

Resource subsidies, top predators, and community regulation in stream ecosystems

by

William Atlas

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APPROVAL

Name: William Atlas

Degree: Master of Science

Title of Thesis:

Resource subsidies, top predators, and community regulation in stream ecosystems

Examining Committee:

Chair: Dr. S. Bisgrove, Associate Professor

Dr. W. Palen, Assistant Professor, Senior Supervisor
Department of Biological Sciences, S.F.U.

Dr. N. Dulvy, Professor
Department of Biological Sciences, S.F.U.

Dr. J. Finlay, Associate Professor
Department of Ecology, Evolution and Behavior, University of Minnesota

Dr. J. Moore, Assistant Professor
Department of Biological Sciences, S.F.U.
Internal Examiner

5 April 2012

Date Defended/Approved

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Abstract

Resource subsidies in the form of energy, materials, and organisms support the productivity of recipient ecosystems. When subsidies increase the abundance of top predators, theory predicts that top-down interactions will be strengthened. However, empirical evidence demonstrating stronger trophic cascades in the presence of resource subsidies is limited, and the degree to which subsidies intensify predation should be constrained by the strength of interactions between predators and their prey. Using both experimental and modeling approaches we tested the degree to which short term patterns of predation are mediated by the availability of terrestrial subsidies, and whether resource subsidies supported two stream predators, steelhead (*Oncorhynchus mykiss*) and Pacific giant salamander (*Dicamptodon tenebrosus*), potentially resulting in stronger top-down control. Results were consistent between both experimental and model food webs where despite high predator biomass, there was little support for a trophic cascade or increased predation of most herbivores in the absence of terrestrial subsidies. Most herbivores were relatively invulnerable to predation, emphasizing that behavioral and morphological adaptations can temper predator prey interactions in highly subsidized ecosystems.

Keywords: resource subsidies; terrestrial-aquatic linkages; trophic cascades; stream ecosystems; experimental ecology; food webs

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Chapter 1. Food falling from the sky: subsidized predators and trophic cascades in a freshwater ecosystem

Abstract

Resource subsidies in the form of energy, materials, and organisms support the productivity of recipient ecosystems. When subsidies increase the abundance of top predators, theory predicts that top-down interactions will be strengthened. However, empirical evidence demonstrating stronger trophic cascades in the presence of resource subsidies is limited, and the degree to which subsidies intensify predation should be constrained by the strength of interactions between predators and their prey. We tested if terrestrial prey subsidies intensified top-down regulation by two stream predators, steelhead (*Oncorhynchus mykiss*) and Pacific giant salamander (*Dicamptodon tenebrosus*). We reduced terrestrial prey and manipulated the presence of predators in 32 stream reaches. Despite high predator biomass, there was little support for a trophic cascade or increased predation of herbivores in the absence of terrestrial subsidies. Most herbivores were relatively invulnerable to predation, demonstrating that behavioral and morphological adaptations can temper predator prey interactions in highly subsidized ecosystems.

Introduction

Trophic cascades are widely studied phenomena whereby predators depress the abundance of prey species with effects propagating through multiple trophic levels ultimately affecting primary productivity (Polis et al. 2000). Trophic cascades occur in a diversity of ecosystems (Pace et al. 1999) and typically result from predation on grazers and other basal consumers (Paine 1974, Carpenter et al. 1985). Trophic cascades have garnered significant attention in the ecological literature, but their importance for

community dynamics is not ubiquitous across ecosystems. While predation often limits the biomass of prey species, cascading effects on primary producers are more rare (Shurin et al. 2002). The consequences of predation within a community can depend on the physical and biological context (Menge et al 1994), and habitat complexity, landscape heterogeneity and the composition of prey and predator assemblages all affect the strength of top-down regulation (Polis et al. 1989, Power 1992, Rosenheim et al. 1993, Wootton et al. 1996, Finke and Denno 2004). The availability of resource subsidies may also play an important role in mediating the strength of trophic cascades (Polis et al. 1997).

In many systems, the movement of nutrients, organic material, and prey from adjacent habitats can subsidize primary and secondary production above what could be supported from *in situ* resources alone (Polis and Strong 1996). Early synthesis on the effects of resource subsidies in recipient communities highlighted that in cases where subsidies increase predator or consumer abundance, the balance of community regulation may shift towards top-down control, intensifying trophic cascades (Polis et al. 1997). While this has been a central premise in theoretical developments surrounding the dynamics of highly subsidized ecosystems (Holt 1984, Huxel and McCann 1998, Leroux and Loreau 2008), empirical evidence of short term changes in the strength of trophic cascades resulting from resource subsidies is fairly limited (but see Polis and Hurd 1996, Henschel et al. 2001). In contrast to predictions that subsidies will increase predator biomass to the detriment of local prey species, experimental studies have demonstrated that when predators preferentially use prey from donor ecosystems (Nakano et al. 1999a), their effect on local herbivore populations may be less than predicted by their biomass alone, tempering top-down control within recipient ecosystems (Nakano et al. 1999b, Sabo and Power 2002, Spiller et al. 2010).

In tributary stream ecosystems, where light availability is limited by dense overhead canopy, terrestrial resource subsidies play an important role in supporting biotic communities (Vannote et al. 1980, Richardson et al. 2010). Inputs of dissolved organic carbon, and leaf litter subsidize stream food webs by increasing the productivity of the stream environment from the bottom up, and subsidies of terrestrial invertebrates often support elevated predator biomass (Webster and Meyer 1997, Wallace et al. 1997, Nakano et al. 1999a, Kawaguchi and Nakano 2001). Predatory fish are widely

recognized as having important effects in river food webs, and may initiate trophic cascades (Power et al. 1985, Power 1990, Nakano et al. 1999b). However, the top-down effects of predation by fish are spatially and temporally variable (Power 1992, Wootton et al. 1996), and may depend on the degree to which community biomass is supported by allochthonous resources (Power and Dietrich 2002, McNeely and Power 2007) as well as the immediate availability of resource subsidies (Nakano et al. 1999b, Baxter et al. 2004). Several previous studies of fish induced trophic cascades in river food webs have been conducted in large mainstem rivers (Power et al. 1985, Power 1990) where the majority of ecosystem energy is derived from in situ primary production (Finlay 2001), however theory predicts that trophic cascades should be particularly strong in highly subsidized tributary reaches where predator biomass is disproportionately high relative to the *in situ* productivity of the stream ecosystem (Polis et al. 1997, Leroux and Loreau 2008).

Here we tested the theoretical prediction that highly subsidized tributary stream food webs would experience strong trophic cascades. Using a three way factorial experiment which manipulated the availability of terrestrial prey, and the presence of two top predators we tested the importance of terrestrial prey subsidies for the strength of top-down control by juvenile steelhead trout (*Oncorhynchus mykiss*) and Pacific giant salamanders (*Dicamptodon tenebrosus*), as well as how terrestrial subsidies influence interactions between the two predators. We predicted that over the course of the two month experiment these highly subsidized stream predators would depress the biomass of aquatic herbivores, releasing primary producers from grazer control and inducing a trophic cascade indicated by an increase in primary producer biomass in the presence of predators (Fig. 1). We also predicted that in the absence of terrestrial prey subsidies, steelhead would shift towards a more aquatic prey base, further depressing aquatic herbivore biomass amplifying the cascading effects of predation. Patterns of top-down regulation by salamanders, which feed primarily on aquatic prey, were not expected to change in the absence of terrestrial prey subsidies. However, we predicted that the aforementioned shift in resource use by steelhead trout would increase competition between steelhead and the more benthic salamanders. Contrasting these predictions, if morphological and behavioral attributes of the aquatic invertebrate community limit steelhead and salamander predation, we predicted that neither predator species would

initiate a trophic cascade, and that steelhead would experience reduced growth in the absence of terrestrial prey.

Methods

Study Site

We manipulated 32 reaches of Fox Creek, a tributary of the South Fork Eel River (2.8 km² drainage area, 39° 43'45" N, 123° 38'40" W) protected within the Angelo Coast Range Reserve in Mendocino Co. California, and part of the University of California Natural Reserve system. The creek is relatively high gradient and is dominated by step-pool channel morphology. Rainfall is highly seasonal with most rainfall occurring during winter and a protracted summer dry season. Consequently, winter base flows are typically an order of magnitude higher than summer base flow. Peak stream temperatures are observed from late July to early August. Vertebrate predators within Fox Creek include Pacific giant salamander (*Dicamptodon tenebrosus*) as well as both young of the year (YOY) and age 1 and older (1+) juvenile steelhead (*Oncorhynchus mykiss*).

Experimental Protocol

For two months (July-August) during summer 2010, we manipulated replicate reaches of Fox Creek to test the role of terrestrial subsidies in mediating the top-down effects of juvenile steelhead trout and Pacific giant salamanders on trophic dynamics in a stream food web. We selected 32 comparable pools; habitat units large enough (> 7 m²) and with adequate depth (> 0.25 m) to support 1+ steelhead and large salamanders throughout the summer, spread throughout the anadromous reach of Fox Creek (1.3 km). Pools were randomly assigned to one of 8 treatments resulting from the factorial combination of the presence or absence of both predator species and the availability of terrestrial prey subsidies, and each treatment was replicated 4 times. However, due to an initial assignment error one treatment, reduced terrestrial subsidy with both predators was replicated 5 times and another, reduced terrestrial subsidy with salamander predators only, was replicated 3 times. Fences buried in the stream substrate and extending above the surface of the water were constructed at the top of the upstream

riffle, and below each pool (3 mm Vexar® mesh) to limit the movement of animals during the study. Each experimental unit included the pool as well as the upstream riffle, ensuring that benthic invertebrates drifting from immediately upstream of the focal pool remained available to predators. For experimental reaches assigned reduced terrestrial subsidy treatments, we installed covers extending over the entire reach constructed of transparent polyethylene plastic and window screen stretched over PVC hoops. Covers were designed to allow maximum light penetration (<8% reduction in visible light), while blocking terrestrial organic matter and invertebrate in-fall. Upstream fences prevented the downstream drift of most organic material and terrestrial invertebrates however small invertebrates may have been able to pass through the mesh. Two small (<10 cm in diameter) ventilation holes were cut into the apex of each cover to allow emerging aquatic insects to escape.

Experimental contrasts in the vertebrate predator community were established by first removing all *O. mykiss* and *D. tenebrosus* through a combination of snorkel, hand capture, and electrofishing until no new animals were captured. All animals were weighed (mg), measured (mm), tagged, and released according to the assigned treatment. 100 mm TL is thought to be the smallest size at which salamanders regularly consume YOY steelhead (Parker 1993) and this was chosen as the minimum size cut off in our predatory salamander treatments. Steelhead were divided into two age groups based on size; young of year (YOY) and 1+ steelhead were marked with small adipose fin clips, and 1+ steelhead and predatory salamanders (> 100mm TL) were tagged individually with passive integrated transponder (PIT) tags (HPT8, 8.4 mm, Biomark; Boise, ID, USA). Experimental densities for YOY (1.25 fish/m²) and 1+ steelhead (0.26 fish/m²) were standardized to mean densities previously observed in Fox Creek, and salamanders density (>100mm) was set based on densities observed during the first two days of sampling (0.52 salamanders/m²). At the conclusion of the experiment, each experimental unit was searched as above, and all *O. mykiss*, and *D. tenebrosus* were weighed and measured.

The aerial flux of terrestrial prey to experimental units was quantified using pan traps deployed five times at five locations across the longitudinal extent of the experiment. Paired traps (37 cm * 26.5 cm) were set inside and outside of the experimental enclosures above the stream surface with a few centimeters of water and

2-3 drops of surfactant to capture any falling invertebrates. The percentage of leaf litter and other organic matter excluded was quantified using buckets (23 cm dia.) deployed over an 11 day period near the end of the experiment at five locations with six buckets at each location, three inside and three outside covered experimental units. Leaf litter samples were dried for 48 hours at 60° C to obtain dry weight, then placed in a muffle furnace at 550°C for 4 hours, and measured immediately after to estimate ash free dry mass and carbon content. Changes in the biomass and composition of stream dwelling aquatic invertebrates were quantified using sticky traps and benthic rock sampling. To sample the emergence of aquatic invertebrates from our experimental pools, three sticky traps were deployed within each experimental unit three times at approximately two week intervals throughout the duration of the experiment. Traps were constructed of 21.6 * 27.9 cm clear overhead transparencies which were sprayed on both sides with the agricultural adhesive Tangle-Trap® (Contech; Victoria, BC, Canada) and were deployed perpendicular to the direction of flow and left for 48 hours. The biomass and composition of benthic aquatic invertebrates in our experimental pools were estimated by sampling 6 randomly selected benthic rocks from each unit at the end of the experiment. Invertebrates captured in pan traps or sampled from benthic rocks were stored in 70% ethanol, identified to family and genus when possible, measured to the nearest 0.1 mm, and converted to biomass estimates using taxa specific length-weight relationships (Hodar 1996, Benke et al. 1999, Sabo et al. 2002). Sticky traps were frozen for later identification to order, and biomass was estimated as above. Average percent canopy cover was estimated for each pool using a spherical densitometer as a proxy for light availability.

To test for experimentally induced effects on primary production, we incubated 12 unglazed ceramic tiles (4.8 cm * 4.8 cm) in each pool over the duration of the experiment. Four tiles were destructively sampled during the course of the experiment at weeks 5, 7, and 9 to test for changes in algae and biofilm standing stock using ash-free dry mass (AFDM) and chlorophyll-a concentration. Algae and biofilms were sampled by scrubbing each tile with a toothbrush and filtered stream water. The resulting slurry was sub-sampled for further analysis, with 20 ml filtered through pre-combusted 0.7µm glass fiber filters (Whatman GF-F, 47mm), and then ashed (550°C for 24 hrs) to estimate AFDM. A 4 ml sub-sample was filtered onto 0.7µm glass fiber filters (Whatman GF-C,

25mm) and frozen for later estimation of chlorophyll-a using ethanol extraction and fluorometry (Steinman and Lamberti 1996). To evaluate whether the observed responses to our covered treatments were due to changes in temperature we placed temperature loggers (ibutton®, MAXIM: Sunnyvale, CA, USA) in 12 experimental units; 6 covered and 6 in uncovered pools along the longitudinal extent of the experiment. Temperatures were then compared by one-way ANOVA to test for an effect of cover.

Analysis

We evaluated the response of predators, herbivores, and primary producers to our experimental treatments by fitting a range of competing linear and linear mixed effects models (Zuur et al. 2009). We used an information theoretic approach based on Aikake's information criterion adjusted for small sample sizes (AICc) to examine the response of the aquatic food web to experimental treatments and background environmental variability such as light availability. For each response variable we considered all possible combinations of our main effects (presence or absence of predatory steelhead, predatory salamander density, presence or absence of terrestrial prey) and their interactions, as well as percent canopy cover as a proxy for light availability. For benthic invertebrate responses we modeled total biomass and tested for responses at the level of order and functional group. Data for the biomass of emerging aquatic invertebrates did not meet the assumptions of normality and were therefore log transformed. Community response metrics which were sampled on a single date such as benthic invertebrates, as well as predator and YOY growth were modeled using linear regression in R. Response metrics with repeated samplings throughout the summer such as chlorophyll-a, AFDM, and aquatic insect emergence were fit using linear mixed effects models (R package nlme) estimated using maximum likelihood, including sample date as a random effect to account for repeated measurements. Models were then ranked based on their relative likelihood (w_i). To avoid over fitting we report only model's within 4 Δ AICc units (Burnham and Anderson 2002) of our top model, and we report weighted coefficients based on all models within this threshold.

There was a high degree of immigration and emigration among predatory salamanders during the experiment, and final salamander densities did not reflect initial treatment contrasts. Consequently, we considered models that included either initial

salamander treatment (presence or absence) or salamander density at the conclusion of the experiment in our candidate model set. Experimental pools without covers provided little inference about the emergence of aquatic insects since capture efficiency on sticky traps was lower than in units with covers and because of the potential for capturing invertebrates emerging from areas outside of the experiment. As a result, we excluded uncovered pools from the analysis of aquatic insect emergence, and report only the results for covered pools.

Results

Terrestrial subsidy

Covered units experienced a dramatic reduction in the flux of terrestrial material during the experiment. The mean daily flux of terrestrial prey to uncovered units was estimated to be $523.1 \pm 101.3 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, and covered pools experienced a 27-fold reduction in this prey subsidy ($18.86 \pm 5.06 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$). Similarly, terrestrial leaf litter subsidies were reduced more than 90 fold, from $800.5 \pm 121 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in open pools to $8.7 \pm 5.05 \text{ mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in covered. Stream temperature was not affected by the presence of covers (mean temp: covered $14.20 \pm 0.17 \text{ SE } ^\circ\text{C}$, uncovered $14.28 \pm 0.15 \text{ SE } ^\circ\text{C}$; $p=0.755$).

Steelhead and salamanders

On average 1+ and YOY steelhead grew approximately 1.23 g and 1.12 g respectively during the duration of the experiment. Growth of juvenile steelhead from both age classes (1+, YOY) was best predicted by the availability of terrestrial prey; however models of YOY growth which included light availability (% canopy cover) also received some support. In the absence of terrestrial prey both YOY and 1+ steelhead experienced substantial reductions in growth (Fig. 1.2A & B, Table 1.1, coefficients: $-2.30 \pm 0.77\text{g}$ and respectively $-0.51 \pm 0.18\text{g}$). The growth of predatory salamanders was not reduced in the absence of terrestrial subsidies (Fig. 1.2C). There was no indication that the growth of 1+ steelhead was altered by the presence of salamander predators and neither predator species significantly reduced the growth of YOY steelhead. Salamander growth was best predicted by a model that included only the presence of 1+

steelhead, with steelhead facilitating significantly higher growth in salamanders over the course of the experiment ($1.86 \pm 0.67\text{g}$) (Fig. 1.2C), however there was limited support for an intercept only model as well (Table 1.1).

Food web response

Neither predator appeared to depress the total biomass of aquatic herbivores, regardless of the availability of subsidies (Fig. 1.2D, Table 1.2). The majority (65%) of the aquatic invertebrate biomass sampled from benthic rocks in Fox Creek was comprised of relatively predator-invulnerable taxa such as armored and case building caddisflies (Order Trichoptera), which are rarely found in the diets of steelhead and salamanders (Parker 1994, Wootton et al. 1996). When the biomass of vulnerable and invulnerable (armored) taxa were analyzed separately, the biomass of benthic invertebrates vulnerable to predation declined with increasing salamander density ($-69 \pm 31 \text{ mg}\cdot\text{m}^{-2}$) (Fig. 1.3A) and predatory steelhead depressed the biomass of vulnerable herbivores ($-11.3 \pm 5.4 \text{ mg}\cdot\text{m}^{-2}$, Fig. 1.2E). Total aquatic invertebrate biomass was higher in pools with greater light availability and there was support for an interaction between steelhead predators and light availability (% canopy cover). The total invertebrate biomass increased along an increasing gradient of light availability; however the slope of that positive relationship biomass was steeper in the presence of steelhead (Fig. 1.3B).

The biomass of aquatic invertebrates emerging from covered experimental units was influenced by the presence of both predators and by light availability. We were unable to identify emergent insects beyond the level of order, and this limited our ability to partition emergence biomass into vulnerable and invulnerable categories. Despite that limitation, effects of predation by salamanders and steelhead on the biomass of emergent aquatic insects were apparent. The top model predicting the biomass of emerging aquatic invertebrates in covered pools included a three-way interaction between the presence of predatory steelhead (1+), light availability (% canopy cover), and final salamander density (Table 1.2) such that emergence biomass declined along increasing gradients in canopy cover and salamander density, and was reduced in the presence of predatory steelhead.

The amount algae and biofilms appeared to be strongly influenced by the availability of light in our study system. The top model for ash free dry mass (AFDM) included only a single factor, % canopy cover, with AFDM declining with increasing canopy cover ($-3.78 \pm 0.91 \text{ g} \cdot \text{m}^{-2} \cdot \% \text{ canopy}^{-1}$). However, a model which included % canopy cover and steelhead as fixed factors received almost equal support, with AFDM increasing in the presence of steelhead, and a third model included an interaction between in steelhead predators and % canopy cover but received considerably less support (Fig. 1.2F, Table 1.3). The concentration of chlorophyll-a was positively related to % canopy cover ($17 \pm 3.99 \text{ } \mu\text{g} \cdot \text{m}^{-2}$) (Fig. 1.2G). Several other models fell within the 4 ΔAIC unit cut off, making the inference about the importance of other variables for chlorophyll-a difficult (Table 1.3).

Discussion

Subsidy theory predicts that top-down regulation should be strengthened by the flux of prey from adjacent habitats if subsidies increase predator biomass above the carrying capacity of the recipient ecosystem (Polis et al. 1997, Leroux and Loreau 2008). However, in some stream ecosystems predatory fish may preferentially consume terrestrial prey (Nakano et al. 1999a), moderating the top-down impacts of these predators (Nakano 1999b). Theory and limited empirical evidence suggest that interactions between predator species may also alter their respective impact on lower trophic levels (Polis et al. 1989, Finke and Denno 2004), but the degree to which resource subsidies alter multiple predator dynamics has rarely been tested (but see Baxter et al. 2004). We tested the top-down effect of two predators, steelhead trout (*O. mykiss*) and Pacific giant salamander (*D. tenebrosus*), in a tributary food web to evaluate the strength of top-down control in a highly subsidized ecosystem and the degree to which predation is mediated by the availability of terrestrial subsidies.

We found that neither predator species initiated a trophic cascade over the 9 weeks of the experiment. Inputs of allochthonous prey in our study system do appear to support higher biomass of predatory steelhead, but experimental removal of predators did not lead to increased herbivore biomass over the course of the experiment, suggesting that steelhead and salamanders do not exert strong top-down control at this

timescale. Steelhead and salamanders both depressed the total biomass of emerging aquatic invertebrates (Fig. 1.4); however neither species had a measurable effect on the biomass of benthic herbivores. When vulnerable and armored benthic taxa were analyzed separately we found that steelhead did depress the biomass of vulnerable herbivores (Fig. 1.2E). Similarly, predation by Pacific giant salamanders reduced the biomass of vulnerable benthic invertebrates regardless of their functional group (Fig. 1.3A); however the effects of predation by salamanders and steelhead on aquatic consumers were apparently not widespread enough for them to propagate to the level of primary producers (Fig. 1.2). While predators did reduce the biomass of some aquatic herbivores over the course of the summer, natural variation in light availability within Fox Creek appeared to be the most important driver of our two indexes of primary productivity (AFDM and chlorophyll-a). There was some support for the inclusion of both predators in models for AFDM and chlorophyll-a suggesting that they may play a secondary role in the abundance of primary producers, possibly via nutrient recycling (Vanni et al. 2006). We found that juvenile steelhead were highly dependent on terrestrial prey, and when subsidies were reduced, both cohorts (1+ and YOY) experienced marked declines in growth (Fig. 1.2A, 1.2C). Predatory salamander (>100 mm) growth was unaffected by the absence of terrestrial prey over the course of this experiment, however they benefited from the presence of steelhead predators regardless of the availability of terrestrial prey (Fig. 1.2B).

Terrestrial subsidies are a major source of energy for light-limited tributary streams (Vannote et al. 1980, Wallace et al. 1997, Finlay 2001, Nakano and Murakami 2001), where allochthonous prey support high predator biomass (Kawaguchi et al. 2003). While terrestrially derived carbon is known to support a significant proportion of the productivity of light limited tributary streams, algae may be a disproportionately important source of energy for aquatic consumers despite relatively low *in situ* primary productivity (McCutchan and Lewis 2002, McNeely et al. 2007). If prey subsidies supported elevated predator biomass in our study system, we predicted that tributary stream food webs should experience strong top-down control by vertebrate predators resulting in increased primary productivity. Furthermore, if experimentally interrupting terrestrial prey subsidies caused a shift by predatory steelhead or salamanders towards a more aquatic prey base, we predicted that it would intensify top-down predation

leading to more pronounced cascading effects on primary productivity. However, these predictions were dependent on the ability of predators to exert strong top-down control of the herbivore guild, and we found no evidence that either predator species significantly depressed aquatic herbivore biomass. Rather, we found that reductions in the availability of terrestrial prey simply reduced the growth of predatory steelhead, with most 1+ fish losing mass during the 9 week long experiment. This pattern of reduced growth suggests that 1+ steelhead were unable to meet the energetic demands of maintaining mass without terrestrial prey. Steelhead trout in our system appear to have only a limited capacity to exploit local consumer biomass, as they did not shift to more aquatic prey sources in the absence of terrestrial prey, suggesting that despite the high biomass of steelhead predators in our study system, the top-down effects of predation may be limited to the small pool of vulnerable aquatic invertebrates.

Pacific giant salamanders and steelhead have substantial dietary overlap (Parker 1994), however we found no evidence of resource competition between steelhead and salamanders, and isotopic evidence suggests that steelhead relied on terrestrial prey to a much greater degree (*Appendix A*). Contrary to the prediction that competition between predator species would increase in the absence of terrestrial subsidies, the presence of predatory steelhead led to increased growth among recaptured salamanders. We propose that the presence of 1+ steelhead may have allowed salamanders to more efficiently exploit aquatic prey. Steelhead are mobile predators that feed in the water column, and are known to elicit changes in the behavior of their prey (Douglas et al. 1994, Post et al. 1998). If behavioral changes by prey in response to the threat of steelhead predation increased their vulnerability to predation by more sedentary, benthic salamanders, it may explain increased salamander growth in the presence of predatory steelhead (Sih et al. 1998)

The top-down effects of predatory fish are well established in the ecological literature in a wide range of aquatic and marine ecosystems (Carpenter et al. 1985, Power et al. 1986, Power 1990, Pace et al. 1999). However, the degree to which predatory fish in river food webs elicit changes in herbivore communities, which result in trophic cascades depends in part on the vulnerability of the aquatic invertebrate community (Power 1992). For instance, inter-annual variability in the strength of trophic cascades in rivers has been linked to flood pulse events which scour the stream bottom

removing large armored caddisflies, leaving behind an aquatic invertebrate community comprised of more predator vulnerable taxa which are strongly regulated by trout (Wootton et al. 1996). In tributary streams in northern California, the multivoltine *Glossosoma pentium* are the dominant armored caddisfly, and maintain high standing biomass for much of the year despite the low primary productivity of these streams. Persistent high densities of *Glossosoma* in tributaries such as Fox Creek result in strong herbivore control of algal biomass and limit the availability of *in situ* production to other un-armored aquatic consumers that are more readily available to predatory fish and salamanders (McNeely et al. 2007). When invulnerable herbivores predominate, there is limited scope for trophic transfer of aquatically derived energy to higher order consumers (Wootton et al. 1996) such as predatory fish and salamanders. Over the course of our study, the effect of steelhead and salamander predation was concentrated on vulnerable invertebrate taxa, with armored herbivores unaffected by the presence of either predator species. Under these circumstances, predators may be unable to initiate trophic cascades.

The absence of strong top-down control by predatory steelhead and salamanders in a highly subsidized stream food web is therefore almost certainly due to the fact that *Glossosoma* and other armored herbivore taxa consume the majority of *in situ* production and are rarely consumed by trout and salamanders. Because of their invulnerability, these taxa serve as a trophic cul-de-sac (Bishop et al. 2007), limiting the biomass of other vulnerable grazers via competition, reducing the trophic transfer of algal biomass to higher trophic levels, and diminishing the ability of top-down predation to propagate through the food web. At the conclusion of our experiment, armored herbivores comprised on average 56% of the benthic biomass across all treatments, increasing the degree to which steelhead must depend on terrestrially derived prey and ensuring that, despite their high biomass relative to *in situ* production, steelhead and salamanders cannot exert strong top-down control on the food web. A similar lack of top-down control over detrital processing by aquatic invertebrates may occur in our study system (Konishi et al. 2001), however because leaf litter and dissolved organic carbon from the terrestrial environment are donor controlled inputs (Polis and Strong 1996) we chose to focus on changes in the biomass of algae in response to subsidized predation in our study system.

The duration of our experimental manipulation limited our inference about the food web response to subsidized predators to a period of about two months during summer base flow conditions. Despite this limitation, there is ample scope for strong community level responses to our manipulations. For example, previous work by McNeely et al. (2007) manipulated the presence of the caddisfly *Glossosoma*, the dominant armored grazer in Fox Creek and found that in the absence of *Glossosoma*, chlorophyll-a in Fox Creek doubled, suggesting that short term experimental manipulations can induce changes in patterns of grazer control and primary productivity. However, the invertebrate community in Fox Creek likely reflects the legacy of predators, and the pre-existing community assemblage may have limited the potential for experimentally induced changes in the strength of trophic cascades in our study. The importance of resource subsidies for populations of predators may operate on longer time scales, by increasing the carrying capacity of the stream for juvenile steelhead. While our experiment was not designed to explicitly address long-term population level responses of predators to resource subsidies, dramatic reductions in growth experienced by 1+ steelhead in the absence of terrestrial prey suggest that their populations are supported in large part by terrestrial prey subsidies. Consequently, while experimental manipulations of the availability of resource subsidies and the predator assemblage did not elicit short-term changes in the strength of top-down control, these resource subsidies may serve to strengthen top-down control over the long term.

Contrary to predictions of strong trophic cascades in highly subsidized tributary streams (Leroux and Loreau 2008); our data suggests that armored herbivores serve to compartmentalize tributary food webs into two parts. One, which consists of a closed loop between algal primary production and armored herbivores, and another in which aquatic consumers are much more closely linked to the productivity of the surrounding terrestrial environment, both from the bottom of the food web via terrestrial detritus and from the top by prey subsidies. While predators in recipient ecosystems undoubtedly benefit from the influx of allochthonous prey (Polis et al. 1997), the degree to which the effect of subsidies propagates through multiple trophic levels depends upon the pre-existing interactions between species in the subsidized food web. In our study system, herbivores limit primary producer biomass (McNeely et al. 2007), however the invulnerability of the herbivore guild ultimately governs the trophic consequences of

predation. This finding is perhaps not surprising given the co-evolution of the aquatic predators and herbivore communities in these subsidized food webs. Because predator biomass in these systems is largely decoupled from *in situ* productivity, the persistence of the aquatic herbivore guild through time is dependent on morphological and behavioral traits that limit their vulnerability to predation. Our results highlight the degree to which the trophic consequences of prey subsidies are influenced by the composition of the *in situ* prey community, and challenge the conventional expectation that subsidized predators will necessarily initiate strong trophic cascades.

Tables

Table 1.1: AICc model selection of linear regression models for response of predator growth to experimental contrasts and light availability (% canopy cover). Table includes $\Delta AICc$ scores, model weights (ω_i) and R-squared values for each candidate model. Models within 4 $\Delta AICc$ units were included in the table, intercept only models are also included as a reference.

<i>Response variable</i>	<i>Model</i>	<i>$\Delta AICc$</i>	<i>ω_i</i>	<i>R^2</i>
1+ steelhead growth	Terrestrial prey (+/-)	0	0.917	0.346
	Intercept	4.8	0.083	
Salamander growth	Steelhead (+/-)	0	0.815	0.406
	Intercept	2.96	0.185	
Yoy growth	Terrestrial prey (+/-)	0	0.511	0.229
	% Canopy cover + terrestrial prey(+/-)	0.7	0.360	0.259
	% Canopy cover * terrestrial prey (+/-)	3.42	0.092	0.236
	Intercept	5.27	0.037	

Table 1.2: AICc model selection of linear regression models for response of benthic aquatic invertebrates and aquatic invertebrate emergence to experimental contrasts and light availability (% canopy cover). Table includes $\Delta AICc$ scores, model weights (w_i) and R^2 values for each candidate model. Models within 4 ΔAIC units were included in the table, intercept only models are also included as a reference.

Response variable	Model	$\Delta AICc$	w_i	R^2
Total herbivore biomass	Intercept	0	1	
Vulnerable herbivore biomass	Steelhead (+/-)	0	0.721	0.105
	Intercept	1.9	0.279	
Total emergence biomass	% Canopy cover * salamander density * steelhead (+/-)	0	0.282	0.427
	% Canopy cover * salamander density + % canopy cover * steelhead (+/-)	1.732	0.119	0.311
	% Canopy cover* salamander density	2.708	0.073	0.199
	Salamander density + steelhead (+/-)	2.88	0.067	0.147
	% Canopy * steelhead (+/-) + salamander density * steelhead (+/-)	2.938	0.065	0.293
	% Canopy + salamander density + steelhead (+/-)	3.179	0.058	0.191
	Salamander density	3.774	0.043	0.080
	Intercept	6.126	0.013	

Table 1.3: AICc model selection of linear regression models for response of two indexes of aquatic primary productivity (AFDM and chl-a) to experimental contrasts and light availability (% canopy cover). Table includes $\Delta AICc$ scores, model weights (ω_i) and R^2 values for each candidate model. Models within 4 ΔAIC units were included in the table, intercept only models are also included as a reference.

<i>Response variable</i>	<i>Model</i>	<i>$\Delta AICc$</i>	<i>ω_i</i>	<i>R^2</i>
Ash Free Dry Mass (AFDM)	% Canopy cover	0	0.409	0.153
	% Canopy cover+ steelhead (+/-)	0.032	0.403	0.173
	% Canopy cover * steelhead (+/-)	1.564	0.187	0.180
	Intercept	13.899	0.000	
Chlorophyll-a	% Canopy cover + terrestrial prey(+/-)	0	0.234	0.235
	% Canopy cover + steelhead (+/-) + terrestrial prey (+/-)	1.494	0.111	0.243
	% Canopy cover + salamander density + terrestrial prey (+/-)	1.579	0.106	0.244
	% Canopy cover	1.765	0.097	0.205
	% Canopy cover * steelhead (+/-) + terrestrial prey (+/-)	2.302	0.074	0.252
	% Canopy cover * salamander density + terrestrial prey (+/-)	2.433	0.069	0.252
	% Canopy cover * salamander density * steelhead (+/-)	2.681	0.061	0.302
	% Canopy cover * salamander density	2.795	0.058	0.231
	% Canopy cover * steelhead (+/-) + salamander density + terrestrial prey (+/-)	2.903	0.055	0.256
	Intercept	16.476	0	

Figures

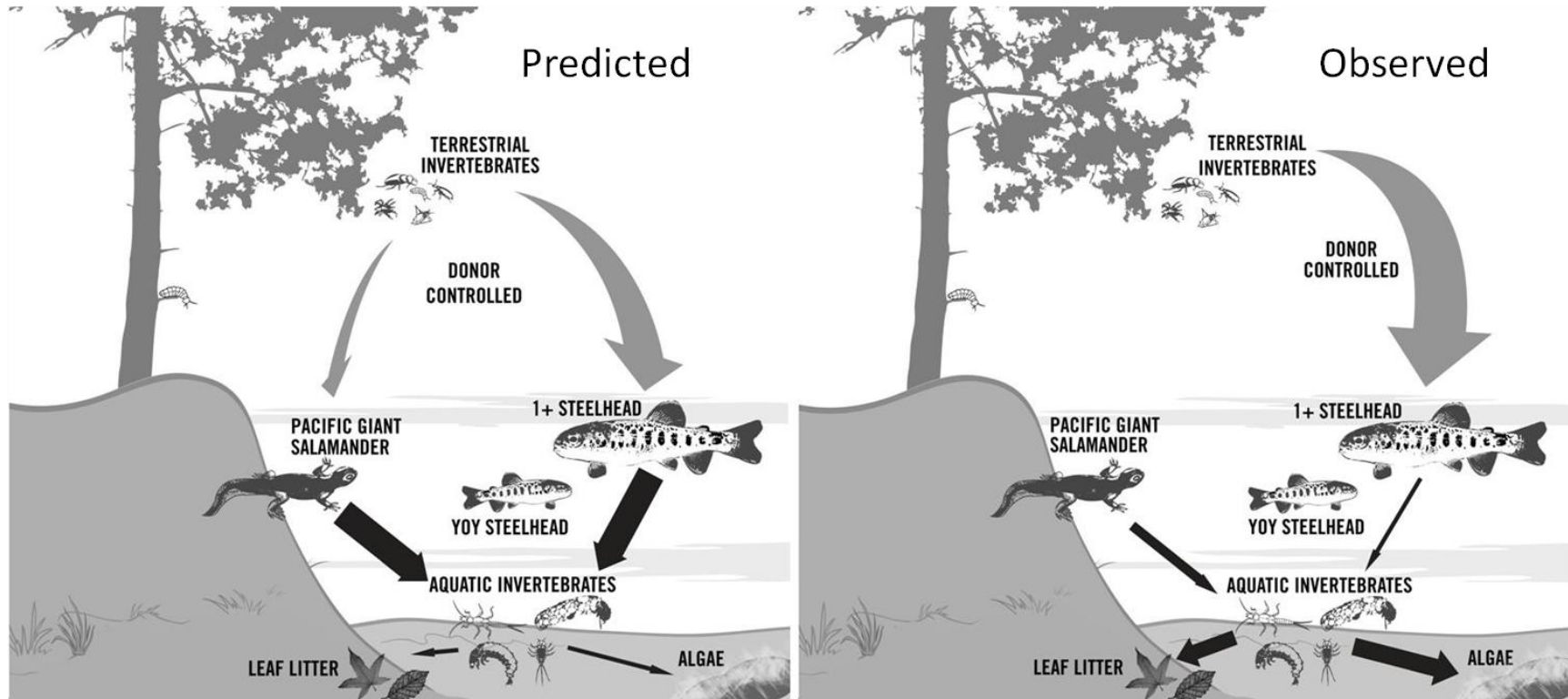


Figure 1.1: Food web diagram depicting predictions and observations of the importance of donor control terrestrial prey subsidies for aquatic predators, and the strength of trophic cascades induced by both salamanders and steelhead. Gray arrows represent donor controlled prey subsidy inputs, arrow size represents the degree to which predator growth depends on resource subsidies. Black arrows represent top-down control in our aquatic food web, with the size of the arrow indicating the strength of interactions between aquatic consumers and their resources.

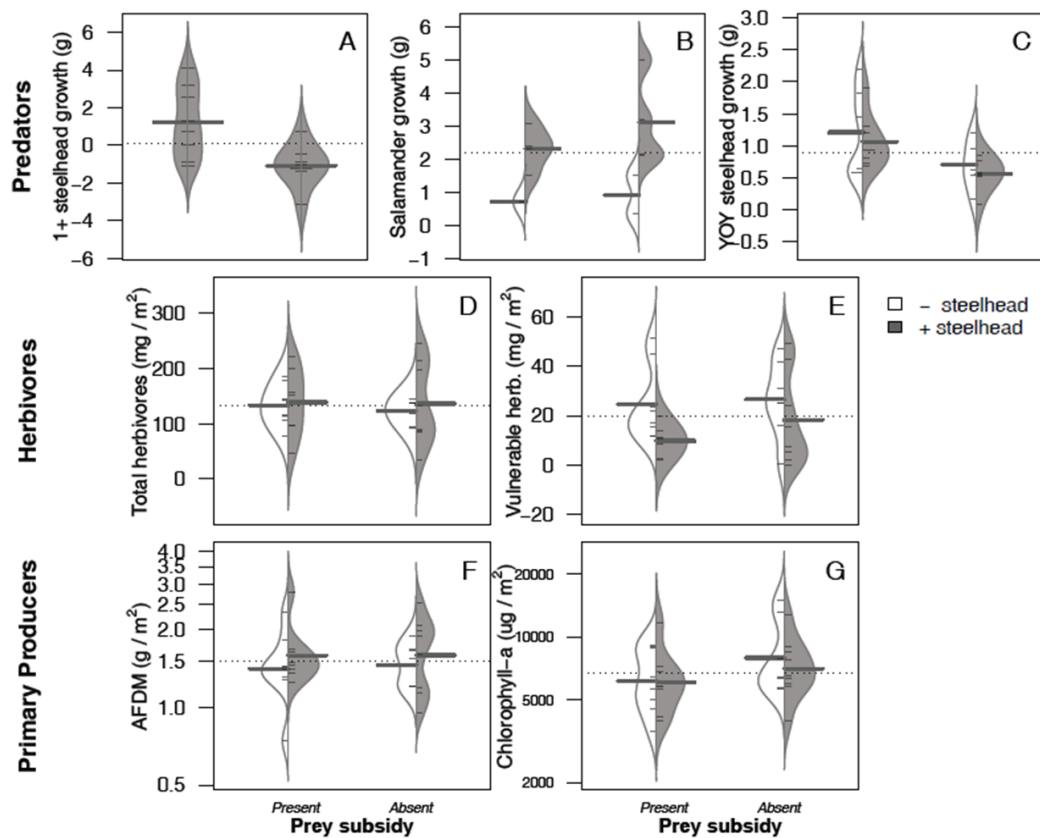


Figure 1.2: (A) Change in 1+ steelhead growth in response to variation in the availability of terrestrial prey subsidies. Change in (B) YOY steelhead growth, (C) salamander growth, (D) final herbivore biomass, (E) final biomass of vulnerable herbivores, (F) algal/biofilm biomass (ash free dry mass), (G) chlorophyll-a in response to experimental manipulations of terrestrial prey availability and the presence of predatory 1+ steelhead. Terrestrial prey availability treatment is depicted on the x-axis of each plot, and steelhead treatments are indicated by the shading within the plotted areas. Pools with predatory steelhead are shaded grey and pools without are white. Plots depict the distribution of responses within our replicate pools, with large bars representing the median value for each treatment.

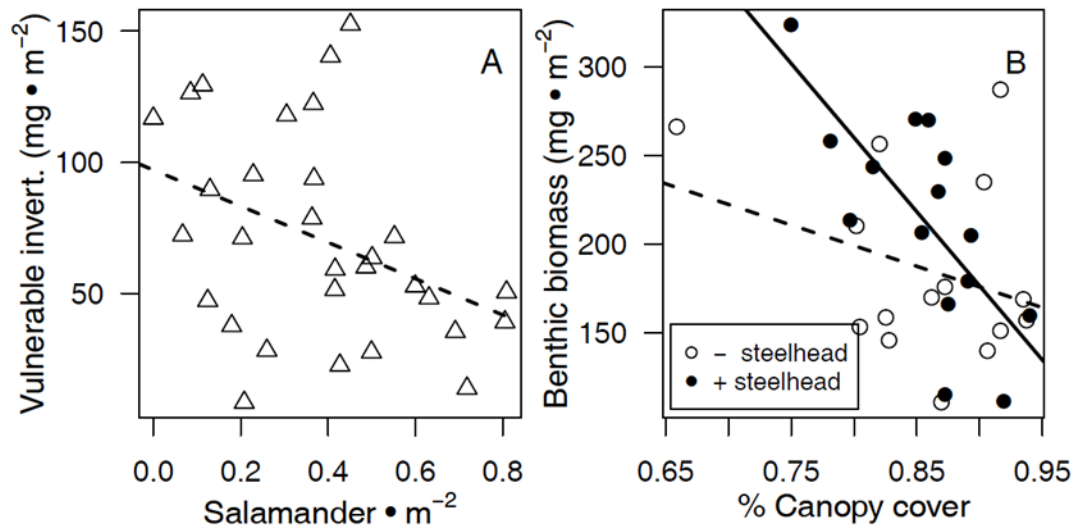


Figure 1.3: (A) Relationship between the biomass of vulnerable benthic invertebrates sampled at the end of the experiment and observed final salamander density. (B) Interaction between light availability (% canopy cover) and steelhead (+/-) for final benthic aquatic invertebrate biomass. Solid line and circles indicate experimental units with steelhead predators, and dashed line and open circles represent steelhead exclusion plots.

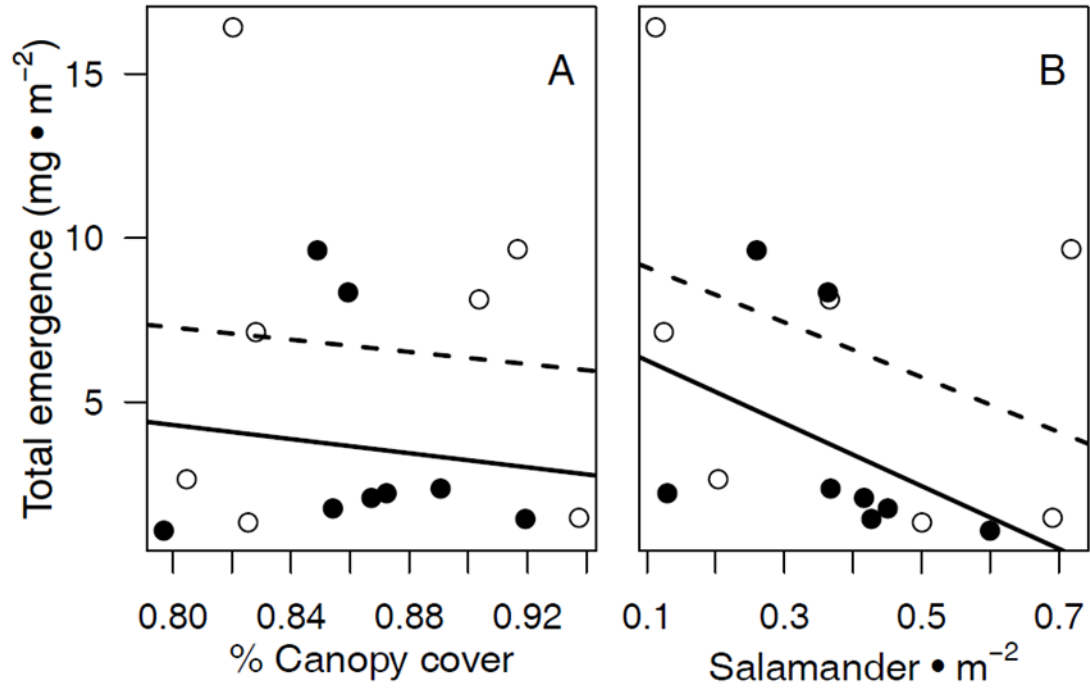


Figure 1.4: Effect of light availability (% canopy cover) (A), and final salamander density (B), with and without predatory steelhead on the total biomass of emerging aquatic invertebrates averaged across three sample dates from covered experimental pools. Lines and circles as for figure 3.1.

Chapter 2. Detritus and prey: food web responses to alternative resource subsidy pathways

Abstract

Resource subsidies often increase the productivity of recipient ecosystems and may have important consequences for the dynamics of recipient food webs. However, the consequences of these flows of allochthonous resources depend on the magnitude of resource subsidies, the trophic level at which they enter the food web, and the composition of the recipient community. In light limited tributary streams large inputs of organic material and prey from the surrounding terrestrial environment support consumer biomass. Consequently, patterns of productivity and community regulation are through to be largely driven by resource subsidies. Using a multi-trophic model we sought to test the differing trophic consequences of prey and detrital subsidies in a tributary stream ecosystem, and how the two subsidy pathways alter patterns of community regulation. We also tested the importance of armored primary consumers, which are common in many tributary streams, both for the food web response to resource subsidies as well as the flow of energy through the food web. We found that resource subsidies resulted in increased biomass of recipient consumers; however the presence of armored invertebrates limited the propagation of subsidy impacts across multiple trophic levels.

Introduction

While ecologists have traditionally studied food web interactions within ecosystems, pioneering work recognizing the importance and ubiquity of linkages between adjacent ecosystems (e.g. Vannote et al. 1980, Polis and Strong 1996) has led to widespread understanding of the degree to which the flow of organisms and materials

from outside local food webs may have fundamentally important consequences for the dynamics of ecosystems (Polis et al. 1997). Resource subsidies involving the flow of nutrients, detritus and prey between adjacent habitats are typically donor controlled, meaning that recipient consumers cannot directly affect the renewal rate or dynamics of the subsidy resource (Polis and Strong 1996). These cross ecosystem fluxes can increase the productivity of recipient consumers, (Nakano and Murakami 2001, Marczak et al. 2007) and may alter the strength of interactions between species in recipient ecosystems (Polis et al. 1997, Nakano et al. 1999b). Resource subsidies may also serve to increase the stability of recipient ecosystems by buffering consumers from variability in local resource pools (Post et al. 2000, Anderson and Polis 2001). Consumer biomass in subsidized ecosystems is often supported above levels that can be sustained by *in situ* productivity alone (Polis and Hurd 1995, Rose and Polis 1998, Sabo and Power 2002, Kawaguchi et al. 2003). In these instances consumers can become decoupled from the dynamics of local resources, resulting in strong top-down control within the subsidized community (Flaherty 1969, Holt 1984) and a strengthening of trophic cascades (Polis and Hurd 1996, Polis et al. 1997, Leroux and Loreau 2008). Across a broad range of ecosystems, resource subsidies increase the productivity of recipient consumers; however major gaps remain in our ability to predict the degree to which resource subsidies will alter the dynamics of recipient food webs. The food web consequences of subsidies should depend on a number of factors, including the timing and magnitude of subsidy inputs (Nakano and Murakami 2001, Leroux and Loreau 2012), the trophic level at which resource subsidies enter recipient food webs (Huxel and McCann 1998), the relative quality of allochthonous material and prey (Marcarelli et al. 2011), the composition of the prey and predator communities, and the strength of interactions between species in the recipient food web (McCann et al. 1998, Huxel et al. 2002).

Tributary streams offer an ideal venue for studying the consequences of subsidies for recipient food webs, as they receive large inputs of both detritus and prey from the surrounding terrestrial environment (Vannote et al. 1980, Nakano and Murakami 2001). Leaf litter and other organic detritus support elevated biomass of primary consumers in stream ecosystems (Fisher and Likens 1972, Vannote et al. 1980, Wallace et al. 1997), and direct subsidies of prey contribute to the biomass of predatory

fish which may derive more than 50% of their diet from terrestrial invertebrates (Nakano and Murakami 2001, Kawaguchi et al. 2003). Because large fluxes of allochthonous material and prey are known to support the productivity of tributary stream communities, previous theoretical work has posited that these systems should experience strong top-down control when subsidies support predator biomass above what could be supported by *in situ* resources alone (Leroux and Loreau 2008). However, experimental evidence to support this theory is lacking and the response of tributary stream food webs to resource subsidies likely depends on the trophic level at which subsidies enter the food web, the relative magnitude of detritus and prey subsidy inputs, and the ability of subsidized predators to exploit local prey. Armored aquatic invertebrates are common in stream food webs, and may limit the ability of predators to exploit primary consumer biomass (Wootton et al. 1996, McNeely et al. 2007). When basal consumers possess morphological or behavioral adaptations that make them invulnerable to predation they may serve as a trophic cul-de-sac, inhibiting the flow of energy to higher trophic levels and limiting ability of predators to exert strong top-down control (Bishop et al. 2007). Wootton et al. (1996) examined the importance of large armored grazers for the strength of trophic cascades in the Eel River, California. However, the mainstem Eel River food web is autotrophic and consumer biomass does not depend on resource subsidies, and the degree to which patterns of top-down control are driven by the presence of armored primary consumers may differ in highly subsidized tributary streams. The role of prey invulnerability in limiting the strength of top-down control in subsidized food webs has not been explicitly studied, and we sought to understand the degree to which food web responses to resource subsidies are limited by the presence of armored prey.

We used a multi-trophic model (*sensu* Wootton and Power 1993) to explore the response of a tributary stream food web to resource subsidies, and the degree to which the presence of armored invertebrates limited the propagation of subsidy effects throughout the food web. This multi-trophic model included two top predators, steelhead trout (*Oncorhynchus mykiss*) and Pacific giant salamander (*Dicaptodon tenebrosus*), both armored and vulnerable aquatic invertebrates partitioned into two general guilds based on their feeding ecology (herbivore, detritivore), as well as pools of algae and detritus within the stream food web. To test the effects of terrestrial invertebrate prey and terrestrial detritus subsidies, we modeled changes in the biomass of predators, primary

consumers, and basal energy pools in response to variation in the magnitude of prey and detritus subsidies, holding subsidy inputs constant through one trophic pathway (i.e. prey subsidies) while manipulating the magnitude of subsidy inputs in the other (i.e. detritus). We also tested the strength of top-down control by both predator species, and the degree to which food web responses to resource subsidies depend on the vulnerability of the aquatic prey community.

Data gathered during a large scale field experiment designed to test the degree to which resource subsidies mediate patterns of top-down control within a tributary stream food web (Atlas et al. *in prep*) offered the unique opportunity to parameterize an ecosystem model using values measured in the field, and to compare experimental outcomes with the responses of our model community to variation in subsidy magnitude and prey vulnerability. We predicted that resource subsidies would increase the abundance of recipient consumers, with prey subsidies resulting in an increase in the biomass of predators and detrital subsidies resulting in an increase in the biomass of primary consumers. We further predicted that prey subsidies which increased the biomass of predators would lead to stronger top-down control, and that detrital subsidies would increase productivity throughout the food web by stimulating greater production of detritivores. However, we predicted that the flow of detrital energy up through the food web and the strength of top-down control by subsidized predators would be limited by the presence of armored invertebrates. We also predicted that the propagation of subsidy effects through our model food web would be strengthened in the absence of armored prey.

Methods

We modeled the dynamics of a tributary stream food web using a multi-trophic modeling framework (Wootton and Power 1993) which included two top predators, both armored and vulnerable primary consumers, algae and detritus. Resources entered the model food web through three pathways, *in situ* primary production, inputs of terrestrial detritus, and inputs of terrestrial invertebrate prey. Both terrestrial detritus and prey were modeled as donor controlled subsidies and entered the food web at a constant rate determined from empirical data. Steelhead trout and salamander biomass increased in

response to the availability of both *in situ* invertebrate prey and inputs of terrestrial invertebrate prey. Both armored and vulnerable invertebrate biomass increased in response to the availability of basal energy (terrestrial detritus and algae) and was limited by predation. Algal biomass increased as a function of light availability which was held constant in our model food web, and the pool of available detritus increased in response to a constant influx of terrestrial detritus. The biomass in both pools of basal energy in our model system was limited by invertebrate primary consumers.

To evaluate the role of terrestrial detritus and algae as drivers of bottom-up production in our model food web and to facilitate evaluation of the effect of subsidies on the two sources of basal energy, aquatic invertebrates were pooled into only two groups. In natural stream ecosystems high species diversity of stream invertebrates is often simplified into functional feeding groups (e.g. shredders, scrapers, collectors, predators, etc), and these functional groups may derive their biomass from both aquatic and terrestrial energy sources (Finlay 2001). However, because we explicitly sought to test relative importance of *in situ* algal biomass and allochthonous detritus for the productivity and dynamics of our model food web we simplified the functional diversity of stream invertebrates further, dividing invertebrate biomass into two pools: herbivores which consumed algae and detritivores which consumed terrestrial detritus. Many aquatic invertebrates in temperate streams are armored and are not readily exploited by many top predators (McNeely and Power 2007), so invertebrate biomass was further partitioned into two groups based on their vulnerability to predation. One group included invertebrates vulnerable to both predator species, and the second included armored invertebrates which were only marginally vulnerable to salamanders and were entirely invulnerable to predatory steelhead.

Using this multi-trophic modeling framework we were able to relate changes in the size of each biomass pool in the food web to a range of model scenarios, which included changes in the magnitude of subsidy inputs and variation in the composition of the predator and prey communities.

Model Structure

Algae and detritus

Changes in the biomass of algae (A) were modeled using an equation (Equation 1) that included the availability of light and consumption by grazers (c_a) (Wootton and Power 1993). In particular the equation related the conversion efficiency of light to algae (b_a); set at 15% a value within the expected range of trophic transfer efficiencies (Pauly and Christensen 1995), the standing biomass of algae (A), light availability expressed as % canopy cover (L) and a theoretical consumption rate by algae (c_a). The relationship between algal biomass and canopy cover was estimated from field data (Atlas et al. *in prep*), and the consumption rate by algae (c_a) was derived using estimates of grazing intensity from McNeely and Power (2007). We then solved the equation for c_a by setting canopy cover to 90%, reflecting the typical amount of light availability in a tributary stream. Algal biomass in our model system was limited by grazing which was a function of the consumption rate of algivores (c_{alg}) and the biomass of both vulnerable (H_{alg}) algivores and armored (G_{alg}) algivores.

$$(1) \frac{dA}{dt} = b_a A L e^{-C_a A} - c_{alg} H_{alg} A - c_{alg} G_{alg} A$$

The change in the biomass of terrestrial detritus over time was modeled (Equation 2) assuming a constant input of detritus (I) minus consumption by armored (G_{det}) and vulnerable detritivores (H_{det}) which was a product of the daily consumption rate (c_{det}), the biomass of detritivores, and the standing stock of detritus (D).

$$(2) \frac{dD}{dt} = I - c_{det} H_{det} D - c_{det} G_{det} D$$

Invertebrates

Invertebrates were divided into two general groups, one was vulnerable to predation by both trout and salamanders, and another was armored and therefore invulnerable to predation by trout and only marginally vulnerable to predation by salamanders. The biomass of predator vulnerable invertebrates (H) was modeled separately for algivores (H_{alg}) (Equation 3) and detritivores (H_{det}) (Equation 4). We estimated changes in invertebrate biomass as a function of the daily consumption rate of

basal energy, which differed for algivores (c_{alg}) and detritivores (c_{det}), and three sources of biomass loss; predation by trout and salamanders, emergence (e_h) into aerial adults, and background natural mortality (m_h). Predation by both trout and salamanders was modeled using a type III functional response which limited exploitation of prey at low densities. Predator specific consumption rates were a function of each predator's daily consumption (c_t and c_s), the total vulnerable prey density (H) and handling time of the prey (a). Total predation on each group of predator vulnerable aquatic invertebrates was therefore a product of the predator specific consumption rates, the biomass of the prey pool and the biomass of the two predators (T , S).

$$(3) \frac{dH_{alg}}{dt} = b_{alg}c_{alg}AH_{alg} - (c_t H^3/a-H^3) H_{alg}T - (c_s H^3/a-H^3) H_{alg}S - m_h H_{alg} - e_h H_{alg}$$

$$(4) \frac{dH_{det}}{dt} = b_{det}c_{det}DH_{det} - (c_t H^3/a-H^3) H_{det}T - (c_s H^3/a-H^3) H_{det}S - m_h H_{det} - e_h H_{det}$$

We modeled changes in the biomass of armored (predator invulnerable) invertebrates for each of the two functional groups, algivores (Equation 5) and detritivores (Equation 6). The biomass of armored invertebrates within each functional group changed as a function of consumption of algae (c_{alg}) or detritus (c_{det}), and was limited by a small degree of predation by salamanders, and the two sources of non-predator loss previous outlined for vulnerable invertebrates. Unlike vulnerable invertebrates armored taxa in our model were not subject to predation by trout and experienced only limited predation by salamanders. Salamander consumption rates on armored invertebrates were based on findings by Parker (1994) indicating that while armored taxa may make up the majority of invertebrate biomass in a tributary stream, they comprised only 6.5% of salamander diets by volume. Predation by salamanders on armored taxa was modeled as a type III functional response; however in accordance with reported values, consumption rates by salamanders were limited to a maximum of 6.5% of their daily consumption (c_s).

$$(5) \frac{dG_{alg}}{dt} = b_{alg}c_{alg}AG_{alg} - ((c_s * 0.065) G^3/a-G^3) G_{alg}S - m_h G_{alg} - e_h G_{alg}$$

$$(6) \frac{dG_{det}}{dt} = b_{det}c_{det}AG_{det} - ((c_s * 0.065) G^3/a-G^3) G_{det}S - m_h G_{det} - e_h G_{det}$$

Finally, we summed the biomass of emerging aquatic invertebrates (Equation 7) from both predator vulnerable and armored groups. The emergence coefficient (e_h) was derived from empirical data, using estimates of total benthic biomass and total daily emergence to fit a linear relationship between emergence biomass and final benthic biomass.

$$(7) \text{ Emergence} = e_h(G + H)$$

Predators

Changes in the biomass of our two predator species; steelhead trout (*O. mykiss*), and Pacific giant salamander (*D. tenebrosus*) were modeled separately. While the two species do overlap in their consumption of many types of aquatic invertebrate prey (Parker 1994, *W. Palen pers. comm.*), steelhead trout in tributary stream food webs are known to rely heavily on terrestrial invertebrates for their growth (Kawaguchi and Nakano 2003, Atlas et al. *in prep*). While salamanders do consume terrestrial invertebrates, terrestrial prey typically comprise a much smaller fraction of their diets (Parker 1994). Furthermore, the two species differ markedly with regards to their metabolic demands (Munshaw et al. *in prep*), growth rates (Atlas et al. *in prep*), and life histories.

We modeled changes in trout biomass (Equation 8) as a function of the growth efficiency of trout (b_t), the consumption of vulnerable aquatic invertebrates (H), and the consumption of terrestrial prey (X). Trout predation of vulnerable aquatic invertebrates was modeled as a type III functional response, which results in low consumption rates at low prey densities, and an asymptotic maximum consumption rate at high prey densities. The type III functional relationship was used because it allowed the persistence of aquatic invertebrate populations, even at high predator biomass. Trout also gained biomass due to the consumption of donor controlled terrestrial prey subsidies (X). Because prey subsidies are donor controlled, trout consumption of this resource was modeled as the product of the daily consumption rate of trout (c_t) and the biomass of trout (T). However, the total daily consumption of terrestrial prey subsidies by trout ($c_t T$) could not exceed the total magnitude of the input (X) and was bounded at that level.

$$(8) \text{ if } X > c_t T; \quad dT/dt = b_t(c_t H^3/a-H^3) HT + b_t c_t T - m_t T$$

$$\text{if } X < c_t T; dT/dt = b_t(c_t H^3/a-H^3) HT + b_t X - m_t T$$

Salamander biomass was similarly modeled as increasing due to consumption of vulnerable aquatic invertebrates but also included the more limited consumption of armored invertebrates (Equation 9). Salamanders benefitted from access to terrestrial prey only when trout biomass was incapable of fully exploiting the resource (ie $X > c_t T$). The pool of terrestrial prey available to salamanders was therefore modeled as $(X - c_t T)$. Like trout, salamanders' maximum consumption of terrestrial prey $c_s S$ could not exceed the magnitude of the available prey subsidies and the maximum potential salamander consumption of terrestrial prey could not exceed the size of the pool of available prey $(X - c_t T)$.

$$(9) \text{ if } X - c_t T > c_s S; dS/dt = b_s(c_s H^3/a-H^3) HS + b_s((c_s*0.065) G^3/a-G^3) GS + b_s c_s S - m_s S$$

$$\text{if } X - c_t T < c_s S; dS/dt = b_s(c_s H^3/a-H^3) HS + b_s((c_s*0.065) G^3/a-G^3) GS + b_s(X - c_t T) - m_s S$$

A complete list of parameters and their units can be found in Table 2.1.

Parameter Estimation

Bioenergetic parameters within the model were derived from a combination of field data and values taken from the literature. Consumption rates and growth efficiencies for aquatic invertebrates were estimated separately for detritivores and algivores using values from the scientific literature. Consumption rates for detritivores (c_{det}) were estimated as 0.35 g/g/day (McDiffet 1970, Grafius and Anderson 1979), and consumption rates for algivores (c_{alg}) were estimated at 0.2 g/g/day (Johnson and Brinkhurst 1971). Growth efficiencies for detritivores (b_{det}) and algivores (b_{alg}) were set at 0.065 g/g and 0.195 g/g respectively (Benke and Wallace 1980), reflecting the relatively poor nutritional quality of most detrital food. Daily consumption rates for predatory steelhead trout (c_t) were estimated using the average daily stream temperature in Fox creek (see below) from late-June to late-August to derive temperature-dependent consumption rates (Wurtsbaugh and Davis 1976). Daily consumption rates were then averaged across the summer to produce a single consumption rate for trout (0.075 g/g/day). Consumption rates of salamanders (c_s) were estimated directly from diets of Pacific giant salamanders assuming a 6 hour gut clearance time (0.02236 g/g/day). We

assumed a growth efficiency of 10% for both predators (Pauly and Christensen 1995). Diet studies suggest that the consumption of armored invertebrates by Pacific giant salamanders is limited to a small proportion of the total volume of their diets. Consequently, we included a limited amount of consumption of armored invertebrates by salamanders, up to 6.5% of their daily consumption rate (Parker 1994).

Initial biomass values for each trophic level in the model were set according to values measured in Fox creek (2.8 km² drainage area) is a tributary of the South Fork Eel River (39° 43'45" N, 123° 38'40" W). Fox creek supports low algal productivity due to dense canopy cover (average ~86%), receives large inputs of both terrestrial detritus (1.7 g/m²/day) and prey (0.523 g/ m²/day), and supports populations of Pacific giant salamanders and steelhead trout. The biomass of steelhead trout and salamanders was estimated by depletion sampling 32 pools across the longitudinal extent of the creek in late June 2010. Predators were removed from replicate pools through a combination of snorkel, hand capture, and electrofishing until no new animals were captured. All animals were weighed (g) and measured (mm) and pool area measurements were used to calculate the biomass of each predator species per unit area (steelhead = 5.12 g/m², salamanders = 13.42 g/m²). Standing biomass of algae was quantified using unglazed ceramic tiles (4.8 cm * 4.8 cm) incubated for 8 weeks in each of the 32 replicate pools during peak summer productivity (mean AFDM = 1.59 g/m²). Average percent canopy cover was estimated for each pool using a spherical densitometer. Emergence of aquatic invertebrates was quantified using replicate sticky traps, deployed perpendicular to the direction of flow within each of our 32 replicate pools and left for 48 hours. The biomass and composition of benthic aquatic invertebrates were estimated with by sampling 6 randomly selected benthic rocks from each pool (H~0.1 g/m², G~0.13 g/m²). The input of terrestrial prey to our study system was quantified using pan traps deployed five times throughout the summer, at five locations across the longitudinal extent of Fox Creek. Traps (37 cm * 26.5 cm) were set above the stream surface with a few centimeters of water and 2-3 drops of surfactant to capture falling invertebrates for a 24 hour period. All invertebrate data from sticky traps, benthic sampling and pan traps were then converted to biomass estimates using taxa specific length-weight relationships (Hodar 1996, Benke et al. 1999, Sabo et al. 2002).

Natural background input of detritus was estimated using leaf litter traps which collected in-fall from the riparian forest and lateral debris traps which sampled any surface litter transport ($I=1.7\text{g}/\text{m}^2/\text{day}$) (McNeely *et al. Unpublished data*). Buckets (0.25 m in diameter) placed at the surface of the water paired with lateral leaf litter baskets placed along the edge of the stream bank. Buckets and litter baskets were deployed at 10 locations throughout Fox Creek and collected 4 times between early summer and early fall. Samples were dried at 60°C for 48 hours and then weighed. Dry weights were divided by area (m^2) and the duration of sampling yielding an average total daily input of detritus during the summer sampling period.

Model Scenarios and Evaluation

Using the modeling framework described above, we evaluated the relative importance of terrestrial prey and detritus subsidies for the productivity and dynamics of a tributary stream food web. Background daily inputs of prey and detritus (estimated at $0.523\text{ g}/\text{m}^2$ and $1.7\text{ g}/\text{m}^2$ respectively) were used to represent the levels best supported by our empirical data, and we consider these rates as the basis for our reference model (see below). To evaluate food web responses to changes in the magnitude of terrestrial prey and detritus subsidies, we simulated a range of different input rates into a model stream community while holding light availability constant. While canopy cover (light availability) and inputs of terrestrial detritus and prey are probably not independent of one another in natural ecosystems, holding light levels constant allowed us to specifically test the response of the model community to variation in subsidy magnitude. Five levels of terrestrial detritus and prey subsidies were simulated independently of one another, including 0%, 50%, 100%, 150% and 200% of natural background subsidy inputs. We also evaluated the effects of simultaneous changes in both subsidies. Models under these alternative subsidy scenarios were run for 90 daily time steps to simulate a period of over-summer growth. At the conclusion of the 90 day model run, changes the biomass of steelhead trout, salamanders, vulnerable invertebrates, armored invertebrates, algae, and the standing pool of terrestrial detritus were used to compare food web responses to subsidy scenarios.

To test the effects of prey invulnerability for the strength of top-control and the food web response to resource subsidies, we compared the final biomass of each

trophic group within our model food web (i.e. steelhead, vulnerable invertebrate, algae, etc.) under reference subsidy levels when armored invertebrates were included in our model community and when all invertebrates were modeled as being vulnerable to predation by steelhead and salamanders. We also evaluated the degree to which prey vulnerability mediates the strength of top-down control by both predator species in our model system, running the same vulnerability scenarios described above with only steelhead, only salamanders, both predators at reference densities, and neither predator species.

Model Evaluation

Models scenarios were evaluated both qualitatively by comparing the final biomass of each trophic group in our model community, and quantitatively through the use of Log Response Ratios (Hedges et al. 1999). Log response ratios were calculated as $LRR_E = \ln(X_E) - \ln(X_C)$, where E is the “treatment”, in our case simulations of different subsidy inputs, prey vulnerability, and predator assemblage. X_E is the biomass of a given trophic group at day 90 (e.g. steelhead trout, armored invertebrates, etc) in response to that change, and X_C is the biomass of that trophic group in the control group. Log response ratios (LRR) offer a simple, easily interpretable measure of community level changes induced by each model scenario.

Results

Food web responses to variation in terrestrial subsidies

Predators

While both predator species in our model system consumed both aquatic and terrestrial prey during the simulation, model results across the range of subsidy scenarios suggest that variation in predatory steelhead biomass is driven almost entirely by inputs of terrestrial prey. Increasing the magnitude of prey subsidies from 0% to 100% natural inputs resulted in a sharp increase in trout biomass at the end of the 90-day model run ($LRR_{100\%} = 0.6307$, Table 2.2) (Figs. 2.1, 2.2). Trout biomass at the end of the 90 day simulations did not vary in response to changes in the inputs of terrestrial detritus ($LRR_{100\%} = 0.0014$, Table 2.2) (Figs. 2.2, 2.3). Reduced inputs of terrestrial prey

(0% and 50% of reference input) resulted in dramatic reductions in trout biomass (- 46.8 % and - 21.5 % respectively). However, predatory trout consumption of terrestrial prey was nearly saturated at reference subsidy levels, and increasing the magnitude of prey subsidies to 200% of the natural input resulted in only a small increase in final trout biomass ($LRR_{200\%} = 0.0347$, Table 2.2) (Figs. 2.1, 2.2). Salamander biomass estimated at the end of the 90 day simulations reflected changes in both prey and detrital subsidies (Figs. 2.1, 2.2, 2.3). When the magnitude of detrital subsidies increased, salamander biomass increased, tracking the response of their aquatic invertebrate prey ($LRR_{200\%} = 0.0135$, Table 2.2). The relationship between salamander biomass and terrestrial prey subsidies was non-linear; at low levels, salamanders did increase in response to terrestrial prey subsidies ($LRR_{100\%} = 0.0257$, Table 2.2), however at high subsidy levels salamanders appeared to benefit substantially from terrestrial prey ($LRR_{200\%} = 0.1726$, Table 2.2) increasing their final biomass by 22% relative to reference subsidy levels.

Aquatic Invertebrates

In simulations that included predatory salamanders and steelhead, the biomass of vulnerable aquatic invertebrates was strongly limited by predation ($LRR_{both} = -3.8001$, Table 2.2). Over the course of the 90 day simulation, the biomass of vulnerable invertebrates initially increased, and peaked shortly after the beginning of the simulation tracking a short-term increase in the amount of detrital biomass available to aquatic consumers (Figs. 2.2, 2.3). Following this peak, predation by salamanders and steelhead trout resulted in a decline of vulnerable aquatic invertebrates to a relatively low but stable biomass. Despite the short-term response to the influx of terrestrial detritus, vulnerable invertebrate biomass did not increase substantially when detrital inputs were increased to 200% of reference subsidy levels ($LRR_{200\%} = 0.0038$, Table 2.2) (Figs. 2.2, 2.3). Predators exerted strong top-down control on the biomass of vulnerable aquatic invertebrates. However, increased predator biomass in response to elevated terrestrial prey subsidies did not substantially increase the strength of top-down control ($LRR_{200\%} = 0.0110$, Table 2.2) (Figs. 2.1, 2.2). By contrast, we found that the biomass of armored aquatic invertebrates was not strongly affected by predation ($LRR_{both} = 0.2343$, Table 2.2) and responded positively to increased detrital subsidies ($LRR_{100\%} = 2.8896$, $LRR_{200\%} = 0.6785$, Table 2.2). The biomass of armored invertebrates increased asymptotically with the upper limit of biomass determined by the availability of

terrestrial detritus (Figs. 2.2, 2.3). In general these predator invulnerable primary consumers were unaffected by variation in the influx of terrestrial prey, except in the highest prey subsidy scenarios (150% and 200% of reference input), where salamander biomass increased sufficiently to depress the biomass of armored invertebrates slightly ($LRR_{200\%} = -0.0528$, Table 2.2) (Figs. 2.1, 2.2).

Over the course of each 90-day food web simulation, the biomass of armored invertebrates greatly exceeded the biomass of vulnerable invertebrates regardless of the magnitude terrestrial subsidies. As such, armored invertebrates comprised the majority of the biomass of emergent aquatic invertebrates. Daily emergence of aquatic invertebrates increased asymptotically during the 90 day simulations, and was strongly influenced by the magnitude of detrital subsidies ($LRR_{100\%} = 2.7381$, $LRR_{200\%} = 0.6703$, Table 2.2) (Fig. 2.4B), but not by terrestrial prey subsidies ($LRR_{100\%} = -0.0093$, $LRR_{200\%} = -0.0571$, Table 2.2) (Fig. 2.4A). On average, inputs of terrestrial prey and detritus ($0.523 \text{ g/m}^2/\text{day}$ and $1.7 \text{ g/m}^2/\text{day}$) exceeded the export of emergent aquatic invertebrates from the aquatic environment which ranged from $0.0039 \text{ g/m}^2/\text{day}$ in the absence of detrital subsidies to $0.1039 \text{ g/m}^2/\text{day}$ when detrital subsidies were increased to 200%.

Algae and Detritus

In general, increases in the availability of resource subsidies increased predator biomass, but did not initiate a trophic cascade in our model ecosystem. With the exception of the 0% detritus subsidy scenario, algal biomass followed the same temporal pattern, declining slightly initially before gradually increasing throughout the duration of the 90 day model simulation as predators suppressed vulnerable herbivore biomass. Under reference conditions, terrestrial prey subsidies had no apparent effect on *in situ* primary productivity ($LRR_{100\%} = 0.0063$). However, the highest level of terrestrial prey subsidy (150% and 200% reference input), salamander biomass increased dramatically resulting in a modest increase in algal biomass ($LRR_{200\%} = 0.0206$), (Figs. 2.1, 2.2). Increases in the magnitude of terrestrial detritus subsidies above reference conditions did not appear to affect algal biomass ($LRR_{200\%} = 0.0015$), however the lowest algal biomass at the end of the 90 day simulation was observed in the absence of detrital subsidies ($LRR_{0\%} = -0.1328$) (Figs. 2.2, 2.3). Temporal changes in the pool of available

terrestrial detritus throughout the duration of 90-day simulations were characterized by a sharp increase, followed by a decline to a stable level only slightly lower than the initial detritus biomass. The final biomass of terrestrial detritus in our model system did not track increases in magnitude of detrital subsidies ($LRR_{200\%} = 0.0043$, Table 2.2) (Figs. 2.2, 2.3), and like algal biomass, prey subsidies had only minimal effects on the pool of detrital biomass ($LRR_{100\%} = 0.0087$, $LRR_{200\%} = 0.0480$) (Figs. 2.1, 2.2).

Food web responses to variation in prey vulnerability

Overall, the relative invulnerability of a large proportion of the aquatic invertebrate community dramatically reduced the flow of energy to top predators (Fig. 2.5), especially steelhead. When all invertebrates were modeled as being vulnerable to predation, consumption of aquatic prey by trout and salamanders increased, routing algal and detrital energy to top predators, resulting in increased growth by steelhead trout ($LRR = 0.0385$) which tracked the magnitude of detrital subsidies (Fig. 2.5). Steelhead benefitted from increased prey vulnerability regardless of the presence of salamander competitors ($LRR_{+Sal} = 0.0385$, $LRR_{-Sal} = 0.0597$), whereas salamanders benefitted very little from increased prey vulnerability except in the absence steelhead trout competitors ($LRR_{+Sthd} = 0.0014$, $LRR_{-Sthd} = 0.0211$), or when the absence of prey subsidies led to a decline in the total biomass of steelhead (Fig. 2.5).

In reference models (*Armored*) when armored taxa were included in the community, predatory steelhead had no effect on the total biomass of primary consumers in the model food web (Detritivores: $LRR_{Sthd} = 0.0504$, Herbivores: $LRR_{Sthd} = 0.1329$), and did not exert strong top-down control on basal resources (Detritus: $LRR_{Sthd} = -0.0491$, Algae: $LRR_{Sthd} = -0.0241$, Table 2.2). There was strong top-down control of primary consumers by predatory salamanders (Detritivores: $LRR_{Sal} = -0.3893$, Herbivores: $LRR_{Sal} = -0.9598$, Table 2.2), which were capable of exploiting armored prey on a limited basis (Fig. 2.6). Predation by salamanders on primary consumers led to increased accumulation of terrestrial detritus ($LRR_{Sal} = 0.3884$, Table 2.2) and elevated biomass of algae ($LRR_{Sal} = 0.3844$, Table 2.2). When all aquatic invertebrate taxa were modeled as being vulnerable to predation, both trout (Detritivores: $LRR_{Sthd} = -0.4385$, Herbivores: $LRR_{Sthd} = -18.3906$, Table 2.2) and salamanders (Detritivores: $LRR_{Sal} = -0.1343$, Herbivores: $LRR_{Sal} = -9.3845$, Table 2.2) depressed the biomass of aquatic

invertebrates, resulting in increased algal production (Fig. 2.6). Herbivore biomass rapidly declined to near zero (Fig. 2.6) and algal biomass was uniformly high (Fig. 2.6). When all invertebrates were modeled as being predator vulnerable, detritivore biomass was also depressed to low levels by predation. However, the biomass of this guild stabilized, albeit at a much lower level than in reference models and did not approach zero (Fig. 2.6).

Discussion

The effect of subsidies in our model system was generally limited to the trophic level at which they entered the food web, and subsidies did not lead to changes in patterns of top-down control. Both detritus and prey subsidies resulted in increased productivity of recipient consumers in our model system. Consistent with a large body of research documenting the benefits of prey subsidies for predators (Polis and Hurd 1995, Rose and Polis 1998, Kawaguchi and Nakano 2003), direct subsidies of terrestrial prey into our model system led to increased predator biomass. But contrary to theory (Holt 1984, Polis et al. 1997, Leroux and Loreau 2008) increasing the availability of allochthonous prey did not strengthen top-down control. Similarly, inputs of terrestrial detritus dramatically increased the biomass of detritivores in our model system. However in general, increased production of primary consumers provided little benefit to predators. These model results and the response of the community to predation by steelhead and salamanders in a large scale field experiment (Atlas et al. *in prep*) suggest that the ability of resource subsidies to propagate through recipient food webs is mediated by the vulnerability of *in situ* prey.

We found that vulnerable aquatic invertebrate biomass was depressed in the presence of both predator species regardless of the availability of terrestrial prey, and armored taxa were largely unaffected by prey subsidies since they were not vulnerable to predation by steelhead trout. Similarly, recent experimental tests of predation in a tributary stream ecosystem demonstrated top-down control of predator vulnerable invertebrates by both salamanders and trout (Atlas et al. 2012 *in press*). In our model food web, terrestrial prey subsidies benefitted salamanders primarily when large inputs of terrestrial prey exceeded the consumptive capacity of steelhead trout (ie. $X > c_t T$).

When this occurred large quantities of unconsumed terrestrial prey became available to salamanders, resulting in a dramatic increase in their biomass. Subsidy driven increases in salamander biomass served to strengthen top-down control, because salamanders in our model were capable of exploiting armored prey on a limited basis. Parker (1994) found armored caddisflies in the diets of salamanders, suggesting that they do access armored prey to some extent, but our recent experimental work suggests that salamander predation is not of sufficient intensity to elicit changes in the biomass of these armored taxa (Atlas et al. *in prep*). While prey subsidies did intensify predation by salamanders leading to stronger top-down control of primary consumers and increased algal biomass, the magnitude of this trophic cascade was small enough that it could be difficult to detect in a variable natural ecosystem. Experimental results suggest that abiotic factors such as light availability play a much larger role in determining primary productivity when the majority of the herbivore community consists of armored taxa (Atlas et al. *in prep*).

Many studies have highlighted the importance of aquatic insect emergence for terrestrial predators (e.g. Henschel et al. 2001, Sabo and Power 2002). However, the shape of watersheds mean that gravity will necessarily move material downhill, resulting in high inputs of allochthonous material and prey into streams and other water bodies (Power et al. 2004, Leroux and Loreau 2008), and we found that our simulated aquatic ecosystem was a net sink of energy. The total flux of aquatic invertebrates back to the terrestrial ecosystem ($0.0529\text{g/m}^2/\text{day}$) was on average an order of magnitude smaller than inputs of terrestrial prey ($0.523\text{ g/m}^2/\text{day}$) into the aquatic system. As the most abundant group of aquatic invertebrates (~95% of final invertebrate biomass), armored detritivores contributed disproportionately to emergence in our model stream ecosystem. Emergence tracked the biomass of detrital inputs closely, but the majority of detritivores were armored and largely invulnerable to predation. The prevalence of armored invertebrates in the model food web meant that very little of the energy which entered the aquatic food web as terrestrial detritus was available to aquatic predators. Consequently, the majority of the detrital energy that entered the aquatic food web was quickly routed back into the terrestrial environment via emerging insects, where it likely benefits terrestrial predators. Many riparian predators depend on emerging aquatic insects as prey (Henschel et al. 2001, Sabo and Power 2002, Power et al. 2004, Baxter

et al. 2005); however our model results suggest that there may be as much as a tenfold difference in the magnitude of reciprocal aquatic and terrestrial prey fluxes. This imbalance may be alleviated in part if emerging aquatic invertebrates are more vulnerable to terrestrial predators than terrestrial invertebrate prey. The timing of terrestrial and aquatic productivity may also lead to seasonal variation in the importance of aquatic prey subsidies for terrestrial consumers (Nakano and Murakami 2001). We modeled these fluxes as constant rates, however if seasonal pulses in subsidy magnitude overlap with periods of low productivity in the recipient food web, subsidies may play a disproportionate role in sustaining consumer biomass (Nakano and Murakami 2001, Baxter et al. 2005).

We propose that the presence of armored taxa limits the ability of predators to induce trophic cascades (Wootton et al. 1996, Atlas et al. *in prep*), and the absence of a strong trophic cascading response to resource subsidies in our model food web was attributable to the high biomass of relatively predator invulnerable armored invertebrates. In our reference model, when armored invertebrates were present at natural densities at the start of our simulation, predatory steelhead trout were unable to access most of the invertebrate biomass in the aquatic food web and relied primarily on terrestrial prey subsidies. A manipulative field experiment that removed armored grazers from experimental reaches of a tributary stream found that armored grazers can limit the biomass of other, more vulnerable invertebrate taxa (McNeely et al. 2007). By outcompeting vulnerable grazers, armored invertebrates reduce the productivity of aquatic food web for higher order consumers and limit the scope for top-down control. However, there may be tradeoffs associated with armoring that limit the dominance of armored invertebrates in the aquatic community. For instance, Wootton et al. (1996) found that the strength of trophic cascades in a river ecosystem could be predicted by the intensity of scouring winter floods, known to induce high mortality among heavily armored grazers, leaving an invertebrate community dominated by more vulnerable taxa which could be readily exploited by predatory fish. Dispersal is an important driver of the distribution patterns of aquatic invertebrates (Malmqvist 2002) and flood disturbance may serve to maintain the diversity of the aquatic invertebrate community if vulnerable invertebrates have higher survival during floods or if they may more readily colonize stream reaches following scouring floods. Morphological and behavioral traits which offer

defense against predators also come at the expense of growth rates and competitive ability (Wellborn 2002), and prey species diversity may be maintained in part by variation in the way that different species balance predation risk, foraging and growth efficiency trade-offs (McPeck et al. 2001). With their heavy rock or stick cases, armored invertebrates may face a trade-off whereby reduced vulnerability to predators comes at the cost of mobility; reducing grazing efficiency and limiting their ability disperse in search of higher quality foraging opportunities.

Model scenarios that included only vulnerable invertebrates contrast sharply with the reference model, and the high biomass of subsidized predators relative to local prey led to strong top-down control and trophic cascades, matching theoretical predictions (Holt 1984, Polis et al. 1997, Leroux and Loreau 2008). When all invertebrates were modeled as being vulnerable, predation by trout, which had previously been limited to a small subset of the invertebrate community, expanded such that it impacted the entire food web. Increased predation by trout and elevated predation rates by salamanders resulted in stronger top-down control leading to marked changes in the biomass of the invertebrate community and the balance between herbivores and detritivores. The biomass of the herbivore guild quickly declined to zero and detritivore biomass was depressed dramatically, releasing algae and detritus from consumer control and initiating a strong trophic cascade as measured by log response ratios (Table 2.2). Interestingly, salamander predators only appeared to benefit from increased prey vulnerability in the absence of the terrestrial prey subsidy, when the biomass of trout competitors declined throughout the 90-day model run. While consumption rates of armored prey by salamanders were relatively low, the invulnerability of this invertebrate guild to predation by trout meant that salamanders benefitted exclusively from this large pool of aquatic invertebrate biomass. Consequently, when armored taxa were eliminated from the invertebrate community there was a sharp increase in the degree of resource overlap and competition between salamanders and trout. Resource overlap is thought to reduce persistence within ecological communities (Schoener 1974, Huxel et al 2002). However in this case, trout and salamanders were resilient to this overlap because of the availability of donor controlled terrestrial prey subsidies, which cannot be overexploited by local predator populations. While model outcomes suggest the potential for competition between salamander and trout populations, empirical evidence suggest that

competition does not limit the growth of either predator species (Atlas et al. 2012 *in prep*). While steelhead and salamanders are known to have a high degree of overlap in aquatic prey resources (Parker 1994), experimental results suggest that steelhead trout may facilitate salamander growth, likely due to changes in prey behavior which increase the vulnerability of prey species in the presence steelhead (Atlas et al. 2012 *in prep*).

The use of a multi-trophic model allowed us to explore the role resource subsidies in recipient food webs and to simulate the interactions between food web members across a range of biologically plausible scenarios. We modeled predators, prey, and basal energy as biomass pools allowing us to ask broad questions about the flow of energy across trophic levels and the interaction between bottom-up and top-down regulation, and resource subsidies. While our findings yield insight into the general dynamics of subsidized ecosystems, modeling complex ecological interactions necessarily involves simplifications, with a resulting loss in biological realism. In real food webs, interactions between predator and prey occur at the individual level, and predator induced behavioral changes in patterns of foraging and habitat use by prey species may have important consequences for trophic dynamics (Lima 1984, Schmitz et al. 1997). The behavior of prey in the presence of predators may also play an important role in mediating patterns of predation, however the functional relationship between the presence of predators and the behavior of prey remains unknown and was not included in our model. Additionally, the response of predators to changes in prey availability may be unpredictable, leading to unforeseen effects in real food webs (Nakano et al. 1999, Baxter et al. 2004). Interactions between competing species in size-structured populations may change throughout their ontogeny (Werner and Gilliam 1984), and depending on their size, salamanders and trout may act as either predator and prey for one another (Resetarits 1991, Parker 1993). This intra-guild predation could have important consequences for the dynamics of both predator populations (Polis et al. 1989), and may dampen top-down control (Finke and Denno 2004). The ecological consequences of intra-guild predation, facilitation, and potentially competition should depend on the size of the individual predators. However, because steelhead trout and salamanders were treated as single biomass pools within our model system, our results do not capture these interactions. Despite these shortcomings, our results match observations and recent experimental results from tributary food webs in the South Fork

Eel watershed where the majority of our parameters are derived from (McNeely et al. 2007, Atlas et al. *in prep*). Furthermore, model results allow us to explore a range of food web scenarios not feasible in natural ecosystems.

Our model results confirm that consumers in recipient communities benefit substantially from resource subsidies. However, increased productivity of subsidized consumers does not necessarily translate into changes in the dynamics of the recipient communities, and we found that prey invulnerability strongly limited the scope of subsidy effects in our model food web. However, even limited consumption of armored prey by salamanders resulted in cascading effects of predation, suggesting that when predator biomass is high, even low predation rates may result in substantial top-down impacts on food webs. Overall, we find that morphological adaptations of prey that limit their susceptibility to predation appear to play a key role in the persistence of prey assemblages. Such adaptations may be ubiquitous among prey in highly subsidized ecosystems where predator biomass greatly exceeds the capacity of the local food web (e.g. *in situ* resources). We conclude that a deeper understanding of patterns of prey vulnerability across different subsidized ecosystems would represent an important advance in understanding the dynamics of spatially subsidized food webs.

Tables

Table 2.1: List of parameters used in multi-trophic model and their units.

Symbol	Meaning	Units
A	Algae biomass	g/m^2
L	Light availability	% canopy cover
D	Detritus standing stock	g/m^2
I	Daily input of detritus	$\text{g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$
X	Daily input of terrestrial prey	$\text{g} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$
H_{alg}	Vulnerable herbivore biomass	g/m^2
G_{alg}	Armored herbivore biomass	g/m^2
H_{det}	Vulnerable detritivore biomass	g/m^2
G_{det}	Armored detritivore biomass	g/m^2
T	Predatory steelhead trout biomass	g/m^2
S	Predatory salamander biomass	g/m^2
b_a	Conversion efficiency of algae	$\text{g} \cdot \% \text{ canopy}^{-1} \cdot \text{d}^{-1}$
c_a	Per capita consumption rate of algae	$\text{m}^2 \cdot \text{g}^{-1} \cdot \text{d}^{-1}$
b_{alg}	Conversion efficiency of herbivores eating algae	g/g
c_{alg}	Per capita consumption rate of algivores	$\text{m}^2 \cdot \text{g}^{-1} \cdot \text{d}^{-1}$
b_{det}	Conversion efficiency of detritivores eating detritus	g/g
c_{det}	Per capita consumption rate of detritivores	$\text{m}^2 \cdot \text{g}^{-1} \cdot \text{d}^{-1}$
b_t	Conversion efficiency of steelhead eating invertebrate prey	g/g
c_t	Per capita consumption rate of steelhead	$\text{m}^2 \cdot \text{g}^{-1} \cdot \text{d}^{-1}$
b_s	Conversion efficiency of salamanders eating invertebrate prey	g/g
c_s	Per capita consumption rate of salamanders	$\text{m}^2 \cdot \text{g}^{-1} \cdot \text{d}^{-1}$
m_h	Mortality of aquatic invertebrates not due to predation	d^{-1}
m_t	Background mortality of steelhead	d^{-1}
m_s	Background mortality of salamanders	d^{-1}
e_h	Emergence rate of aquatic invertebrates	d^{-1}

Table 2.2: Log Response Ratios for model community responses to variation in subsidy magnitude as well as predator assemblage under both armored and invulnerable prey scenarios. 100% columns represent food web response to an increase in subsidy magnitude from 0% to 100% of natural subsidy inputs, and 200% columns represent an increase in subsidy magnitude from 100% to 200% natural subsidy input.

	Prey subsidy		Detritus subsidy		(+/-) Trout		(+/-) Salamander		(+/-) Predators	
	100%	200%	100%	200%	Armored	Vulnerable	Armored	Vulnerable	Armored	Vulnerable
Detritus (g/m ²)	0.009	0.048	1.678	0.004	-0.049	0.432	0.388	0.142	0.396	2.525
Algae (g/m ²)	0.006	0.021	0.133	0.002	-0.024	0.013	0.384	0.008	0.452	0.917
Vulnerable Invert. (g/m ²)	-0.107	0.011	0.516	0.004	-0.367	-0.439	0.222	-0.134	-3.8	-2.592
Armored Invert. (g/m ²)	-0.008	-0.053	2.89	0.679	0.062	-0.439	-0.425	-0.134	0.234	-2.627
Steelhead Trout (g/m ²)	0.631	0.035	0.001	0.001	--	--	-0.002	-0.023	--	--
Salamanders (g/m ²)	0.026	0.173	0.013	0.014	-0.174	-0.197	--	--	--	--
Emergence (g/m ² /day)	-0.009	-0.052	2.738	0.67	0.053	-0.439	-0.417	-0.134	-0.425	-2.61
Herbivores (g/m ²)	-0.025	-0.117	-0.475	-0.003	0.133	-18.391	-0.95	-9.385	-0.974	-41.015
Detritivores (g/m ²)	-0.009	-0.049	5.141	0.689	0.05	-0.439	-0.389	-0.134	-0.396	-2.544

Figures

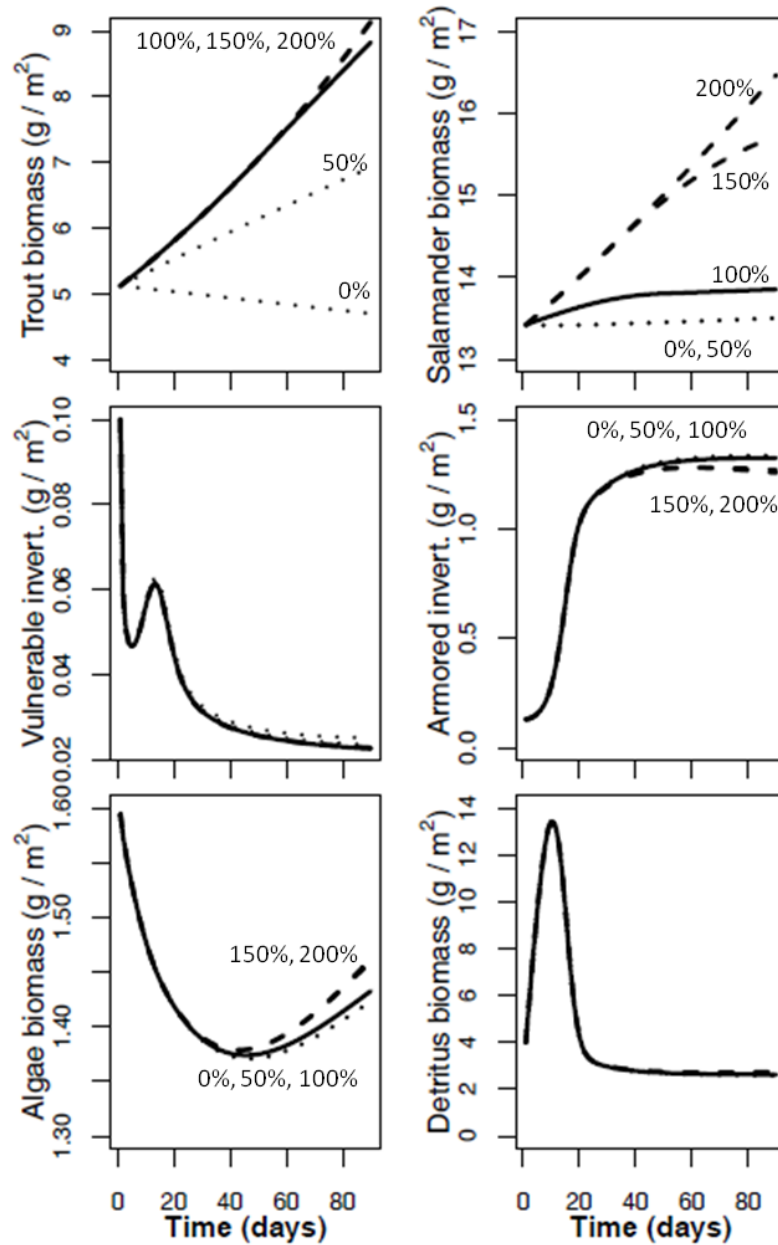


Figure 2.1: Response of model food web to changes in the magnitude of prey subsidies over 90 day model run. Solid line indicates natural background level of prey subsidy (100%, 0.523 g/m^2), short dashed lines represent lower levels of prey subsidy relative to natural (0%, 50%), and long dashed lines represent high levels of prey subsidy relative to natural influx (150%, 200%).

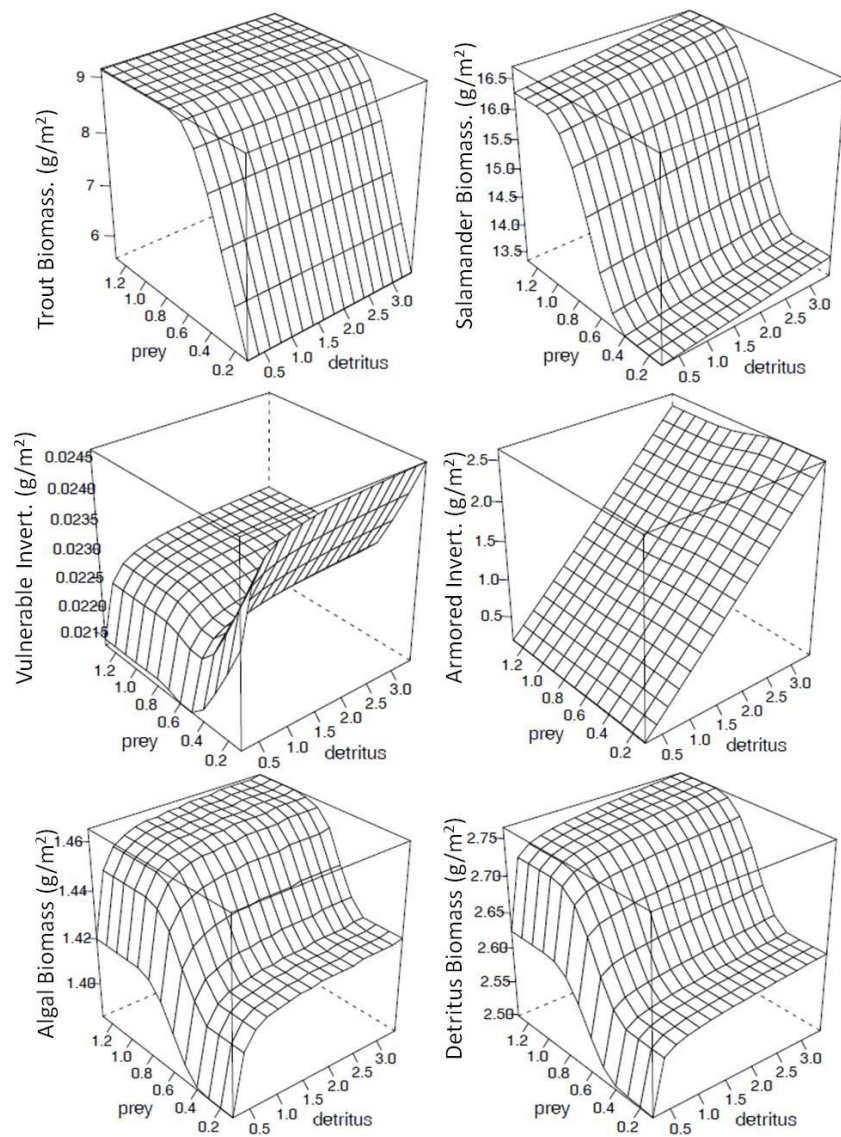


Figure 2.2: 3-D plot of model food web responses to simultaneous variation in the magnitude of detritus and prey subsidies across a range of subsidy inputs. Vertical axis represents the biomass of each trophic group at the end of the 90-day model run. Prey axis represents the daily influx of terrestrial prey subsidies, ranging from 0 to 1.3 g/m²/day. Detritus axis represents daily influx of detritus ranging from 0 to 3.4 g/m²/day.

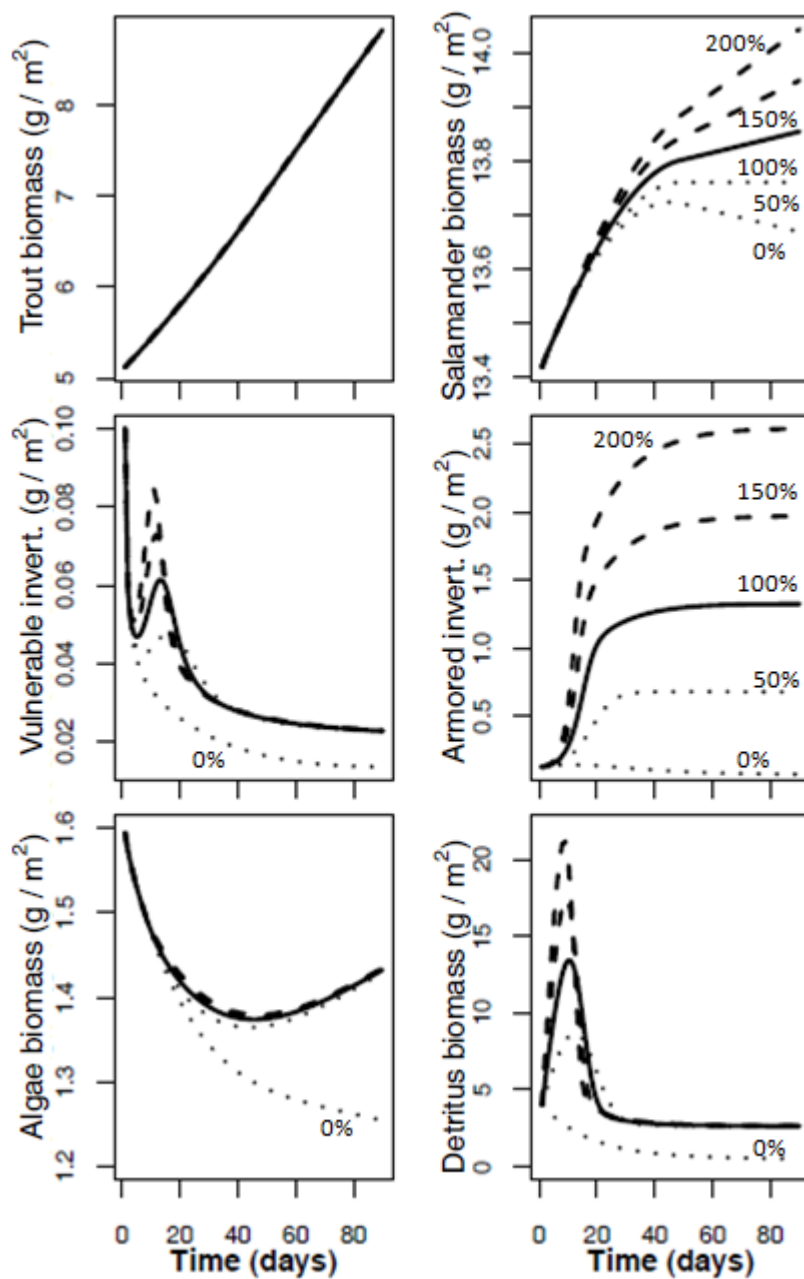


Figure 2.3: Response of model food web to changes in the magnitude of allochthonous detritus subsidy. Solid line indicates natural background level of detrital subsidy (100%, 1.7 g/m^2), short dashed lines represent lower levels of detrital subsidy relative to natural (0%, 50%), and long dashed lines represent high levels of detrital subsidy relative to natural influx (150%, 200%).

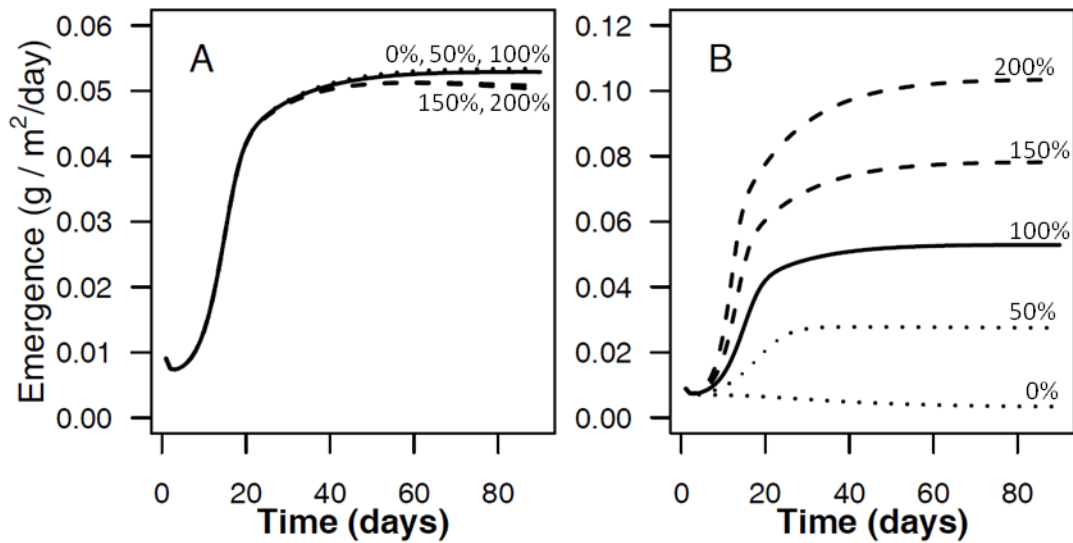


Figure 2.4: Response of daily emergence biomass to changes in the magnitude of (A) terrestrial prey subsidies and (B) terrestrial detritus subsidies. Solid line indicates natural background level of subsidy (100%), short dashed lines represent lower levels of subsidy relative to natural (0%, 50%), and long dashed lines represent high levels of subsidy relative to natural influx (150%, 200%).

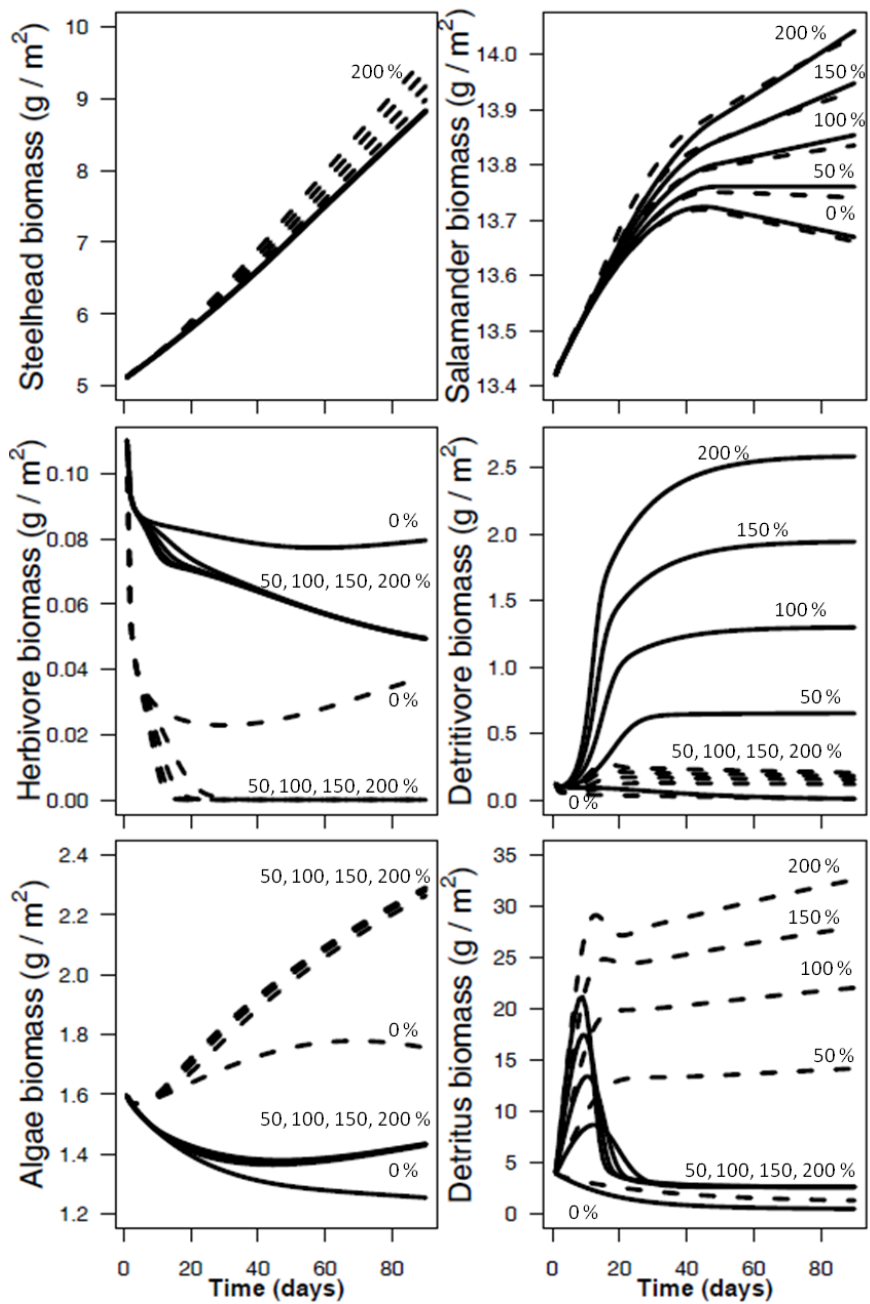


Figure 2.5: Effect of prey armoring on the response of the model community to variation in the magnitude of detrital subsidies, ranging from 0% natural background inputs to 200%. Solid lines represent scenarios with the natural community composition, including armored invertebrates. Dashed lines are scenarios in which the invertebrate community consisted of only vulnerable prey.

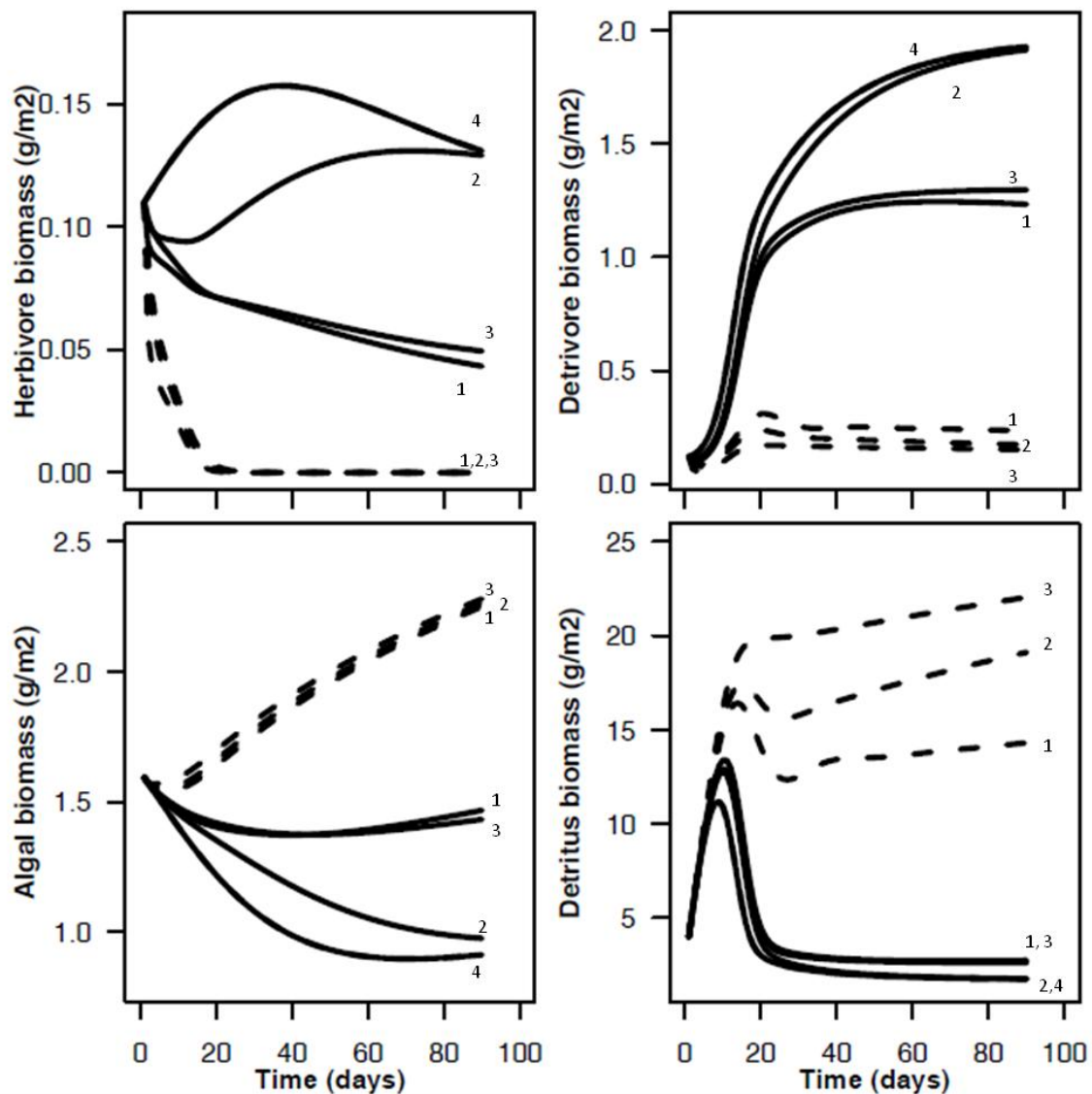


Figure 2.6: Changes in the herbivore and detritivore biomass in response to predation, and the strength of trophic cascades initiated by each predator species (1) salamander only (2) steelhead trout only (3) both predators present (4) neither predator present. Solid lines indicate natural community scenario (armored invertebrates present), dashed lines indicate vulnerable prey community scenario (only vulnerable invertebrates).

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Appendices

Appendix A

Isotopic Sampling

At the conclusion of the field experiment (Ch.1), small non-lethal tissue samples were taken from a subset of recaptured 1+ steelhead and *D. tenebrosus* (>100 mm TL) for comparisons of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ across treatments and between species. $\delta^{13}\text{C}$ values for algae and terrestrial detritus have been shown to be distinct and stable isotope analysis can allow for an estimate of the contribution of terrestrial versus aquatically derived energy in animal tissues (Finlay 2001). Fin and salamander tail tissue was dried in the laboratory (<60°C), ground, weighed to the nearest 0.001 mg, and enclosed in tin capsules. Isotope analysis was conducted at the University of California Davis, Stable Isotope Facility using an isotope ratio mass spectrometer. Isotope ratios are expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, which represent the levels of enrichment of the heavier isotope relative to the standard (N_2 , Pee Dee Belemnite). Fin and tail tissues are thought to reflect the isotopic signature of the diet within a few months of sampling (Miller 2006), roughly the same duration as the experiment.

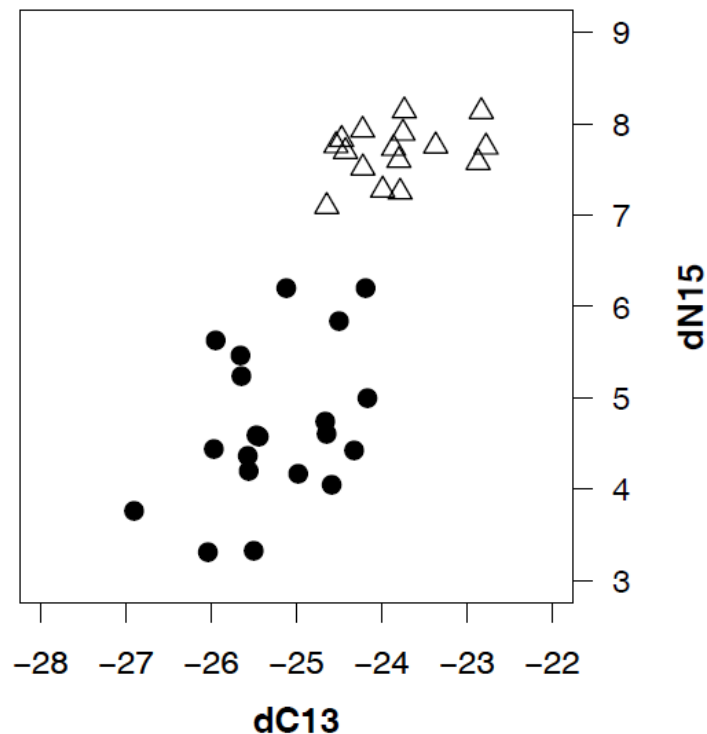


Figure A.1: Isotopic comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of salamanders and steelhead trout sampled at the conclusion of the experiment in Fox Ck. Open triangles represent steelhead trout, closed circles represent Pacific giant salamanders.

References

- Finlay, J.C. (2001). Stable-carbon-isotope ratios of river biota: implications for energy flow in lotic food webs. *Ecology*, 82, 1052-1064.
- Miller, T.W. (2006). Tissue-specific response of $\delta^{15}\text{N}$ in adult Pacific herring (*Clupea pallasii*) following an isotopic shift in diet. *Environmental Biology of Fishes* 76, 177-189.

Appendix B

Table B.1: Weighted model average coefficient estimates for benthic invertebrate responses to experimental manipulations.

Response Variable (units)	Coefficient	S.E.	Rel. Import.
<i>Benthic invertebrates (mg/m²)</i>			
Total benthic invertebrate biomass			
Intercept	481.6	173.7	
% Canopy cover	-340.5	199.8	1
Steelhead (+/-)	369.4	330.8	0.71
% Canopy cover * Steelhead (+/-)	-603.9	318.6	0.47
Total vulnerable benthic invertebrate biomass			
Intercept	160.97	97.13	
% Canopy cover	-163.01	115.08	0.46
Salamander density	-68.46	32.08	1
Total ephemeroptera biomass			
Intercept	89.206	50.58	
% Canopy cover	-92.15	50.76	0.75
Steelhead (+/-)	-10.91	6.138	0.73
Ephemeroptera scrapers			
Intercept	25.595	3.801	
Steelhead (+/-)	-11.279	5.376	NA
Coleoptera scrapers			
Intercept	23.421	6.921	
Salamander (+/-)	15.669	9.787	NA
Trichoptera shredders			
Intercept	117.74	64.73	
% Canopy cover	-117.94	75.39	NA

Table B.2: Weighted model average coefficient estimates of invertebrate emergence response to experimental manipulations.

Variable (units)	Coefficient	S.E.	Rel. Import.
Emergence (mg/m²/day)			
ln(Total emergence biomass)			
Intercept	-5.227	9.764	
% Canopy cover	10.215	12.092	0.89
Salamander density	-8.37	15.833	1
Steelhead (+/-)	36.891	38.901	0.88
% Canopy cover * Salamander density	12.331	25.124	0.48
% Canopy cover * Steelhead (+/-)	-50.756	45.107	0.76
Salamander density * Steelhead (+/-)	-116.195	74.799	0.35
% Canopy cover * Salamander density * Steelhead (+/-)	168.159	64.435	0.29
ln(Trichoptera emergence)			
Intercept	37.35	21.85	
% Canopy cover	-51.98	20.71	0.88
Salamander density	-104.92	33.92	0.88
Steelhead (+/-)	-0.23	1.04	0.31
% Canopy cover * Salamander density	120.46	39.51	0.88
ln(Ephemeroptera emergence)			
Intercept	-27.86	11	
Steelhead (+/-)	144.37	29.85	NA
Salamander density	19.69	21.09	NA
% Canopy cover	34.45	13.25	NA
Steelhead (+/-) * Salamander density	-268.65	59.31	NA
Steelhead (+/-) * % Canopy cover	-169.41	34.86	NA
Salamander density * % Canopy cover	-27.81	24.48	NA
Steelhead (+/-) * Salamander density * % Canopy cover	315.43	69.41	NA

Variable	Coefficient	S.E.	Rel. Import.
<i>Emergence contd.</i>			
In(Diptera emergence)			
Intercept	-6.78	5.14	
% Canopy cover	9.50	6.22	1
Salamander density	-1.29	8.84	1
Steelhead (+/-)	27.89	19.02	1
% Canopy cover * Salamander density	-6.73	18.32	0.28
% Canopy cover * Steelhead (+/-)	-32.67	22.07	1
Salamander density * Steelhead (+/-)	-45.25	54.52	0.33
% Canopy cover * Salamander density * Steelhead (+/-)	109.25	48.18	0.16
Plecoptera emergence			
Intercept	3.71	1.09	
Salamander density	-5.54	2.55	NA

Table B.3: Weighted model average coefficient estimates of predator growth response to experimental manipulations.

Variable (units)	Coefficient	S.E.	Rel. Import.
Animal growth (g)			
Salamander (>100mm) growth			
Intercept	0.85	0.57	
Steelhead (+/-)	1.86	0.67	NA
1+ steelhead growth			
Intercept	1.23	0.55	
Terrestrial subsidy(+/-)	-2.30	0.77	NA
Yoy steelhead growth			
Intercept	2.07	1.54	
% Canopy cover	-2.31	1.96	0.47
Terrestrial subsidy (+/-)	-0.34	1.24	1
% Canopy cover * Terrestrial subsidy (+/-)	-2.19	4.1	0.1

Table B.4: Weighted model average coefficient estimates of Ash Free Dry Mass (AFDM) and chl-a response to experimental manipulations.

Variable (units)	Coefficient	S.E.	Rel. Import.
primary producers			
AFDM (g/m²)			
Intercept	46.82	8.49	
% Canopy cover	-37	9.82	1
Steelhead (+/-)	6.08	11.62	0.59
% Canopy cover * Steelhead (+/-)	-16.53	19.6	0.19
Chlorophyll-a (µg/ m²)			
Intercept	-8891.8	10229	
% Canopy cover	18248.2	12037.7	1
Terrestrial (+/-)	1194.9	650.2	0.68
Salamander Density	-13818.1	30338.3	0.42
Steelhead (+/-)	-2920.6	17599	0.37
% Canopy cover * Salamander Density	51191.9	43379.4	0.15
% Canopy cover * Steelhead (+/-)	11768	39353.7	0.1
Salamander Density * Steelhead (+/-)	58065.7	80126.9	0.08
% Canopy cover * Salamander Density * Steelhead (+/-)	-165556.2	68193.1	0.03