Dependence of stream predators on terrestrial prey fluxes: food web responses to subsidized predation

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Abstract. Resource subsidies in the form of energy, materials, and organisms can support the productivity of recipient ecosystems. When subsidies increase the abundance of top predators, theory predicts that top-down interactions will be strengthened. However, the degree to which subsidies intensify predation should be constrained by the strength of interactions between predators and their prey. To test the potential for subsidies to drive strong top-down control 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. Prey subsidies supported elevated growth of predatory steelhead in our study system and in the absence of allochthonous prey steelhead experienced a 187% reduction in growth. Despite the high biomass of subsidized predators, there was little support for strong top-down control of herbivore biomass, or a trophic cascade as measured by changes in AFDM and chlorophyll-a. This result was consistent across subsidy treatments, suggesting that predatory steelhead are unable to increase exploitation of aquatic prey in the absence of terrestrial prey subsidies. The potential for top-down control was apparently limited by the fact that most (82%) herbivores in our study system were armored and relatively invulnerable to predation. These results demonstrate the potential importance of behavioral and morphological adaptations that can temper predator prey interactions in highly subsidized ecosystems.

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INTRODUCTION

Resource subsidies, the movement of nutrients, organic material, and prey from adjacent habitats, support elevated primary and secondary production in many ecosystems, and play an important role in mediating the dynamics of recipient food webs (Polis et al. 1997). The response of food webs to resource subsidies will depend in part on the trophic level at which subsidies enter the recipient food web (Marczak et al. 2007). Subsidies of nutrients and organic material that support higher productivity at the base of the food web can influence community composition (Hocking and Reynolds 2011) and patterns of food web regulation (Polis and Hurd 1996, Spiller et al. 2010). Subsidies of prey can support elevated biomass of predators (Rose and

Polis 1998, Hilderbrand et al. 1999, Sabo and Power 2002, Wipfli and Gregovich 2002, Kawaguchi et al. 2003), creating the potential for strengthened top-down control of in situ prey through the process of apparent competition (Holt 1984, Polis et al. 1997, Henschel et al. 2001, Murakami and Nakano 2002). In such instances, subsidized predators may elicit changes in the biomass and composition of multiple trophic levels within the recipient food web (Polis and Hurd 1996, Henschel et al. 2001, Leroux and Loreau 2008).

Although the ability of prey subsidies to influence patterns of top-down control is well documented in the literature, the response of communities to prey subsidies will depend on prey traits as well as the demographic and behavioral responses of predators to resource subsidies. For a cross ecosystem flux of prey to influence the dynamics of a recipient food web via apparent competition, subsidies must elicit a demographic response within the predator guild supporting higher biomass of predators than would otherwise be sustained by in situ productivity, and increased predator biomass must result in greater predation on in situ prey (Polis et al. 1997). Thus, the ability of subsidized predation to elicit changes in trophic level biomass will also depend acutely on the composition of the community, and ability of predators to exploit local prey. Alternatively, if subsidized predators exhibit strong selectivity for high quality allochthonous prey (Nakano et al. 1999a, Marcarelli et al. 2011), the effect of subsidies may be positive for in situ prey and top-down control may be weaker than expected in recipient food webs. In such cases, interrupting the availability of terrestrial prey subsidies may result in prey switching with increased exploitation of in situ prey (Sabo and Power 2002, Spiller et al. 2010) triggering trophic cascades (Nakano et al. 1999b, Baxter et al. 2004).

In small tributary stream ecosystems where light availability is often limited by dense overhead tree canopies, 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 from the surrounding terrestrial environment increase the productivity of streams from the bottom-up (Wallace et al. 1997, Finlay

2001), and subsidies of terrestrial invertebrates often support elevated biomass of predatory fish (Nakano et al. 1999a, Kawaguchi and Nakano 2001). Predatory fish can play a key role in mediating dynamics in river food webs, and may exert strong top-down control resulting in 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 this variability may be partially due to the composition of the primary consumer guild. 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 food webs are primarily supported by in situ primary production (Finlay 2001). Theory predicts that trophic cascades should be particularly strong in highly subsidized tributaries, where the majority of ecosystem energy is derived from allochtonous sources (Finlay 2001), resulting in predator biomass that is disproportionately high relative to the in situ productivity of the stream ecosystem (Polis et al. 1997, Leroux and Loreau 2008).

Here we experimentally tested the response of a highly subsidized tributary stream food web comprised of three trophic levels to changes in the short term availability of resource subsidies. Using a three-way factorial experiment we tested the strength of top-down control by two predators, juvenile steelhead trout (Oncorhynchus mykiss) and Pacific giant salamander (Dicamptodon tenebrosus), how the effects of these predators are mediated by the availability of terrestrial prey, and the degree to which predator biomass was supported by the availability of terrestrial prey resources. We predicted that over the course of the short-term experiment (~9 weeks) the presence of both predator species would depress the biomass of herbivorous aquatic invertebrates, releasing primary producers from grazer control, thereby inducing a trophic cascade as indicated by an increase in primary producer biomass in the presence of predators (Fig. 1). Furthermore, we predicted that, if terrestrial prey subsidies supported elevated biomass of steelhead resulting in stronger top down control of aquatic consumers, we would see reductions in steelhead growth in the absence of terrestrial prey subsidies which should result in a weakening of
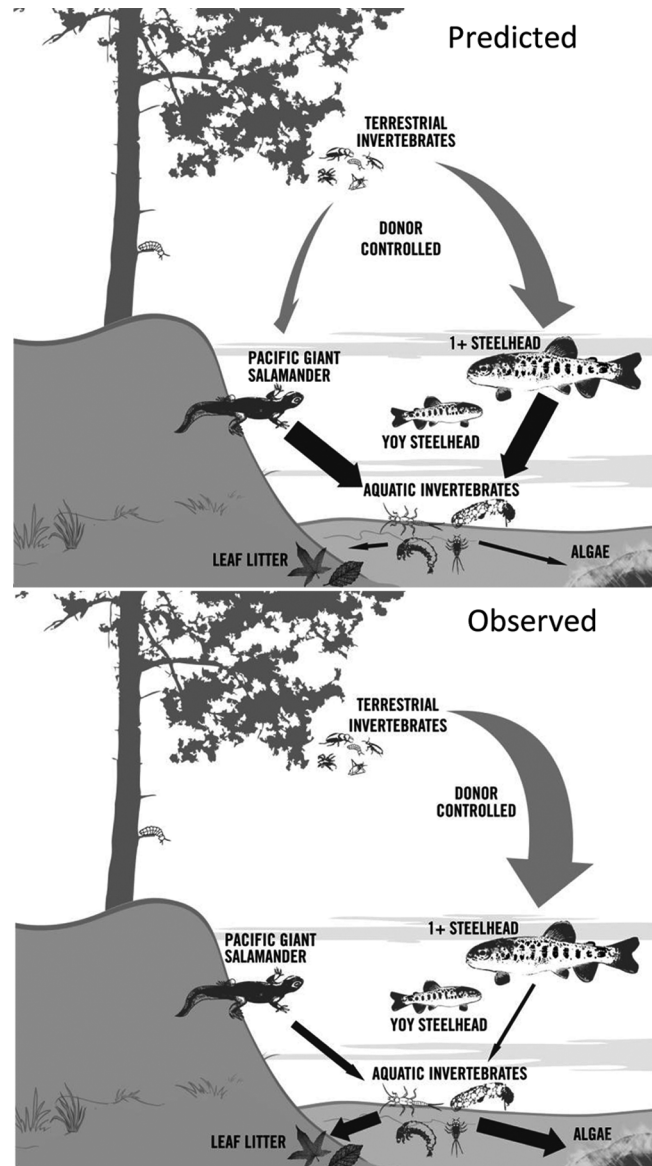
Fig. 1. Food web diagram depicting the predicted and observed effects of terrestrial resource subsidies in the Fox Creek food web. Gray arrows represent the degree of predator dependence on terrestrial prey subsidies and black arrows depict the strength of top-down control over a given biomass pool. The authors predicted that subsidized predators would exert strong top-down control over aquatic consumer biomass, such that predator removal would result in a release of primary consumers from predator control triggering a trophic cascade with reductions in primary producer biomass.

trophic cascades over time. Alternatively, if predatory steelhead preferentially exploit terrestrial prey resulting in a positive effect of resource subsidies on in situ consumers, we predicted that experimental reductions in terrestrial prey in-fall would necessitate a shift in predation by trout towards a more aquatic prey base, depressing aquatic herbivores and amplifying trophic cascades relative to treatments where terrestrial prey were available. Patterns of top-down regulation by salamanders, which feed primarily on benthic aquatic prey (Parker 1994), were not expected to

change in the absence of terrestrial prey subsidies. However, the predicted shift in resource use by steelhead trout was expected to increase competition between steelhead and salamanders, reducing the growth of steelhead and the benthic dwelling salamanders. Contrasting these predictions, if morphological and behavioral attributes of the aquatic invertebrate community limit predation by steelhead and salamanders, we predicted that neither predator species would initiate a trophic cascade, and steelhead would experience dramatic reductions 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 km^2 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 (*D. tenebrosus*) as well as both young of the year (YOY) and age 1 and older (1+) juvenile steelhead (*O. mykiss*). While both resident and anadromous *O. mykiss* may be present in Fox Creek, the majority are thought to spend 2 years in freshwater before migrating to sea. However, the life-history of any individual fish could not be visually distinguished and all *O. mykiss* in Fox Creek are therefore referred to as steelhead.

Experimental protocol

For nine weeks (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 throughout the

length of Fox Creek that is accessible to fish (1.3 km). These pools represented habitat with sufficient area (>7 m^2) and with adequate depth (>0.25 m) to support 1+ steelhead and large salamanders throughout the summer. 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 (Table 1). 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. Upstream riffle habitats were included to ensure that drifting benthic invertebrates from immediately upstream of the focal pool remained available to predators. For experimental reaches assigned to 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) and ventilation, 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. Pools were then visually searched via snorkeling in the weeks following the start of the experiment to confirm the robustness of the predator contrasts. The smallest size at which salamanders regularly consume

Table 1. Factors included in three-way factorial experiment including the presence/absence of 1+ steelhead predators, salamanders (>100) and terrestrial prey in-fall. Food web arrangement within 32 individual pool habitats was manipulated with a combination of levels across each of the three factors resulting in 4 replicates of 8 unique experimental treatments.

Level	Factor	Background density or rate	Treatment density or rate
+/−	1+ steelhead (>85 mm)	0.26 fish/m^2	0 fish/m^2
+/−	Salamanders (>100 mm TL)	0.52 salamanders/m^2	0 salamanders/m^2†
+/−	Terrestrial prey subsidy	523.1 mg·m^{-2}·d^{-1}	18.86 mg·m^{-2}·d^{-1}

† Tagged salamanders exhibited high degree of movement during the course of the experiment, such that final salamander density was unrelated to the initial treatment Experimental contrasts in salamander presence were not included in the analysis.

YOY steelhead is thought to be 100 mm total length (TL) (Parker 1993), and this was chosen as the minimum size cut off in our predatory salamander treatments. Salamanders smaller than this threshold were not manipulated. Steelhead were divided into two age groups based on size; young of year (YOY) and 1+ steelhead (>85 mm), both marked with small adipose fin clips. Predatory salamanders (>100 mm TL) and 1+ steelhead and were tagged individually with passive integrated transponder (PIT) tags (HPT8, 8.4 mm, Biomark; Boise, ID, USA). Experimental densities for YOY (1.25 fish/m^2) and 1+ steelhead (0.26 fish/m^2) were standardized to mean densities previously observed in Fox Creek (W. Palen, *unpublished data*), and salamanders density (>100 mm) was set based on densities observed during the first two days of sampling (0.52 salamanders/m^2). At the conclusion of the 9-week experiment, each experimental unit was searched as above, and all *O. mykiss*, and *D. tenebrosus* were weighed, measured, and released. Experimental contrasts in 1+ steelhead density were well maintained throughout the course of experiment with final densities closely matching initial treatments (+steelhead treatment: 0.29 fish/m^2; −steelhead treatment: 0.06 fish/m^2). However, salamanders showed a high degree of emigration and immigration possibly due to their ability to move short distances over land and final densities did not reflect initial treatment contrasts (+salamander treatment: 0.34 salamanders/m^2; −salamander treatment: 0.39 salamanders/m^2). Key response variables for vertebrates included batch growth estimated as the change in the mean mass for young-of-year steelhead in each pool, as well as the growth of individually marked 1+ steelhead and salamanders.

Pan traps and leaf buckets were used to quantify the in-fall of terrestrial prey and leaf litter into Fox Creek. The aerial flux of terrestrial prey into experimental units was quantified using pan traps deployed five times at five locations across the longitudinal extent of the experiment (1.3 km). 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 from covered treatments 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.

Responses by the aquatic invertebrate community to experimental contrasts were estimated using sticky traps which indexed aquatic insect emergence, and by sampling benthic aquatic invertebrates from rocks within each experimental pool. To sample the emergence of aquatic insects from experimental pools, three sticky traps were deployed within each experimental unit three times at approximately two-week intervals throughout the duration of the experiment (9 weeks). 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. Traps collected at uncovered pools likely captured

insects from adjacent areas and were therefore dropped from the analysis of emergence response. Within covered pools sticky traps were assumed to have equal capture efficiency, allowing us to compare the effects of our predator treatments on aquatic insect emergence. 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 as in McNeely et al. (2007). Each rock was moved quickly from the stream bottom into a net positioned downstream and placed in a tray to minimize the escape of more mobile aquatic insects. The entirety of each rock was then cleaned with a garden sprayer and visually inspected to ensure the capture of all aquatic invertebrates. Invertebrate biomass was then standardized by the surface area of the 6 rocks sampled. 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 dry mass estimates using taxon 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. Key response variables for aquatic invertebrates included the biomass of benthic invertebrates, partitioned into groups based on functional feeding groups, as well as the biomass of emerging aquatic insects as indexed by sticky traps.

For the purpose of our analysis all members of the scraper functional group were considered herbivores. This assumption was based on previous work demonstrating that members of this functional group disproportionately rely on in situ production in our study system (McNeely et al. 2007). Invertebrates were further partitioned into groups based on their relative vulnerability to predation, with armored invertebrates such as cased caddisflies classified as invulnerable, and soft-bodied invertebrates such as mayflies classified as vulnerable.

To test for experimentally induced effects on primary producer biomass, 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 0.7 μm glass fiber filters (Whatman GF-F, 47 mm), and then ashed (550°C for 24 hrs) to estimate AFDM. A 4 ml sub-sample was filtered onto 0.7 μm glass fiber filters (Whatman GF-C, 25 mm) 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 experimental covers.

Statistical analyses

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 in the statistics program R version 2.13.2 (R Development Core Team 2011). We used an information theoretic approach based on Akaike's information criterion adjusted for small sample sizes (AICc) (R-package AICcmodavg) (Mazerolle 2011) 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 as well as the biomass of two categories of herbivores (vulnerable, armored) with invertebrate taxa partitioned into these groups based on the presence of physical armoring such as rock or

stick cases. 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) (Pinhero et al. 2012) estimated using maximum likelihood, including sample date as a random effect to account for repeated measurements. Data for the biomass of emerging aquatic invertebrates did not meet the assumptions of normality and were therefore log transformed. Models were then ranked based on their relative likelihood (ωi). To avoid over fitting we removed "pretending variables", variables which receive support in the AICc framework but do not change model deviance. We report only model's within 2 ΔAICc units (Burnham and Anderson 2002) of our top model, and we report weighted coefficients based on all models within this threshold (Appendix A).

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 261.5 $\pm$ 50.6 mg DM·m^{-2}·d^{-1}, and covered pools experienced a 27-fold reduction in this prey subsidy (9.43 $\pm$ 2.53 mg DM·m^{-2}·d^{-1}). Similarly, terrestrial leaf litter subsidies were reduced more than 90 fold, from 800.5 $\pm$ 121 mg DM·m^{-2}·d^{-1} in open pools to 8.7 $\pm$ 5.05 mg DM·m^{-2}·d^{-1} in covered. Stream temperature was not affected by the presence of covers (covered, 14.20°C $\pm$ 0.17°C [mean $\pm$ SE]; uncovered, 14.28°C $\pm$ 0.15°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 with YOY growth declining across a gradient of increasing canopy closure (-2.31 ± 1.96 g). In the absence of terrestrial prey, most individual fish (1+ steelhead and YOY) experienced negative growth over the course of the experiment (Fig. 2A, C, Table 2; coefficients: -2.30 ± 0.77 g and -0.51 ± 0.18 g, respectively). There was no indication that the growth of 1+ steelhead was altered by the presence of salamander predators and neither predator species limited the growth of YOY steelhead. The growth of predatory salamanders was not reduced in the absence of terrestrial subsidies (Fig. 2B), and was instead best predicted by a model that included only the presence of 1+ steelhead. The presence of steelhead facilitated higher growth in salamanders over the course of the experiment (1.86 $\pm$ 0.67 g; Fig. 2B), though there was limited support for an intercept only model as well (Table 2).

Food web responses

Neither predator depressed the total biomass of aquatic herbivores, and AICc indicated a lack of support for top-down control of herbivore biomass regardless of the availability of subsidies (Fig. 2D, Table 2). The majority (65% of biomass) of aquatic invertebrates sampled from benthic rocks in Fox Creek were 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 there was support for top-down control
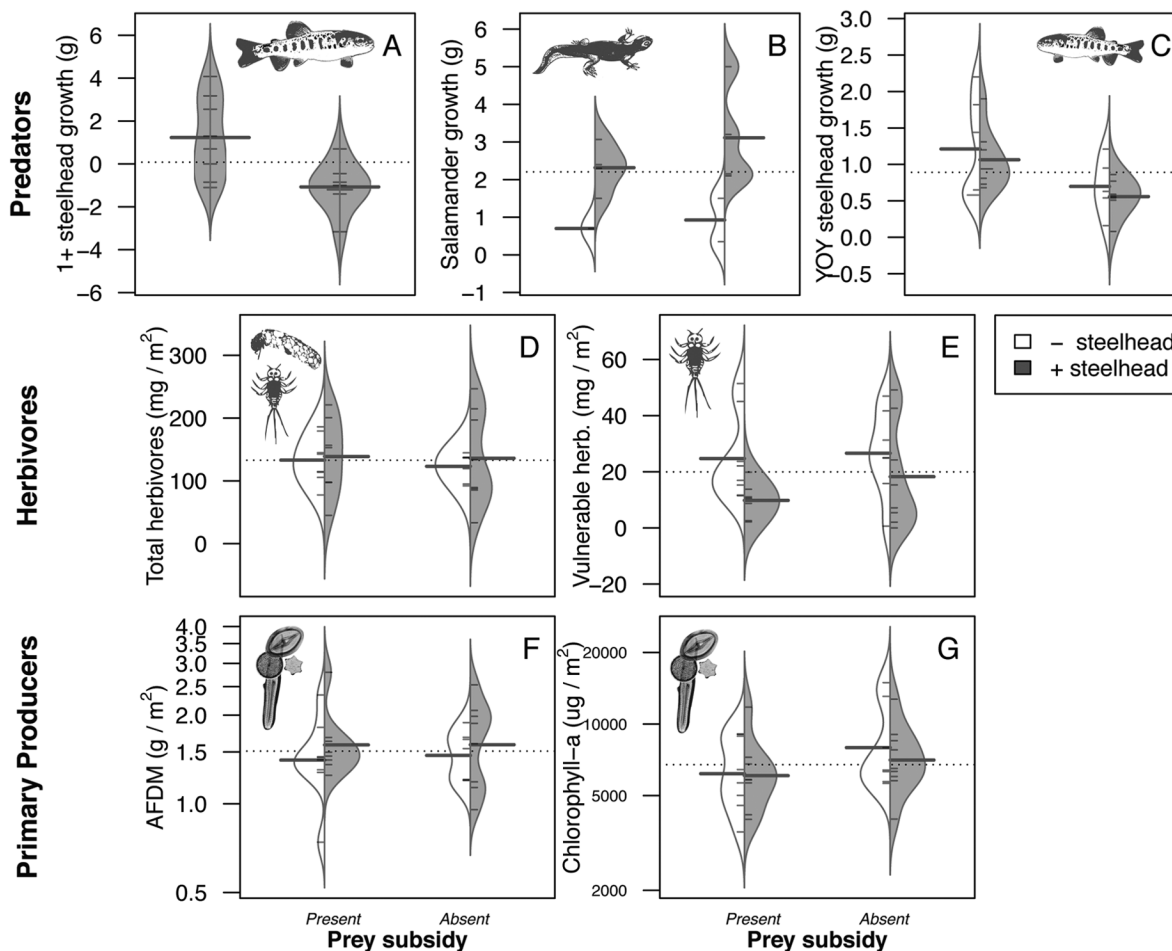
Fig. 2. Food web response to experimental manipulation of predator assemblage and availability of terrestrial prey. Terrestrial prey availability treatment is depicted on the x-axis of each plot, grey areas indicate experimental treatments with steelhead predators. Dark horizontal bars represent mean values for each treatment, and curves represent the distribution of response data. (A) Response of 1+ steelhead growth to reductions in terrestrial prey availability. (B) Growth of recaptured salamanders (>100 mm), (C) growth of young of year steelhead, (D) final herbivore biomass, (E) final biomass of vulnerable herbivores, (F) primary producer biomass indexed by AFDM and (G) chlorophyll-a response to experimental changes in terrestrial prey availability and 1+ steelhead presence.

of vulnerable herbivore biomass in experimental units with steelhead (-11.3 ± 5.4 mg DM·m^{-2}, Fig. 2E). However total aquatic invertebrate biomass increased in the presence of predatory steelhead (369.4 ± 323.9 mg DM·m^{-2}) and decreased along a gradient from 0 to 100% in canopy cover (-340.5 ± 193.1 mg DM·m^{-2}). There was also support for a positive interaction between steelhead predators and light availability (% canopy cover) such that the slope of the positive relationship between total benthic biomass and light availability was steeper in the

presence of steelhead (-603.9 ± 193.1 mg DM·m^{-2}; Fig. 3).The top model for aquatic insect emergence included an interaction between % canopy cover and steelhead as well as the main effect of salamander density, however a model which included an interaction between canopy and salamander density also fell within the 2 ΔAICc unit threshold (Table 2). The biomass of aquatic insects emerging from covered experimental units showed a similar pattern to total benthic invertebrate biomass. The biomass of insect emergence was higher in the presence of

Table 2. AICc model selection of linear regression models for response variables including R^2 values for each model. Variables include % canopy cover, steelhead predators (presence/absence), final salamander density, and the availability of terrestrial prey.

Response variable	Model	ΔAICc	ω_i	R^2
Predator growth				
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	0.569	0.229
	% Canopy cover + terrestrial prey (+/−)	0.7	0.413	0.259
	Intercept	5.27	0.037	
Aquatic invertebrates				
Total invertebrate biomass	Steelhead (+/−) × % Canopy cover	0	0.554	0.305
	% Canopy	0.811	0.369	0.196
	Intercept	5.75	0.031	
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 × steelhead (+/−) + salamander density	0	0.680	0.292
	% Canopy cover × salamander density + % canopy cover × steelhead (+/−)	1.718	0.298	0.311
	Intercept	6.112	0.032	
Primary producers				
Ash free dry mass (AFDM)	% Canopy cover	0	0.686	0.153
	% Canopy cover × steelhead (+/−)	1.564	0.314	0.180
	Intercept	13. 9	0.001	
Chlorophyll-a	% Canopy cover + terrestrial prey (+/−)	0	0.530	0.235
	% Canopy cover + steelhead (+/−) + terrestrial prey (+/−)	1.494	0.251	0.243
	% Canopy cover	1.765	0.219	0.205
	Intercept	16.476	0.000	

steelhead (16.45 ± 7.07 mg DM·m^{-2}) and there was a positive interaction between steelhead and light availability (−19.58 ± 8.2 mg DM·m^{-2}) such that the slope of the relationship between light availability and emergence biomass steepened in the presence of steelhead. Because of the high degree of movement in and out of experimental enclosures by tagged salamanders, the true response of the stream food web to the presence of salamanders was difficult to discern and estimated model coefficients were suspect.

The amount of algae and biofilm were 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 biofilm AFDM declining across an increasing gradient in canopy cover from 0 to 100% (−3.78 ± 0.91 g AFDM·m^{-2}). However, a model which included an interaction between % canopy cover and steelhead received some support, with AFDM increasing in the presence of steelhead (−1.653 ± 1.93 g AFDM·m^{-2}; Fig. 2F,
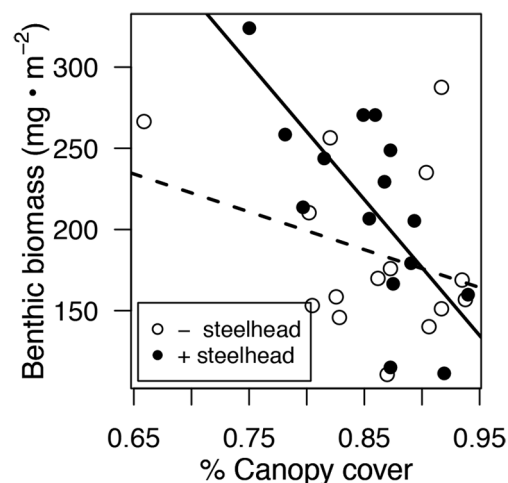

Fig. 3. Effect of % canopy cover in mediating response of total benthic biomass to manipulations in the presence of predatory steelhead. Solid line and circles indicate experimental units with steelhead.

Table 2). Like AFDM, the concentration of chlorophyll-a was positively related to light availability (0–100% canopy: 17 ± 3.99 μg·m^{-2}), which was included in every model receiving support (Table 2, Fig. 2G).

Discussion

We found clear evidence that terrestrial prey subsidies support the growth of predatory steelhead in tributary stream food webs during the course of our 9-week experiment. Throughout the summer, fish in pools with experimental covers experienced dramatic reductions in growth, with many losing mass during the 2-month experiment. While this finding suggests high potential for apparent competition between terrestrial prey and in situ prey species, the top-down effect of steelhead on the biomass of benthic invertebrates was limited to a small subset of the aquatic community (vulnerable herbivores), and was not strengthened in the absence of terrestrial prey. This weak top-down control is likely due to the abundance of morphologically predator-resistant invertebrates in this tributary stream food web (McNeely et al. 2007), with approximately 65% of the total benthic invertebrate biomass and 82% of herbivore biomass classified as armored and invulnerable to predation. Though predatory fishes have also been shown to induce trophic cascades on detrital processing rates (Konishi et al. 2001, Boyero et al. 2007,, but see Ruetz et al. 2002), we did not estimate changes in the processing of terrestrial detritus as part of this study. We expect that the processing rates by aquatic invertebrates may be similarly insensitive to top-down control in our study system due to the high abundance of armored taxa within shredder and scraper functional feeding groups. Given the relative invulnerability of most aquatic prey in our study system, it appears that rather than subsidizing fish predation on local invertebrates, terrestrial prey may serve as the primary source of energy in supporting predatory fish in the Fox Creek food web. Consequently, when terrestrial subsidies were interrupted, there was little scope for intensified predation on in situ prey as observed in other studies (Nakano et al. 1999b, Baxter et al. 2004).

Previous work in stream food webs has found

that the degree to which predatory fish exert top-down control depends in part on the vulnerability of the aquatic invertebrate community (Power 1992). In the South Fork Eel River, inter-annual variability in the strength of trophic cascades has been linked to flood-pulse events that scour the stream bottom and remove large armored caddisflies (Genus *Dicosmoecus*). These large winter floods leave behind an aquatic invertebrate community comprised of more predator vulnerable taxa resulting in dramatic changes in year-to-year patterns of top-down control by predatory steelhead trout (Wootton et al. 1996, Power et al. 2008). In tributary streams in northern California, the smaller, multivoltine *Glossosoma pentium* are the dominant armored caddisfly, and this taxon maintains 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 aquatic consumers that are more readily available to predatory fish and salamanders (McNeely et al. 2007). The food web consequences of reduced prey vulnerability are well documented, and prey species that escape predation by attaining large body size may be resource limited despite high predator biomass (Chase 1999, Sinclair et al. 2003). Similarly, species which employ heavy armored cases may be largely invulnerable to predation and may 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.

Despite the prevalence of armored aquatic prey in Fox Creek and the lack of strong experimentally induced trophic cascades, we did identify several notable effects of predatory steelhead on the food web. When we partitioned herbivores into armored versus more vulnerable groups and analyzed food web responses separately, we found strong evidence for top-down control of the biomass of vulnerable herbivores over the course of the experiment (Table 1, Fig. 2E). Light availability (% canopy cover) was the most important factor influencing indices of primary production (AFDM, chl-a), models that

included steelhead as well as light availability also received support (Table 2), with steelhead having a positive effect on AFDM and appearing to reduce the concentration of chl-a. Despite the lack of top-down control by steelhead on the total biomass of herbivores, this interaction (predator × light) suggests a positive effect of steelhead on primary producer biomass such that the positive effect of increasing light availability was greater in the presence of steelhead, possibly due to nutrient recycling by steelhead (Vanni et al. 2006, Munshaw et al. 2013) (Fig. 3). Similarly, there was support for a positive effect of predatory steelhead on the total biomass of benthic invertebrates as well as the emergence of aquatic insects from experimental pools, as well as an interaction between steelhead and light availability. The conformity of the response of primary producers and benthic invertebrates to the presence of predatory fish and light availability suggest that fish and other predators may mediate food web productivity in tributary streams from the base of the food web via nutrient recycling, with fish excretion ultimately influencing the magnitude of reciprocal subsidies into the riparian forest.

As predicted, a two month long reduction in the influx of terrestrial prey subsidies did not appear to negatively affect the growth of Pacific giant salamanders. This finding is consistent with previous observations that salamander diets are dominated by benthic aquatic invertebrates (Parker 1994). Further, given the high biomass of predatory and largely benthic feeding Pacific giant salamanders that we found in Fox Creek, occurring at twice the density of 1+ steelhead (0.52 salamanders/m^2 vs. 0.26 steelhead/m^2), we predicted that benthic invertebrate biomass would be depressed in their presence. However, low recapture rates and movement by individuals outside of our study reaches made it difficult to detect the food web effects of salamanders. We also predicted that YOY steelhead would have reduced growth in the presence of large 1+ steelhead and salamanders, but did not detect any effect of either predator on their growth. Despite considerable diet overlap between salamanders and 1+ steelhead (Parker 1994, Munshaw et al. 2013), the presence of salamanders had no detectable effect on the growth of 1+ steelhead, regardless of the availability of terres-

trial prey. Limited isotope samples collected in conjunction with the experiment suggest that steelhead relied on terrestrial prey to a much greater degree during the summer than large (>100 mm SVL) salamanders (Appendix B). 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 regardless of the availability of terrestrial prey. While this conclusion is tempered by the low sample size of salamanders recaptured at the end of our experiment (n = 19), we propose that the presence of 1+ steelhead 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 (including young of year steelhead) 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 nine week duration of our experimental manipulation during the peak window of summer productivity limits our inference about the response of the Fox Creek food web to subsidized predators over longer time scales. Given the short duration of our experiment, we were unlikely to capture the full range of possible invertebrate population responses to our imposed food web manipulations. However, our experimental treatments do provide important inference about how short-term changes in the intensity of predation can affect local aquatic invertebrate biomass, invertebrate movement, and growth. The invertebrate community present within our experimental stream reaches certainly reflected the legacy of interactions with both predators, and the pre-existing herbivore assemblage may have limited the potential for experimentally induced changes in the strength of trophic cascades in our study over the two month time period we ran the experiment. Despite this limitation, previous work conducted over a similar duration has resulted in strong community level responses. For example, when McNeely et al. (2007) experimentally removed the caddis-

fly *Glossosoma*, the dominant armored grazer in Fox Creek, chlorophyll-a in Fox Creek doubled, suggesting that short-term manipulations can induce changes in grazer control and primary productivity. The importance of terrestrial resource subsidies for predator populations likely also manifests over longer time scales. For example, subsidies may increase the carrying capacity of the recipient ecosystem for predators increasing population productivity and carrying capacity for salamanders and trout. Subsidies of leaf litter and other organic material also serve to increase food web productivity from the base of the food web, however given the relatively long turn over time of this organic material in the stream food web we cannot draw inference about the long-term consequences of reduced detrital subsidies. Our experiment was not designed to explicitly address long-term population level responses of predators to resource subsidies, however dramatic reductions in growth experienced by 1+ steelhead in the absence of terrestrial prey suggest that current population sizes are supported in large part by terrestrial prey subsidies. Due to the nature of our experimental enclosures, fish were not allowed to move in response to manipulations in resource availability. However, the reductions in fish growth observed in our study coupled with previous experimental work demonstrating high rates of emigration by trout in the absence of terrestrial prey (Kawaguchi et al. 2003) suggest that in general terrestrial prey subsidies support predatory stream fish biomass in tributary stream food webs.

Our results support the prediction that the presence of armored herbivores in Fox Creek 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 tied 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, the degree to which subsidies propagate through multiple trophic levels depends upon the ability of predators to exploit *in situ* prey. In our study system herbivores are known to limit primary producer biomass (McNeely et al. 2007), yet the invulnerability of much of the herbivore guild ultimately limits the importance of predation. Even in the absence of terrestrial prey, aquatic predators did not appear capable of expanding their exploitation of local herbivore biomass. This finding is perhaps not surprising given the co-evolution of the aquatic predators and herbivore communities in these subsidized food webs. Because predators are largely decoupled from in situ productivity in these systems, the persistence of the aquatic herbivore guild through time has likely been 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 raise interesting questions about the degree to which morphological and behavioral traits conferring low vulnerability to predation may be ubiquitous in highly subsidized food webs.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Model averaged coefficient estimates for the response of vertebrate growth to experimental manipulations for all models within 2 ΔAICc threshold.

Variable	Coefficient	SE	Rel. Import.
Salamander (>100 mm) growth (g)			
Intercept	0.85	0.57	
Steelhead (+/−)	1.86	0.67	NA
1+ steelhead growth (g)			
Intercept	1.23	0.55	
Terrestrial subsidy (+/−)	2.30	0.77	NA
YOY steelhead growth (g)			
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 A2. Model averaged coefficient estimates for the response of aquatic invertebrates to experimental manipulations for all models within 2 ΔAICc threshold.

Response variable	Coefficient	SE	Rel. Import.
Total benthic invertebrate biomass (mg/m^2)			
Intercept	481.6	168	
% Canopy cover	−340.5	193.1	1
Steelhead (+/−)	369.4	323.9	0.71
% Canopy cover × Steelhead (+/−)	−603.9	303.8	0.47
Vulnerable herbivores (mg/m^2)			
Intercept	25.6	3.8	
Steelhead (+/−)	−11.3	5.4	NA
Emergence biomass (mg/m^2)			
Intercept	−6.96	7.7	
% Canopy cover	11.25	9.3	1
Salamander density	−9.5	13.6	1
Steelhead (+/−)	16.5	7.1	1
% Canopy cover × Steelhead (+/−)	−19.6	8.2	1
% Canopy cover × Salamander density	22.9	21.8	0.3

Table A3. Model averaged coefficient estimates for primary producer responses to experimental manipulations for all models within 2 ΔAICc threshold.

Variable	Coefficient	SE	Rel. Import.
AFDM (g/m^2)			
Intercept	4.7	0.85	
% Canopy cover	−3.7	0.98	1
Steelhead (+/−)	0.6	1.15	0.59
% Canopy cover × Steelhead (+/−)	−1.65	1.9	0.19
Chlorophyll-a (μg/m^2)			
Intercept	−11324	4904	
% Canopy cover	21304	5666	1
Terrestrial (+/−)	1204	637	0.74
Steelhead (+/−)	−611.5	637	0.25

Appendix B

At the conclusion of the experiment, small non-lethal tissue samples were taken from a subset of recaptured 1+ steelhead and *D. tenebrosus* (>100 mm TL) for comparisons of $\delta^{13}C$ and $\delta^{15}N$ across treatments and between species. $\delta^{13}C$ 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 $\delta^{13}C$ and $\delta^{15}N$ 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.
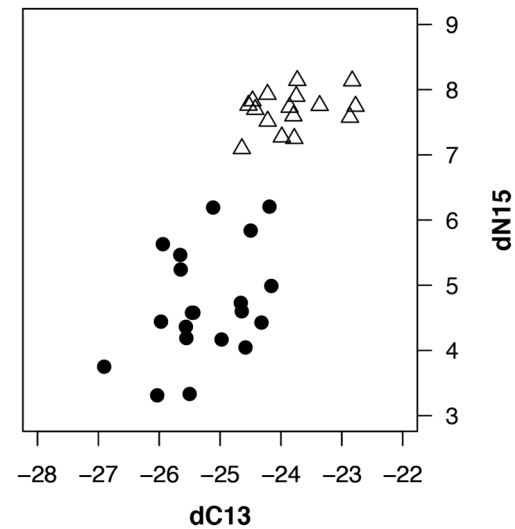

Fig. B1. Isotopic comparison of $\delta^{13}C$ and $\delta^{15}N$ signatures of salamanders and steelhead trout sampled at the conclusion of the experiment in Fox Creek. Open triangles represent steelhead trout, closed circles represent Pacific giant salamanders. More negative $\delta^{13}C$ values for steelhead are indicative of a greater reliance upon terrestrially derived carbon.