

Quantitative gradient of subsidies reveals a threshold in community-level trophic cascades

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Abstract. Evidence varies on how subsidies affect trophic cascades within recipient food webs. This could be due to complex nonlinearities being masked by single-level manipulations (presence/absence) of subsidies in past studies. We predicted that trophic cascade strength would increase nonlinearly across a gradient of subsidies. We set out to reveal these complex, nonlinear relationships through manipulating a quantitative gradient of detrital subsidies to lake benthic food webs along with the presence/absence of trout. Contrary to our prediction, we found that trophic cascades only occurred at low subsidy levels, disappearing as subsidies increased. This threshold in trophic cascade strength may be due to an increase in intermediate predators in the absence of top predators, as well as changes in the proportion of armored vs. un-armored primary consumers. Future studies on the effect of subsidies on trophic cascade strength need to incorporate naturally occurring gradients to reveal the complex direct and indirect interactions within food webs.

Key words: allochthonous material; benthic; cross-ecosystem; freshwater; indirect effect; lake; nonlinear effects; subsidy; threshold; top-down processes; trophic cascade.

INTRODUCTION

Donor-controlled materials and organisms that move across ecosystem boundaries (subsidies) are accepted as an integral part of the composition and function of recipient ecosystems (Polis et al. 1997, Baxter et al. 2005, Richardson et al. 2010). The classic examples of subsidies, such as kelp detritus on beaches or spawning salmon transferring marine-derived nutrients upstream (Spiller et al. 2010, Wipfli and Baxter 2010), are now known to influence interactions with the recipient community (Sabo and Power 2002, Marczak et al. 2007, Yang et al. 2010). Subsidies have bottom-up effects on consumers at multiple levels that influence communities beyond the controls of in situ production (Polis and Strong 1996). Besides direct effects on consumers, subsidies may influence food-web dynamics, such as trophic cascades where predators indirectly influence in situ producers (Nakano et al. 1999, Knight et al. 2005, Piovia-Scott et al. 2011).

Consumer–resource models predict stronger trophic cascades with an increase in the supply of subsidies because of increased bottom-up resources (Huxel and McCann 1998, Leroux and Loreau 2008). However, empirical studies show varied responses of trophic cascade strength to increased subsidies. Not only do subsidies that enter the food web at different trophic

levels cause different responses in trophic cascade strength (e.g., compare Nakano et al. 1999 and Nystrom et al. 2003), but there are also varied responses in trophic cascade strength between studies that investigated subsidies entering at the same trophic level (Nakano et al. 1999, Henschel et al. 2001, Halaj and Wise 2002, Piovia-Scott et al. 2011).

The differences in empirical results could be due to simplifications that do not reflect the range of processes, or the complex relations (nonadditivities, nonlinearities, and so on) by which consumer–resource dynamics operate in communities. One simplification is the binary manipulation of a subsidy through either completely removing it from a system or adding it in a single quantity. In nature, subsidy input rates often differ along a continuous gradient and can be patchy in abundance in both space and time (Minshall et al. 1983, Hoover et al. 2006, Wesner 2010). The natural gradient in the amount of resource can affect population abundances and reproduction as well as the behavior of organisms within a community (Yang et al. 2010). These interactions may lead to complex, nonlinear changes in trophic cascade strength along a gradient of subsidy input rates. Therefore, manipulation of subsidies by a single level may not reflect the full range of dynamics, and likely tells only a part of the story. Although theoretical models have addressed the effects of gradients of subsidies on food webs (Huxel and McCann 1998, Leroux and Loreau 2008), they use simplified food webs that are most applicable to “species-level” trophic cascades that occur in compartments or chains of food webs (Polis et al. 2000). In

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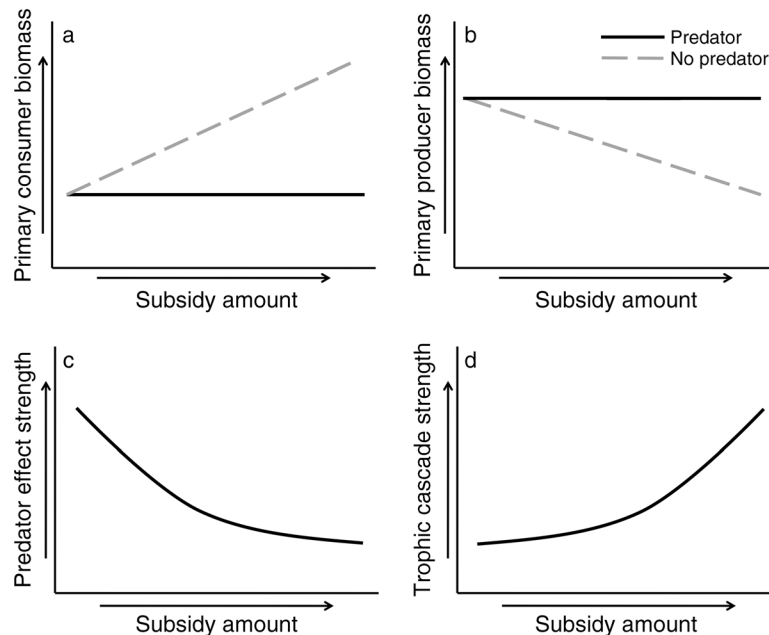


FIG. 1. Predictions of how increasing subsidy amount affects response variables: (a) primary consumer biomass and (b) primary producer biomass in the presence/absence of predators and (c) direct effects of predators on primary consumers (predator effect strength) and (d) indirect effects of predators on primary production (trophic cascade strength). When calculated as log ratios from two linear regressions, predator effect strength and trophic cascade strength are predicted to be nonlinear.

whole, empirical food webs, the effects of predators on complete animal and plant communities (made up of multiple compartments and chains) are crucial in understanding whether there is top-down control in the whole food web. Therefore, it is important to describe “community-level” or whole food-web trophic cascades (Polis et al. 2000). Incorporating these complexities into theoretical and empirical studies is the next step in revealing possible nonlinear effects of subsidies on trophic cascade strength.

The purpose of this study was to investigate whether trophic cascade strength changes along a quantitative gradient of subsidy input. We conducted an in-lake cage experiment in which we manipulated the presence/absence of a top predator (trout) and the biomass of alder detritus, as leaf litter subsidies are a crucial resource to consumers in many freshwater ecosystems (Richardson 1991, Wallace et al. 1999, Solomon et al. 2008, Klemmer et al. 2012). We hypothesized that, in the absence of trout, an increase in detritus resources would increase primary consumer biomass (Fig. 1a), and therefore decrease algal biomass (Fig. 1b). However, in the presence of trout, the suppression of primary consumers would negate any positive influence of increasing detritus on primary consumer biomass (Fig. 1a) and subsequent reductions in algal biomass (Fig. 1b). This would lead to a nonlinear decrease in predator effect strength on primary consumers (Fig. 1c) and nonlinear increase in trophic cascade strength with subsidies (Fig. 1d).

METHODS

Study site

Our study took place at Marion Lake in the Malcolm Knapp Research Forest (MKRF; 49°18'35" N, 122°32'58" W) in the Coast Mountain Range of British Columbia, Canada. MKRF is a temperate rainforest with the main canopy consisting of western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), and Douglas-fir (*Pseudotsuga menziesii*) with deciduous trees such as red alder (*Alnus rubra*) and vine maple (*Acer circinatum*) around riparian zones (Kominoski et al. 2011). Marion Lake, which is a shallow (maximum depth 7 m) oligotrophic lake at an altitude of 300 m, is described in detail by Winterbourn (1971).

Experimental design

In October 2010, we placed 30 experimental cages (0.81 m² surface area, 0.50 m height) along the western shore ~1 to 2 m from shore, ~0.25 m apart, and in ~0.25 m water depth. The bottom and sides of the cages were covered with 1-cm mesh screening to allow for open colonization and movement of lake benthic organisms, yet contain added leaf detritus. The tops of the cages were covered with 0.3-cm mesh screening to prevent trout escape and the input of additional leaf subsidies from the terrestrial ecosystem. The experiment was designed as a replicated regression (Cottingham et al. 2005) with three replicates of each of five amounts of leaf detritus (0, 6.2, 12.3, 24.7, and 49.4 g/m²), representing the natural range of variation in detritus

standing stocks. Leaf input was crossed by the presence or absence of cutthroat trout (*Oncorhynchus clarkii*) (~10-cm fork length). Treatments were randomly assigned to the cages. Cages were pushed into lake sediment with three large rocks inside to provide substrate.

Red alder leaves (*Alnus rubra*) were gathered after senescence in October 2009 from alder trees around the University of British Columbia's campus (Vancouver, Canada) and air dried for 11 months. In September 2010, the appropriate detritus density was added to each of the cages and allowed to inoculate for 7 d to encourage microbial colonization of the detritus and benthic invertebrate colonization of the cages. The experiment was initiated on 1 October 2010, when one cutthroat trout was added to half of the cages.

The experiment ran for 25 d, after which the cages were removed from the lake by sliding a 1-mm mesh net around the cages to capture the benthic invertebrate community. All coarse detritus (>1 mm; Appendix A) and invertebrates were frozen until processing. Any three-spined sticklebacks (*Gasterosteus aculeatus*) that were found in the cages at the end of the experiment were counted and released back into the lake, and the cutthroat trout were returned to their original habitat.

Benthic invertebrate composition

Invertebrate samples were thawed, separated from the detritus, and preserved in 70% ethanol. Individuals were then measured (length of body or width of shell) using an optical micrometer and identified to genus where possible (Cannings and Stuart 1977, Thorp and Covich 1991, Wiggins 1996, Merritt et al. 2008). Taxa were assigned to feeding groups, i.e., primary consumers and predatory invertebrates (Merritt et al. 2008). The primary consumer group included invertebrates that feed on algae and/or detritus. The dry mass and biomass of each individual was estimated using length–mass regressions (Appendix B: Table B1).

Benthic algal biomass

Three 25-cm², non-glazed, ceramic tiles were placed in the southwest corner of each cage one week prior to the start of the experiment to pre-colonize. Tiles were removed at the end of the experiment to measure net benthic algae chlorophyll *a* (chl *a*) biomass and frozen at –18°C until analysis. The tiles were processed for chlorophyll *a* (chl *a*, as mg/m²; using U.S. EPA method 445.0) with a Turner Designs fluorometer (model TD-700, Sunnyvale, California, USA). The average of the three tiles was used for cage chl *a*.

Trophic cascade strength

Relative predator (trout) impact on the adjacent (primary consumer invertebrates, predator effect strength) and nonadjacent trophic level (benthic algae biomass, trophic cascade strength) was calculated using

log ratio to estimate trophic cascade strength (Shurin et al. 2002, Leroux and Loreau 2008):

$$\log \text{ratio} = \ln(RV_1/RV_0)$$

where RV is the response variable (chl *a* or primary consumer invertebrates) in cages with trout (RV₁) and without trout (RV₀). Treatment means of the response variables were used to calculate log ratios. Positive/negative values indicate a positive/negative (respectively) effect on response variables. Larger values indicate strong predator regulation.

Statistical analyses

The effect of increasing subsidy inputs on response variables (chl *a*, primary consumer dry mass, snail-only density, and primary consumer invertebrate density without snails ["density without snails"]) for predator (trout) and no-predator (no trout) treatments were analyzed using analysis of covariance (ANCOVA) with predator presence as the categorical variable, and detritus subsidy input as the continuous variable, along with the predator by subsidy interaction. Response variables were subsequently analyzed with separate linear regressions for predator and no-predator treatments and for nonsignificant regressions means were reported on graphs. The relationship between predator effect strength and trophic cascade strength was analyzed using linear regression. All assumptions of normality and equal variance were met. All statistical analyses were conducted using R (R Development Core Team 2011).

RESULTS

Predator presence increased primary consumer biomass to four times greater than the no-predator treatment at the highest subsidy input level. Yet without predators, there was no significant change in primary consumer biomass with increasing subsidies (Fig. 2a, Table 1b). The direct effect of predators on primary consumers (predator effect strength) was highest in the high subsidy treatments (Fig. 2c). At the lowest subsidy inputs, chl *a* in predator treatments was twice that in the no-predator treatments. But, past the threshold, in treatments with ≥12.4 g of detritus inputs, predators had a significant negative impact on chl *a* compared to no-predator treatments. In the absence of trout, there was no significant effect of detritus on chl *a* (Fig. 2b, Table 1a). The indirect positive effect of trout on chl *a* (trophic cascade strength) was only present at no-subsidy and lowest subsidy treatments (Fig. 2d). The negative relationship between predator effect strength and trophic cascade strength was significant ($P = 0.03$, $r^2 = 0.83$).

Predatory invertebrate density increased (Table 1c, Fig. 3a) and stickleback density decreased (Appendix C: Fig. C1) with subsidies but with no effect of trout, although we observed a trend of certain predatory invertebrate taxa decreasing with trout (Appendix D:

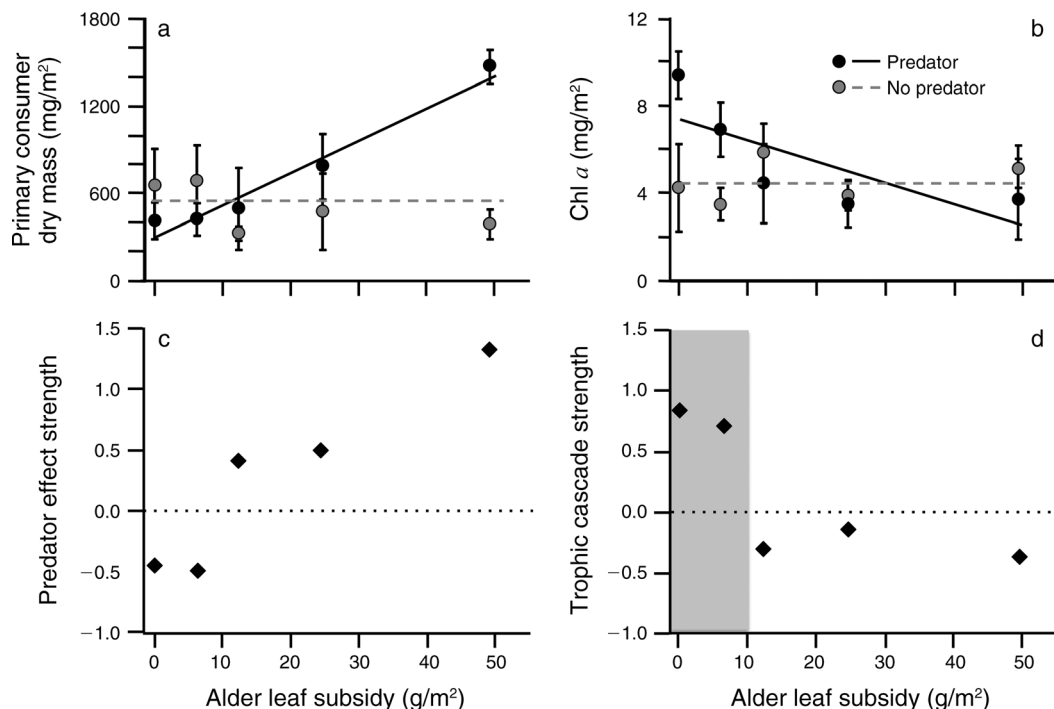


FIG. 2. Effect of alder leaf detritus on (a) primary consumer invertebrate dry mass, (b) chlorophyll *a*, (c) predator effect strength (log ratio of means of predator and no-predator treatments for primary consumer invertebrates), and (d) trophic cascade strength (log ratio of means of predator and no-predator treatments for chl *a*; the gray box indicates presence of trophic cascade). Data presented on graphs for panels (a) and (b) are treatment means \pm SE with black solid lines representing linear regressions for predator treatments and gray dashed lines representing treatment average for the no-predator treatment. The dotted line at 0 in panels (c) and (d) indicates the difference between positive and negative effects of predators.

Fig. D1). Increasing subsidies had a significant positive effect on snail density with predators present, but no effect when predators were absent (Table 1d, Fig. 3b). However, increasing subsidies had no effect on total primary consumer density when snails were excluded ("without snails") in predator and no-predator treatments (Table 1e, Fig. 3c). At the highest subsidy level without trout, snail density was lower than the density of the rest of the primary consumer community, whereas with trout snails dominated the primary consumer assemblage.

DISCUSSION

We predicted that trophic cascade strength would increase with an increased supply of subsidy. Without predators, primary consumer numbers would increase with subsidies, which would decrease algal biomass. With predators, primary consumer numbers would be suppressed, therefore releasing algal biomass from grazing. However, the trends we observed in our experiment were opposite of our predictions; only the no-subsidy and the lowest subsidy treatments showed strong positive indirect effects of predators on algae (trophic cascade). Conversely, the three highest detritus treatments did not demonstrate positive indirect effects of predators on algal biomass. This threshold in trophic cascades between low and high subsidies was unexpected

and reveals how abrupt changes in species interactions can be along a gradient in resources quantity (Polis and Hurd 1996, Nakano et al. 1999, Leroux and Loreau 2008).

Trophic cascade strength

Theoretical and empirical studies have provided mixed results on how subsidies affect trophic cascade strength; with inputs of subsidies, some provide evidence for increases in trophic cascade strength while others provide evidence for decreasing trophic cascade strength (Polis and Hurd 1995, Nakano et al. 1999, Halaj and Wise 2002, Leroux and Loreau 2008). These discrepancies may be due to a single-level manipulation of subsidies. In the context of our findings, a comparison between the two lowest subsidy levels vs. the lowest and highest subsidy levels reveals different results (no change in trophic cascade strength vs. a decrease in trophic cascade strength, respectively). Only studying two subsidy levels may miss the nonlinear complexities, resulting in different interpretations.

We observed a positive effect of predators on algal biomass at 0 and 6.2 g/m² of subsidies. However, the change from 6.2 to 12.3 g/m² of subsidies created a switch from a positive indirect effect of trout on algae to no, or even negative, indirect effects. The threshold we observed in the trophic cascade strength was mirrored in

TABLE 1. Linear models for (a) chlorophyll *a*, (b) primary consumer dry mass, (c) ln(predatory invertebrate density), (d) snail density, and (e) primary consumer invertebrate density when snails were excluded ("density without snails").

Variable	Intercept	Slope	<i>F</i>	df	<i>P</i>	<i>r</i> ²
a) Chl <i>a</i> (mg/m ²)						
No predator (linear regression)	4.21	0.02	0.33	1, 13	0.57	0.03
Predator (linear regression)	7.41	-0.09	6.11	1, 13	0.03	0.32
Predator main effect			1.41	1, 26	0.24	
Subsidy main effect			14.97	1, 26	0.12	
Predator × subsidy interaction			30.93	1, 26	0.03	
b) Primary consumer dry mass (mg/m ²)						
No predator (linear regression)	599.51	-5.03	1.05	1, 13	0.32	0.07
Predator (linear regression)	299.97	22.48	26.8	1, 13	0.0001	0.67
Predator main effect			3.36	1, 26	0.08	
Subsidy main effect			7.08	1, 26	0.01	
Predator × subsidy interaction			17.61	1, 26	0.0003	
c) ln(predatory invertebrate density)†						
Subsidy effect (linear regression)	2.69	0.02	9.63	1, 28	0.004	0.26
Predator main effect			2.99	1, 26	0.10	
Subsidy main effect			9.99	1, 26	0.004	
Predator × subsidy interaction			0.08	1, 26	0.78	
d) Snail density (number/m ²)						
No predator (linear regression)	11.51	0.13	1.40	1, 13	0.26	0.10
Predator (linear regression)	7.90	1.13	9.89	1, 13	0.008	0.43
Predator main effect			5.28	1, 26	0.03	
Subsidy main effect			11.23	1, 26	0.002	
Predator × subsidy interaction			7.21	1, 26	0.01	
e) Density without snails (number/m ²)						
No predator (linear regression)	19.93	0.51	1.77	1, 13	0.21	0.12
Predator (linear regression)	28.68	0.21	1.24	1, 13	0.29	0.09
Predator main effect			73.36	1, 26	0.67	
Subsidy main effect			2.84	1, 26	0.10	
Predator × subsidy interaction			0.51	1, 26	0.48	

Note: *P* values in boldface type are significant (*P* < 0.05).

† Originally measured as number/m².

the predator effect strength on primary consumers, providing support for threshold responses to subsidies across the chain of interactions that make up trophic cascades. Evidence for thresholds in subsidy supply where indirect predator effects change from positive to negative have not been observed before in empirical studies of subsidy effects on trophic cascades.

Community-level responses

Piovia-Scott et al. (2011) showed that when seaweed was added to beaches, detritivore numbers increased, and predators switched from feeding on herbivores to detritivores, which reduced the positive indirect effect of predators on plants. Similarly, our results show that in the absence of alder detritus, cutthroat trout had a positive indirect effect on algal biomass, which decreased with the addition of alder leaf detritus. However, we did not find evidence of a switch from predators feeding on herbivores to detritivores with subsidy addition. We found instead that the biomass of primary consumers increased with subsidy inputs, but only in the presence of predators. While this potentially explains the threshold in trophic cascade strength, the mechanisms behind the unexpected increase in primary consumers with top predators is unclear.

There are two potential mechanisms for why primary consumers increased with resources only in the presence of trout. The first is that the trout did not directly influence primary consumer numbers, but influenced the presence of predatory invertebrates creating a four-level trophic cascade. We found a trend, albeit not statistically significant, of lower predatory invertebrate density in the presence of trout, supporting this possible mechanism (Appendix D). Without trout, increased predatory invertebrates may have suppressed primary consumers explaining the unpredicted result of primary consumers not increasing with resources in the absence of trout. The second possible mechanism is that predators released a subset of consumers from competition. We found that snail densities increased with subsidies only in the presence of trout, whereas the density of other primary consumers did not increase in the presence of trout. Out of the three snail taxa, *Gyraulus* and *Planorbella* are classified as detritus and algal consumers, whereas *Pseudosuccinea* is an algal consumer. Trout preferentially consume vulnerable soft-bodied primary consumers (such as mayfly larvae; McIntosh 2002, Nystrom et al. 2003), and in doing so, may have released armored primary consumers (snails) from competition (McNeely et al. 2007), enabling them to track the increased subsidy quantities.

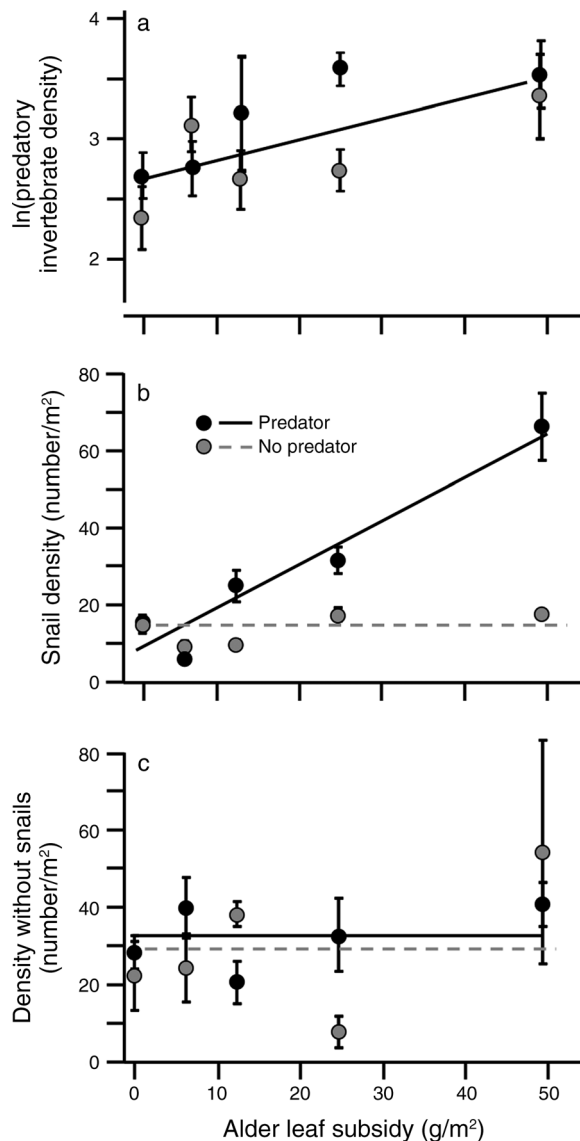


FIG. 3. Effect of alder leaf mass on (a) predatory invertebrate density (linear regression includes predator and no-predator treatments; originally measured as number/m²), (b) snail density, and (c) primary consumer invertebrate density when snails were excluded ("density without snails") in the presence and absence of predators. Data presented on graphs are treatment means \pm SE, with the black solid line in panel (a) representing linear regression of increasing subsidies (predator/no-predator treatment not included in analysis), the black solid line in panel (b) representing linear regression for predator treatment, and the black solid line in panel (c) representing the average for the predator treatment. Gray dashed lines in panels (b) and (c) represent the treatment average for the no-predator treatment.

Conclusions

Our results provide evidence that different quantities of subsidies will affect trophic cascade strength in a nonlinear way. We observed a threshold response in trophic cascade strength along a continuous gradient of subsidies, where there was a loss of trophic cascade

strength past low subsidy densities. This threshold response in cascade strength is a novel empirical result, which was likely due to the suppression of intermediate predators by top predators, combined with a change in community composition of primary consumers. Quantitative gradients of subsidies are prevalent in nature (Hoover et al. 2006, Wesner 2010), which, combined with our results, stresses the importance of studying food-web level effects of subsidies across a range of input amounts. Our study has broad implications, as the uptake of subsidies within food webs is similar across aquatic and terrestrial systems (Bartels et al. 2012). With anthropogenic changes altering subsidy inputs to systems (Lecerf and Richardson 2010, Piovia-Scott et al. 2011, Greig et al. 2012), it is important to note how slight the changes need to be to affect whole food-web dynamics.

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LITERATURE CITED

- Bartels, P., J. Cucherousset, K. Steger, P. Eklov, L. J. Tranvik, and H. Hillebrand. 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* 93:1173–1182.
- Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201–220.
- Cannings, R. A., and K. M. Stuart, editors. 1977. The dragonflies of British Columbia. First edition. British Columbia Provincial Museum, Victoria, British Columbia, Canada.
- Cottingham, K. L., J. T. Lennon, and B. L. Brown. 2005. Knowing when to draw the line: designing more informative ecological experiments. *Frontiers in Ecology and the Environment* 3:145–152.
- Greig, H. S., P. Kratina, P. L. Thompson, W. J. Palen, J. S. Richardson, and J. B. Shurin. 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. *Global Change Biology* 18:504–514.
- Halaj, J., and D. H. Wise. 2002. Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. *Ecology* 83:3141–3151.
- Henschel, J. R., D. Mahsberg, and H. Stumpf. 2001. Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. *Oikos* 93:429–438.
- Hoover, T. M., J. S. Richardson, and N. Yonemitsu. 2006. Flow-substrate interactions create and mediate leaf litter resource patches in streams. *Freshwater Biology* 51:435–447.
- Huxel, G. R., and K. McCann. 1998. Food web stability: The influence of trophic flows across habitats. *American Naturalist* 152:460–469.
- Klemmer, A. J., S. A. Wissinger, H. S. Greig, and M. L. Ostrofsky. 2012. Nonlinear effects of consumer density on multiple ecosystem processes. *Journal of Animal Ecology* 81:770–780.
- Knight, T. M., M. W. McCoy, J. M. Chase, K. A. McCoy, and R. D. Holt. 2005. Trophic cascades across ecosystems. *Nature* 437:880–883.

- Kominoski, J. S., L. B. Marczak, and J. S. Richardson. 2011. Riparian forest composition affects stream litter decomposition despite similar microbial and invertebrate communities. *Ecology* 92:151–159.
- Lecerf, A., and J. S. Richardson. 2010. Litter decomposition can detect effects of high and moderate levels of forest disturbance on stream condition. *Forest Ecology and Management* 259:2433–2443.
- Leroux, S. J., and M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecology Letters* 11:1147–1156.
- Marczak, L. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* 88:140–148.
- McIntosh, A. R. 2002. Impact of introduced trout on *Nesameletus* mayfly populations measured using electrofishing. *Archiv für Hydrobiologie* 154:375–392.
- McNeely, C., J. C. Finlay, and M. E. Power. 2007. Grazer traits, competition, and carbon sources to a headwater-stream food web. *Ecology* 88:391–401.
- Merritt, R. W., K. W. Cummins, and M. B. Berg, editors. 2008. An introduction to the aquatic insects of North America. Fourth edition. Kendall-Hunt Publishing, Dubuque, Iowa.
- Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, and R. L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs* 53:1–25.
- Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. *Ecology* 80:2435–2441.
- Nystrom, P., A. R. McIntosh, and M. J. Winterbourn. 2003. Top-down and bottom-up processes in grassland and forested streams. *Oecologia* 136:596–608.
- Piovia-Scott, J., D. A. Spiller, and T. W. Schoener. 2011. Effects of experimental seaweed deposition on lizard and ant predation in an island food web. *Science* 331:461–463.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Polis, G. A., and S. D. Hurd. 1995. Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proceedings of the National Academy of Sciences USA* 92:4382–4386.
- Polis, G. A., and S. D. Hurd. 1996. Allochthonous input across habitats, subsidized consumers, and apparent trophic cascades: Examples from the ocean-land interface. Pages 275–285 in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of pattern and dynamics*. Chapman and Hall, New York, New York, USA.
- Polis, G. A., A. L. W. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology and Evolution* 15:473–475.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.
- R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richardson, J. S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology* 72:873–887.
- Richardson, J. S., Y. X. Zhang, and L. B. Marczak. 2010. Resource subsidies across the land-freshwater interface and responses in recipient communities. *River Research and Applications* 26:55–66.
- Sabo, J. L., and M. E. Power. 2002. River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology* 83:1860–1869.
- Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecology Letters* 5:785–791.
- Solomon, C. T., S. R. Carpenter, J. J. Cole, and M. L. Pace. 2008. Support of benthic invertebrates by detrital resources and current autochthonous primary production: results from a whole-lake C-13 addition. *Freshwater Biology* 53:42–54.
- Spiller, D. A., J. Piovia-Scott, A. N. Wright, L. H. Yang, G. Takimoto, T. W. Schoener, and T. Iwata. 2010. Marine subsidies have multiple effects on coastal food webs. *Ecology* 91:1424–1434.
- Thorpe, J. H., and A. P. Covich, editors. 1991. *Ecology and classification of North American freshwater invertebrates*. Academic Press, San Diego, California, USA.
- Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69:409–442.
- Wesner, J. S. 2010. Seasonal variation in the trophic structure of a spatial prey subsidy linking aquatic and terrestrial food webs: adult aquatic insects. *Oikos* 119:170–178.
- Wiggins, G. B. 1996. *Larvae of the North American caddisfly genera (Trichoptera)*. Second edition. University of Toronto Press, Toronto, Ontario, Canada.
- Winterbourn, M. J. 1971. Life histories and trophic relationships of Trichoptera of Marion Lake, British Columbia. *Canadian Journal of Zoology* 49:623–635.
- Wipfli, M. S., and C. V. Baxter. 2010. Linking ecosystems, food webs, and fish production: subsidies in salmonid watersheds. *Fisheries* 35:373–387.
- Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse-consumer interactions. *Ecological Monographs* 80:125–151.

SUPPLEMENTAL MATERIAL

Appendix A

Analysis of detritus remaining at the end of the experiment ([Ecological Archives E094-175-A1](#)).

Appendix B

Length-mass regression equations used to calculate invertebrate biomass ([Ecological Archives E094-175-A2](#)).

Appendix C

Analysis of sticklebacks found in cages at the end of the experiment ([Ecological Archives E094-175-A3](#)).

Appendix D

Redundancy analysis (RDA) on community composition in experimental cages ([Ecological Archives E094-175-A4](#)).