

Aquatic predation alters a terrestrial prey subsidy

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Abstract. Organisms with complex life histories (CLH) often cross habitat or ecosystem boundaries as they develop from larvae to adults, coupling energy flow between ecosystems as both prey (bottom-up) and consumers (top-down). Predation effects on one stage of this life cycle can therefore cascade across ecosystems, magnifying the impact of local predation. The majority of predation studies have assessed effects only on a local level, within the habitat of the predator. I used large outdoor stream mesocosms to test the hypothesis that predation in an aquatic habitat alters the magnitude and trophic structure of a prey assemblage in a terrestrial habitat. I also tested how a consumer in the terrestrial habitat (web-weaving spiders) responded to these changes in prey export. Two fish species were the predators (red shiner, *Cyprinella lutrensis* and orangethroat darter, *Etheostoma spectabile*) in an experiment with three treatments: both fish species monocultures plus a fishless control. Fish predation reduced aquatic insect emergence biomass by 50% compared to the fishless control and altered the trophic structure of the emergent community, reducing emerging insect predator biomass by 50%, but had no effect on other insect trophic groups. Spiders captured only insects that were unaffected by fish predation (mostly chironomids) and therefore did not respond numerically to overall changes in insect abundance or biomass. Patterns of insect emergence were largely driven by a strong negative relationship between fish and a predatory dragonfly (*Pantala flavescens*). The results of this experiment show that predation in one habitat can have strong effects on the biomass and trophic structure of subsidies entering adjacent habitats, resulting in contrasting predictions for the role of these subsidies in recipient food webs. In the absence of fish, aquatic habitats produced terrestrial insect communities with higher biomass (bottom-up potential) and a higher proportion of predators (top-down potential) than when fish were present.

Key words: aquatic–terrestrial linkages; *Cyprinella lutrensis*; dragonflies; emergence predation; *Etheostoma spectabile*; fish; food webs; habitat coupling; mesocosm experiment; *Pantala flavescens*; subsidies.

INTRODUCTION

Predation studies typically focus on direct or indirect effects of predation on local prey communities. However, a large percentage of organisms (~80%) exhibit ontogenetic niche shifts (Werner and Gilliam 1984), in which an organism's niche changes during development. In organisms with complex life histories (CLH) such as amphibians and insects, niche shifts often occur between larval and adult stages, with each stage in separate habitats (Werner and Gilliam 1984). When prey communities are dominated by organisms that exhibit coupled ontogenetic and habitat shifts, predation effects in a local habitat can cascade across habitat or ecosystem boundaries, altering the abundance and biomass of the prey community in a second habitat or ecosystem (Baxter et al. 2004). These alterations can have strong effects on the structure and dynamics of food webs in the recipient habitat (Polis and Hurd 1996,

Nakano and Murakami 2001, Baxter et al. 2004, Knight et al. 2005, Marczak and Richardson 2007).

Spatial subsidies involve the flow of nutrients, material, and organisms across ecological boundaries, with their bottom-up effect in recipient food webs determined by the magnitude of the subsidy (Nakano and Murakami 2001, Sabo and Power 2002, Baxter et al. 2004). When subsidies consist of an assemblage of organisms, as opposed to nutrient subsidies, top-down effects may also be important, and will vary according to the trophic structure of the subsidy assemblage. Subsidy communities that are equal in magnitude, but different in species composition, may have different impacts on recipient food webs if the species occupy different trophic levels. For example, insects that emerge from aquatic to terrestrial habitats subsidize consumers in terrestrial food webs (Nakano and Murakami 2001, Baxter et al. 2004). Many aquatic insects do not feed as adults (e.g., chironomids, mayflies, caddisflies), while some are predators (e.g., damselflies and dragonflies), and can have strong consumptive effects in terrestrial ecosystems (Knight et al. 2005). Hence, the primary impact in terrestrial food webs of a subsidy assemblage of chironomids and

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mayflies (nonconsumers) is likely as an energy source for terrestrial consumers. In contrast, a subsidy assemblage composed of damselflies and dragonflies (predators) may represent the same amount of biomass as the former subsidy, but could also exert strong top-down effects in a terrestrial food web.

Recent theory has emphasized how changes to the quality of larval habitat can influence the consumer potential of CLH communities in the adult habitat. Increased resources in the larval habitat can cause a counterintuitive decrease in larval abundance over time if adult reproduction is limited by low resource levels in the adult habitat, and vice versa. Such alternative stable states are thereby maintained by altering productivity in only one system (Schreiber and Rudolf 2008). Similarly, increased mortality of aquatic tadpoles decreases adult frog abundance around ponds. Because adult frogs are predatory, a decrease results in contrasting predator profiles around ponds ("predator shadows"). When applied to the landscape scale across a series of natural ponds, such reductions in adult predators alter the spatial patterning of terrestrial trophic cascades, based only on dynamics in aquatic habitats (McCoy et al. 2008).

In addition to resource availability, predation in the larval habitat may also regulate the consumer potential of prey subsidies in recipient food webs (sensu Knight et al. 2005), but this has not been studied. Additionally, to my knowledge only two studies have assessed the effect of predation in larval habitats on the magnitude of a subsidy entering a recipient habitat (Baxter et al. 2004, Finlay and Vredenburg 2007). In both cases predatory trout reduced the biomass of organisms emerging from aquatic to terrestrial habitats. Fish are often the top predators in permanent aquatic habitats. Fish species identity is typically related to feeding strategy, which can determine the strength of predation. Benthic feeding fishes may have stronger effects on stream secondary productivity than surface-feeding fishes because surface-feeding fishes are subsidized by terrestrial input, reducing pressure on benthic invertebrates (Dahl and Greenberg 1996). Knowledge of factors controlling both the magnitude and trophic structure of organism subsidies is needed to more fully understand how food web changes in one habitat can cascade into adjacent habitats.

I tested the hypothesis that top predators in aquatic habitats alter the magnitude and trophic structure of organisms entering adjacent terrestrial habitats. Using two fish species as predators, I predicted that fish predation would alter the trophic structure and reduce biomass of insects emerging from aquatic mesocosms into the surrounding terrestrial habitat, causing a reduction in abundance of terrestrial spiders that feed on emerging insects. I also predicted that the strength of the predation effect would correspond to fish-feeding strategy.

METHODS

Predators

I manipulated the presence of two predatory fish species with different functional feeding strategies: benthic invertivore (*Etheostoma spectabile*) and water-column invertivore (*Cyprinella lutrensis*). Both species are common and widespread throughout the central United States and often co-occur. The orangethroat darter (*Etheostoma spectabile*) is an invertivore common to streams throughout eastern Oklahoma and feeds exclusively on the benthos, primarily on insects (chironomids, stoneflies, mayflies [Martin 1984, Miller and Robison 2004]). Red shiner (*Cyprinella lutrensis*) is an abundant invertivorous local minnow in North American prairie streams (Matthews 1985). It typically lives in the water column and feeds at all levels of the water column, including benthic, mid-water, and surface habitats (Hale 1963). Insects are the primary prey of red shiner, but its diet can also include substantial amounts of algae and other invertebrates (Gido and Matthews 2001).

A predatory dragonfly species (*Pantala flavescens*) aerially colonized the mesocosms within minutes after filling with them water, acting as an extra potential predator on aquatic insects in the mesocosms. I did not manipulate *P. flavescens* abundance. *P. flavescens* feeds on invertebrates (e.g., midges) and small vertebrates (tadpoles) (Sherratt and Harvey 1989).

Description of mesocosms and experimental design

This experiment was conducted using large outdoor aquatic mesocosms at the University of Oklahoma Biological Station (UOBS) near Lake Texoma, Oklahoma, USA (Matthews et al. 2006) over 46 days in June and July 2007 (see Plate 1). Each mesocosm consisted of an individual pool (183 cm diameter and 46 cm deep) with a riffle (122 cm long and 5–10 cm deep) both "upstream" and "downstream" (Fig. 1). The side of each mesocosm has a Plexiglas viewing window (22 × 10 cm) just below water level. Partial shade was provided with shade cloths suspended ~150 cm above each mesocosm. The substrate was a mixture of cobble and gravel taken from Brier Creek (Marshall County, Oklahoma, USA). Mesocosms were separated by marine plywood dividers placed in the riffles to prevent water from mixing between units. Plastic mesh screens (0.32 cm diameter) at the upper and lower attachment of each riffle restricted fish to pools. Flow was maintained by Little Giant submersible pumps (2500 L/h) (Little Giant Pump, Oklahoma City, Oklahoma, USA). All units were filled with well water from a public supply (Marshall County Water Corporation) over a 24-h period on 24–25 May and flow was initiated immediately after. On 25 May, a slurry of algae obtained from nearby Brier Creek was added equally to each unit to introduce periphyton and filamentous algae. Small snails, cladocerans, and some larval insects were likely included in the algal inocula-

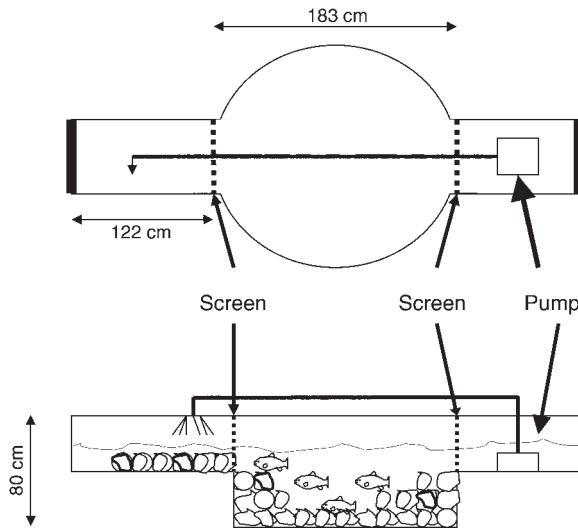


FIG. 1. Schematic of a single mesocosm at the University of Oklahoma Biological Station, near Lake Texoma, Oklahoma, USA. The shade cloth is not shown.

tions. Units were maintained with flow but without fish for 17 days (25 May–11 June) to allow establishment of algae and aerial colonization by invertebrates (mostly midges and dragonflies; Table 1). Mesocosms were not covered at any point during the experiment, allowing continuous oviposition. Temperature ($31.3^{\circ} \pm 2.0^{\circ}\text{C}$) and dissolved oxygen ($9.3 \pm 1.0 \text{ mg/L}$) were measured several times during the experiment. Conductivity was not measured in this experiment, but was measured between 385 and 490 μS in a previous experiment using the same mesocosms (Gido and Matthews 2001). Temperature, dissolved oxygen, and conductivity in the mesocosms are within the natural ranges of nearby streams (Miller and Golloday 1991).

The experiment included six replicates of each of three treatments: water column feeder (*C. lutrensis*), benthic feeder (*E. spectabile*), and fishless control. Treatments were assigned randomly among 18 individual mesocosm units. Approximately 150 individuals of similar size for each fish species were collected from nearby streams by seining on 11 June 2007. This marked the beginning of the experiment (Table 1). On the same day, 20 individuals of each species were assigned to each of six units, resulting in a density of 10.6 fish/m², commensurate with natural densities. All remaining fish were held in separate units, and were used to replace any dead fish (<10 fish total, checked daily) on the day they were found.

Fish from a single randomly selected replicate from each fish treatment were observed three times over the course of the experiment (Table 1). Observations lasted 5 min during early afternoon following methods described in Hargrave (2009). Notes were taken at 30-s intervals on the number of fish visible and their position in the pool: benthic, water column, or surface. Feeding attempts and their location also were noted whenever they occurred during the 5-min period. At the end of the experiment all fish were preserved in 10% formalin. Gut contents of 15 fish from each species (at least two per replicate) were identified to the lowest taxonomic level possible and classified as larval or winged. I compared fish diet overlap using the Morisita-Horn index (C_{MH}) (Gelwick and Matthews 2006):

$$C_{\text{MH}} = \left[2 \times \sum (n_{i,a}n_{i,b}) \right] / [d_a + d_b]N_a \times N_b$$

where N_a is the number of individual prey in fish species A; N_b is the number of individual prey in fish species B; $n_{i,a}$ is the number of individual prey of the i th species in fish species A; $n_{i,b}$ is the number of individual prey of the

TABLE 1. Timeline showing dates of experimental setup and sampling of aquatic and terrestrial food web components from stream mesocosms at the University of Oklahoma Biological Station, near Lake Texoma, Oklahoma, USA.

Date in 2007	Day of experiment	Event
25 May		all mesocosms filled with water and inoculated with algae and small invertebrates; aerial colonization begins
29 May		periphyton substrates placed in each mesocosm
9 June		first spider counts
11 June	0	all fish collected and placed in mesocosms; beginning of experiment
18 June	7	first fish observations
19 June	8	first benthos sample
25 June	14	second fish observations
26 June	15	collected periphyton; first odonate counts; set emergence traps
27 June	16	measured temperature and dissolved oxygen
28 June	17	first emergence collection
2 July	21	second odonate counts; second spider counts
4 July	23	set emergence traps
7 July	26	second emergence collection; second benthos sample; third odonate counts
10 July	29	third fish observations; first macrophyte measurements
16 July	35	measured temperature and dissolved oxygen; fourth odonate counts; third spider counts
19 July	38	set emergence traps
22 July	41	fourth spider counts; second macrophyte measurements
23 July	42	third emergence collection; third benthos sample; fifth odonate counts; fish diet analysis; second periphyton collection (lost); end of experiment

*i*th species in fish species B; $d_a = \sum n_{i,a}^2/N_a^2$ and $d_b = \sum n_{i,b}^2/N_b^2$ (d_a and d_b are the sum of the square of the number of individual prey taxa in each species divided by the square of the total number of prey for each fish species). C_{MH} has values between 1 and 0, where 1 indicates that diets are identical with respect to proportional prey composition, and 0 indicates that fish diets are completely different.

Periphyton was sampled using 10 porous silica discs (2.5 cm diameter), placed randomly on the substrate in each pool 13 days before the start of the experiment. Periphyton was collected on days 15 and 42. On day 15, four discs were collected from each mesocosm and frozen overnight to lyse cells. The discs were then extracted overnight in 90% acetone. Chlorophyll *a* was estimated for each treatment spectrophotometrically with a correction for phaeophytin (American Public Health Association 1998). Periphyton samples from day 42 were lost.

Floating emergence traps were deployed continuously for 2–4 days during three sampling periods (Table 1). Traps were made using a galvanized steel frame with a collection area of 0.16 m². Styrofoam was attached to the bottom of the traps for buoyancy. Nylon fabric surrounded the trap and was attached to a plastic collection bottle at the top, which was fitted with an inverted funnel. A small piece of an insecticidal strip was placed in each collecting jar (the active ingredient was dichlorvos; Hot Shot No-Pest Strip, United Industries, St. Louis, Missouri, USA). Upon collection, insects were transferred to individually labeled vials, and stored dry or in 95% ethanol. All insects were identified to family using Triplehorn and Johnson (2005), and measured for length to the nearest 0.1 mm for regression estimation of biomass (Sabo et al. 2002). Adult insects were classified as predators, omnivores, or nonconsumers according to descriptions of family-level adult feeding roles in Triplehorn and Johnson (2005).

The emergence traps collected insects whose life cycle contained a floating pupa stage, but underestimated insects that crawl out of the water to emerge (e.g., odonates). Odonate emergence was estimated by collecting exuviae from the upstream and downstream screens. Limiting collections to screens underestimated total dragonfly emergence for the pool. To correct for this and create a common area metric for analyses with emergence trap data, I multiplied the proportion of the pool circumference surveyed (0.16) by the pool area (2.6 m²). All dragonfly collections were divided by the resulting area (0.4176 m²) to estimate emergence density. All mesocosms were checked for exuviae at least twice per week for the first four weeks, and then almost daily afterward. All exuviae were preserved in 70% ethanol and stored for later identification and measurement. Biomass of dragonflies was estimated based on published regression equations using exuviae head width, measured to the nearest 0.1 mm (Sabo et al. 2002).

Benthic macroinvertebrates were sampled three times during the experiment using a steel cylinder (50 cm²). The cylinder was driven ~5 cm into the substrate and the contents scooped into a sieve (500 μm), drained, and preserved in ethanol (70%). Three samples were taken from each pool and combined into a single sample. Macroinvertebrates were identified to order or family using Merritt and Cummins (1996).

Shifts in foraging behavior under the threat of fish predation are common (Sih 1980). To test for this potential effect in this experiment, I counted larval dragonflies that were perched on clay tiles five separate times (Table 1). I assumed the clay tiles represented risky habitats for dragonflies because they contained no refuge and had light backgrounds. In addition, I observed dragonflies feeding from the tiles on several occasions through the viewing windows early in the experiment. On each observation date I approached each mesocosm slowly to avoid disturbing the dragonflies, and quickly counted the number of dragonflies on each tile. Four tiles were in each mesocosm, but algal growth sometimes obscured 1–2 tiles. I corrected for this by dividing the counts by the number of tiles observed.

Macrophytes can serve as refuge for benthic invertebrate prey (Gilinsky 1984), as can mats of filamentous algae. I measured this structural refuge by multiplying the percent cover of benthic filamentous algae by the mean height of filaments to use the volume of filamentous algae as an estimate of prey refuge. Two measurements were made toward the end of the experiment (Table 1). I measured height by placing a meter stick on the substrate in three random locations and recording the height (± 1 cm) of each filament that touched the meter stick (usually 3–4 filaments).

Spiders naturally colonized the tops of mesocosms and served as terrestrial consumers. I measured their response to insect emergence by visual counts of occupied webs directly over each pool on four nights: two nights before fish introductions and then on three nights after fish introductions (Table 1). Most spiders were tetragnathids, which commonly build webs on riparian vegetation and include a large percentage of emerging chironomid and mayfly insects in their diet (Williams et al. 1995). Webs were usually attached to the emergence trap cages, edges of the mesocosm, and/or the PVC pipe running above each pool.

Data analysis

I tested the null hypothesis of no differences between treatments using a separate repeated-measures ANOVA (rmANOVA) for abundance of common taxa, abundance and biomass of trophic groups, proportion of each trophic group, overall biomass, and overall abundance. Fish treatment was the between-subjects factor, and time was the within-subjects factor. Relative abundance of macroinvertebrates in fish diets was analyzed with a one-way ANOVA using fish species as the predictor variable. Linear regression was used to test

for a relationship between overall insect emergence and spider abundance. If an ANOVA was significant for any variable, I used Tukey's honestly significant difference (hsd) post hoc test, which corrects for family-wise Type I error (Quinn and Keough 2002). Abundance data were log-transformed, counts of larval odonates were square-root-transformed, and proportional data were arcsine square-root-transformed when needed to satisfy assumptions for ANOVA (Quinn and Keough 2002). For rmANOVA, sphericity was tested using Mauchly's *W*, and adjusted degrees of freedom were used when significant following the Greenhouse-Geisser adjustment. All statistical analyses were performed using SPSS 16.0 for Macintosh (SPSS, Chicago, Illinois, USA).

RESULTS

Both fish species reduced emergent insect biomass by at least 55% compared to the fishless control (Fig. 2a, Table 2), and significantly altered the trophic structure of the emergent community, reducing the proportion of predators when fish were present (Fig. 2b). Predators averaged 55% of emergent biomass in the fishless treatment, but only 28% and 24% in *C. lutrensis* and *E. spectabile* treatments, respectively. This reduction was significant in the *E. spectabile* treatment and approached significance in the *C. lutrensis* treatment (Table 2). Overall predator proportion by biomass increased over time (Fig. 2b, Table 2) with the onset of *P. flavescens* emergence (Table 2), but there was no interaction between time and treatment (rmANOVA within subjects, $F_{2,24} = 1.127, P = 0.356$).

Fish had a strong negative effect on the emergence of a predatory dragonfly, *Pantala flavescens*, but not on any other taxon. Fish reduced emergence abundance of *P. flavescens* by at least 57% compared to the control (rmANOVA between subjects, $F_{2,14} = 10.314, P = 0.002$; Tukey's hsd post hoc comparisons between *C. lutrensis* vs. control, $P = 0.016$; *E. spectabile* vs. control, $P = 0.006$). Due to their relatively large size, reduction in *P. flavescens* emergence drove the large reductions in emergence of overall biomass and predator biomass. Overall predator biomass (*P. flavescens* and long-legged flies [Diptera: Dolichopodidae]) was reduced nearly fivefold in both fish treatments compared to the control (Table 2), and there was a significant treatment \times time

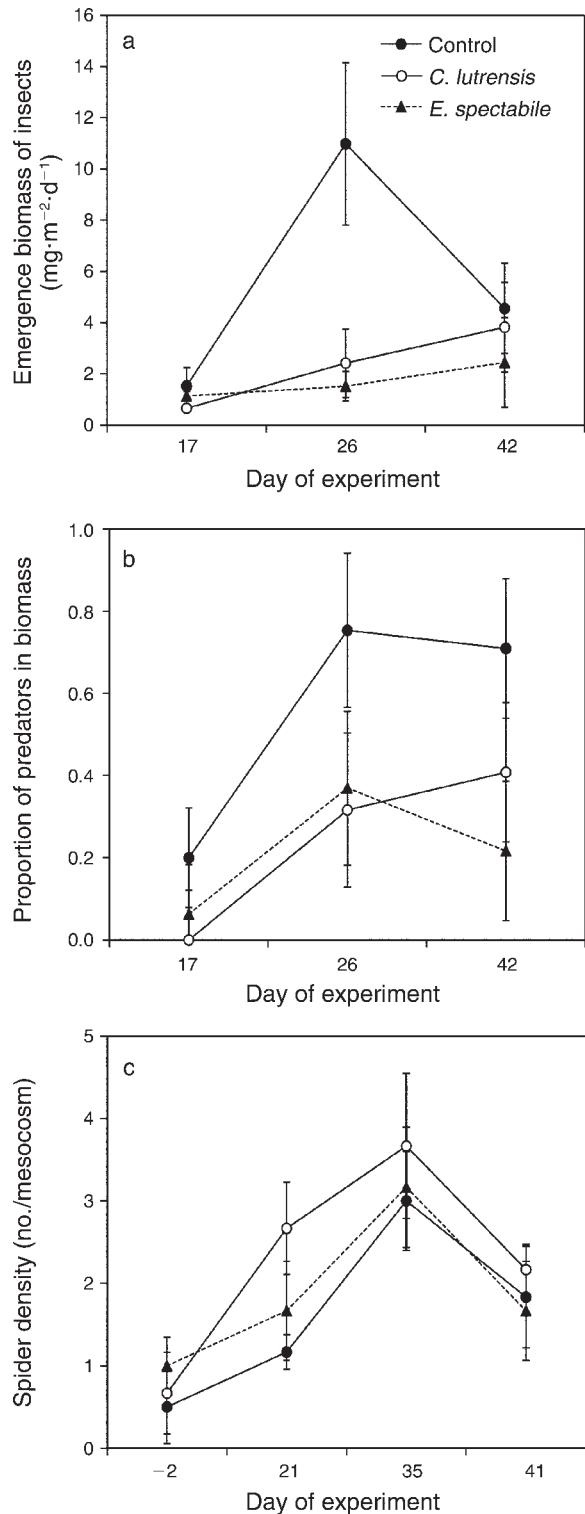


FIG. 2. Response of emerging insects and spiders to the presence of two predatory fish species (red shiner, *Cyprinella lutrensis* and orangethroat darter, *Etheostoma spectabile*) and a fishless control in stream mesocosms in June and July 2007 at the University of Oklahoma Biological Station. (a) Emergence biomass of adult aquatic insects over three sample dates, (b) proportion of predator biomass in emergent insect assemblage over three sample dates, (c) counts of web-weaving spiders above aquatic mesocosms over four sample dates. Data are means \pm SE. Day of experiment refers to the number of days since fish were introduced to the mesocosms. Spiders (mostly

Tetragnathidae and Lycosidae) were counted above each mesocosm to determine whether terrestrial consumers responded to changes in insect emergence. Insect assemblages were dominated numerically by non-feeding Chironomidae and a predatory dragonfly (*Pantala flavescens*). Fish strongly reduced emergence of *P. flavescens*, causing a reduction in the proportion of predator biomass emerging from mesocosms.

TABLE 2. Repeated-measures ANOVA and Tukey's hsd post hoc comparisons of selected response variables.

Response	Source and post hoc	Hypothesis df	Error df	Effect size	<i>P</i>
Emergence					
Total abundance	treatment	2	15		0.549
Total biomass	treatment	2	15		0.018
	<i>E. spectabile</i> vs. control			0.91	0.040
	<i>C. lutrensis</i> vs. control				
Total predators, biomass	time	1.57	23.54†		0.025
	treatment	2	15		0.010
	treatment × time	1.57	23.54†		0.025
	<i>E. spectabile</i> vs. control			0.97	0.011
	<i>C. lutrensis</i> vs. control			0.69	0.041
Trophic structure, predator abundance (%)	treatment	2	13		0.222
Trophic structure, predator biomass (%)	time	2	22		0.004
	treatment	2	12		0.036
	<i>E. spectabile</i> vs. control			0.40	0.049
	<i>C. lutrensis</i> vs. control			0.59	0.064
Visual dragonfly counts	time	4	48		0.024
	treatment	2	12		0.003
	<i>E. spectabile</i> vs. control			1.70	0.006
	<i>C. lutrensis</i> vs. control			1.70	0.004
Chlorophyll <i>a</i> , day 16	treatment‡	2	17		0.360
Spiders					
Abundance (no./mesocosm)	time	2	30		0.001
	treatment	2	15		0.427

Notes: Units are as follows: abundance (no.·m⁻²·d⁻¹), biomass (mg·m⁻²·d⁻¹), trophic structure (proportion of predators by abundance biomass). Effect size is the difference between mean treatments/standard deviation. The predatory fish are *Etheostoma spectabile* and *Cyprinella lutrensis*. Time and treatment × time interactions are excluded unless significant.

† Degrees of freedom represent Greenhouse-Geisser adjustments.

‡ One-way ANOVA.

interaction (Table 2). Fish reduced emerging predator biomass on day 26 (one-way ANOVA, $F_{2,15} = 7.368$, $P = 0.006$), when *P. flavescens* emergence was at its peak, but had no effect on days 17 (one-way ANOVA, $F_{2,15} = 0.543$, $P = 0.592$) or 42 (one-way ANOVA, $F_{2,15} = 0.657$, $P = 0.532$).

Non-feeding insects (Chironomidae, Ephemeroptera, and Trichoptera) made up >90% of non-odonate individuals by abundance and were unaffected by fish presence. A total of 638 individuals representing nine insect taxa emerged from the mesocosms during the experiment. Fish had no effect on overall emergent insect abundance (Table 2).

Spiders were present above at least 83% of all mesocosms on each sampling date ($n = 4$ observations), but density was low (mean, 2.33 spiders/mesocosm; range, 0–8). I did not identify spiders below order (Araneae) during observations, but abundance appeared to be dominated by tetragnathids (Araneae: Tetragnathidae), horizontal orb-weaving spiders that have been found to respond to fluctuations in aquatic insect abundance (Baxter et al. 2004, Marczak and Richardson 2007). Linear regression revealed no relationship between spider density and insect abundance ($R^2 = 0.0212$, $P = 0.5646$) or biomass ($R^2 = 0.0624$, $P = 0.3175$). Spiders showed no preference for fish treatments (Table 2) despite the reduction in emergent biomass when fish were present. On several dates I qualitatively examined spider webs to ensure that aquatic insects were being

trapped. Food items in webs appeared to consist almost exclusively of chironomids, suggesting that spiders were subsidized by aquatic production. *Pantala flavescens* was not observed in any webs.

Benthic invertebrate abundance was dominated by small snails (64%; Gastropoda: Planorbidae) and chironomid larvae (21%). Among benthic insects, chironomid larvae made up ~90% of all insects by abundance. Fish had no impact on the abundance of any benthic invertebrate taxon (Table 2). *Pantala flavescens* was too rare in benthic samples to analyze, appearing in no more than three of the 18 pools on any sample date. This is in contrast to their relative abundance shown by exuvia counts, and suggests a sampling bias, which was likely due to the ability of *P. flavescens* larvae to evade capture during benthic samples due to their high mobility. In contrast to their rarity in benthic samples, visual benthic surveys of *P. flavescens* on clay tiles revealed a five- to sixfold higher density in fishless treatments (0.24 larvae/tile) relative to either *C. lutrensis* (0.03 larvae/tile) or *E. spectabile* (0.05 larvae/tile) treatments (rmANOVA between subjects, $F_{1,12} = 31.015$, $P = 0.011$; Tukey's hsd post hoc comparisons with control, $P \leq 0.019$).

I observed fish from a single pool for each species on three dates (Table 1). No darters were observed on day 30, because filamentous algal growth blocked them from my view. Nearly all of the 20 initial darters were collected at the end of the experiment and very little



PLATE 1. Stream mesocosms with emergence traps at the University of Oklahoma Biological Station, Oklahoma, USA. The inset shows an adult dragonfly emerging from a mesocosm pool, with exuviae below. Fish in mesocosm pools drastically reduced dragonfly emergence, which drove a reduction in overall emergence biomass and altered the trophic structure of the adult aquatic insect prey subsidy. Photo credits: J. S. Wesner.

mortality occurred over the course of the experiment, meaning that darters were simply hidden on the benthos during observation periods. On days 7 and 14, I observed two and three darters, respectively. These individuals appeared to be actively feeding on the benthos. They moved in and out of rock crevices and under tiles and remained almost constantly in contact with the substrate. In contrast, nearly all red shiner individuals were observed on each day, and spent almost all of their time in the water column. On each occasion, only 2–3 shiners were seen feeding on the benthos at any time. The rest of the individuals remained in the water column and often broke the surface to feed. Diet analysis using the Morisita-Horn index (C_{MH}) revealed strong overlap in prey composition ($C_{MH} = 0.98$). On average, *C. lutrensis* fed on more terrestrial input (30%) than *E. spectabile* (<1%), but terrestrial input in *E. spectabile* was too rare ($n = 1$) to analyze statistically. Prey composition for both species was dominated by *Bosmina* spp. (Cladocera: Bosminidae), which made up 60% of food items. Cladoceran species typically occupy benthic and water-column habitats (Dodson and Frey 2001). The next most common food items, pooled for both species, were: chironomid larvae (12%), spiders (5%), *P. flavescens* (4%), unknown terrestrial insects (4%), terrestrial dipterans (3%), Collembola (3%), Planorbidae (3%), unidentifiable prey (2%), copepods (<1%), chironomid pupae (<1%), Plecoptera (<1%), and Megaloptera (<1%).

Chlorophyll *a* was similar across treatments on day 16 (6.85 ± 2.77 mg/m², mean \pm SE; Table 2). Prey refuge, estimated as volume of filamentous algae (mostly *Chara*

spp. and *Oedogonium* spp.), was similar across treatments on day 29 ($F_{2,16} = 0.785$, $P = 0.475$) and day 41 ($F_{2,15} = 2.971$, $P = 0.087$).

DISCUSSION

This study showed that predation by fish in an aquatic habitat strongly altered the trophic structure and biomass of an insect prey subsidy entering the terrestrial habitat. To my knowledge only two empirical studies have assessed the impact of predation in aquatic habitats on terrestrial food webs (Baxter et al. 2004, Knight et al. 2005). Trout predation reduced insect biomass export to the terrestrial system by nearly half, altering the abundance of terrestrial web-weaving spiders (Baxter et al. 2004), and predatory sunfish altered a terrestrial trophic cascade by reducing the abundance of predatory adult dragonflies in terrestrial habitats around ponds (Knight et al. 2005). My study complements the findings of Baxter et al. (2004) and Knight et al. (2005), showing that fish predation can simultaneously affect the magnitude and trophic structure of adult aquatic insect assemblages in terrestrial habitats. When predatory fish were present, insect emergence biomass was low and dominated by non-feeding insects. When predatory fish were absent, insect emergence biomass was high and dominated by predatory insects. The contrasting adult aquatic insect assemblages created by fish predation in this study are likely to have different effects in terrestrial food webs. In the presence of fish, the primary effect of adult aquatic insects in terrestrial food webs is likely bottom-up, as an energy source for terrestrial consumers (Fig. 3). In the absence of fish, the likely effect of adult

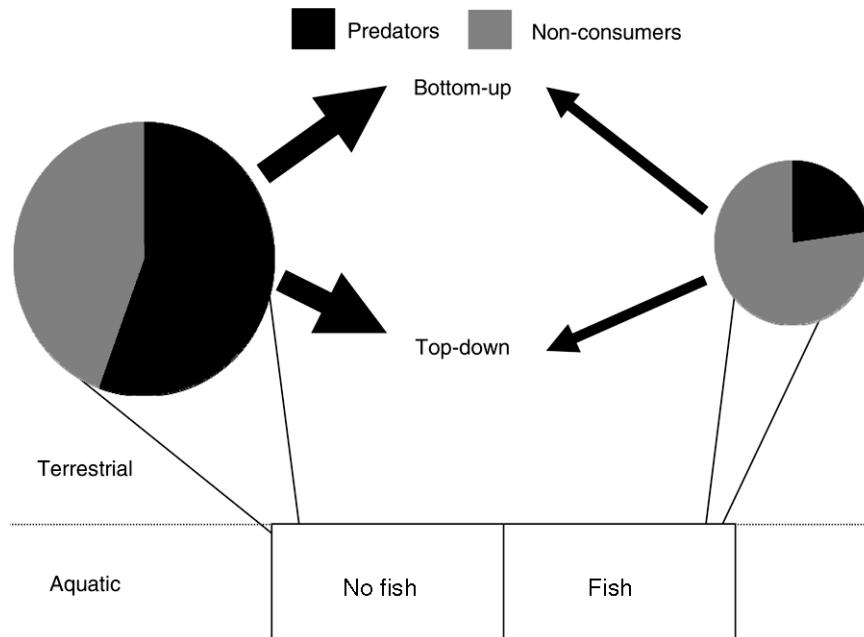


FIG. 3. Potential roles of alternative adult aquatic communities in terrestrial food webs created by different predator regimes in aquatic habitats. Different sizes of pie charts reflect differences in total biomass of emergent insects seen in this study. Different arrow sizes reflect the magnitude of the impact of each community predicted from this study (top-down = consumption of terrestrial prey; bottom-up = energy source for terrestrial consumers).

aquatic insects is bottom-up and top-down, as both prey and predators in terrestrial food webs (Fig. 3).

Fish reduced emergence of adult insect predators by ~50%, nearly identical to the reduction found by Knight et al. (2005, as estimated from their Fig. 2b). Modeling showed that a similar reduction in frog emergence from ponds reduced the predation profile around ponds (predator shadows), and led to an increase in herbivorous insect biomass, thereby reversing a trophic cascade (McCoy et al. 2008). Such effects of consumer movement across habitat and ecosystem boundaries are relatively unknown, but should be emphasized in future empirical studies to further understand the cascading effects of habitat alteration, especially when these habitats contain organisms with complex life histories.

Terrestrial web-weaving spiders did not respond to reductions in insect emergent biomass, in contrast to recent studies showing that this predatory guild is sensitive to such alterations. Baxter et al. (2004) showed that tetragnathid spiders were reduced along stream reaches with invasive rainbow trout (*Onchorhynchus mykiss*), due to a 35% reduction in emergent insect biomass. In their study, spiders were surveyed 2–4 m from the stream edge. In my study, spiders were surveyed directly above the water. Therefore, insects that crawl out of the water to emerge from the mesocosm walls (i.e., hemimetabolous insects) may have been able to avoid capture in spider webs, and the bulk of insects that spiders trapped were insects that emerge directly from the water surface (i.e., holometabolous

insects). Such differences in emergence strategy could explain the lack of correlation between spider abundance and insect emergence because chironomid emergence was similar across replicates, and chironomids were the most abundant prey taxon in spider webs. These data highlight the importance of prey and consumer functional traits in predicting the impact of subsidies (Marczak et al. 2007).

Fish in this experiment represented two different feeding strategies: benthic invertivore and water-column invertivore. Both fish species had similar overall predation effects, although *C. lutrensis* (water-column feeder) had somewhat more terrestrial insects in their diet than *E. spectabile* (benthic feeder; 30%, <1% of diet, respectively). When both fish species showed significant effects compared to the control, they were always stronger, based on *P* values, in the *E. spectabile* treatment. Additionally, while both species reduced predatory insect emergence, only *E. spectabile* caused a reduction strong enough to significantly reduce the proportion of predator biomass in the emergent community.

Fish fed on a variety of prey items, but significant predation effects were limited to a single dragonfly species, *P. flavescens*. It is possible that fish reduced populations of prey taxa other than *P. flavescens*, but that these were masked by increased dragonfly predation on the same prey taxa in the control treatments (sensu Thorp and Bergey 1981). Several studies have found a strong predation effect of dragonflies on benthic aquatic

community structure (Thorp and Cothran 1984) and abundance (Van Buskirk 1988). Cladocerans were the numerically dominant food item for both fish species, though were likely less important energetically than larger invertebrates given their small size. Cladocerans typically occur at all levels of the water column, though I only sampled invertebrates on the benthos. I do not know whether Cladocerans were present in the water column, or whether their prevalence in fish guts was due to both species feeding on the benthos or due to the presence of cladocerans at all levels of the water column.

Reduced insect emergence in the presence of fish could result from either direct or indirect predation. Direct predation occurs when predators consume prey. Indirect predation occurs when predators alter the behavior of prey by, for example, reducing oviposition in larval habitats with predators. It is likely that direct predation by fish on dragonfly larvae, and not behavioral avoidance by ovipositing dragonflies of mesocosms with fish, was the primary mechanism regulating insect emergence patterns in this study for the following reasons. The minimum development time from oviposition to emergence for *P. flavescens* is ~38 days (Suhling et al. 2004). Pools in my experiment were fishless for 17 days prior to fish introductions, meaning that initial oviposition occurred across pools that were equal in their predator threat. Peak dragonfly emergence occurred ~43 days after the mesocosms were filled with water, suggesting that the majority of *P. flavescens* emerging were the result of oviposition before fish introductions. While it is possible that dragonflies ovipositing after fish introductions avoided pools with fish (behavioral avoidance), this mechanism would not explain the strong differences seen in dragonfly emergence at the middle of the experiment. An alternative hypothesis is that *P. flavescens* larvae delayed emergence in fish treatments. Delayed emergence of a dragonfly species (*Lestes sponsa*) of up to seven days was caused by the presence of a predatory fish (*Perca fluviatilis*) in a study by Brodin (2005). *P. flavescens* emergence from the *C. lutrensis* treatment increased in the final four days of the experiment (2.33 individuals·m⁻²·d⁻¹ vs. 0.12 individuals·m⁻²·d⁻¹ during the rest of the experiment), but this was due entirely to a single treatment, and emergence was not significantly different across treatments in the final collection period. Thus, direct predation by fish on larval *P. flavescens* was likely the primary mechanism driving emergence patterns, though it should be noted that indirect predation effects could create similar patterns in other systems.

Oviposition in the mesocosms began almost immediately upon filling with water. The source of insects is unknown, but is likely Lake Texoma, a large permanent reservoir located several hundred yards from the mesocosms. The exception is that some insects, snails, and cladocerans were likely introduced during algal inoculations at the beginning of the experiment, though it should be noted that the source of *P. flavescens* is

almost certainly aerial because it does not occur in the algal source habitat. Drift from the upstream riffles and flow rate in the mesocosms is low. The dynamics of colonization and predation therefore likely resemble small, isolated, slow-flowing pool-riffle streams, all of which are common but understudied habitats in the central United States (Matthews 1988).

This study shows that predation in a donor habitat alters the magnitude and trophic structure of a prey subsidy entering an adjacent habitat. Subsidies alter food web dynamics in recipient systems from the bottom-up, as an energy subsidy to terrestrial consumers (Nakano and Murakami 2001, Baxter et al. 2004, Marczak et al. 2007) or from the top-down, as consumers themselves in recipient food webs (Knight et al. 2005). The type of impact is necessarily determined by both the magnitude and trophic structure of the subsidy, which in turn is determined by the quality of larval habitat (e.g., predation threat or resource abundance). Empirical studies have largely focused on the role of predation in regulating the biomass of prey subsidies. In this study, predation in the larval aquatic habitat altered both the biomass and trophic structure (proportion of predators) of a prey subsidy, reducing the amount of energy and predators entering the adult terrestrial habitat.

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