soils through water transport of dissolved salmon nutrients (e.g. nitrogen + phosphorus), but also through active transport of salmon carcasses by bears (*Ursus* spp.) and other wildlife to riparian areas [29,30]. Salmon subsidies can thus affect forest soil communities in two ways: through nutrients entering the bottom of the food web and through specialists that are associated with the breakdown of salmon carcasses [31,32].

We contrast forest soil size spectra from before and during salmon spawning beside two streams that each support large runs of salmon versus control areas above waterfall barriers that prevent salmon migration. First, we hypothesized that temperate forest soil communities would be size structured, exhibiting a negative relationship between abundance and body mass. Second, we hypothesized that nutrients from salmon that enter the bottom of the food web would increase abundance across all size classes (increasing the intercept of the abundance–mass scaling

relationship), and that these increases in abundance would remain year-round, including pre-spawning periods. Finally, we hypothesized that large-bodied carcass specialists would increase in abundance during salmon spawning, resulting in a transient shallowing of the $N \sim M$ slope when salmon are present. Overall, we show the utility of using size-based methods to evaluate the relative benefits of resource subsidies to species and individuals in food webs.

2. Material and methods

(a) Study sites

This study was conducted beside the Clatse and Neekas rivers, near the Heiltsuk First Nation village of Bella Bella, on the central coast of British Columbia, Canada. Both streams remain minimally influenced by human disturbances, and are bisected by waterfalls 5–10 m high, resulting in a downstream area accessible to salmon and a similar salmon-free upstream reach, which for our purposes serves as a control. These waterfalls block salmon and limit the length of the salmon-bearing reach to 0.9 km on the Clatse River and 2.1 km on Neekas River. Chum (*Oncorhynchus keta*), pink (*Oncorhynchus gorbuscha*) and coho (*Oncorhynchus kisutch*) salmon spawn from late August to early November, returning at average biomasses of 39 016 and 61 594 kg km^{-1} to the Clatse and Neekas spawning reaches, respectively, in the 10 years prior to sampling (1992–2001). Each year, an estimated 16–48 per cent of the chum salmon biomass and 4–6 per cent of the pink salmon biomass is transferred to the forest by black bears (*Ursus americanus*) and wolves (*Canis lupus*) [33].

(b) Forest soil community

We monitored a grid of pitfall traps to estimate the relative abundance of species in a forest soil community within 20 m of the Clatse and Neekas rivers. Three 10×10 m plots were established both above (no salmon) and below (salmon) the waterfall barrier based on similarities in slope, canopy cover, forest structure and proximity to the waterfall in June prior to salmon spawning (pre-spawning) and in September during the spawning period (spawning) of 2001 [34]. Within each plot, we set up nine pitfall traps (each 10 cm diameter) in a 3×3 grid. Each trap was open for a total of 18 days (nine per season) and had three 15×20 cm drift fences to increase capture rates. Plots above versus below the waterfalls were separated by 300–600 m, limiting the likelihood of species dispersal among treatments.

All individuals caught in pitfall traps were sorted into the lowest taxonomic level possible in separate species categories (hereafter 'species') based on their feeding guild, life stage and body size (see the electronic supplementary material, table S1). The greatest taxonomic diversity occurred within the Coleoptera, Diptera and Hymenoptera. Individual samples ($n = 1–188$) of each species were weighed to estimate species body mass (M). The abundance (N) of each species was summed across pitfall traps for each plot. The trap catch could be biased towards larger and more mobile individuals, which would result in a shallower than expected abundance–mass scaling. However, the replicated spatial and temporal contrasts provide a robust test of how a resource subsidy may affect a body size–abundance relationship sampled in a consistent (if slightly biased) manner using pitfall traps.

(c) Statistical description of species and individual $N \sim M$ relationships

We calculated both species and individual body size–abundance relationships of the forest soil community. First, the species-level

relationship was bounded using quantile regression to estimate the 90th quantile slope of $\log_{10}(\text{abundance})$ by $\log_{10}(\text{body size})$ of all species using the package ‘quantreg’ in R. Local size–density relationships are often characterized by constraint triangles or polygons where species inhabiting the outer boundaries are the most likely to reflect and define the limits of mass-specific energy availability [10–12]. The quantile regression technique provides a linear model at a given quantile, where the main decision to be made is which quantile(s) best represent the outer boundaries of the data [35]. We chose the 90th quantiles because although any particular quantile is correlated with those nearby, the 95th and 99th quantiles showed much greater sensitivity to outliers coupled with larger error terms.

Second, we calculated a size spectrum, more familiar to aquatic ecologists, by placing individuals, irrespective of species identity, within five \log_{10} body size classes starting at the following sizes: 10^{-1} , 10^0 , 10^1 , 10^2 and 10^3 mg, based on a range in body size of 0.1–3000 mg. The largest size class was truncated; however, our results are robust to changes in the number of size classes and the exclusion of the largest partial size class. Abundance was summed across all individuals in each class by plot and M was given as the lower bound of each class. Because we used species mean masses, this assumes that there is only small variation in body size for each species relative to differences between classes, an assumption that would often be violated in more highly size-structured fish-dominated aquatic systems [13], but which is likely met here [16]. For example, one of the most variable species were cyclorrhaphan Diptera larvae, which ranged in mass from 8.0 to 54.2 mg ($n = 188$, mean ~ 20 mg), with 96 per cent of individuals falling within one \log_{10} size class (10^1 mg = 10–100 mg), and only 4 per cent (seven of 188) falling in the previous \log_{10} size class (10^0 mg = 1–10 mg).

We used generalized least squares to model the intercept and slope of $N \sim M$ of the individual size spectrum. This method is identical to linear regression, but allows us to account for spatial correlation in the model [36]. Because of the nested spatial design of the data, we applied a compound symmetry correlation structure of salmon (above waterfalls versus below waterfalls) within stream (Clatse, Neekas). This model thus behaves like a mixed-effects model, although it does not contain any random effects, and instead has a symmetrical dependence structure between communities surveyed on the same stream [36].

(d) Hypothesis testing and model selection

For both the species and the individual approaches, we used a model selection framework to test the effect of salmon subsidies on the $N \sim M$ relationship of the forest soil community. We used an initial full-fixed model that contained the main effects of season (June, pre-spawning; September, spawning), salmon (above waterfalls, no salmon; below waterfalls, salmon) and stream (Clatse, Neekas), and the *a priori* hypothesized interactions $M \times \text{season}$, $M \times \text{salmon}$, $\text{season} \times \text{salmon}$ and $M \times \text{season} \times \text{salmon}$. The interactions with M tested for changes in the $N \sim M$ slope (e.g. changes in energy transfer between trophic levels), whereas the main effects and the $\text{season} \times \text{salmon}$ interaction tested for differences in the intercept (e.g. total energy available). We also tested the transience of the salmon subsidy effects; for example, system-wide increases in abundance across all size classes may occur only during the salmon spawning season (indicated by the $\text{season} \times \text{salmon}$ interaction). In comparison, salmon subsidies may disproportionately increase the abundance of large-bodied predators compared with smaller size classes, resulting in a shallower $N \sim M$ slope that remains throughout the year ($M \times \text{salmon}$ interaction), or only when salmon carcasses are available ($M \times \text{season} \times \text{salmon}$ interaction).

We evaluated the relative strength of support of these hypotheses using an ‘all model combinations’ approach ($n = 38$

models), where model uncertainty was assessed using the Akaike information criterion (AICc) and multi-model averaging [37]. Models with lower AICc values have a better trade-off between complexity and fit than models with higher AICc scores. When there are several similarly weighted top models, model averaging can be used to incorporate the model uncertainty into the estimated parameters [37]. We used the MuMIn package in R, and the ‘zero’ method to compare models and calculate multi-model averaged parameter estimates from the set of models with $\Delta\text{AICc} < 4$ (see the electronic supplementary material, table S2) [38]. AICc weights (w_i) were calculated for each model (see the electronic supplementary material, table S3) and for each parameter to estimate relative variable importance (RVI). In the ‘zero’ method, a zero is substituted into the estimation of effect size when a given variable is absent from a model in the top model set, which thus decreases the multi-model parameter estimate (and error) of variables that only appear in models with low weights [38]. The number one ranked models and unstandardized parameter estimates are also shown in the electronic supplementary material, table S4. Because unstandardized parameter estimates (or coefficients) are only interpretable within the scale of each explanatory variable, we also compare relative effect sizes by centring each numeric variable (subtracting the mean) and dividing by two times the standard deviation [39]. This method allows reported coefficients (standardized parameter estimates) to be directly comparable with one another. All analyses were conducted in R v. 2.10.1 [40].

3. Results

Using a grid of pitfall traps, we caught and identified a total of 14 816 individuals from a forest soil community beside salmon spawning and control reaches, and during pre-spawning and spawning periods at two streams in coastal British Columbia. These were sorted into 104 species from at least 29 orders and 66 families, and were dominated by insects, arachnids, collembola and molluscs (see the electronic supplementary material, table S1). The dominant guilds included detritivores, predators and saprophages, followed by herbivores, fungivores and parasitoids.

Salmon arrival caused a transient doubling of the abundance and biomass of this forest soil community. During the autumn salmon spawning, pitfall traps in the salmon-bearing reaches below the waterfalls typically captured greater than twice the number of individuals and biomass compared with control reaches above waterfalls (figure 1). However, contrary to our original prediction, the abundance and biomass of these forest soil communities in the summer prior to salmon arrival was similarly lower between salmon-bearing and control reaches.

We found strong evidence for size structuring in this forest soil community using both species and individual approaches. At the species level, body size–abundance relationships showed a consistent triangular shape with wide-ranging abundance at small body sizes and low abundance of large-bodied species (figure 2*a,b*; electronic supplementary material, figure S1). There was a consistent outer-bound slope across the 90th quantile of abundance, which scaled negatively with body size as $N \sim M^{-0.50}$ (see the electronic supplementary material, table S2). At the individual level, abundance scaled negatively with body size as $N \sim M^{-0.59}$ when the abundance of all individuals were summed across five \log_{10} body size classes (figure 2*c,d*; electronic supplementary material, figure S2 and table S2).

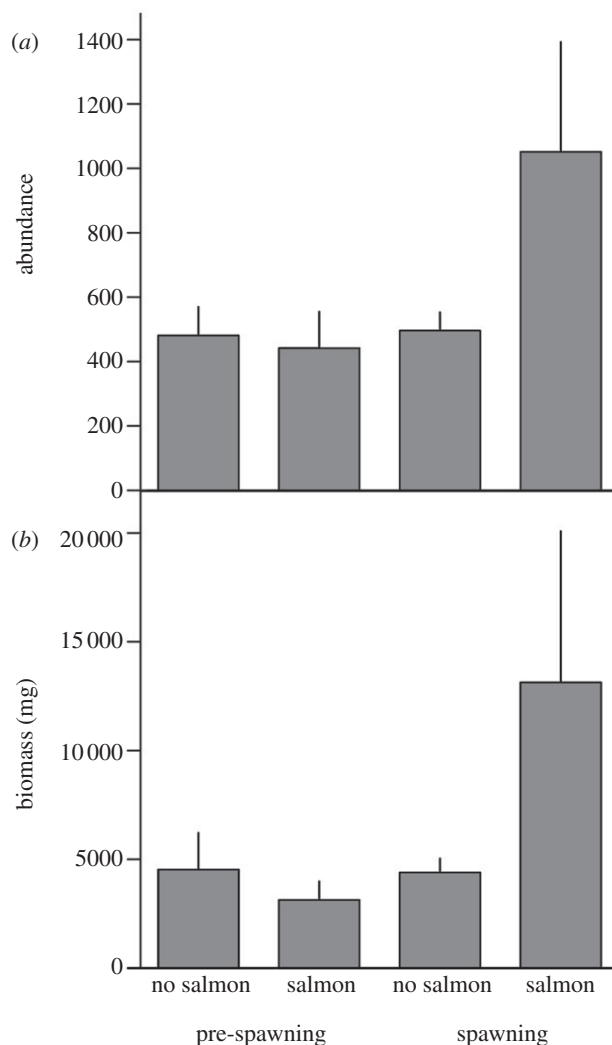


Figure 1. (a) Mean abundance and (b) standing biomass in mg (\pm s.e.m.) per plot of all individuals captured using pitfall traps in forest soil communities beside streams that support spawning Pacific salmon and above waterfall barriers with no salmon. Data were collected from two streams in early summer (before salmon spawn) and in the autumn (during salmon spawning).

For both species and individual approaches, a single outlier in numbers at mass (i.e. abundance at a given body size) was observed at an intermediate body size, but only when salmon were present. This outlier was cyclorrhaphan fly larvae, probably of two dominant families (Calliphoridae and Dryomyzidae), originating from salmon carcasses dropped in the forest by bears within several metres of the pitfall trap locations. During autumn salmon spawning, these larvae contributed 94 per cent and 90 per cent of the total pitfall-trapped abundance and biomass, respectively, within the 10–100 mg \log_{10} body size class. This results in a 20-fold increase in abundance and a 10-fold increase in biomass in the 10–100 mg \log_{10} body size class below the waterfalls with salmon compared with above the waterfall with no salmon (table 1). These fly larvae were not present below or above the waterfalls during the pre-spawning period.

Contrary to our original expectation, salmon carcass subsidies caused only transient increases in abundance across all size classes (table 1), and little change in the relative distribution of that abundance among smaller versus larger size classes (no change in slope). Across both streams, the $N \sim M$ intercept was higher below the waterfalls with salmon compared with control sites above the waterfalls

without salmon, although this only occurred during the salmon spawning season (strong season \times salmon interaction; table 2). The individual effects of salmon and season were found in all models with $AIC_c < 4$ ($RVI = 1$), and the interaction between season and salmon was also important (species model: $RVI = 1$; individual model: $RVI = 0.91$). By contrast, we observed little support for changes in the relative abundance among size classes as would be diagnosed by shifts in the body size–abundance slope with subsidies of salmon (low RVI and standardized estimates for $M \times$ season, $M \times$ salmon and $M \times$ season \times salmon; table 2). While there were differences in intercept between streams (species model: $RVI = 0.66$; individual model: $RVI = 1$), our findings were consistent across streams (see the electronic supplementary material, figures S1 and S2). The top models of the species ($w_i = 0.25$) and individual analyses ($w_i = 0.54$) both contained the same parameters (see the electronic supplementary material, tables S3 and S4).

4. Discussion

We have shown that energy flow across species and individuals is size structured in forest soil communities beside streams in a temperate rainforest in western Canada. We also show that a resource subsidy, with energy derived from Pacific salmon carcasses, causes a transient doubling of the standing biomass of these communities when salmon are available, and enables salmon carcass-specialist species—fly larvae that have fed on salmon carcasses—to reach higher than expected abundances, and hence escape the local size spectrum. Counter to our original hypotheses, salmon subsidies did not disproportionately benefit larger size classes, nor affect the biomass of the food web throughout the year, but affected a guild of carcass specialists that are intermediate in size, and hence reside in the middle of this size spectrum.

Size structuring was found using both species- and individual-based approaches. While fish-dominated aquatic systems are well known to be size structured [13,14], examples in terrestrial communities are less common. Several studies have demonstrated size structuring across trophic levels in soil communities, where species and/or individuals use similar amounts of available energy [15,16,41]. Using a species-based approach, we found a consistent triangular shape to a local forest soil community, with many rarer species and several dominant ones bounded by an outer slope of $M^{-0.50}$. This triangular shape can occur because local species abundance distributions are often right-skewed, with only a few very abundant species and many rarer ones [42,43]. For example, species tend to be abundant in a small portion of their range and rarer elsewhere [44]. The community dominants are thus most likely to be experiencing energy limitation [10–12], whereas rarer species may have more specialized niches with different energy sources, or may have other ecological limits such as competition [45] or predation [46].

An alternative to the species approach is to sum abundance across individuals of different sizes. Using an individual approach, we found a scaling of $M^{-0.59}$, and similar top models to the 90th quantile approach with all species. Across trophic levels in individual size spectra, it is predicted that inefficient energy transfer will yield steeper

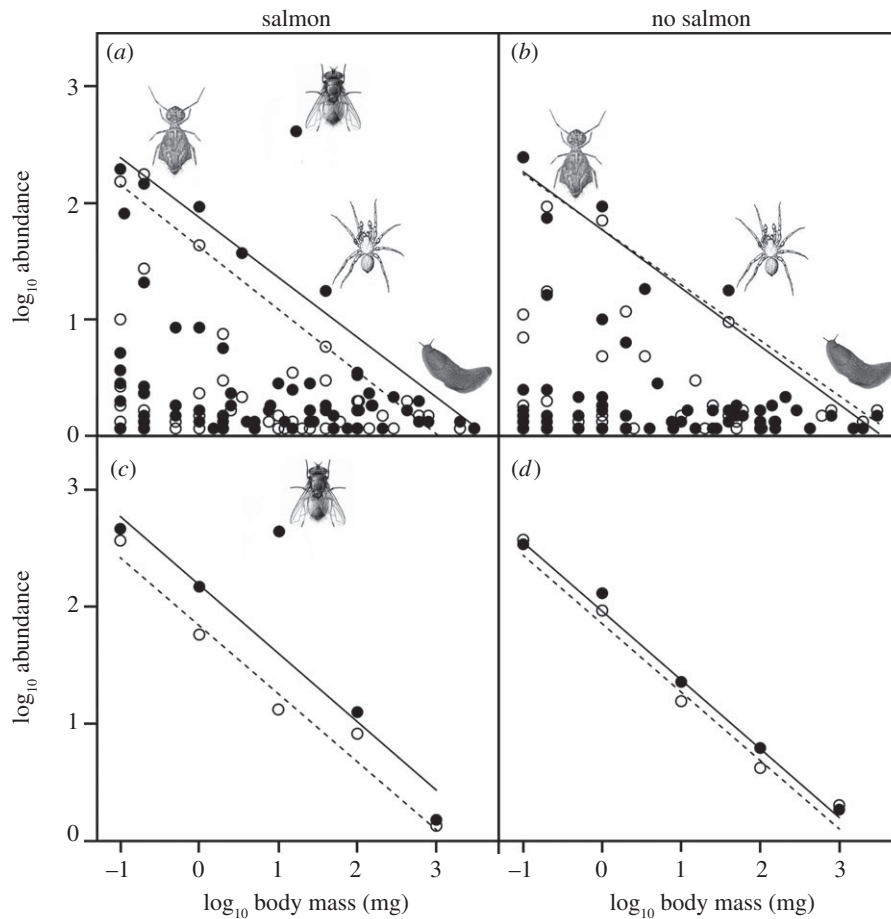


Figure 2. (*a,b*) Species and (*c,d*) individual body size (M)–abundance (N) relationships in forest soil communities (*a,c*) beside streams with spawning Pacific salmon and (*b,d*) above waterfall barriers without salmon. When salmon carcasses are available, we observe systemic increases in the intercept, and specialist species—fly larvae that have consumed salmon carcasses—escaping the size spectrum of this forest soil community. $N \sim M$ relationships were modelled across the 90th quantile of abundance for all species in the community, and by summing across all individuals within five \log_{10} body size categories. Surveys occurred in two time periods: in early summer before salmon have arrived (open circles and dotted lines), and in the autumn when salmon spawn (solid lines and filled circles). Abundance is averaged across two streams, and lines are fitted from multi-model parameter estimates (see the electronic supplementary material, table S2). Pictures relate to the nearest data points and highlight several of the major species/groups sampled along the gradient in body mass (collembola: *Ptenothrix maculosa*; flies: cyclorrhaphan Diptera larvae; spiders: *Cybaeus reticulatus*; slugs: Arionidae spp.).

Table 1. Average proportional change in abundance and biomass by individual \log_{10} body size class (mg) in forest soil communities subsidized by salmon compared with control reaches with no salmon. Sampling occurred in autumn salmon spawning and in early summer during pre-spawning. Abundance (N) and biomass (B) ratios = N or B below waterfalls with salmon/ N or B above waterfalls with no salmon.

season	\log_{10} body size class (mg)	abundance ratio	biomass ratio
autumn (during spawning): (spawning reach/control reach)	0.1–1	1.36	1.55
	1–10	1.14	1.37
	10–100	19.95	10.71
	100–1000	2.23	2.11
	1000–10 000	0.60	0.56
summer (pre-spawning): (spawning reach/control reach)	0.1–1	0.99	1.18
	1–10	0.62	0.64
	10–100	0.84	0.75
	100–1000	2.26	1.51
	1000–10 000	0.33	0.31
autumn ratio/summer ratio	0.1–1	1.38	1.32
	1–10	1.84	2.13
	10–100	23.78	14.34
	100–1000	0.98	1.39
	1000–10 000	1.80	1.79

Table 2. Relative variable importance (RVI) and standardized parameter estimates (std.est.) predicting species and individual abundance in forest soil communities subsidized by Pacific salmon carcasses. Greater relative variable importance was observed for shifts in the intercept than for shifts in the slope with salmon subsidies.

method	parameter	test of	RVI	std.est.
species size–density relationship 90th quantile regression	body mass (M)	slope	1	–1.22
	salmon	intercept	1	0.11
	season	intercept	1	0.02
	stream	intercept	0.66	0.05
	salmon \times season	intercept	1	–0.28
	$M \times$ season	slope	0.13	0.06
	$M \times$ salmon	slope	0.52	0.04
	$M \times$ salmon \times season	slope	0.32	–0.11
individual size distribution generalized least squares	body mass (M)	slope	1	–1.67
	salmon	intercept	1	0.23
	season	intercept	1	–0.10
	stream	intercept	1	0.20
	salmon \times season	intercept	0.91	–0.24
	$M \times$ season	slope	0.19	0.01
	$M \times$ salmon	slope	0.19	0.01
	$M \times$ salmon \times season	slope	0	0

scalings of $N \sim M$ (e.g. $M^{-1.2}$), an observation common in aquatic food webs [13]. However, declines in species diversity with increasing body size can also compensate for inefficient energy transfer between trophic levels, bringing scalings closer to $M^{-0.75}$ [16]. In forest soil communities, shallow slopes across the individual size distribution (mean = $M^{-0.44}$) are common, which may be because of higher than expected trophic transfer efficiency [16]. Alternatively, it could be because of fractional predator–prey mass ratios, as found in other detrital systems such as marine benthic infauna, where larger individuals feed at lower trophic levels and have greater relative access to available energy [47]. Thus, the expected slope of forest soil communities remains an open question, although we remain cautious about the interpretation of our slope of $M^{-0.59}$, because pitfall traps may tend towards increased catch of larger individuals.

Here, we show how size spectra can be used to detect and contextualize the beneficiaries of resource subsidies. We hypothesized that salmon subsidies would increase the standing biomass across the community (the intercept) year-round, and cause transient increases in abundance of larger-bodied scavengers and predators (shallowing of the slope) when salmon are available. In riparian areas beside salmon streams, the nutrients provided by spawning salmon can shift plant communities, and increase the nitrogen content and growth of associated forests [48,49]. Through links between above- and below-ground biota, these nutrient effects may influence the abundance of soil detritivores and predators, including in summer when salmon are not present [50]. For example, long-term subsidies to organic farms can increase the abundance of detritivores such as earthworms [16]. We found evidence for our initial hypothesis that salmon subsidies cause systemic increases in abundance across all size classes. However, contrary to our predictions, the increases in the size spectrum intercept were transient and only observed when salmon were

available. Further, salmon subsidies did not affect the distribution of that abundance (the slope). This means that shifts in the soil food web occur primarily in the short term, with energy ultimately derived from salmon, where species across a range of body sizes benefit. When salmon are not available, the community below the waterfall barrier then relaxes to the same scaling relationship as above the waterfalls, where salmon are always absent [51].

Strong competition for subsidized resources often favours species with specialized life history and mobility traits that enable a quick response to subsidies [52]. These transient outliers in numbers at mass occur commonly in aquatic systems, for example through upwelling events, which can then cause cascading mesopredator release effects for other species [25,26]. We observed transient 20-fold increases in abundance and 10-fold increases in biomass within an intermediate size class when salmon were available compared with control sites with no salmon. Ninety per cent of these increases are composed of one species group (cyclorrhaphan fly larvae), which escape the size spectrum of this forest soil community. Fly larvae are commonly observed as dominant consumers of salmon carcasses and are a key part of the streamside food web [29,31,33,53]. They overwinter in the soil near carcasses for at least eight months, and during this time are consumed by at least 21 soil invertebrate and 16 vertebrate species [33], including large-bodied species such as the carrion beetle *Nicrophorus investigator*, but also small-bodied parasitic wasps and rove beetles (Family Staphilinidae). In the late spring and summer, the surviving larvae pupate into adult flies and emerge from the soil *en masse*, which can affect the bloom timing of local plant species [54], and provides one mechanism by which top predators such as songbirds may have higher densities along these same salmon streams and estuaries [55–57].

In summary, we illustrate how body size–abundance distributions can be used as a framework for evaluating the food

web beneficiaries of resource subsidies. In particular, tests that take advantage of spatial and temporal contrasts across subsidy and habitat gradients will be useful in identifying the location of subsidy effects in food webs and the resulting trophic cascades. For example, despite several decades of research on Pacific salmon, it is still debated how these pulses of marine-derived nutrients and energy affect terrestrial ecosystems. Applying a size-based approach may yield new insight into the role of salmon subsidies in recipient streams, lakes and forests, including the size structuring of aquatic food webs, as well as predictions regarding the population densities and body sizes of top predators such as grizzly bears.

We greatly acknowledge the Heiltsuk Nation for research partnerships in their traditional territory. Thanks to Katie Christie, Chris

Darimont, Ted Gladstone, Simon Hocking, Larry Jorgenson, Ian McAllister, Karen McAllister, Danny Windsor and Michael Windsor for field and logistical support. We thank the following invertebrate taxonomists: Jan Addison, Andrew Bennett, Rob Bennett, Matt Buffington, Henri Goulet, Graham Griffiths, Dave Kavanaugh, Jan Klimaszewski, Zoe Lindo, Steve Marshall, Stuart Peck, Geoff Scudder and Monty Wood. Thanks to Sean Anderson, Doug Braun, Rob Hocking, Wendy Palen, Rowan Trebilco, the Reimchen and Ring laboratories at the University of Victoria, and the Earth to Ocean group at Simon Fraser University for discussion and analytical support. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada, the Pacific Salmon Foundation, the Leading Edge Endowment Fund, the David Suzuki Foundation, and the Hakai Network for Coastal People, Ecosystems and Management. Author contributions: M.D.H. designed and performed research, analysed data and wrote the paper; N.K.D. designed the data analysis and wrote the paper; J.D.R. supported research and wrote the paper; R.A.R. supported taxonomic identifications and designed data collection; T.E.R. designed and supported data collection.

References

1. Elton CS. 1927 *Animal ecology*. New York, NY: Macmillan Co.
2. Hutchinson GE. 1959 Homage to Santa-Rosalía or why are there so many kinds of animals. *Am. Nat.* **93**, 145–159. (doi:10.1086/282070)
3. Marquet PA, Navarette SA, Castilla JC. 1990 Scaling population density to body size in rocky intertidal communities. *Science* **250**, 1125–1127. (doi:10.1126/science.250.4984.1125)
4. Srivastava DS, Lawton JH. 1998 Why more productive sites have more species: an experimental test of theory using tree-hole communities. *Am. Nat.* **152**, 510–529. (doi:10.1086/286187)
5. Kaspari M, O'Donnell S, Kercher JR. 2000 Energy, density, and constraints to species richness: ant assemblages along a productivity gradient. *Am. Nat.* **155**, 280–293. (doi:10.1086/303313)
6. Cohen JE, Jonsson T, Carpenter SR. 2003 Ecological community description using the food web, species abundance, and body size. *Proc. Natl Acad. Sci. USA* **100**, 1781–1786. (doi:10.1073/pnas.232715699)
7. Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004 Toward a metabolic theory of ecology. *Ecology* **85**, 1771–1789. (doi:10.1890/03-9000)
8. Damuth J. 1981 Population density and body size in mammals. *Nature* **290**, 699–700. (doi:10.1038/290699a0)
9. Peters RH. 1983 *The ecological implications of body size*. Cambridge, UK: Cambridge University Press.
10. Blackburn TM, Brown VK, Doube BM, Greenwood JJD, Lawton JH, Stork NE. 1993 The relationship between abundance and body-size in natural animal assemblages. *J. Anim. Ecol.* **62**, 519–528. (doi:10.2307/5201)
11. White EP, Ernest SKM, Kerkhoff AJ, Enquist BJ. 2007 Relationships between body size and abundance in ecology. *Trends Ecol. Evol.* **22**, 323–330. (doi:10.1016/j.tree.2007.03.007)
12. Kaspari M, Weiser MD. 2012 Energy, taxonomic aggregation, and the geography of ant abundance. *Ecography* **35**, 65–72. (doi:10.1111/j.1600-0587.2011.06971.x)
13. Jennings S, Mackinson S. 2003 Abundance–body mass relationships in size-structured food webs. *Ecol. Lett.* **6**, 971–974. (doi:10.1046/j.1461-0248.2003.00529.x)
14. Jennings S, De Oliveira JAA, Warr KJ. 2007 Measurement of body size and abundance in tests of macroecological and food web theory. *J. Anim. Ecol.* **76**, 72–82. (doi:10.1111/j.1365-2656.2006.01180.x)
15. Meehan TD. 2006 Energy use and animal abundance in litter and soil communities. *Ecology* **87**, 1650–1658. (doi:10.1890/0012-9658(2006)87[1650:EUAAL]2.0.CO;2)
16. Reuman DC, Mulder C, Raffaelli D, Cohen JE. 2008 Three allometric relations of population density to body mass: theoretical integration and empirical tests in 149 food webs. *Ecol. Lett.* **11**, 1216–1228. (doi:10.1111/j.1461-0248.2008.01236.x)
17. Polis GA, Anderson WB, Holt RD. 1997 Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* **28**, 289–316. (doi:10.1146/annurev.ecolsys.28.1.289)
18. Pace ML, Cole JJ, Carpenter SR, Kitchell JF, Hodgson JR, Van de Bogert MC, Bade DL, Kritzberg ES, Bastviken D. 2004 Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. *Nature* **427**, 240–243. (doi:10.1038/nature02227)
19. Jansson M, Persson L, De Roos AM, Jones RI, Tranvik LJ. 2007 Terrestrial carbon and intraspecific size-variation shape lake ecosystems. *Trends Ecol. Evol.* **22**, 316–322. (doi:10.1016/j.tree.2007.02.015)
20. Polis GA, Hurd SD. 1995 Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proc. Natl Acad. Sci. USA* **92**, 4382–4386. (doi:10.1073/pnas.92.10.4382)
21. Spiller DA, Piovia-Scott J, Wright AN, Yang LH, Takimoto G, Schoener TW, Iwata T. 2010 Marine subsidies have multiple effects on coastal food webs. *Ecology* **91**, 1424–1434. (doi:10.1890/09-0715.1)
22. Boudreau PR, Dickie LM. 1992 Biomass spectra of aquatic ecosystems in relation to fisheries yield. *Can. J. Fish. Aquat. Sci.* **49**, 1528–1538. (doi:10.1139/f92-169)
23. Carbone C, Gittleman JL. 2002 A common rule for the scaling of carnivore density. *Science* **295**, 2273–2276. (doi:10.1126/science.1067994)
24. Blanchard JL, Jennings S, Law R, Castle MD, McCloghrie P, Rochet MJ, Benoit E. 2009 How does abundance scale with body size in coupled size-structured food webs? *J. Anim. Ecol.* **78**, 270–280. (doi:10.1111/j.1365-2656.2008.01466.x)
25. Pope JG, Shepherd JG, Webb J. 1994 Successful surf-riding on size spectra: the secret of survival in the sea. *Phil. Trans. R. Soc. Lond. B.* **343**, 41–49. (doi:10.1098/rstb.1994.0006)
26. Kimmel DG, Roman MR, Zhang X. 2006 Spatial and temporal variability in factors affecting mesozooplankton dynamics in Chesapeake Bay: evidence from biomass size spectra. *Limnol. Oceanogr.* **51**, 131–141. (doi:10.4319/lo.2006.51.1.0131)
27. Gende SM, Edwards RT, Willson MF, Wipfli MS. 2002 Pacific salmon in aquatic and terrestrial ecosystems. *Bioscience* **52**, 917–928. (doi:10.1641/0006-3568(2002)052[0917:PSIAAT]2.0.CO;2)
28. Naiman RJ, Bilby RE, Schindler DE, Helfield JM. 2002 Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems* **5**, 399–417. (doi:10.1007/s10021-001-0083-3)
29. Reimchen TE. 2000 Some ecological and evolutionary aspects of bear-salmon interactions in coastal British Columbia. *Can. J. Zool.* **78**, 448–457. (doi:10.1139/z99-232)
30. Quinn TP, Carlson SM, Gende SM, Rich HB. 2009 Transportation of Pacific salmon carcasses from streams to riparian forests by bears. *Can. J. Zool.* **87**, 195–203. (doi:10.1139/Z09-004)
31. Hocking MD, Ring RA, Reimchen TE. 2009 The ecology of terrestrial invertebrates on Pacific salmon carcasses. *Ecol. Res.* **24**, 1091–1100. (doi:10.1007/s11284-009-0586-5)

32. Holtgrieve GW, Schindler DE, Jewett PK. 2009 Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. *Ecol. Res.* **24**, 1125–1135. (doi:10.1007/s11284-009-0591-8)
33. Hocking MD, Reimchen TE. 2006 Consumption and distribution of salmon (*Oncorhynchus* spp.) nutrients and energy by terrestrial flies. *Can. J. Fish. Aquat. Sci.* **63**, 2076–2086. (doi:10.1139/f06-110)
34. Hocking MD, Reimchen TE. 2002 Salmon-derived nitrogen in terrestrial invertebrates from coniferous forests of the Pacific Northwest. *BMC Ecol.* **2**, 4. (doi:10.1186/1472-6785-2-4)
35. Scharf FS, Juanes F, Sutherland M. 1998 Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* **79**, 448–460. (doi:10.1890/0012-9658(1998)079[0448:IERFTE]2.0.CO;2)
36. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009 *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.
37. Burnham KP, Anderson DR. 1998 *Model selection and multimodel inference: a practical information-theoretic approach*. New York, NY: Springer.
38. Grueber CE, Nakagawa S, Laws RJ, Jamieson IG. 2011 Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* **24**, 699–711. (doi:10.1111/j.1420-9101.2010.02210.x)
39. Gelman A. 2008 Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27**, 2865–2873. (doi:10.1002/sim.3107)
40. R Development Core Team. 2009 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <http://www.R-project.org>.
41. Mulder C, Cohen JE, Setälä H, Bloem J, Breure AM. 2005 Bacterial traits, organism mass, and numerical abundance in the detrital soil food web of Dutch agricultural grasslands. *Ecol. Lett.* **8**, 80–90. (doi:10.1111/j.1461-0248.2004.00704.x)
42. McGill BJ *et al.* 2007 Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol. Lett.* **10**, 995–1015. (doi:10.1111/j.1461-0248.2007.01094.x)
43. Morlon H *et al.* 2009 Taking species abundance distributions beyond individuals. *Ecol. Lett.* **12**, 488–501. (doi:10.1111/j.1461-0248.2009.01318.x)
44. Brown JH, Mehlman DW, Stevens GC. 1995 Spatial variation in abundance. *Ecology* **76**, 2028–2043. (doi:10.2307/1941678)
45. Ernest SKM. 2005 Body size, energy use, and community structure of small mammals. *Ecology* **86**, 1407–1413. (doi:10.1890/03-3179)
46. Woodward G, Hildrew AG. 2002 Body-size determinants of niche overlap and intraguild predation within a complex food web. *J. Anim. Ecol.* **71**, 1063–1074. (doi:10.1046/j.1365-2656.2002.00669.x)
47. Dinmore TA, Jennings S. 2004 Predicting abundance–body mass relationships in benthic infaunal communities. *Mar. Ecol. Prog. Ser.* **276**, 289–292. (doi:10.3354/meps276289)
48. Hocking MD, Reynolds JD. 2011 Impacts of salmon on riparian plant diversity. *Science* **331**, 1609–1612. (doi:10.1126/science.1201079)
49. Drake DC, Naiman RJ. 2007 Reconstruction of Pacific salmon abundance from riparian tree-ring growth. *Ecol. Appl.* **17**, 1523–1542. (doi:10.1890/06-1200.1)
50. Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH, Wall DH. 2004 Ecological linkages between aboveground and belowground biota. *Science* **304**, 1629–1633. (doi:10.1126/science.1094875)
51. Marquet PA, Quiñones RA, Abades S, Labra F, Tognelli M, Arim M, Rivadeneira M. 2005 Scaling and power-laws in ecological systems. *J. Exp. Biol.* **208**, 1749–1769. (doi:10.1242/jeb.01588)
52. Marczak LB, Thompson RM, Richardson JS. 2007 Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* **88**, 140–148. (doi:10.1890/0012-9658(2007)88[140:MTLHAP]2.0.CO;2)
53. Meehan EP, Seminet-Reneau EE, Quinn TP. 2005 Bear predation on Pacific salmon facilitates colonization of carcasses by fly maggots. *Am. Midland Nat.* **153**, 142–151. (doi:10.1674/0003-0031(2005)153[0142:BPOPSF]2.0.CO;2)
54. Lisi PJ, Schindler DE. 2011 Spatial variation in timing of marine subsidies influences riparian phenology through a plant–pollinator mutualism. *Ecosphere* **2**, 101. (doi:10.1890/ES11-00173.1)
55. Christie KS, Hocking MD, Reimchen TE. 2008 Tracing salmon nutrients in riparian food webs: isotopic evidence in a ground-foraging passerine. *Can. J. Zool.* **86**, 1317–1323. (doi:10.1139/Z08-110)
56. Christie KS, Reimchen TE. 2008 Presence of salmon increases passerine density on Pacific Northwest streams. *Auk* **125**, 51–59. (doi:10.1525/auk.2008.125.1.51)
57. Field RD, Reynolds JD. 2011 Sea to sky: impacts of residual salmon-derived nutrients on estuarine breeding bird communities. *Proc. R. Soc. B* **278**, 3081–3088. (doi:10.1098/rspb.2010.2731)