Canadian Journal of Fisheries and Aquatic Sciences
Journal canadien des sciences halieutiques et aquatiques

Getting Quantitative about Consequences of Cross-Ecosystem Resource Subsidies on Recipient Consumers

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2016-0242.R1
Manuscript Type:	Article
Date Submitted by the Author:	21-Jul-2016
Complete List of Authors:	Richardson, John; University of British Columbia, Wipfli, Mark; University of Alaska Fairbanks, Department of Biology and Wildlife
Keyword:	Allochthonous inputs, detritus, fish, resource pulse, subsidy

Getting Quantitative about Consequences of Cross-Ecosystem Resource Subsidies
on Recipient Consumers

John S. Richardson¹, Mark S. Wipfli²

¹ John.Richardson@ubc.ca, Department of Forest and Conservation Sciences, the University of
British Columbia, Vancouver, B.C., V6T 1Z4, Canada.

² mwipfli@alaska.edu, US Geological Survey, Alaska Cooperative Fish and Wildlife Research
Unit, Institute of Arctic Biology, University of Alaska Fairbanks, USA

Draft

Abstract

Most studies of cross-ecosystem resource subsidies have demonstrated positive effects on recipient consumer populations, often with very large effect sizes. However, it is important to move beyond these initial addition-exclusion experiments to consider the quantitative consequences for populations across gradients in the rates and quality of resource inputs. In our Introduction paper to this special issue, we describe at least four potential models that describe functional relationships between subsidy input rates and consumer responses, most of them asymptotic. Here we aim to advance our quantitative understanding of how subsidy inputs influence recipient consumers, and the communities they are part of. In the papers following, fish were either the recipient consumers or the subsidy as carcasses of anadromous species. Advancing general, predictive models will enable us to further consider what other factors are potentially co-limiting (e.g. nutrients, other population interactions, physical habitat, etc.) and better integrate resource subsidies into consumer-resource, bio-physical dynamics models.

Keywords

Allochthonous inputs, detritus, fish, resource pulse, subsidy

Introduction

The importance of cross-ecosystem resource subsidies has been recognised in a variety of ecosystems for decades. Leaf detritus or dissolved organic matter entering freshwater food webs, sea wrack decomposing on beaches, salmon returning from the oceans to freshwater, and the emergence of the adult stages of aquatic insects are all well-studied examples of cross-ecosystem resource subsidies. However, the synthesis of the topic by Polis et al. (1997) helped focus on the process and allowed for generalisations of this particular consumer-resource interaction across ecosystems. There is now theory available that allows for more formal consideration of population and community dynamics in response to these spatially subsidised, donor-controlled resource fluxes (e.g. Yang et al. 2008; Holt 2008; Takimoto et al. 2009). We now know that relative differences in primary productivity between adjacent habitats is not a sufficient predictor of which direction across ecosystem boundaries will result in impacts of subsidies on productivity of recipient consumers (Marczak et al. 2007a). However, if one considers directly comparable resource types (e.g. specific sizes of terrestrial prey and not simply all terrestrial prey), focussing on consumer-specific trophic levels and not just overall productivity, it will allow evaluation of the contributions of subsidies to recipient populations (Marczak et al. 2007a).

There have been a very large number of studies of the impacts of cross-ecosystem resource subsidies on recipient populations and communities (see Polis et al, 1997; Richardson et al. 2010). A long history of observation of the roles of subsidy inputs over the past century has evolved to a more quantitative approach, but there are still ways that this field can become more quantitatively predictive to test more refined hypotheses. In this introduction to our special issue we suggest possible advances from qualitative predictions about the responses to resource

subsidies (e.g., simply predicting increases), to predicting the magnitude of changes in productivity or population numbers of particular recipient populations. This would serve to facilitate empirical tests of the quantitative contributions of spatially subsidised, donor-controlled resources to population and community dynamics. In this paper we briefly review some examples of the progress made in recent decades towards understanding the consequences of resource subsidies for populations of recipient consumers, and ways in which our predictions from hypotheses could be more quantitative. In the second half of the paper we introduce the papers included in this special issue, and then end with considerations of ideas to serve as guidance for future research.

Consumer responses to natural variation in subsidy input rates

Many studies have noted the importance of cross-ecosystem resource subsidies, from observations of terrestrial prey in consumer stomachs to the large numbers of obligate detritivorous organisms in freshwaters (e.g., Polis et al. 1997). Such observations have many decades of history. In the past several decades, more and more studies have observed that in general populations of consumers are more abundant or productive where subsidy inputs are higher.

In general, recipient populations generally show a positive relation in terms of growth, density or population biomass as resource subsidy input rate increases. For instance, Swain et al. (2014) showed a positive relation of invertebrate densities, algae and sculpin densities along a gradient of long-term escapement numbers of spawning Sockeye Salmon in central British Columbia. Wipfli and Musselwhite (2004) and Piccolo and Wipfli (2002) demonstrated higher rates of invertebrate subsidies from upland forested streams to downstream habitats as riparian

alder increased in coastal Alaska. Similarly, reductions in subsidy inputs can have negative consequences for recipient ecosystems. Gergs et al. (2014) showed that densities of an invasive, non-native amphipod in the Rhine River were negatively associated with the rates of emergence of adult aquatic insects, and was linked to lower densities of terrestrial spiders.

Quantitative effects of experimental manipulations

There are many experimental studies of the addition or exclusion of a large diversity cross-ecosystem resource subsidies. For instance, experimental additions (e.g., Richardson 1991) or exclusion (e.g., Wallace et al. 1999) of leaf litter to streams have demonstrated that detritus is an important subsidy resource for particular consumer populations and overall productivity of streams. Additions or removal of sea wrack on small Caribbean islands has shown that this too is a key resource affecting recipient populations (e.g., Piovia-Scott et al. 2011). Exclusion of terrestrial arthropods from dropping into a stream resulted in reduced growth and shifts in foraging by trout (Nakano et al. 1999), and exclusion of nematomorph-infected crickets from streambanks resulted in much lower growth rates of char compared to control reaches (Sato et al. 2011). Exclusion of adult aquatic insects from riparian areas show many web-building spiders use this resource (Marczak and Richardson 2007). However, almost all of these manipulations have been binary, i.e. addition or exclusion of some cross-ecosystem resource subsidy relative to an ambient “control”.

Some examples of manipulations to create experimental gradients of subsidy input rates have appeared in recent years. Wipfli et al. (1998, 1999) demonstrated that biofilm growth and densities of benthic invertebrates were positively related to the amount of salmon carcass added to experimental streams in Alaska. Manipulation of input rates of periodical cicadas to pond

mesocosms demonstrated a positive response of biofilms and consumers along the input gradient (Nowlin et al. 2007). Klemmer and Richardson (2012) created a gradient of leaf litter abundance in cages in a lake with or without trout present, and demonstrated a positive and generally asymptotic response in the numbers of detritivores. Jones and Lennon (2015) created an experimental gradient in the concentrations of dissolved organic carbon (DOC) in a series of ponds, which led to increased bacterial productivity along that concentration gradient, although overall system productivity was hump-shaped due to the light attenuation effect of colored DOC and reduced primary productivity. What is missing from the literature is a more general predictive framework of how populations could respond to quantitative differences or variation in the input rates of subsidy resources.

Yang et al. (2008) and Holt (2008) have developed models to predict how the subsidy pulse duration relative to the generation time of the consumer, as well as the pulse magnitude would result in consumer population responses. Many studies have used short-term pulses in experiments. However, we still need to do more to scale these subsidy pulses in ways that can be incorporated into consumer-resource dynamics and models, such as those mentioned above (Yang et al. 2008; Holt 2008).

Conversion efficiency: another way of looking at responses to subsidies

The majority of these studies have not considered the rates of increase in the relations of consumer population response relative to subsidy inputs in terms of whether they are proportional to some conversion rate such as assimilation efficiency. That is, one might be able to examine the slope of the input rate (energy or biomass) versus response (functional response or numerical response) of consumer biomass. By definition the slope must be <1.0 , but the slope

would be predicted to be very much smaller than 1.0 for detritivores than for stream fishes eating terrestrial prey. For instance, Mehner et al. (2016) found that consumers incorporated only 5% of inputs of particulate organic matter to lakes, a very low ecological efficiency. Such uses of conversion efficiencies are common to ecosystem energetics models. However, to date this approach has not been used much for quantifying responses of recipient consumer populations to subsidy resources.

Alternate trajectories of consumer population responses to subsidy input rates

As discussed above, experimental studies of resource subsidies have primarily used exclusion or addition of a single treatment level to test for recipient consumer responses. From such studies, one would initially draw a straight line from the ambient rates to the manipulated rates, with relatively little consideration of how the responses might vary with response to different rates of subsidy inputs (Figure 1). As a first approximation this first model assumes a linear response over the natural range of subsidy inputs. Few studies have considered whether these relations are linear across the full range of natural variation of input rates, which might be unlikely as other processes begin to limit or co-limit recipient responses, for instance, space limitation or limitation by other resources, or even build up of predators and pathogens (Figure 1). This would lead to a non-linear response of consumer populations to increasing subsidy input rates.

It is likely that the shape of the consumer populations' response surface might be asymptotic as our second suggested curve (Figure 1), as proposed by Richardson (1993). Several examples of such relations have been published. Wipfli et al. (1999) experimentally demonstrated an asymptotic response of algae and freshwater invertebrates to incremental

increases of salmon subsidies in experimental channels and a small natural stream in Alaska. Dose-response relationships at broader spatial and temporal scales would advance our understanding of quantitative subsidy effects on consumers and ecosystems.

As a third option, response surfaces to subsidy inputs could be sigmoid, which would line up with the large literature on prey switching found in the predation literature (e.g., Townsend et al. 1986). The switching curve (sigmoid) may reach an asymptote for many potential reasons, the most obvious would be the co-limitation of other variables (as in model 2 above), but could also be limited by functional responses within generations of longer-lived recipient species, or even by top-down control by predators. Sato and Watanabe (2014) showed that as input rates of terrestrial prey increased, stream fishes switched from *in situ* prey to the terrestrial prey, but at low prey input rates they did not feed on subsidy prey.

Another potential recipient response function to subsidy inputs could be hump shaped, stimulating at low input rates and toxic at high rates (Figure 1), consistent with the subsidy-stress gradient hypothesis. This hypothesis was proposed for the non-linear responses in a population or community across a gradient of inputs (Odum et al. 1979). Most of these inputs were regarded as stimulating to recipient systems at low to moderate input rates, but stressful at higher input rates leading to deceleration of the productivity of the recipient. The form of this relation is shown as a hump-shaped response curve along the gradient. It is easy to appreciate this when one considers the inputs of nutrients which could be stimulating at low concentrations, assuming a nutrient-limited system, and becoming toxic at high concentrations (Odum et al. 1979). For instance, an example of this is to be found in Woodward et al. (2012) showing that modest inputs of nutrients (N and P) to streams stimulated decomposition rates of terrestrial leaf litter and input to food webs, whereas high concentrations decreased decomposition rates, presumably through

toxicity of high N concentrations. Another example of this hump-shaped response surface was demonstrated in an experimental manipulation of DOC to ponds (Jones and Lennon 2015). In that experiment increased concentrations of DOC led to increases in bacterial production increasing along the entire gradient of DOC additions. However, the increase in microbial production was more than offset in the other direction by light attenuation due to the colored DOC, and thus beyond a peak response at low concentrations of DOC, measures of zooplankton, chlorophyll *a* and respiration declined due to reduced primary production (Jones and Lennon 2015). Another example where a potential marine subsidy can become lethal comes from Southeast Alaska and shows how too many returning adult pink salmon can rapidly deplete stream O₂ concentrations (Leon Shaul, Alaska Dept of Fish and Game, personal communication) (Figure 2). In this case not only does the potential subsidy die prior to spawning, but it causes extensive mortality in the recipient consumers (juvenile coho salmon in this case). Although apparently rare, these types of die-offs appear to be happening more frequently in some areas with strong salmon returns, coupled with warm and sunny (summer), low-water periods.

It is possible that there could be other consumer-resource responses for recipient populations, but these four cover the primary dynamical outcomes. Of course, there are many potential higher-order consequences at a community level, driven through trophic and indirect interactions. For instance, terrestrial arthropods eaten by stream fishes can lead to trophic cascades as pressure on *in situ* resources is relaxed (e.g. Nakano et al. 1999; Sato et al. 2016). Additional prey as a result of sea wrack can reduce predation pressure by island lizards on herbivorous insects leading to indirect effects from a subsidy resource at the shoreline resulting in benefits to plants (Piovia-Scott et al. 2011). There are several other very good examples of community-level effects, directly and indirectly resulting from subsidy inputs, but it is not our

purpose to review all those here. Resource subsidies could also be potentially destabilising as biomass of a subsidised population returns to feeding on *in situ* resources and potentially over-consuming instantaneous production (Yang et al. 2008). Nowlin et al. (2007) and Jones and Lennon (2015) showed that increased subsidy inputs (cicada carcasses and DOC concentration, respectively) resulted in decreased stability across an intermediate level of subsidy input rates. A large range of community and ecosystem-level dynamics may be influenced by cross-ecosystem resource subsidies, and this is a topic for continuing research.

In Richardson and Sato (2015) there were 5 key questions posed regarding future directions of the study of cross-ecosystem resource subsidies. These included questions of duration and magnitude (e.g., Yang et al. 2008), resource quality (size, nutritional value, protective chemicals, etc. (e.g., Marcarelli et al. 2011)), influence on intensity of trophic cascades, and impacts on recipient system stability. The final question was about quantitative predictions, the subject of this special issue of the Canadian Journal of Fisheries and Aquatic Sciences. We now have sufficient knowledge of these processes that we should be able to become more quantitative about our predictions and in our studies of consumer population responses.

Special Issue

In this special issue we include eight papers presented at a special symposium of the annual American Fisheries Society meeting in August, 2015. These papers present examples of consumer responses to cross-ecosystem resource subsidies, including to and from streams and lakes. All of these papers involve either fish as the recipient consumer or their carcasses as the

subsidy, and these studies demonstrate the range of ways subsidy resources affect consumer populations and their communities.

Although there have been many studies of cross-ecosystem resource subsidies with salmonids either as the subsidy (carcasses of anadromous species) or the consumer, they are not the only group of fishes that are involved in these dynamics. As Weaver et al. (this issue) show, Atlantic lamprey returning to east coast streams can contribute to a pulse subsidy of nutrients and biomass to streams. Weaver et al. (this issue) demonstrated that experimental additions of lamprey carcasses along a stream reach enhanced the local productivity of a stream food web by alleviating nutrient limitation of biofilms through increased N as ammonium from the carcasses. Moreover, along their experimental study reach they were able to show increasing concentrations of ammonium as the cumulative totals of lamprey carcasses increased, with concomitant patterns in algal biomass. The slope of the line relating algal biomass to cumulative lamprey biomass was very shallow ($\ll 1$) suggesting other factors limited the potential for this subsidy to limit the potential for increases due the subsidy inputs.

Subsidies are not just important in small streams. As Rine et al. (this issue) demonstrated, terrestrial (invertebrates) and marine (salmon carcasses) subsidies provide measurable trophic contributions to juvenile Coho Salmon and Chinook Salmon along a 97-km stretch of a large, complex glacial river in Alaska. These contributions varied relative to each other and seasonally, and were secondary to freshwater food resources, with the main periods of benefits during summer and early autumn. Moreover, the relative contributions of these subsidy resources varied spatially along habitat units in this large and complex river, and illustrates the importance of considering the broader portfolio of energy and nutrient sources and type, and how they vary across time and space. Most past studies have not taken into account this broader quantitative

view of prey source and utilization across complex habitat mosaics of large floodplain rivers, as shown by Rine et al. (this issue). Li et al. (this issue) also provide evidence for spatial variation (tributaries versus larger streams) and a strong seasonal difference in biomass of terrestrial invertebrates ingested (mass-specific rates) by cutthroat trout and steelhead, despite no sign of differences in growth rates as a result.

Mejia et al. (this issue) used experimental enclosures to assess juvenile Chinook Salmon growth at areas identified as groundwater inflow, streamwater outflow, or neutral sites to factor out temperatures, nutrients and DOC as variables that could contribute to groundwater impacts on instream productivity. Fish enclosed at groundwater inflows had nearly twice the growth rate of fishes at the losing sites, supported by much higher GPP and benthic biomass, as well as by warmer temperatures in this spring-time experiment. This provides another example of how the physical environment interacts with subsidy resources to influence responses of recipient consumers.

Smits et al. (this issue) found that growth rates of Coho Salmon juveniles were related to presence of Sockeye Salmon carcasses (and their eggs), but that the response was modulated by stream temperatures. By using several years' worth of data across seven streams with natural variation in temperatures and Sockeye spawner densities, they used this natural variation to link subsidy supplies and temperatures to consumer responses. However, density of spawning Sockeye Salmon was not a significant contributor to Coho responses, only the presence or absence of Sockeye spawners, which also contrasts with several past studies (e.g. Wipfli et al. 1998, Swain et al. 2014). This exemplifies that additional controls from the physical environment can interact with the subsidy input rates to influence the recipient population's response through variation in allocation of energy.

Boucek et al. (this issue) demonstrate that the rate of subsidy flows into rivers in Florida can vary as a consequence of annual weather patterns due to drought influencing distribution and abundance of invertebrate prey in floodplains that can enter the river. In floodplain river systems, fishes can exploit the floodplain during wet seasons, but following an extreme drought year, the biomass and types of prey available from floodplains was reduced by over 75%. This provides another example of controls of resource subsidies at the level of the donor system related to weather.

Changes in the quality and quantity of subsidies to streams of leaves and terrestrial invertebrates due to shifts in riparian species composition have been shown (e.g. Wipfli 1997, Marcarelli et al. 2011). Roon et al. (this issue) provide another example of how non-native species of riparian trees can alter the quantity (and perhaps timing) of terrestrial invertebrate inputs. Surprisingly, despite much lower input rates of terrestrial invertebrates in reaches with European Birdcherry, Roon et al. (this issue) found no significant differences in feeding rates of Coho Salmon juveniles in their Alaska streams, likely due to prey mixing above and within the stream.

Piovia-Scott et al. (this issue) develop a broad, conceptual model of the influence of two factors, trout presence and elevation, on the relative rates of fluxes of cross-ecosystem resources for lakes in the mountains of California. They demonstrate that elevation and fish presence (most often purposefully introduced) account for the majority of variance in a set of data for subsidy fluxes into and out of lakes. In their paper they provide quantitative estimates of fluxes of resource subsidies in both directions, to and from the lake ecosystems and consider the main hypotheses for the mechanisms by which these flows vary by trout presence and elevation (Piovia-Scott et al. this issue).

Discussion

As a more coherent body of theory develops around the consumer-resource dynamics of donor-controlled subsidy inputs, we should be able to develop a more quantitative approach to the interaction. Theory by Yang et al. (2008) and Holt (2008) scale inputs of subsidy resources by the magnitude and duration of the inputs relative to the consumer resource demand and generation time of the consumers, respectively. This kind of quantification is still missing from a great deal of the empirical research, although Marczak et al. (2007) used a meta-analysis to look at how the relative magnitude of inputs affected consumer populations. Rine et al. (this issue) have taken a step towards quantifying this for river salmonids, building on similar efforts by Wipfli and Baxter (2010). Further development of scaling properties will enable us to advance the ability to predict consumer population responses.

Emerging examples are suggesting that recipient responses are not simple and may interact with other factors, such as interactions in effect sizes from both concentrations and stoichiometry of nutrients in freshwater (Guesewell and Gessner 2009; Bellmore et al. 2014). And consumers vary in the types and sizes of subsidy resources they can use, illustrating that even within species, size classes may respond differently (e.g., Marczak et al. 2007b, Li et al. this issue, Piovia-Scott et al. this issue, Smits et al. this issue). In addition, the seasonal timing of subsidy inputs might be important to the responses by consumer populations (e.g. Sato et al. 2016).

Resource quality may be an important additional factor. There have been many studies over the years of how differences in leaf litter quality affects breakdown rates and rates of consumption by consumers. Knowing input rates, along with quality, may enable us to better predict the consequences for productivity of consumer populations. This likely extends to the

species of terrestrial invertebrates falling into streams, and changes to the complement of species falling depending on the type of vegetative canopy, for instance as seen in Roon et al. (this issue). Quality may include nutritional quality, but it can also include size. For instance, large prey may be differentially eaten in contrast to smaller prey (e.g. Marczak et al. 2007b, Li et al. this issue).

Studies of cross-ecosystem resource subsidies often note that there are flows of resources in both directions across boundaries. These are rarely reciprocal in the sense of creating a positive feedback loop. However, it is rare to have detailed studies such as that Piovita-Scott et al. (this issue) provide, estimating how these flows vary into and out of lakes based on trophic structure (presence of trout) and elevation. More system-wide and quantitative studies of flows in both directions would be informative, as well as explicit consideration of the full range of direct and indirect effects within communities.

The field still needs to develop additional studies to look at the form of the response curves of recipient consumers to different rates of subsidy flows. There is an opportunity to advance the theory in the context of consumer-resource dynamics, and consider the additional feedbacks on population controls associated with co-limitation, density dependence, and additional community interactions, such as predation rates. Cross-ecosystem resource subsidies provide a potentially powerful experimental model for learning about consumer-resource dynamics in a donor-controlled system, where the resource input rates to the system are not controlled by the consumer.

Changes in the timing, magnitudes, and quality of resource subsidy flows due to land use, climate change, and invasive species could lead to unpredicted, and potentially unwanted, outcomes for consumers and their communities. For instance, the temperature dependence of

juvenile salmon responses to salmon carcasses (Smits et al. this issue) or groundwater inflows (Mejia et al. this issue), or the change in terrestrial arthropod inputs from invasive, non-native plants taking over riparian areas (Roon et al. this issue) are just a couple of examples of how impacts of resource subsidies could be altered. This match-mismatch hypothesis has been the focus of a great deal of climate change research, and the potential for shifts in the phenology of cross-ecosystem resource subsidy flows as a result of changes to plant composition and climate change might also alter the responses of recipient populations.

The community and food-web effects of subsidies are being increasingly noted. As several authors have demonstrated, subsidies (or their exclusion) can lead to trophic cascades and other community level impacts (e.g. Nakano et al. 1999; Sato et al. 2016). There are certainly many examples of subsidies boosting production at lower trophic levels that contribute to bottom-up increases at higher trophic levels (e.g. Wallace et al. 1999; Wipfli et al. 1999). Other considerations of how subsidies might contribute to, or reduce, stability are emerging (e.g. Rosenzweig 1971; Nowlin et al. 2007; Jones and Lennon 2015).

Appreciation of the roles of cross-ecosystem resource subsidies as a flow to recipient consumers requires that one correctly identify what limits populations in the first place. At some input rates subsidy resources are predicted to become excess and consumer population responses would be asymptotic, or even hump-shaped. However, resource subsidies may have no impact on consumers if equivalent resources are available and not limiting. In many instances, other resources might be the primary constraint on consumer populations, or other resources may be co-limiting (e.g. Sperfeld et al. 2016). The latter does lead to the question of how such resource flows might contribute to the recipient community if the target consumer does not use them. It is worth considering other consumers and pathways for these resource flows even when the

putative target consumer shows no response. Better understanding the interactions of subsidy resources with constraints based on other resources would be another possible research need.

The papers in this special issue address some of the large range of possible responses by consumer populations. There is still a large scope for advancing this field by linking subsidy resources to consumer-resource dynamics and considering how input rates affect population and community responses depending on rates and quality of inputs, as well as aspects of timing relative to consumer life cycles and duration of the inputs. Quantitative models can provide a tool to consider how subsidy inputs to one trophic level might influence the dynamics at the community level, since most published studies are of durations too short to adequately determine responses at other trophic and ecosystem levels, and longer-term effects.

Acknowledgements

We thank the many reviewers who commented on the earlier versions of papers included here. We are grateful to Ryan Bellmore for his detailed review of our manuscript. We also thank Leon Shaul and Amy Hemenway with Alaska Dept of Fish and Game for use of photos and their insights on relationships between subsidy input rates, water temperature, biological oxygen demand, and juvenile salmon mortality. Our research is funded by grants from the Natural Sciences and Engineering Research Council (Canada) to JSR, and from US Geological Survey and NSF-EPSCoR to the University of Alaska.

References

- 386 Bellmore, J.R., Fremier, A.K., Mejia, F., and Newsom, M. 2014. The response of stream
387 periphyton to Pacific salmon: using a model to understand the role of environmental context.
388 Freshwat. Biol. **59**: 1437-1451.
- 389 Boucek, R.E., Soula, M., Tamayo, F., and Rehage, J.S. A once in ten year drought alters the
390 magnitude and quality of a floodplain prey subsidy to coastal river fishes. Can. J. Fish.
391 Aquat. Sci. this issue.
- 392 Gergs, R., Koester, M., Schulz, R.S., and Schulz, R. 2014. Potential alteration of cross-
393 ecosystem resource subsidies by an invasive aquatic macroinvertebrate: implications for the
394 terrestrial food web. Freshwat. Biol. **59**: 2645–2655.
- 395 Guesewell, S., and Gessner, M.O. 2009. N : P ratios influence litter decomposition and
396 colonization by fungi and bacteria in microcosms. Functional Ecol. **23**: 211-219.
- 397 Holt RD. 2008. Theoretical perspectives on resource pulses. Ecology **89**: 671–681.
- 398 Jones, S.E., and Lennon, J.T. 2015. A test of the subsidy-stability hypothesis: the effects of
399 terrestrial carbon in aquatic ecosystems. Ecology **96**:1550-1560.
- 400 Klemmer, A.J., and Richardson, J.S. 2013. Quantitative gradient of subsidies reveals a threshold
401 in community-level trophic cascades. Ecology **94**: 1920-1926.
- 402 Li, J., Gerth, W., Van Driesche, R., Bateman, D., and Herlihy, A. Seasonal and spatial
403 fluctuations in *Oncorhynchus* trout diet in a temperate mixed-forest watershed. Can. J. Fish.
404 Aquat. Sci. this issue.
- 405 Marcarelli, A.M., Baxter, C.V., Mineau, M.M., and Hall, R.O. Jr. 2011. Quantity and quality:
406 unifying food web and ecosystem perspectives on the role of resource subsidies in
407 freshwaters. Ecology **92**: 1215-1225.

- 408 Marczak, L.B., and Richardson, J.S. 2007. Spiders and subsidies: results from the riparian zone
409 of a coastal temperate rainforest. *J. Anim. Ecol.* **76**: 687-694.
- 410 Marczak, L.B., Thompson, R.M., and Richardson, J.S. 2007a. A meta-analysis of the role of
411 trophic position, habitat type and habitat productivity in determining the food web effects of
412 resource subsidies. *Ecology* **88**:140-148.
- 413 Marczak, L.B., Hoover, T.M., and Richardson, J.S. 2007b. Trophic interception: how a
414 boundary-foraging organism influences cross-ecosystem fluxes. *Oikos* **116**:1651-1662.
- 415 Mehner, T., Attermeyer, K., Brauns, M., Brothers, S., Diekmann, J., Gaedke, U., Grossart, H.-P.,
416 Köhler, J., Lischke, B., Meyer, N., Scharnweber, K., Syväranta, J., Vanni, M.J., and Hilt, S.
417 2016. Weak response of animal allochthony and production to enhanced supply of
418 terrestrial leaf litter in nutrient-rich lakes. *Ecosystems* **19**: 311–325.
- 419 Mejia, F.H., Baxter, C.V., Berntsen, E.K., and Fremier, A.K. Linking groundwater-surface water
420 exchange to food production and salmonid growth. *Can. J. Fish. Aquat. Sci.* this issue.
- 421 Nakano, S. Miyasaka, H., and Kuhara, N. 1999. Terrestrial-aquatic linkages: Riparian arthropod
422 inputs alter trophic cascades in a stream food web. *Ecology* **80**: 2435-2441.
- 423 Nowlin, W.H., González, M.J., Vanni, M.J., Stevens, M.H.H., Fields, M.W., and Valente, J.J.
424 2007. Allochthonous subsidy of periodical cicadas affects the dynamics and stability of
425 pond communities. *Ecology* **88**: 2174–2186.
- 426 Odum, E.P., Finn, J.T., and Franz, E.H. 1979. Perturbation theory and the subsidy-stress
427 gradient. *BioScience* **29**: 349-352.
- 428 Piovia-Scott, J., Spiller, D.A., and Schoener, T.W. 2011. Effects of experimental seaweed
429 deposition on lizard and ant predation in an island food web. *Science* **331**: 461-463.

- 430 Piovia-Scott, J., Sadro, S., Knapp, R.A., Sickman, J., Pope, K.L., and Chandra, S. Landscape-
431 level variation in reciprocal subsidies between lakes and watersheds: Perspectives from the
432 mountains of California. *Can. J. Fish. Aquat. Sci.* this issue.
- 433 Polis, G.A., Anderson, W.B., and Holt, R.D. 1997. Toward an integration of landscape and food
434 web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology*
435 *and Systematics* **28**: 289-316.
- 436 Richardson, J.S. 1993. Limits to productivity in streams: evidence from studies of
437 macroinvertebrates, p.9-15. *In*: Gibson, R.J., and Cutting, R.E. [Eds] *Production of juvenile*
438 *Atlantic salmon, *Salmo salar*, in natural waters.* Canadian Special Publication of Fisheries
439 *and Aquatic Sciences* **118**
- 440 Richardson, J.S., and Sato T. 2015. Resource flows across freshwater-terrestrial boundaries and
441 influence on processes linking adjacent ecosystems. *Ecohydrology* **8**: 406-415.
- 442 Richardson, J.S., Zhang, Y., and Marczak, L.B. 2010. Resource subsidies across the land-
443 freshwater interface and responses in recipient communities. *River Research and Applic.* **26**:
444 55-66.
- 445 Richardson, J.S. 1991. Seasonal food limitation of detritivores in a montane stream: an
446 experimental test. *Ecology* **72**: 873- 887.
- 447 Rine, K.M., Wipfli, M.S., Schoen, E.R., Nightengale, T.L., and Stricker, C.A. Trophic pathways
448 supporting juvenile Chinook and coho salmon in the glacial Susitna River, Alaska: patterns
449 of freshwater, marine, and terrestrial food resource use across a seasonally dynamic habitat
450 mosaic. *Can. J. Fish. Aquat. Sci.* this issue.

- 451 Roon, D.A., Wipfli, M.S., Wurtz, T.L., and Blanchard, A.L. Invasive European bird cherry
452 (*Prunus padus*) reduces terrestrial prey subsidies to urban Alaskan salmon streams. Can. J.
453 Fish. Aquat. Sci. this issue.
- 454 Rosenzweig, M.L. 1971. Paradox of enrichment: Destabilization of exploitation ecosystems in
455 ecological time. Science 171:385-387.
- 456 Sato, T., and Watanabe, K. 2014. Do stage-specific functional responses of consumers dampen
457 the effects of subsidies on trophic cascades in streams? J. Anim. Ecol. 83:907-915.
- 458 Sato, T., Watanabe, K., Kanaiwa, M., Niizuma, Y. Harada, Y and Lafferty, K.D. 2011.
459 Nematomorph parasites drive energy flow through a riparian ecosystem. Ecology **92**:201-
460 207.
- 461 Sato, T., El-Sabaawi, R., Campbell, K., Ohta, T., and Richardson, J.S. A test of the effects of
462 timing of a pulsed resource subsidy on stream ecosystems. J. Anim. Ecol. in press
- 463 Sperfeld, E., Raubenheimer, D., and Wacker, A. 2016. Bridging factorial and gradient concepts
464 of resource co-limitation: towards a general framework applied to consumers. Ecology
465 Letters **19**: 201-215
- 466 Smits, A.P., Schindler, D.E., Armstrong, J.B., Brett, M.T., Carter, J.L., and Santos, B.S. Thermal
467 constraints on stream consumer responses to a marine resource subsidy. Can. J. Fish. Aquat.
468 Sci. this issue.
- 469 Swain, N. R., Hocking, M.D., Harding, J.N., and Reynolds, J.D. 2014. Effects of salmon on the
470 diet and condition of stream-resident sculpins. Can. J. Fish. Aquat. Sci. **71**: 521–532.
- 471 Takimoto, G., Iwata, T., and M. Murakami. 2009. Timescale hierarchy determines the indirect
472 effects of fluctuating subsidy inputs on in situ resources. American Naturalist **173**:200-211.

- 473 Townsend, C.R., Winfield, I.J., Peirson, G., and Cryer, M. 1986. The response of young roach
474 *Rutilus rutilus* to seasonal changes in abundance of microcrustacean prey: a field
475 demonstration of switching. *Oikos* **46**: 372-378.
- 476 Wallace, J.B., Eggert, S.L., Meyer, J.L., and Webster, J.R. 1999. Effects of resource limitation
477 on a detrital-based ecosystem. *Ecol. Monogr.* **69**: 409–442.
- 478 Weaver, D., Coghlan, S., and Zydlewski, J. Sea Lamprey carcasses exert local and variable food
479 web effects in a nutrient-limited Atlantic coastal stream. *Can. J. Fish. Aquat. Sci.* this issue.
- 480 Wipfli, M.S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams:
481 contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. *Can.*
482 *J. Fish. Aquat. Sci.* **54**: 1259-1269.
- 483 Wipfli, M.S., and Musslewhite, J. 2004. Density of red alder (*Alnus rubra*) in headwaters
484 influences invertebrate and detritus subsidies to downstream fish habitats in Alaska.
485 *Hydrobiologia* **520**: 153-163.
- 486 Wipfli, M.S., and Baxter, C.V. 2010. Linking ecosystems, food webs, and fish production:
487 Subsidies in salmonid watersheds. *Fisheries* **35**: 373-387.
- 488 Wipfli, M.S., Hudson, J., and Caouette, J. 1998. Influence of salmon carcasses on stream
489 productivity: response of biofilm and benthic macroinvertebrates in southeastern Alaska,
490 U.S.A. *Can. J. Fish. Aquat. Sci.* **55**: 1503-1511.
- 491 Wipfli, M.S. Hudson, J.P., Chaloner, D.T., and Caouette, J.R. 1999. Influence of salmon
492 spawner densities on stream productivity in Southeast Alaska. *Can. J. Fish. Aquat. Sci.*
493 **56**:1600-1611.
- 494 Woodward, G., Gessner, M.O., Giller, P.S., Gulis, V., Hladyz, S., Lecerf, A., Malmqvist, B.,
495 McKie, B.G., Tiegs, S.D., Cariss, H., Dobson, M., Eloise, A., Ferreira, V., Graca, M.A.S.,

496 Fleituch, T., Lacoursiere, J.O., Nistorescu, M., Pozo, J., Risnoveanu, G., Schindler, M.,
497 Vadineanu, A., Vought, L.B-M., and Chauvet, E. 2012. Continental-scale effects of nutrient
498 pollution on stream ecosystem functioning. *Science* **336**: 1438-1440.

499 Yang LH, Bastow JL, Spence KO, Wright AN. 2008. What can we learn from resource pulses?
500 *Ecology* **89**: 621–634.

501 |

Draft

Figure captions:

Figure 1. Possible response surfaces of recipient populations (biomass, numbers or productivity) along a gradient of cross-ecosystem resource subsidy input rate. Dashed black line indicates the default outcome one derives from two points, assuming a linear consumer response to increases in subsidy input rates. The asymptotic red, solid line shows the potential pattern as some other resource or process becomes limiting or co-limiting to recipient consumers. The dashed magenta line indicates an expected response from a switching consumer (behavioral switch to subsidy resource as input rates increases). Finally, the green (dashed and dotted) line is consistent with the subsidy-stress hypothesis or other mechanism by which too much of a subsidy resource input could have negative consequences on population productivity.

Figure 2. Example of the impacts of too much subsidy leading to lethal outcomes, in this case through returning adult salmon exhausting the oxygen supply in a stream, killing spawning adults (the subsidy) and the resident juvenile Coho Salmon (the potential recipient). Photos courtesy of Amy Hemenway.

Figure 1. Possible response surfaces of recipient populations (biomass, numbers or productivity) along a gradient of cross-ecosystem resource subsidy input rate. Dashed black line indicates the default outcome one derives from two points, assuming a linear consumer response to increases in subsidy input rates. The asymptotic red, solid line shows the potential pattern as some other resource or process becomes limiting or co-limiting to recipient consumers. The dashed magenta line indicates an expected response from a switching consumer (behavioral switch to subsidy resource as input rates increases). Finally, the green (dashed and dotted) line is consistent with the subsidy-stress hypothesis or other mechanism by which too much of a subsidy resource input could have negative consequences on population productivity.

Photo: Amy Hemenway

532

Photos: Amy Hemenway

533

534 **Figure 2.** Example of the impacts of too much subsidy leading to lethal outcomes, in this case
535 through returning adult salmon exhausting the oxygen supply in a stream, killing spawning
536 adults (the subsidy) and the resident juvenile Coho Salmon (the potential recipient). Photos
537 courtesy of Amy Hemenway.

Draft