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Diet shift of lentic dragonfly larvae in response to reduced terrestrial prey subsidies

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Abstract. Inputs of terrestrial plant detritus and nutrients play an important role in aquatic food webs, but the importance of terrestrial prey inputs in determining aquatic predator distribution and abundance has been appreciated only recently. I examined the numerical, biomass, and diet responses of a common predator, dragonfly larvae, to experimental reduction of terrestrial arthropod input into ponds. I distributed paired enclosures ($n = 7$), one with a screen between the land and water (reduced subsidy) and one without a screen (ambient subsidy), near the shoreline of 2 small fishless ponds and sampled each month during the growing season in the southern Appalachian Mountains, Virginia (USA). Screens between water and land reduced the number of terrestrial arthropods that fell into screened enclosures relative to the number that fell into unscreened enclosures and open reference plots by 36%. The $\delta^{13}C$ isotopic signatures of dragonfly larvae shifted towards those of aquatic prey in reduced-subsidy enclosures, a result suggesting that dragonflies consumed fewer terrestrial prey when fewer were available (ambient subsidy: 30%, reduced subsidy: 19% of diet). Overall abundance and biomass of dragonfly larvae did not change in response to reduced terrestrial arthropod inputs, despite the fact that enclosures permitted immigration/emigration. These results suggest that terrestrial arthropods can provide resources to aquatic predators in lentic systems, but that their effects on abundance and distribution might be subtle and confounded by in situ factors.

Key words: resource subsidies, allochthonous input, odonate, IGP, food web.

Ecologists have long understood that ecosystems are connected by the movement of energy and nutrients (Lindeman 1942, Minshall 1960). However, the implications of such movements for food webs have been studied only more recently (e.g., Polis et al. 1997, Power et al. 2004, Baxter et al. 2005). Most research examining the influence of allochthonous inputs on recipient food webs was conducted initially at boundaries with large resource gradients (i.e., between high-productivity and low-productivity habitats like the upwelling ocean and desert islands) (Heatwole 1970, Jackson and Fisher 1986, Polis et al. 2004). As research expanded to interfaces between habitats with more similar productivity, such as forests and temperate waterways (Cloe and Garman 1996, Nakano and Murakami 2001, Power et al. 2004, Paetzold and Tockner 2005), movements of resources across ecosystem boundaries were shown to be more ubiquitous determinants of foodweb dynamics than originally thought (Baxter et al. 2005, Knight et al. 2005, Marczak et al. 2007).

Movements of resources between ecosystems can alter foodweb dynamics in recipient systems in several ways. Inputs can directly subsidize the diet of certain consumers, thereby increasing consumer density and decoupling consumer densities from abundance of in situ resources (Polis and Hurd 1996a, b, Nakano and Murakami 2001, Sabo and Power 2002a, b). For example, aquatic insects emerging from a desert stream provided 37 to 100% of the diet of riparian spiders and increased local spider density up to 10× compared to density when no insects were emerging (Sanzone et al. 2003). Resource subsidies can indirectly affect consumers by changing competitive interactions (Baxter et al. 2004) or by providing alternative prey for intraguild predators (Sabo and Power 2002a). For example, experimental reduction of aquatic insects next to a large river appeared to increase the consumption of insectivorous wolf spiders by insectivorous lizards (Sabo and Power 2002a). On the other hand, characteristics of recipient food webs also can influence the effect of

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subsidies on consumers. Recipient productivity (Huxel and McCann 1998), the ratio of subsidies to in situ resources (Marczak et al. 2007), habitat availability (Greenwood and McIntosh 2008), and higher-order predators (Crooks and Soule 1999, Sabo and Power 2002a) can influence the response of consumers to allochthonous resource inputs.

Because of their physical proximity to terrestrial ecosystems, freshwater food webs have high potential to be influenced strongly by allochthonous resource subsidies. For example, terrestrial plants provide structure and resources in the form of leaves and woody debris to aquatic organisms (especially detritivores) in forested streams (Minshall 1960, Kaplan and Newbold 1993, Meyer et al. 1998). Terrestrial arthropods that fall into the water can provide a direct source of prey for aquatic predators, and affect growth, distribution, and abundance of fish and macroinvertebrates in streams (Kawaguchi and Nakano 2001, Nakano and Murakami 2001, Baxter et al. 2005). Ponds typically receive inputs from the terrestrial environment, but much less is known about the role of allochthonous subsidies in lentic than in lotic systems (but see Schindler and Scheurell 2002, Knight et al. 2005, Regester et al. 2006). Lentic systems often have less edge for a given surface area (Gratton and Vander Zanden 2009) and lower flow rates than do lotic systems. These factors could reduce the quantity of terrestrial inputs to lotic systems but increase residence times.

I used a manipulative field experiment to examine the role of terrestrial prey subsidies in determining the abundance and distribution of a top aquatic predator (dragonfly larvae) in fishless ponds. I used repeated sweeps of the pond and stable isotope signatures (Hall 1995, Hamilton et al. 2004, Pace et al. 2004) to monitor changes in consumer abundance, biomass, and diet in enclosures in relation to the availability of allochthonous resources. The abundances of 2 other common top consumers (newts and crayfish) in enclosures also were monitored to examine their potential effects on dragonfly response to terrestrial prey subsidies.

Methods

I did this study at Mountain Lake Biological Station in the Allegheny Mountains of southwestern Virginia, USA (elevation 1160 m) in 2 permanent fishless ponds. Ponds were constructed in 1965 and were ~500 m apart (Sylvatica: 86.1 m perimeter, 353.5 m^2 area, 0.95 m deep; Horton: 65.9 m perimeter, 223.3 m^2 area, 1.3 m deep). Ponds were filled by rain and surface flow and were surrounded by an open vegetated area (~1–5 m wide) and large trees (mixed deciduous, dominated by northern red oak [*Quercus rubra*] and pitch pine [*Pinus rigida*]). Predominant bottom cover in the ponds was leaf litter from surrounding trees and the pondweed *Elodea* sp. The most common dragonflies emerging from the ponds during the experiment were *Libellula lydia* Drury 1770, *Libellula pulchella* Drury 1773, *Somatochlora elongata* Scudder 1866, *Cordulia shurtleffi* Scudder 1866, *Aeshna umbrosa* Walker 1908, and *Sympetrum rubicundulum* Say 1839. I deposited voucher specimens at the Smithsonian National Museum of Natural History, Washington, DC, USA.

I used a 1-way randomized block design ($n = 7$) to test the effects of 2 levels of terrestrial input (ambient subsidy or reduced subsidy; sensu Sabo and Power 2002a, b) on larval dragonfly diet, biomass, and abundance in field enclosures. I also monitored unmanipulated open plots set ≥ 3 m from enclosures ($n = 4$, i.e., 2 at each pond) for reference. Enclosures were paired by treatment in both study ponds ($n = 5$ ambient/reduced-subsidy pairs at Sylvatica pond and $n = 2$ ambient/reduced-subsidy pairs at Horton pond).

Enclosures (1.5 m long × 2 m high × 1.5 m wide) consisted of a polyvinyl chloride (PVC) pipe frame on a wood base with a plastic flange sunk into the substrate. The tops and ends of cages were covered with plastic hardware cloth (opening 1.27 cm × 1.91 cm) to allow immigration and emigration of focal organisms from enclosures and the open pond while excluding larger predators, such as birds. Focal organisms could move between enclosures, but adult dragonflies could not enter them to oviposit. Thus, numerical responses to treatment resulted from differences in survivorship and migration. Reduced-subsidy enclosures included an additional fiberglass screen top and screen partition between land and water to block terrestrial prey inputs into the enclosure.

I erected cages at the beginning of the growing season in May 2004 before the first sampling period so that pretreatment measurements could be taken in enclosures. I sampled enclosures once a month during the growing season (June–August 2004) and estimated relative abundance and biomass of dragonfly larvae in each sampling plot with a box sampler (Harris et al. 1988). After slowly approaching the sampling area, I quickly pushed the bottomless metal frame of the sampler (1.0 m × 0.5 m × 1.0 m, l × w × h) into the pond substrate. I measured water volume in the sampler as a potential covariate of dragonfly abundance in the enclosures by taking water depth measurements on both sides of the frame. I collected

the contents of the sampler (water column and top layer of substrate) with 3 consecutive sweeps of a snug-fitting net, and picked, counted, and identified all dragonfly larvae from the samples in the field. I also counted and measured (snout-vent length for newts and total length for crayfish) potential intraguild predators (i.e., Eastern red-spotted newts [*Notophthalmus viridescens*] and Tennessee River spiny crayfish [*Orconectes spinosus*], an invasive species in the ponds). These predators were impossible to exclude from enclosures because they were similar in size to dragonfly larvae, and thus, I monitored them for potential effects on dragonfly larval responses to prey subsidies. I returned all animals, except dragonfly larvae, which were removed temporarily for weighing and identification to genus, to enclosures immediately.

I estimated the abundance of terrestrial insects that fell into ponds with floating pan traps (43 cm × 33.5 cm × 11.4 cm grey plastic bins) filled with ~5 L of filtered pond water and 30 mL of diluted dish soap as a surfactant (Nakano and Murakami 2001). I anchored 2 pan traps to the pond floor in each enclosure/control plot for 2 d each sample period. I sieved (500-μm-mesh sieve) and froze pan contents. I identified arthropods to family or order and designated them as aquatic or terrestrial in origin.

Stable isotopes have been used frequently to estimate diet and trophic structure in natural communities (Hall 1995, Collier et al. 2002, Sanzone et al. 2003, Akamatsu et al. 2005). I determined C isotopic signatures for 1 randomly selected dragonfly larva from each sample (n = 7 enclosures/treatment × 2 sampling dates) to estimate diet shifts in dragonfly larvae caused by decreased availability of terrestrial arthropod inputs. I removed abdomens from larvae before sample preparation to reduce incorporation of undigested stomach contents into the estimate of isotopic signature. Isotopic analysis was done with a Carlo Erba elemental analyzer coupled to a Micromass Optima isotope ratio mass spectrometer (GV, Manchester, UK). I report the stable isotope ratio as δX (‰) = $[R_{sample}/R_{standard} - 1] \times 1000$, where $X = {}^{13}C$ and $R = {}^{13}C/{}^{12}C$. Peedee Belemnite (PDB) served as the standard for ${}^{13}C$.

To illustrate the approximate size of any effect on dragonfly larval diet in more intuitive terms than raw $\delta^{13}C$ values, I estimated the proportion of the diet from each potential source with a 3-source mixing model (IsoSource; Phillips and Gregg 2003). IsoSource solves isotope mixing models iteratively where the number of sources is greater than the number of isotopes + 1. I estimated the mean proportion of dragonfly larval diet from terrestrial resources for each treatment from $\delta^{13}C$ values for predator and 3 potential prey sources: aquatic detritivores (midges [Chironomidae]), aquatic herbivores (mayflies [Ephemeroptera]), and terrestrial herbivores (leafhoppers [Cicadellidae:Homoptera]). These prey items were common potential prey in and around the ponds (Kraus 2006, this study). I selected 2 (±1) leafhoppers from sticky traps in reference plots adjacent to pond enclosures and combined them for analysis because of their low mass (n = 4 plots). I collected 1 or 2 chironomid midges from floating emergence traps (n = 7 enclosures/treatment × 2 sampling dates). I also collected mayflies from emergence traps, but they were not abundant, and I collected them from only 2 enclosures (n = 2). The prey $\delta^{13}C$ signatures used in the mixing model were averaged per enclosure (i.e., averaged over time). Dragonfly isotopic signatures used in the mixing model were calculated as mean signatures per treatment. Thus

$$\delta^{13}C_{\text{dragonfly treatment } i} = x\delta^{13}C_{\text{terrestrial prey}} + y\delta^{13}C_{\text{aquatic herbivorous prey}} + (1-x-y)\delta^{13}C_{\text{aquatic detritivous prey}}$$

where i is reduced or ambient treatment, x is the proportion of dragonfly diet from terrestrial herbivores, y is the proportion from aquatic herbivorous prey, and $(1 - x - y)$ is the proportion from aquatic detritivorous prey. The same mean prey values were used for both ambient- and reduced-subsidy mixing models. I tested the assumption that prey $\delta^{13}C$ did not change with treatment where possible (i.e., where animals were sampled from multiple replicates of each treatment). I assumed fractionation of ${}^{13}C$ was negligible based on published estimates for predaceous macroinvertebrates (Jardine et al. 2005).

I used SAS statistical software (SAS 9.1; SAS Institute Inc., Cary, North Carolina) for all data analysis. I used a repeated measures generalized linear mixed model (rmGLMM) to test the effect of subsidy reduction on consumer responses. GLMMs are particularly useful for analyzing data with nonnormal errors of known distribution (Wolfinger and O'Connell 1993, Bolker et al. 2009). I specified link functions to the expected error distribution of each dependent variable (McCullagh and Nelder 1989). I fitted count data to Poisson or negative binomial distributions, and length, mass, and isotopic signatures to the normal distribution (Littell et al. 1996). I modeled error distribution for time as either compound symmetric or autoregressive by 1 time step. I created a set of candidate models for each dependent variable based on these error distributions (for time

and treatment) and inclusion of a random block effect. I chose best-fit model from this set using Akaike's Information Criterion for small sample sizes (AICc, smaller = better) (Burnham and Anderson 1998) and the overdispersion parameter Φ (closer to 1 = better). I evaluated effects of subsidy reduction (ambient- vs reduced-subsidy enclosures) and cages (ambient-subsidy enclosure vs open plots) with post hoc Fisher's Least Significant Difference (LSD) tests. I used data collected in May to examine initial differences among cages before the subsidy reduction screens were installed, and I did all other analyses with data collected after the subsidy reduction screens were erected (June, July, and August). I included pond identity as an effect in the models because differences were detected between ponds after data were collected. All figures represent the least-square mean estimates calculated from the best-fit GLMM and back-transformed to the scale of the data.

Results

When averaged over the season, 36% fewer terrestrial arthropods fell into pan traps in the reduced-subsidy treatment than in the ambient-subsidy treatment, and the number collected did not differ between ambient-subsidy and open plots (Table 1, Fig. 1A). The largest proportion of these arthropods was small herbivorous insects (38% Homoptera, Hemiptera, and Thysanoptera), followed by nonaquatic Diptera (32%), Hymenoptera (9%), and Collembola (7%). Significantly fewer small herbivorous insects were collected in reduced-subsidy than in ambient-subsidy enclosures, and the number collected did not differ between ambient-subsidy and open plots (Table 1, Fig. 1B). Significantly fewer flying aquatic insects (i.e., terrestrial adult stages; 93% aquatic Diptera) fell into pan traps in the reduced-subsidy than in the open plots, but the number collected did not differ between reduced-subsidy and ambient-subsidy enclosures or between ambient-subsidy enclosures and open plots (Table 1, Fig. 1C).

$\delta^{13}C$ signatures of dragonfly larvae were more enriched in ambient-subsidy than in reduced-subsidy enclosures, but did not differ between ambient-subsidy enclosures and open plots (Table 1, Fig. 1D). The most common terrestrial herbivorous prey (leafhoppers) had more enriched $\delta^{13}C$ signatures than aquatic herbivorous prey (mayflies) or aquatic detritivorous prey (chironomid midges) (Student's t-test, $p < 0.001$ for both comparisons; mean $\pm$ SD $\delta^{13}C$, leafhoppers: -27.1 ± 0.7, $n = 4$; mayflies, -38.4 ± 0.4, $n = 2$; midges $= -33.4 \pm 1.9$, $n = 13$ [midges were absent from 1

TABLE 1. Repeated measures generalized linear mixed model statistical output for best-fit models testing the effect of subsidy reduction on prey inputs to ponds, dragonfly C isotopic signature, count, and biomass. Treatment (treat) effect in the model includes both enclosure treatments (ambient and reduced subsidy, $n = 7$) and open plots ($n = 4$). Month effect includes the 3 mo after the subsidy screens were installed in enclosures (June–August). Pond is the post hoc comparison between Horton ($n = 2$) and Sylvatica Ponds ($n = 5$). Spatial block did not improve fit of any model and was not included here. Distribution indicates error distribution used for each response variable (nb = negative binomial, norm = normal). Blocks did not improve model fit and were not used. Estimates of F statistics are analogous to type III Sums of Squares in analysis of variance. Bold indicates $p < 0.05$.

	Prey									Dragonflies								
	Terrestrial arthropods			Herbivorous terrestrial insects			Flying aquatic insects			δC^{13}			Count			Biomass total		
Effects	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Distribution		nb			nb			nb			norm			nb			nb	
Treatment	2,12	9.44	**0.003**	2,12	6.75	**0.011**	2,12	6.23	**0.014**	2,12	5.82	**0.017**	2,12	2.12	0.163	2,12	1.01	0.393
Month	2,30	4.62	**0.018**	2,28	7.75	**0.002**	2,30	11.46	**0.002**	1,11	3.63	0.083	2,29	1.54	0.232	2,29	2.89	0.072
Treat × month	4,30	0.39	0.215	4,28	2.10	0.107	4,30	1.54	0.215	2,11	0.03	0.967	4,29	0.74	0.572	4,29	1.57	0.208
Pond	1,12	2.97	0.359	1,12	0.23	0.643	1,12	0.91	0.359	1,12	82.37	**<0.001**	1,12	0.22	0.648	1,12	4.52	0.055
Treat × pond	2,12	1.40	0.565	2,12	0.52	0.606	2,12	0.60	0.565	2,12	0.62	0.556	2,12	4.34	**0.038**	2,12	1.43	0.278

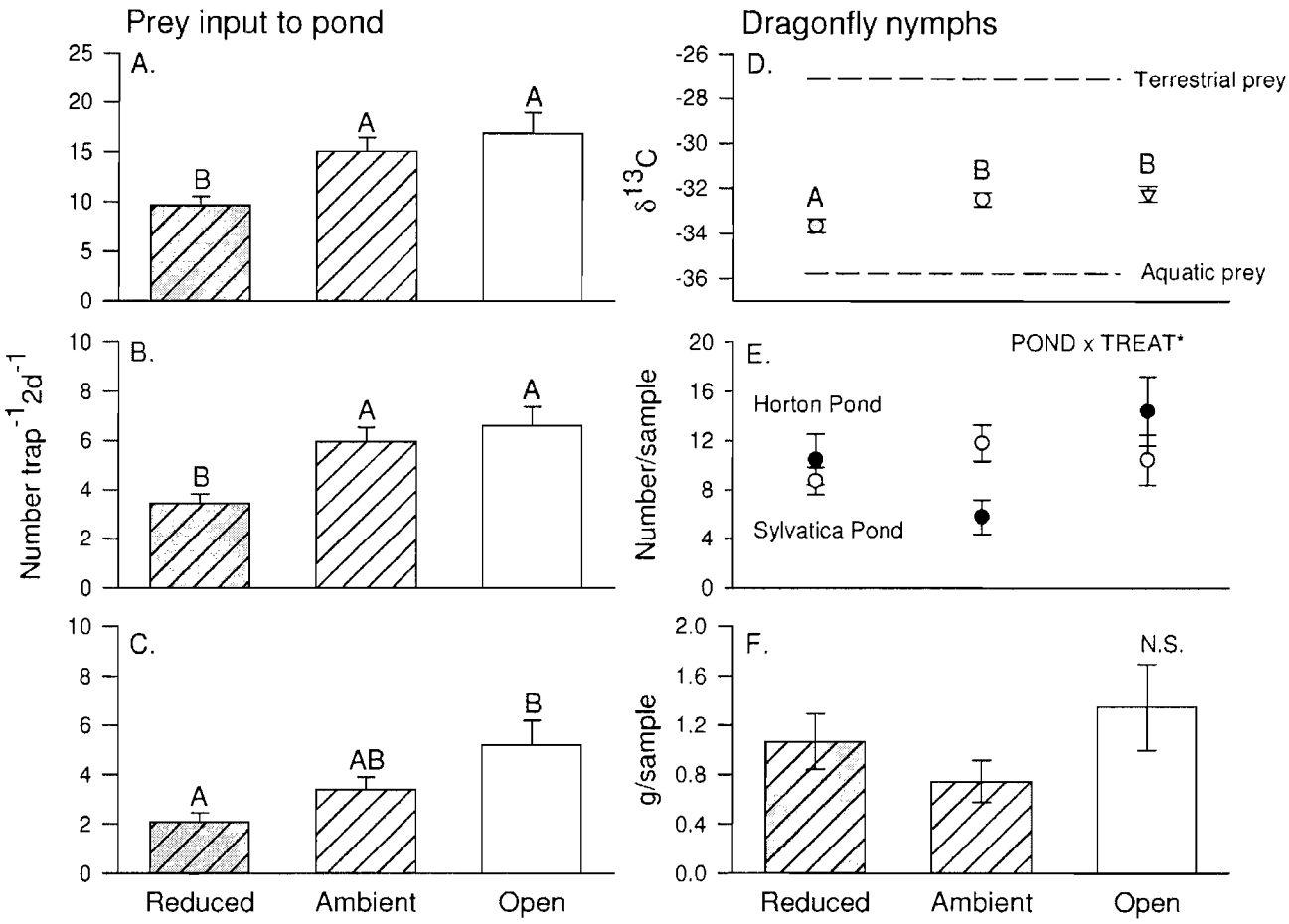

FIG. 1. Mean (+1 SE) total terrestrial arthropods (A), terrestrial herbivores (B), and aquatic flying insects (terrestrial adults) (C) falling into the ponds over 48 h and mean (±1 SE) larval dragonfly δ^{13}C signature (D), abundance (E), and biomass (F) per enclosure and sample date in ambient- vs reduced-subsidy enclosures and open plots. In D, dashed lines represent the mean available prey δ^{13}C signatures based on the average δ^{13}C of aquatic midges and mayflies and the average δ^{13}C of leafhoppers sampled during the experiment. All values are back-transformed from best-fit repeated measures generalized linear mixed model analysis. Within panels, bars with the same letters are not significantly different (Fisher's Least Significant Difference, $p > 0.0\%$). $n = 7$ for all treatment combinations. TREAT = treatment, N.S. = $p > 0.05$, * = significant interaction.

trap]). Chironomid δC^{13} signatures did not differ between ambient-subsidy and reduced-subsidy enclosures (GLMM, treatment $F_{2,14} = 0.43$, $p = 0.66$).

Larval dragonfly δ^{13}C signatures used in the mixing model were −32.8 ± 1.7 (ambient subsidy) and −34.1 ± 1.6 (reduced subsidy) ($n = 6$, excludes 1 block that did not contain larvae in both ambient-and reduced-subsidy treatments). Based on the mean signatures of the 3 prey items, the isotope mixing model suggested that on average 30% ± 12% (99% CI = 9–49%) of dragonfly larval diet in the ambient-subsidy enclosures and 19% ± 12% (99% CI = 0–38%) of dragonfly larval diet in the reduced-subsidy enclosures came from terrestrial arthropods. The overlapping confidence intervals surrounding these proportions suggest they were not significantly different.

Neither subsidy reduction nor enclosures affected the counts or biomass of dragonfly larvae as a whole ($p > 0.05$; Table 1, Fig. 1E, F). However, pond identity influenced the effect of subsidy reduction on dragonfly abundance within enclosures. Dragonfly numbers were lower in the ambient-subsidy enclosures than in the reduced-subsidy enclosures at Horton Pond, whereas this pattern was reversed in Sylvatica Pond (Table 1, Fig. 1E). The number of dragonfly larvae was significantly higher in open plots than in ambient-subsidy enclosures at Horton Pond (Fig. 1E), a result that suggested a potential enclosure effect on the dragonfly

numerical response at Horton Pond. Initial counts and biomass of dragonfly larvae did not differ among treatments in May before subsidy screens were erected ($p > 0.05$). Dragonfly larval response did not change seasonally after screens were erected in June (Table 1).

Individual dragonfly genera responded similarly to the reduced subsidies (Fig. 2A–J), although *Aeshna* larvae showed a marginally significant increase in total biomass (194%, $p = 0.06$; Fig. 2F) in reduced-subsidy enclosures (Table 2). Too few representatives of each dragonfly species were analyzed separately for isotopes to permit statistical examination of the effects of subsidy treatment on diet for each taxon. However, mean responses for *Aeshna*, *Somatochlora*, and *Sympetrum* (taxa for which isotopic signatures were obtained from ≥ 1 enclosure/treatment) all showed the general trend of becoming more aquatic in the reduced-subsidy treatments.

Neither top predator (newts and crayfish) found in the enclosures showed a numerical or biomass response to reduced subsidies (Table 3, Fig. 3A–D). Horton Pond contained almost 4× more newts than Sylvatica Pond, whereas Sylvatica Pond contained 10× more crayfish than Horton Pond (Table 3, Fig. 4A–D). Water volume per sampler did not differ between ambient- and reduced-subsidy enclosures or between enclosures and open plots (GLMM, $F_{2,12} = 0.63$, $p = 0.55$), but did differ between ponds (Horton: 0.12 ± 0.026 m^3, Sylvatica: 0.095 ± 0.020 m^3; GLMM, $F_{1,12} = 6.8$, $p = 0.023$) probably because of the steeper embankment at Horton Pond.

Discussion

I examined the effect of terrestrial prey inputs on odonates in fishless ponds. The results suggest that dragonfly diet can be subsidized by terrestrial arthropod prey. Data from this experiment and previous measurements at these ponds (Kraus 2006) showed that terrestrial herbivores were more enriched in ^{13}C than aquatic insects. The C isotopic signatures of dragonfly larvae were significantly more enriched in enclosures receiving ambient rates of terrestrial arthropod inputs than in enclosures with a 36% reduction in input. This pattern suggests that dragonfly larvae responded to a reduction in terrestrial input by shifting their diet toward aquatic resources. Iterative solutions from the isotope mixing model showed that the use of terrestrial resources was reduced 37% on average (from 30% in ambient subsidy to 19% in reduced subsidy), but these diet percentages had overlapping 99% confidence intervals. Thus, although the C signatures changed significantly with terrestrial input, the proportion of diet coming from terrestrial resources in these treatments was still quite variable. Other models that include source and mixture error (Phillips and Gregg 2001) allow more direct estimation of this variability, but require use of 2 isotopes (e.g., C^{13} and N^{15}) for a 3-source mixing model. δN^{15} was measured initially in my study, but N fractionation in dragonfly tissue was not, and the output from these models is very sensitive to the estimate of N fractionation (Caut et al. 2009).

Consumption of terrestrial insects by dragonfly larvae has not been widely recorded, but dragonfly larvae (i.e., *Aeshna*) that live in the study ponds consumed floating moth adults in laboratory feeding trials (Kraus 2006). *Aeshna*, in particular are the most likely to consume terrestrial insects among the 5 common odonates, because *Aeshna* use multiple foraging strategies (sit and wait vs active) depending on prey behavior and density (Johansson 1991). This plasticity in foraging behavior indicates the ability to use both dying terrestrial prey and living (perhaps more active) aquatic prey. Furthermore, terrestrial C can be an integral part of lentic food webs in lakes and might contribute to dragonfly diets in lakes. For example, Solomon et al. (2008) found that ~25% of dragonfly diet in shallow lakes came from terrestrial or dead autochthonous production, and Carpenter et al. (2005) found that the contribution of terrestrial C to a lake food web was substantial (>50% diet for 5 species of fish).

Despite an overall shift in C isotopic signature in response to reduced terrestrial inputs, dragonfly larvae did not respond numerically to terrestrial arthropod input. The lack of a numerical response suggests a limited role of terrestrial inputs in determining the within-pond distribution of near-shore dragonfly larvae. However, the abundance of dragonflies did appear to be slightly higher in ambient-subsidy enclosures than in reduced-subsidy enclosures at Sylvatica Pond. In view of the large decrease in dragonfly abundance in ambient-subsidy enclosures at Horton Pond, this result suggests that pond-specific factors might have had stronger or opposite effects on dragonfly distributions in the 2 ponds.

Newts and crayfish did not respond to allochthonous inputs, but the large difference in their abundances between ponds might have differentially influenced the response of dragonfly larvae to terrestrial inputs, at least within enclosures. For example, *Aeshna* larvae exhibited the same pond-dependent numerical response to subsidies as total dragonflies, but their biomass increased almost 200% in reduced-subsidy enclosures in both ponds. Thus,

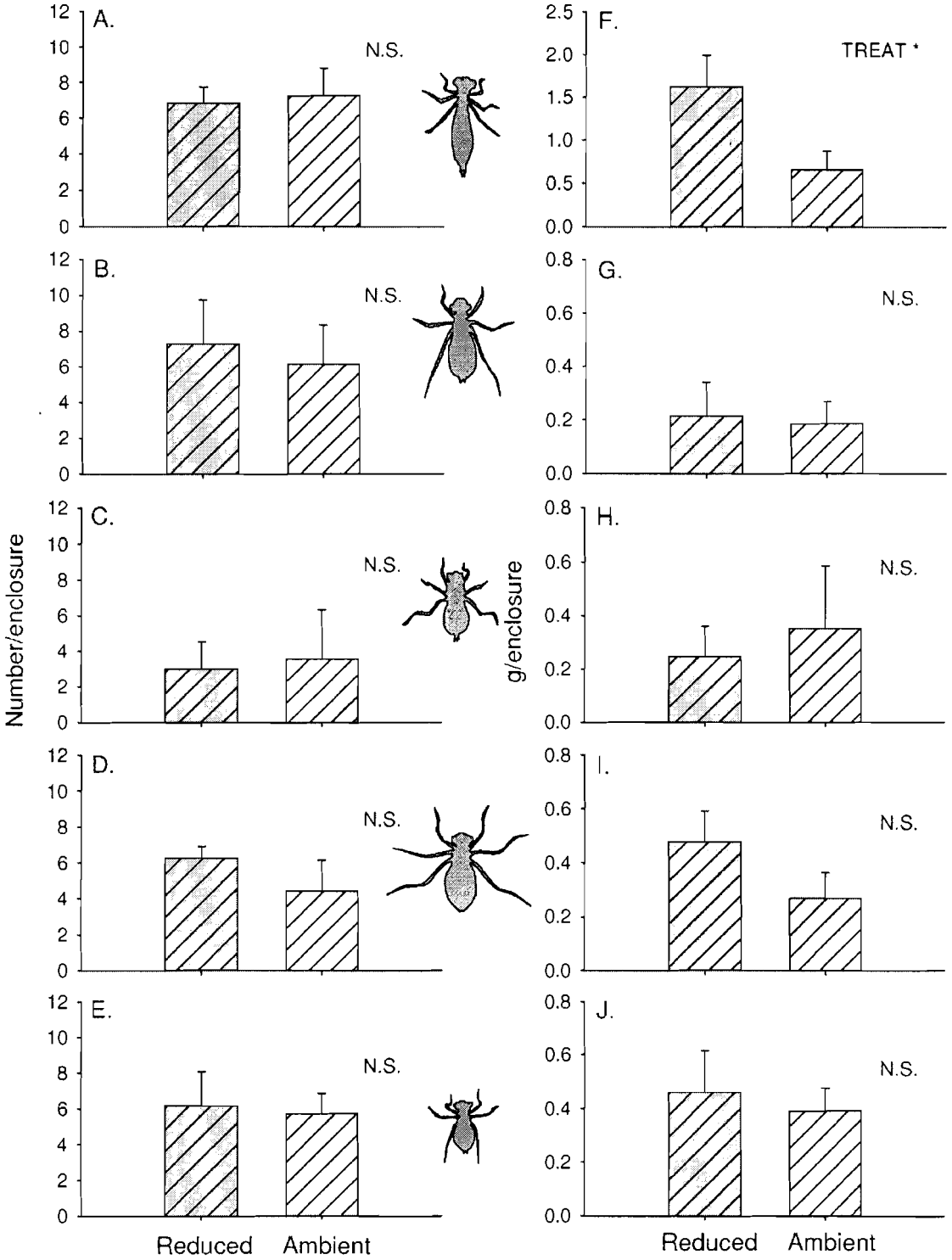

FIG. 2. Mean (+1 SE) number of *Aeshna* (A), *Cordulia* (B), *Somatochlora* (C), *Libellula* (D), and *Sympetrum* (E) larvae and mean wet body mass of *Aeshna* (F), *Cordulia* (G), *Somatochlora* (H), *Libellula* (I), and *Sympetrum* (J) larvae in ambient- and reduced-subsidy enclosures summed over the 3 mo (June–August) of the experiment after treatments were erected. Drawings indicate relative sizes and shapes of genera. All values are back-transformed from best-fit repeated measures generalized linear mixed model analysis. $n = 7$ for all treatment combinations. TREAT = treatment, * = marginally significant at $p = 0.06$, N.S. = $p > 0.05$.

TABLE 2. Generalized linear mixed model statistical output for best-fit models testing the effect of subsidy reduction on total number and biomass of individual species of dragonfly larvae found in enclosures over the duration of the experiment (June–August). Treatment (treat) effect includes only the enclosure treatments (ambient and reduced subsidy; $n = 7$). Pond effect tests differences between Horton ($n = 2$) and Sylvatica Ponds ($n = 5$). Distribution indicates error distribution used for each response and whether spatial block improved model fit (nb = negative binomial, norm = normal, po = Poisson). Best fit models were chosen based first on lowest Akaike Information Criterion for small sample size (AICc) value, and second on the over-dispersion parameter (Φ) being closest to 1. Estimates of F statistics are analogous to type III Sums of Squares in analysis of variance. Bold indicates $p < 0.05$.

	Aeshna			*Cordulia*			*Libellula*			*Somatochlora*			*Sympetrum*		
Effects	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Count															
Distribution	po, no block			nb, no block			nb, no block			po, no block			nb, no block		
Treatment	1,10	1.00	0.342	1,10	0.86	0.374	1,10	0.00	0.999	1,10	3.92	0.076	1,10	0.02	0.901
Pond	1,10	1.88	0.200	1,10	2.42	0.151	1,10	0.00	0.976	1,10	5.30	**0.044**	1,10	0.02	0.965
Treat × pond	1,10	5.06	**0.048**	1,10	0.78	0.397	1,10	0.00	0.999	1,10	2.05	0.183	1,10	0.02	0.901
Biomass															
Distribution	norm, block			norm, no block			norm, no block*			nb, no block*			norm, no block		
Treatment	1,5	5.95	0.059	1,10	0.09	0.770	1,10	0.00	0.999	1,10	0.35	0.565	1,10	0.23	0.645
Pond	1,5	0.05	0.837	1,10	5.86	**0.036**	1,10	0.00	0.977	1,10	0.12	0.739	1,10	0.01	0.937
Treat × pond	1,5	0.44	0.538	1,10	0.07	0.797	1,10	0.00	0.999	1,10	0.01	0.922	1,10	0.12	0.737

[a] Model that included block had lower AICc but was severely underdispersed ($\Phi < 0.07$); effect significances were not different

Aeshna were smaller and less abundant in ambient-subsidy enclosures than in reduced-subsidy enclosures at Horton Pond. One explanation for this pattern is that smaller *Aeshna* might have suffered high mortality in the pond with high abundance of gape-limited predators (i.e., newts; Wilbur et al. 1983). However, in Sylvatica Pond, where gape-limited predators were less abundant and more crayfish were present, small *Aeshna* might have been able to respond numerically to the increased abundance of terrestrial resources. Thus, differences between ponds in the abundance of a gape-limited intraguild predator might have influenced the numerical response of dragonflies to terrestrial subsidies.

Intraguild interactions influence responses to subsidies in other systems (Sabo and Power 2002b, Baxter et al. 2004). At the boundary between a 2nd-order stream and deciduous forest, introduced salmonids used terrestrial resources that fell into the stream and caused native fish to shift to benthic macroinverte-

TABLE 3. Repeated measures generalized linear mixed model statistical output for best-fit models testing the effect of subsidy reduction on number of individual newts and crayfish per enclosure and the total body length of all individuals per enclosure and sample date. Treatment effect in the model includes both enclosure treatments (ambient and reduced subsidy, $n = 7$) and open plots ($n = 4$). Month effect includes the 3 mo after the subsidy screens were installed in enclosures (June–August). Pond is the post hoc comparison between Horton ($n = 2$) and Sylvatica Ponds ($n = 5$). Distribution indicates error distributions used for each response and whether spatial block improved model fit (nb = negative binomial, norm = normal, po = Poisson). Estimates of F statistics are analogous to type III Sums of Squares in analysis of variance.

	Newts						Crayfish					
	No. individuals			Body length			No. individuals			Body length		
Effects	df	F	p	df	F	p	df	F	p	df	F	p
Distribution	po, no block			norm[a], no block			nb, no block			norm[a], block		
Treatment	2,12	1.39	0.287	2,12	1.19	0.338	2,12	1.24	0.325	2,35	0.85	0.436
Month	2,30	1.32	0.282	2,24	2.81	0.080	2,30	3.55	**0.041**	2,35	3.81	**0.032**
Treat × month	4,30	1.50	0.227	4,24	0.64	0.641	4,30	0.59	0.570	4,35	0.35	0.840
Pond	1,12	15.69	**0.002**	1,12	9.00	**0.011**	1,12	18.72	**0.001**	1,35	8.71	**0.006**
Treat × pond	2,12	0.19	0.833	2,12	0.52	0.641	2,12	0.85	0.502	2,35	1.85	0.173

[a] Analysis was done on $\sqrt{(x)}$-transformed values to reduce over-dispersion

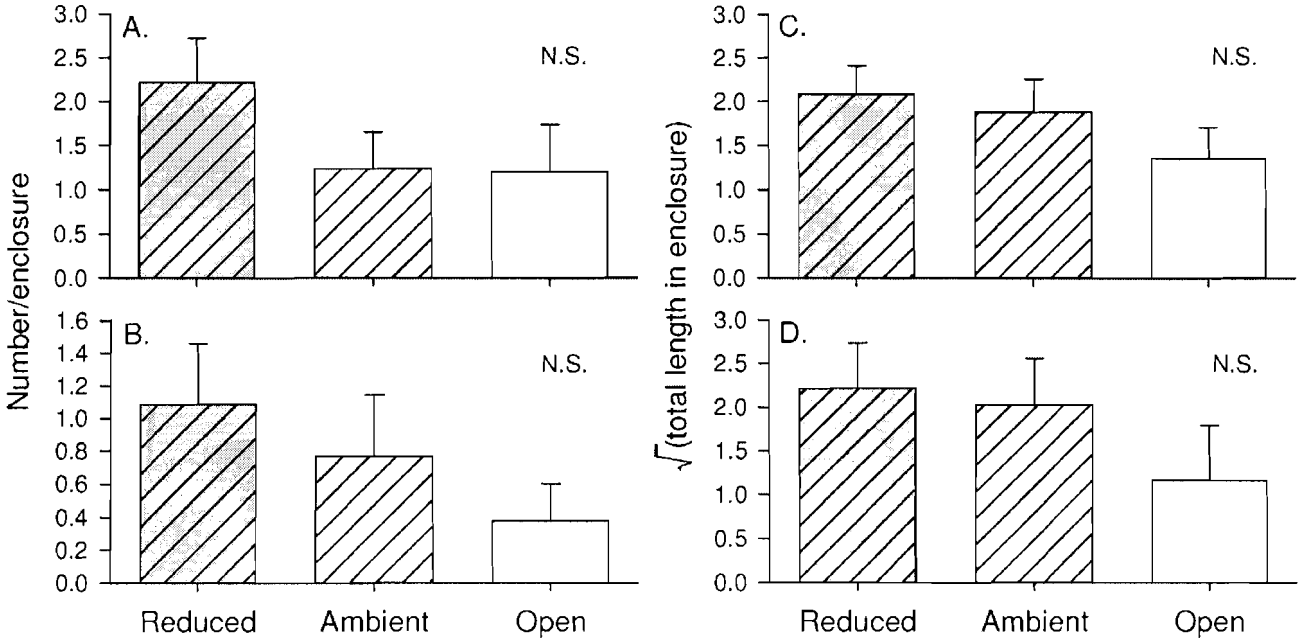

FIG. 3. Mean (+1 SE) number of newts (*Notophthalmus viridescens*) (A) and Tennessee River spiny crayfish (*Orconectes spinosus*) (B) and total length of newts (C) and crayfish (D) per enclosure in ambient- and reduced-subsidy enclosures. All values are back-transformed from best-fit repeated measures generalized linear mixed model analysis. $n = 7$ for all treatment combinations. * = $p < 0.05$, ** = $p < 0.01$, N.S. = $p > 0.05$.

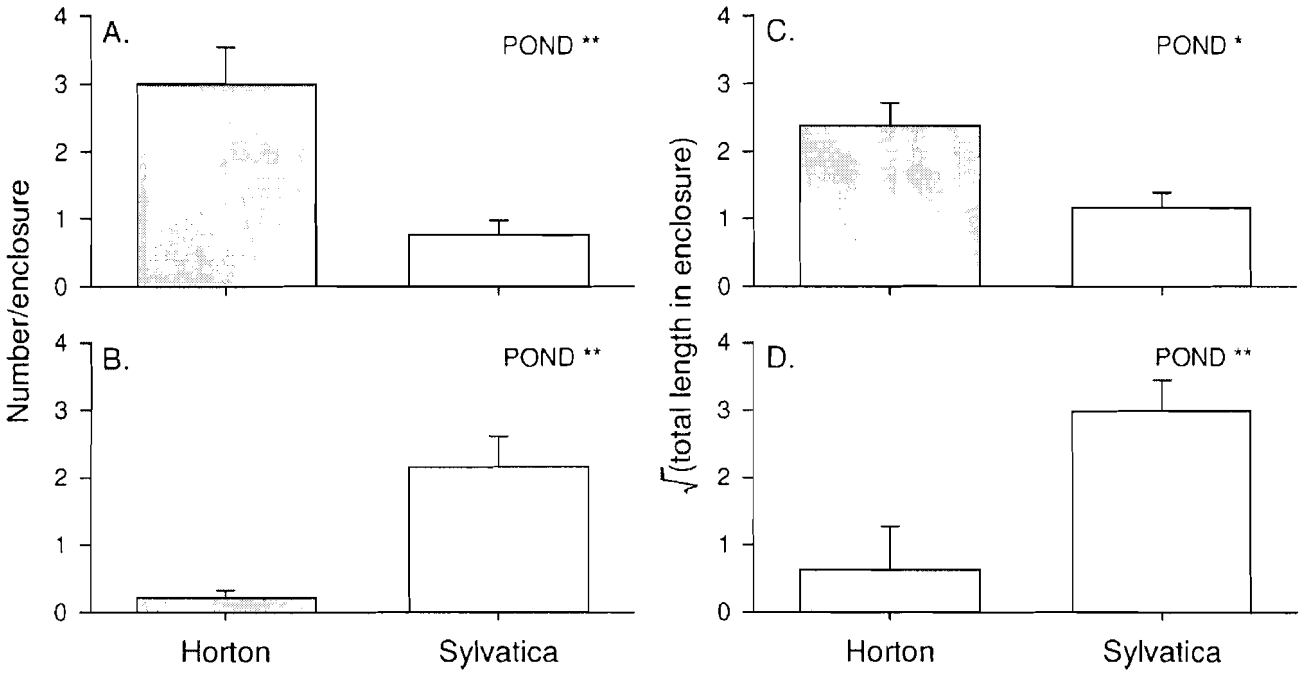

FIG. 4. Mean (+1 SE) number of newts (*Notophthalmus viridescens*) (A) and Tennessee River spiny crayfish (*Orconectes spinosus*) (B) and total length of newts (C) and crayfish (D) per enclosure in Sylvatica Pond and Horton Pond. All values are back-transformed from best-fit repeated measures generalized linear mixed model analysis. $n = 5$ in Sylvatica Pond, $n = 2$ in Horton Pond. * = $p < 0.05$, ** = $p < 0.01$.

brates (Baxter et al. 2004). On a riparian cobble bar, wolf spiders were able to persist in higher numbers in the presence of arthropod-eating lizards, in part because aquatic insects were available as an alternate prey source for both lizards and spiders (Sabo and Power 2002b, Power et al. 2004). Uncovering the extent and variation of intraguild interactions on the impact of terrestrial subsidies is integral to our understanding community patterns and dynamics in freshwater systems, especially in forested ponds and headwater streams where both allochthonous inputs and predator–prey interactions can strongly influence community structure (Wilbur 1997, Nakano and Murakami 2001).

The results of my study suggest that terrestrial arthropods can subsidize the diet of aquatic secondary consumers in lentic systems, although numerical responses (immigration, mortality) to these resources might be limited or determined by in situ factors. I suggested one factor (intraguild predation) that could limit consumer responses to subsidies, but the relative availability of in situ resources, preference for subsidies, and physiological constraints also can influence consumer responses (Huxel and McCann 1998, Power et al. 2004, Marczak et al. 2007). Much of the original work on the effects of resource subsidies to food webs focused on input from very high productivity to very low productivity habitats (e.g., Polis and Hurd 1996a, b, Polis et al. 2004), where in situ control of foodweb dynamics was weak or nonexistent. More empirical work is needed to understand consumer responses to subsidies in systems where characteristics of the recipient food web also might strongly influence consumer abundances and distributions (Baxter et al. 2005, Iwata 2007).

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