# Mobile Consumers track Invertebrate Subsidies from Floating Algal Mats

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## ABSTRACT

During summer, floating algal mats in many rivers host large numbers of larval invertebrates that emerge as flying adults. In late summer, these mats detach and float downstream, subsidizing the cobble bars they strand on. I investigated whether adult odonates and Lycosid spiders, two groups of mobile consumers, track these patchy subsidies. In the South Fork Eel River (39˚44' N, 123˚37' W; 39˚44' N, 123˚38' W), Mendocino County, California, I moved 2.5x1 m$^2$ floating mats of the filamentous alga, *Cladophora glomerata,* along the river shoreline to create 7 experimental blocks, each with 1 algae and 1 no-algae plot. I measured invertebrate emergence from mats and consumer densities within 1m of the plot edge.  Both consumers tracked emergence, which was on average 7% higher from algal plots. Odonates were on average 30% more abundant in plots with algal mats and lycosids on average 11% more abundant. Their ability to track spatially and temporally patchy algal mats, allowed these riparian consumers to exploit a trophic subsidy from aquatic production in the sunlit mainstem river. Mapping the origins, fluxes and fates of organic production that link freshwater, terrestrial, and marine food webs can reveal vital connections of ecosystems threatened by change.

## KEYWORDS

# INTRODUCTION

Ecologists use food webs to depict energy flux and organismal interactions within habitats (Power 1992, Polis et al. 1996). Trophic subsidies are the movement of resources across ecosystems in the form of nutrients, organic matter and organisms (Polis et al. 1997) and can enrich consumers in recipient habitats (Sabo and Power 2002B). Spatial or temporal variation in subsidies allow researchers to explore how mobile consumers make decisions (Polis et al. 1996). For example, the ideal free distribution model predicts that mobile consumers in a heterogeneous landscape will distribute themselves in relation to local resource flux or renewal rates (Fretwell 1972, Kennedy and Gray 1993). A consumer tracking the spatial distribution and timing of resource fluxes may allow for greater foraging success than just following resource abundance (Armstrong et al. 2016). Greater white-fronted geese time their continental migrations to follow the earliest spring plant growth and to forage on the most nutrient-rich vegetation available (van Wijk et al. 2012). Brown bears and Glaucous-winged gulls follow subtle spatial and temporal variation in anadromous Pacific salmon migrations to fuel most of their annual growth in a limited time (Schindler et al. 2013). When consumers track the phenology of seasonal subsidies, they can find the most profitable locations and maximize high-quality foraging time. Effective ecosystem conservation policy incorporates landscape-level understanding of resource heterogeneity (Polis et al. 1997, Power and Rainey 2000, Schindler and Smits 2017) and how recipient consumers respond to resource variation (Schindler et al. 2013, Armstrong et al. 2016).

Subsidy flow connects river and terrestrial systems (Nakano and Murakami 2001) and explains watershed food web dynamics (Sabo and Power 2002B). Terrestrial habitats are sources of primary productivity to rivers, such as leaf litter supporting aquatic detritivores (Cummins et al. 1973, Wallace et al. 1997). Terrestrial nutrients flushed into river headwaters also support the growth of algae (Power 1990). More recently, stream ecology research has focused on the movement on nutrients from rivers into adjacent terrestrial habitats (Sabo and Power 2002B, Power et al. 2004). Pulses of aquatic invertebrates emerge and disperse as subsidies into terrestrial systems (Power 1990, Nakano and Murakami 2001, Power et al. 2004, Schindler and Smits 2017), often providing higher nutritional quality prey than the terrestrial subsidies entering rivers (Schindler and Smits 2017) and a source of fatty acids otherwise limited in terrestrial resources (Torres-Ruiz et al. 2007). Seasonal pulses of emergence can subsidize terrestrial systems at times

when terrestrial invertebrate subsidies are low, benefiting riparian consumers (Nakano and Murakami 2001). In Northern California rivers, researchers study how aquatic invertebrate flux influence different trophic levels of the terrestrial food web (Power 1990, Power et al. 2004).

The South Fork Eel River in Mendocino County, Northern California, experiences seasonal fluxes of emerging aquatic invertebrates (Power 1990). Floating algae mats, *Cladophora glomerata,* protect larval aquatic invertebrates from predatory fish and transport them to the shoreline, where they emerge into their flying adult forms. These invertebrates feed a broad spectrum of terrestrial consumers over a range of mobilities (Power 1990, Sabo & Power 2002B). Filmy-dome spiders contain significant amounts of carbon isotopes found in algae, passed through by insect emergence, despite the immobility of their late-stage webs restricting foraging range (Power et al. 2004). Lycosid spiders track emergence productivity over river channels (Power et al. 2004). *Sceloporus* lizards (*Sceloporus occidentalis* and *Sceloporus gracious*) hunt emerging insects from the cobble bar, which support their growth and reduce their predation on *in-situ* prey, including Lycosid spiders (Sabo and Power 2002A). Bats, the most mobile of the insectivores studied at the Eel River, also concentrate their foraging in aquatic invertebrate emergence near or over the river (Rainey et al. 2006). However, research of the Eel River food system lacks field experiments directly comparing how different insectivores track variation in aquatic insect emergence over similar spatial scales.

In this study, I rearranged floating algal mats to explore how consumers with different mobilities distribute themselves around the same flux of prey. Adult odonates, which forage in the air, and Lycosid spiders, which stalk prey along the cobble bars (Power et al. 2004), consume emerging insects. Do the different foraging styles of the two consumers affect their distribution around the emerging insect subsidy? I established seven pairs of plots with or without algal mats and measured flux of emergent aquatic invertebrates, numbers of Lycosids, and numbers of odonates around plots to test a) the assumption that algal mats would generate more insect emergence, and b) the prediction that both consumers would be more abundant around algal mat plots if these maintained higher numbers and greater biomass of aquatic invertebrate emergence.

**METHODS**

**Study site**

This study took place along a 0.6 km reach (39˚44' N, 123˚37' W; 39˚44' N, 123˚38' W) in the headwaters of the South Fork Eel in UC Berkeley's Angelo Coast Range Reserve, Mendocino County, Northern California (Figure 1).  The food web and landscape in the reserve have been extensively studied (Power 1990, Power 1992, Power and Dietrich 2002), and this project builds on the work of Mary Power and Michael Parker in the mid 90's (Power et al. 2004). In some years, the region's Mediterranean climate experiences heavy winter rainfall that produces scouring floods (Power 1990).  Flooding variation determines the scale of *Cladophora glomerata* blooms during late spring and early summer. Blooms are greater if scouring floods have extirpated large armored caddisfly grazers (*Dicosmoecus gilvipes*) during the previous winter (Power et al. 2008a, 2013, Sculley et al. 2017).  In spring, *C. glomerata* grow as bright green 8-9m turfs along the river's bed and boulder substrate, and eventually detach as floating mats, which senesce and turn yellow to rusty red from heavy overgrowth of diatoms (Power et al. 2008b, Furey et al. 2012). Chironomid midges weave the filamentous strands of the algae mats into retreats for unarmored larval aquatic invertebrates, such as ephemeroptera and trichoptera (Power 1991, Power et al. 2015). *C. glomerata* mats strand on cobble bars, which are dry during summer low flow periods, and serve as launch pads for aquatic invertebrate emergence.
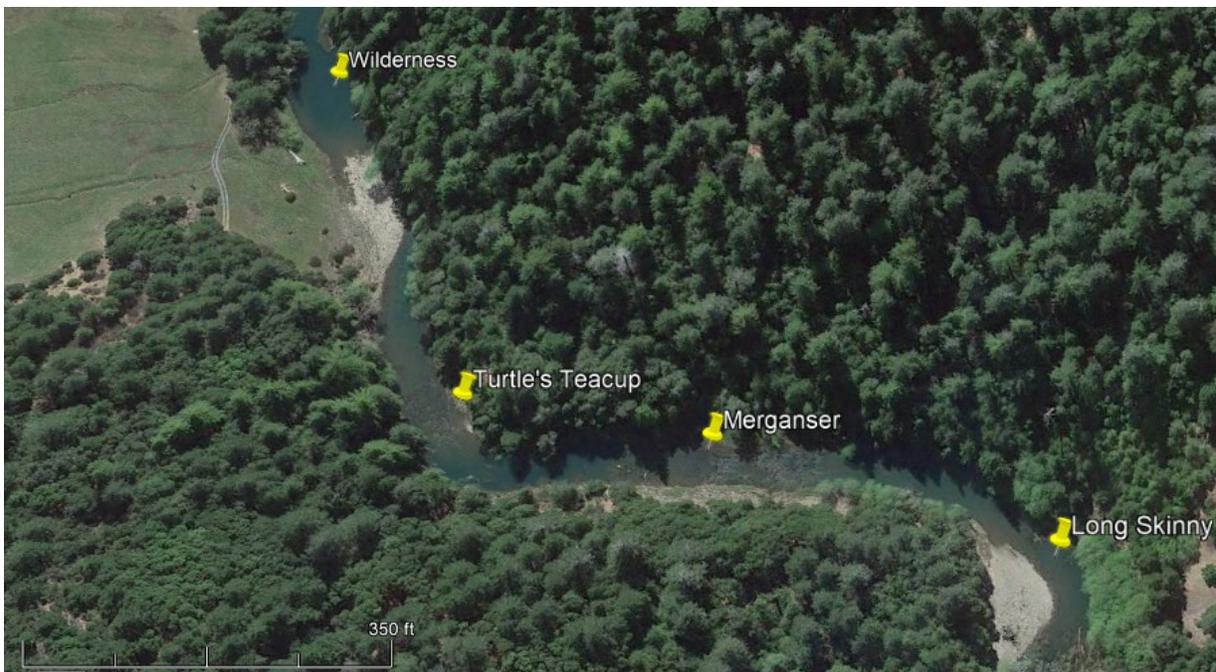


**Figure 1.  Map of study of site at the Angelo Coast Range Reserve.** Yellow markers indicate pool study sites along the South Fork of the Eel River.

**Invertebrate emergence manipulation**

To estimate flux of emergent aquatic invertebrates from *C. glomerata* mats to the shoreline, I surveyed insect emergence with sticky flagging and emergence traps. I transferred floating mats to create 2.5m x 1m patches of algae along the shorelines of four pools. Matching each plot with a no-algae plot of equal size from which all algae were removed, I created seven, 7 m x 1 m paired plots. Paired plots in the same pool were 3m apart. I inserted two transparent 12.5 x 20 cm irrigation flags, covered in Tangle-foot (Tanglefoot, Grand Rapids, Michigan, USA) at 0 m and 1 m from the shore, for a total of four flags per sampling period (Figure 2). Flags stood at 40cm above the ground deployed on metal wire. I sampled emergence continuously for five-day intervals from July 5 – August 2, 2019; each block was sampled four times except for two blocks that were added one week into the study. During the final experimental week (July 26 – August 2, 2019), I placed emergence traps 0.5 m from the shore in the center of each plot. Emergence traps were PVC cylinders, 25.4 cm in diameter and 30 cm high, each with three stacked pairs of 2μm netting mesh windows along the sides. An acetate sheet covered in Tangle-foot and secured with a rubber band covered each emergence trap, the glue side facing downward.
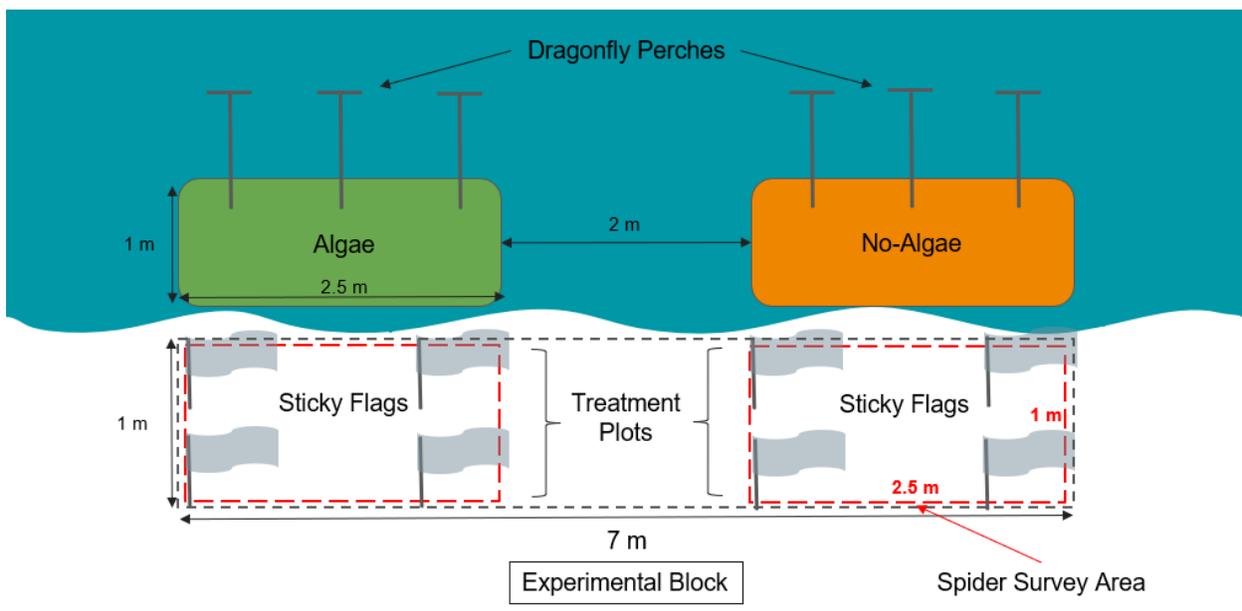


**Figure 2. Paired plot layout of algal and no-algae treatments along the riverbank.** Lycosid surveys took place within each treatment plot. Odonates were counted if present on perches, natural substrates, or flew by during scans. Perches stood at 0.3m tall and total arm-span was 0.3m in length.

After sampling, I brought flags and emergence trap lids to the lab and scanned them with a consumer-grade flatbed scanner. I used ImageJ (ImageJ version 1.52a, Schneider et al. 2012, Mendez et al. 2018) to count individuals and measure their length with mm scale bar. I identified all insects to order and estimated biomass using family-based length to weight regression equations (Sabo et al. 2002).

All analyses and statistical tests were conducted using the statistical program R (R version 3.6.1, R Core Team 2017, and Wickham 2009), specifically the packages effsize, ggplot2, lme4, lmerTest, lubridate, MuMIn, and tidyverse. For both flag and emergence trap data, I used generalized mixed models with Poisson distribution for invertebrate number and linear mixed models for invertebrate biomass data. I assigned abundance or biomass as the response variables and treatment as the explanatory variable with paired plot as a random effect. I found effect size using a $R^2$ function (MuMIn, Selya et al. 2012) to calculate Cohen's $f^2$ between treatments.

**Consumer Distribution Surveys**

*Odonata*

Odonate surveys took place within paired plots from 11 am to 4 pm, when their activity was high. Each treatment plot was surveyed when in direct sunlight. To standardize perch availability among plots, I placed 3 T-shaped bamboo sticks in each algae/non-algae plot, at 0.5 m from the shoreline (Figure 2) for odonates to perch and rest or sally from. I scanned and counted odonates present, noting whether they were sitting or flying by, in each plot every 2 minutes for 5 scans over a total of 8 minutes. I took averages of the 5 scans and then summed across sampling dates to calculate a combined survey average. I identified individuals to species (taxonomy based on Manolis 2003). I used linear mixed-effect models for both total odonates surveyed and for each individual species. I used the sum of the scan averages for all odonates and for each species as response variables and treatment as explanatory variable with a random effect of paired plot. I calculated effect size of treatment with Cohen's $f^2$ functions, in R.

*Lycosid spiders*

I counted all Lycosids (wolf spiders) on the ground of each 2.5 x 1 m treatment plot by turning over all loose pebbles and cobbles within the area (Figure 3; Paetzold et al. 2005, Power et al. 2004). Spider surveys occurred during evenings, from 5 pm to 8 pm, when wolf spiders emerge from their webs under rocks to hunt crepuscularly (Power et al. 2004). I used a generalized linear mixed model with Poisson distributions with treatment as explanatory variable and a random effect of paired plot. I found effect size of treatment with Cohen's $f^2$ functions, in R.



**Figure 3. Set up for algae plot at Merganser 2.** The white box represents my Lycosid spider survey area.

## RESULTS

### Invertebrate emergence

208 sticky flag traps captured a total of 59,950 insects and total biomass of 14,524.79 mg. Diptera dominated both numbers and biomass, followed by coleoptera, ephemeroptera, trichoptera and plecoptera (Table 1). Fewer insects and less biomass were caught on flags set further from the

shoreline the river ($P<0.05$). For this reason, I excluded the farther (1m from water's edge) sets of sticky flag traps from further analysis. Water level decreased throughout the experiment, and flags were held at constant position, so they were displaced slightly away from the river during successive sampling periods. Sticky flagging over algal plots captured on average 7% more insect emergence than flagging over no-algae plots (Figure 4A, generalized mixed, $P < 0.05$). Sticky flags captured an average 7% difference between treatments in insect biomass which was not significant (Figure 4B, linear mixed, $P = 0.32$).

I captured an average 17% more insects with emergence traps over no-algae plots than over algae plots (Figure 4C, generalized mixed, $P < 0.05$). Emergence traps caught an average 4% difference in emerging biomass between treatments, which was not significant (Figure 4D, linear mixed, $P = 0.57$). The 14 emergence traps captured a total of 2718 insects and a biomass of 8981 mg. Diptera again dominated both total insect and biomass estimates, followed by ephemeroptera, coleoptera and trichoptera (Table 1).

**Table 1: The total number, biomass and percentages of dominant emerging taxa captured by sticky flag and emergence traps.**

| Order | Total Insect Number Sticky Flag | | Total Biomass (mg) Sticky Flag | | Total Insect Number Emergence Trap | | Total Biomass (mg) Emergence Trap | |
|---|---|---|---|---|---|---|---|---|
| Diptera | 44801 | 74.7% | 5913 | 40.7% | 2369 | 87% | 5557 | 62% |
| Coleoptera | 3371 | 5.6% | 1158 | 7.9% | 113 | 4% | 787 | 8.7% |
| Ephemeroptera | 1663 | 2.8% | 2022 | 13.9% | 215 | 8% | 2154 | 24% |
| Trichoptera | 1496 | 2.5% | 3325 | 22.9% | 19 | 0.6% | 397 | 4% |
| Orthoptera | 177 | 0.30% | 875 | 6.0% | 2 | 0.7% | 86 | 0.9& |
| Plecoptera | 159 | 0.26% | 1019 | 7.0% | 0 | 0% | 0 | 0% |
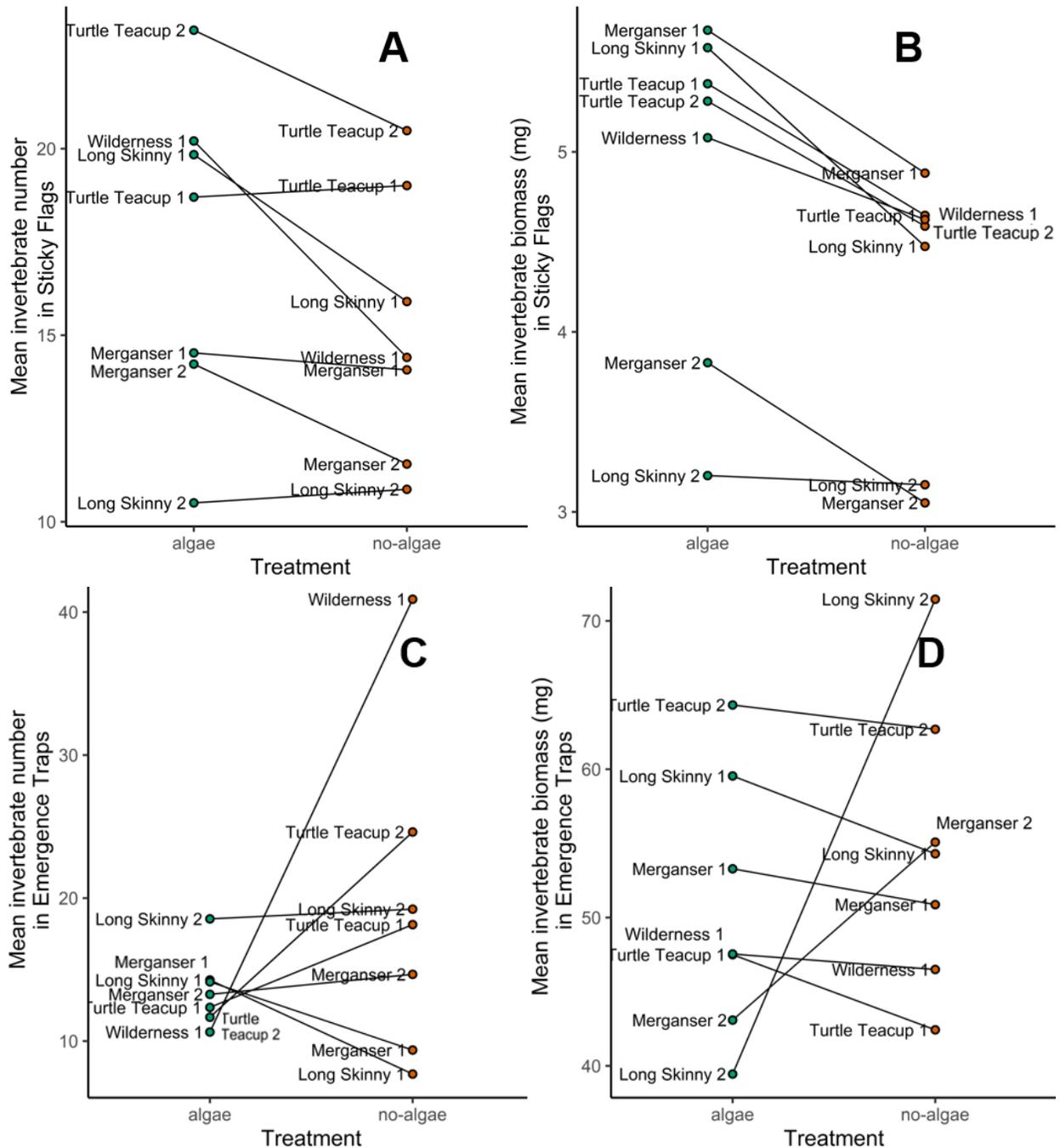
**Figure 4. Lines link algae and non-algae plots within a pair, and names indicate paired plot location. (A) Average number of invertebrates captured by sticky flag traps per paired plot.** Flags caught 27,189 insects in algae plots ($\bar{x}$ = 944.3, s.d. = 53.25, n = 104) and 24,498 insects in no-algae plots ($\bar{x}$ = 845.7, s.d. = 41.6, n = 104). In 5 out of paired plots, there was a small trend towards more invertebrates captured in algae plots than non-algae plots (Table 2, Cohen's $f^2$= 0.04, small effect). **(B) Average invertebrate biomass captured by sticky flag traps per paired plot.** Flags caught 7713.37 mg from algae plots ($\bar{x}$ = 251.5 , s.d. = 7.6, n = 104) and 6811.42 mg from no-algae plots ($\bar{x}$ = 216.1, s.d.= 4.3, n = 104), but treatment difference was modest (Table 2, Cohen's $f^2$= 0.09, small effect). **(C) Average numbers of insects captured in emergence traps per paired plot.** Emergence traps captured 1,135 insects in algae plots ($\bar{x}$ = 94.9, s.d. = 26.9, n = 7) and 1,583 insects in no-algae plots ($\bar{x}$ = 134.6, s.d. = 44.6, n = 7). There was a large trend of more insects in no-algae plots than algae plots (Table 2, Cohen's $f^2$= 0.35, large

effect) with a significant site effect (generalized mixed, P < 0.05). Wilderness and Turtle Teacup comprised 51% of the total emerging insects found in no-algae plots. **(D) Average invertebrate biomass captured by emergence traps per paired plot.** Emergence traps captured 4,269 mg in algae plots ($\bar{x}$ = 354.8, s.d. = 28.7, n = 7) and 4,712 mg in no-algae plots ($\bar{x}$ = 383.3, s.d. = 34.3 , n = 7).  There was a modest difference between treatments (Table 2, Cohen's $f^2$= 0.12, small effect).

## Consumer Distribution

*Odonata*

I surveyed more adult odonates in algal plots ($\bar{x}$ = 47.6, s.d. = 1.2, n = 27) than in non-algal plots ( $\bar{x}$ = 25.7, s.d. = 0.6, n = 27). The difference, an average 30% more individuals in algae plots, was significant (Figure 5A, linear mixed, P = 0.02). Of the sums of the scan averages, 22 were dragonfly species with 14.3 *Libellula saturata* (flame skimmer)*,* 5.8 *Ophiogomphus bison* (bison snaketail), and 1.9 *Aeshna walker* (Walker's darner); I found a summed average of 51.2 damselfly species with 42.8 *Argia lugens* (sooty dancer), 8 *Argia emma* (Emma's dancer) and 0.4 *Argia agrioides* (California dancer). I surveyed an average 28 sooty dancers, the most abundant species, in algae plots and 14.8 in no-algae plots, an average 31 % more in algae plots (P= 0.04), with a small trend of 0.5 less sooty dancers in no-algae plots (Cohen's $f^2$= 0.11, small effect). An average 4.2 bison snaketails were found in algae plots and an average 1.6 bison snaketails in no-algae plots, an average 45% more individuals in algae plots. Bison snaketail distribution showed the same small trend towards less individuals in no-algae plots, with on average 0.09 less individuals in no-algae plots (P = 0.0552, Cohen's $f^2$= 0.07, small effect). I surveyed an average of 10 flame skimmers in algae plots and an average of 4.3 in no-algae plots, with an average 40% more individuals surveyed in algae plots. Flame skimmers also showed a small trend of less individuals in no-algae plots, with on average 0.23 less individuals in no-algae plots (P = 0.15, Cohen's $f^2$= 0.09, small effect).

*Lycosid spiders*

I counted more Lycosid spiders under cobbles and pebbles in algae plots ($\bar{x}$ = 31, s.d. = 2.3, n = 27) than no-algae plots ($\bar{x}$ = 24.8, s.d. = 2.4, n = 27). The difference, an average 11% more

individuals in algae plots, was significant (Figure 5B, generalized mixed, P = 0.02). Of the 206 wolf spiders counted in this study, I found 118 were in algae plots and 88 were in no-algae plots.
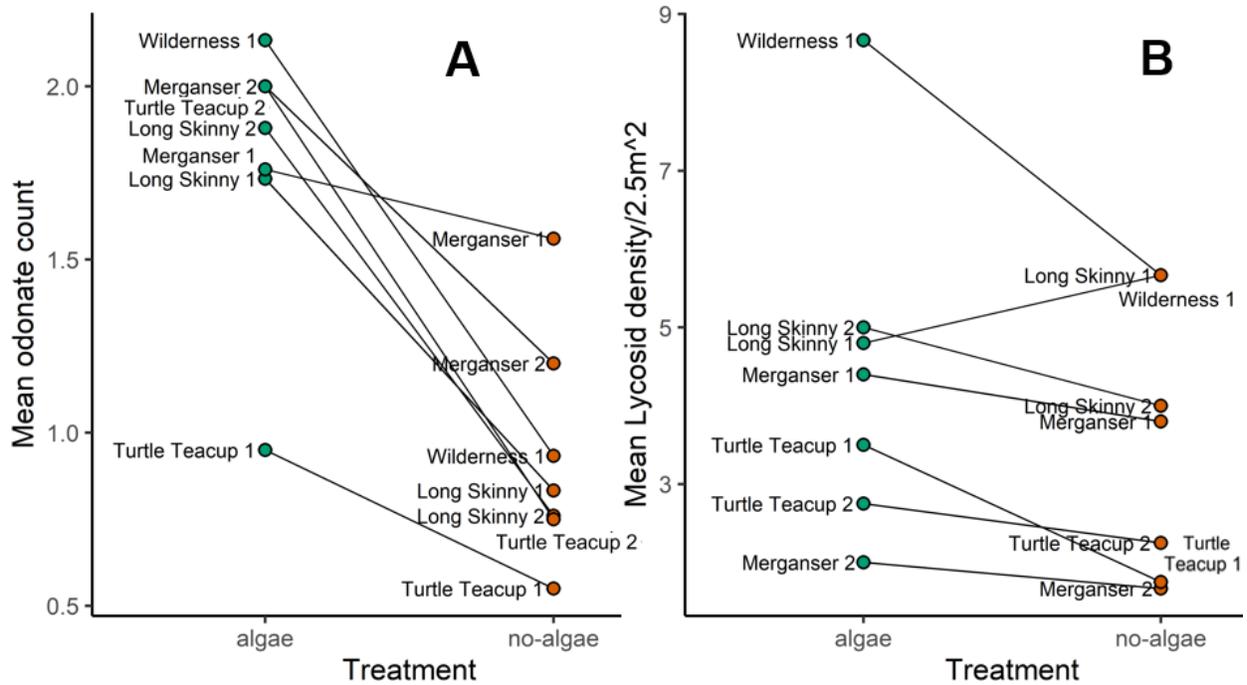


**Figure 5. Lines link algal and non-algal plots within a pair, and names indicate paired plot location. (A) Average odonate count surveyed per paired plot.** We counted a summed average of 73 odonates over 54 surveys. Odonates displayed a small trend towards more individuals in algae plots than no-algae plots (Table 2, Cohen's $f^2$= 0.11, small effect). **(B) Average Lycosid spider density surveyed over a 2.5 m^2 area per paired plot.** There was a small trend of 0.31 less wolf spider per no-algae plot (Table 2, Cohen's $f^2$= 0.12, small effect).

**Table 2: Components of each linear and generalized mixed model used in experimental analysis, with treatment as explanatory variable and random effect of paired plot.** The effect size range for Cohen's f^2: small >= 0.02, medium >= 0.15, large >= 0.35.

| Response Variable | Coefficient for no-algae treatment | Intercept for algae treatment | P value | Effect Size Type | Effect Size |
|---|---|---|---|---|---|
| Invertebrate Number (sticky flags) | -0.12 | 6.12 | <0.05 | Cohen's $f^2$= 0.04 | Small |
| Invertebrate Biomass (sticky flags) | -17.83 | 134.97 | 0.32 | Cohen's $f^2$= 0.09 | Small |
| Invertebrate Number (emergence traps) | 0.33 | 5.05 | <0.05 | Cohen's $f^2$= 0.35 | Large |
| Invertebrate Biomass (emergence traps) | 63.29 | 609.86 | 0.57 | Cohen's $f^2$= 0.12 | Small |
| Sum of averaged odonate scans | -0.8111 | 1.76 | 0.02 | Cohen's $f^2$= 0.11 | Small |
| Lycosid spider count | -0.31 | 2.8 | 0.02 | Cohen's $f^2$= 0.12 | Small |

# DISCUSSION

This study found that odonates and Lycosid spiders tracked uneven emerging insect subsidies over four experimental weeks in four pools of the Eel River. The consumers responded to algae treatment and matched my predictions, despite subsidy sampling methods recording small differences in insect flux between treatments. I captured a total 59,950 insects with sticky flags, but only found an average 7% more emerging invertebrates in algae plots than in the no-algae plot. While this difference was significant and supports my predicted trend of greater emergence in algae plots, I anticipated a larger effect size and percent difference. Emerging biomass displayed the same small trend with on average 7% more emerging biomass in algae plots than in no-algae plots, though this difference was not statistically significant and effect size was small. These limited trends differ from observed insect emergence patterns in the Eel River, which found emergence rates were many times greater from floating mats than bare gravel substrates (Power 1990). Surprisingly, emergence trap data contrasted this finding more starkly, trending in the complete opposite direction.

An average of 17% more invertebrates emerged from no-algae plots into emergence traps than from algae plots, a significant difference. The same trend occurred in emergence trap biomass, though smaller and not significant, with an average 4% more biomass in no-algae plots than algae plots. Emergence trap data had high variation between paired plot locations and two paired plots accounted for over 50% of the total emerging invertebrates captured in no-algae blocks. With those two pools removed, the trend reverses and I found 6% less invertebrates emerge from no-algae plots than algae plots, a significant difference that matches predictions. The conflicting results of the two emergence measuring methods and the high variance between pools suggest problems recording emergence flux. Of the outlier paired plots, diptera represented 97% of the total insects to emerge from no-algae plots for one site and diptera with ephemeroptera represented 98% of the total insects to emerge from the other site. The no-algae plots of these paired plots potentially contained recent dipteran and ephemeropteran oviposition sites. I may have unknowingly placed the emergence traps over these egg masses in the bare river substrate. This would explain why emergence trap data so starkly contrasts with previously observed greater emergence from algae mats than bare substrate (Power 1990, Power et al. 2004).

I did not observe much impact on emergence by adding algae, despite well-documented instances of *C. glomerata* mats holding large numbers of larval invertebrates (Power 1990, Power et al. 2004). The three-dimensional movement of emerging insects makes sampling this subsidy potentially challenging (Power et al. 2004). The sticky traps captured emergence towards one shoreline, and flags were not moved with water level until the last experimental week. Flags farther away from the shoreline likely missed emergence, as invertebrate number and biomass decline exponentially with distance from the river (Power et al. 2004). Ground flags also likely missed dispersal of insects out of the river and up over the forest canopy (Power et al. 2004). The emergence traps caught upward emergence for only the last experimental week, but two pools potentially contained recent diptera and ephemeroptera egg masses. An unusually late summer flood could have also restarted *C. glomerata's* phenology (Power 1991). The available algae in July was bright green at harvest, rather than the rusty-red algae used in previous Eel River emergence research (Power 1991). Green algae color indicates low aquatic invertebrate presence with lower eventual emergence levels to be captured over the course of my study (Power 1991, Furey et al. 2012). Despite these outlier paired plots and my difficulties accurately tracking insect emergence, both consumers successfully tracked the subsidy.

I surveyed an average 30% more odonates in algae plots than in no-algae plots and an average 11% more Lycosid spiders. These results support previous observation that odonates responded to subsidy plots (Sabo and Power 2002A), and prior results that Lycosid spiders track algal mat manipulations (Sabo and Power 2002A, Power et al. 2004). Odonate distribution in algae plots was higher than Lycosid spider distribution. Flight may help odonates track resources better than spiders. Flying allows greater mobility than stalking from the cobble bars, so flying predators may have greater subsidy tracking potential (Power et al. 2004), or at least a greater potential foraging area. Odonates hunt over broad ranges (Manolis 2003) and may pick up on subtle spatial and temporal variations in insect emergence. They can find the most profitable foraging location and maximize their productive foraging time (Armstrong et al. 2016). Yet, this trend breaks down when comparing individual odonate species distributions.

Of the six species of odonate surveyed over the course of the experiment, three species exhibited small trends of higher distribution in algae plots than in no-algae plots. One of the species was a damselfly, the sooty dancer, and had the highest distribution in algae plots. The other two were dragonflies, the bison snaketail and the flame skimmer. The similar trend between species is

unexpected due to the different foraging styles used by damselflies and dragonflies (Manolis 2003). Damselflies perch on taller sedges and cobbles, sallying out to grab insects and returning to their perch with captured prey. Dragonflies hunt in sweeps over broad reaches of the river and catch insects on the wing, a more "mobile" foraging strategy. Including "fly-bys" in my surveys may have overestimated odonate count by mistaking potential territory defense behavior as hunting. Or perhaps a smaller potential hunting area makes locating the most productive cobble bar a greater priority for damselflies, explaining their better resource tracking. Sticky flags unintentionally caught more sooty dancer individuals than any other odonate. Black phoebes *(Sayornis nigricans)* also seemingly tracked algae plots. Sooty dancers are drably colored, a dark ashen gray in males and a dusty brown in females that was potentially less conspicuous to predatory birds than the flashier bison snaketail or flameskimmer. Sooty dancer coloring may camouflage their hunting position, while the dragonflies must constantly forage on the move to avoid predation, limiting their subsidy tracking. The need to avoid predation may complicate the idea of higher mobility allowing greater subsidy tracking, as we found that the most mobile forager was not necessarily the most successful.

Research should continue to explore how food system dynamics and mobility impact resource tracking. We know that consumer mobility aids tracking ability (Power et al. 2004, Armstrong et al. 2016). Higher trophic level consumers may also determine where ephemeral aquatic subsidies enter the food web and the extent of their influence up the food chain. This interaction between river and terrestrial ecosystems through aquatic subsidies means that local management of one community impacts the productivity and structure of both (Polis et al. 1997, Power et al. 2004, Schindler and Smits 2017).

River and terrestrial ecosystems are connected by subsidy flow (Polis et al. 1996, Power et al. 2004, Schindler and Smits 2017), and human impact moves from one to the other. Agricultural run-off and other pollution in rivers can spread into terrestrial ecosystems with emerging aquatic insects and magnify into higher trophic consumers (Schindler and Smits 2017). Urbanizing and simplifying river systems reduces system complexity and so reduces variation in resource subsidies (Schindler and Smits 2017). A lack of system complexity potentially decreases a tracking consumer's success by limiting total productive foraging time with less potential resource patches (Armstrong et al. 2016). By mapping the origins, fluxes and fates of organic production that link freshwater and terrestrial food webs, we can reveal vital connections of ecosystems threatened by

change. Land management policies that prioritize this resource heterogeneity can preserve system resiliency.

## ACKNOWLEDGEMENTS

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## APPENDIX A: EMERGENCE-DISTANCE MODEL OUTPUTS

**Table A1. Generalized and linear mixed model results with distance as explanatory variable and a random effect of paired plot.** The effect size range for Cohen's f^2: small >= 0.02, medium >= 0.15, large >= 0.35.

| Response Variable | Coefficient | P value | Effect Size Type | Effect Size |
|---|---|---|---|---|
| Invertebrate Number | -0.55 | $< 0.05$ | Cohen's f^2 = 0.6 | Large |
| Invertebrate Biomass | -66.4 | $< 0.05$ | Cohen's f^2 = 0.6 | Large |

## APPENDIX B: INSECT EMERGENCE BY TAXA
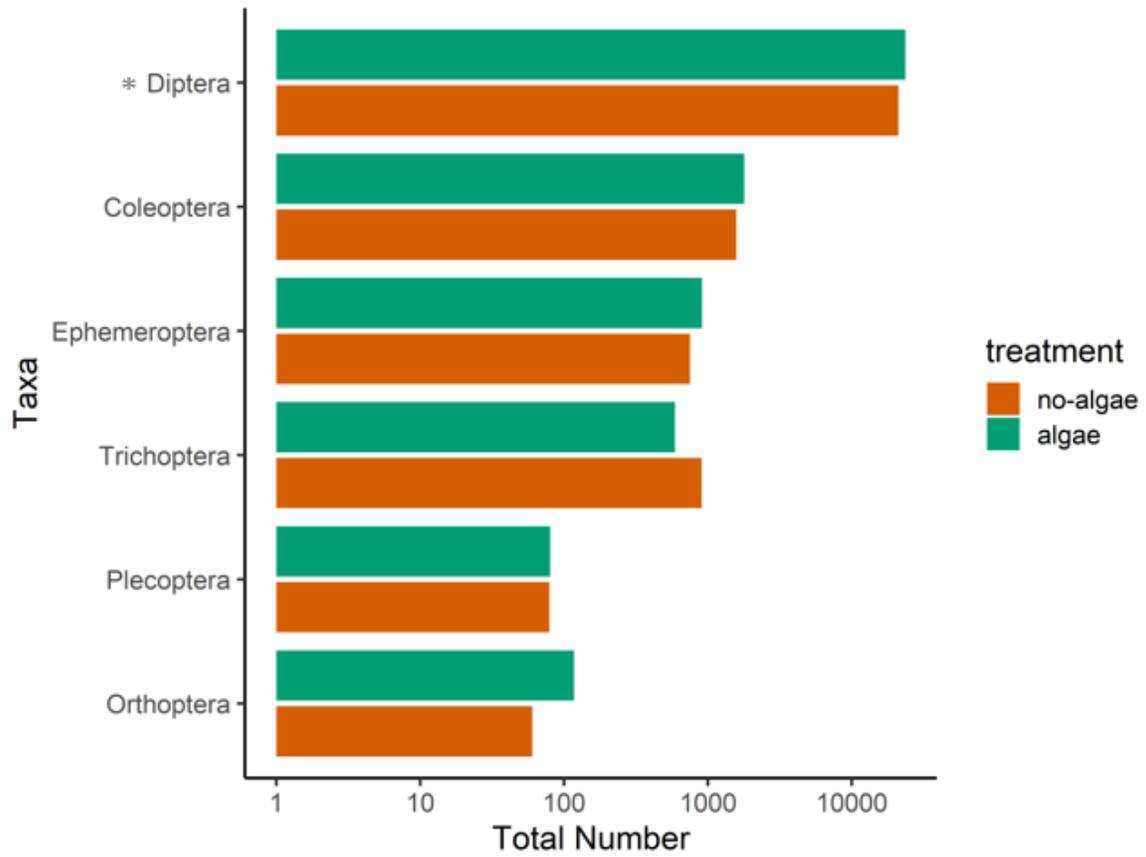


**Figure B1. Total count of insect emergence by taxa per treatment, as captured by terrestrial sticky traps.** Bars display logged invertebrate number to show variance between taxa while x-axis displays not-logged total number. Asterisk indicates significant percentage of total insects captured by sticky traps.

## APPENDIX C: ODONATE DISTRIBUTION BY SPECIES TAXA
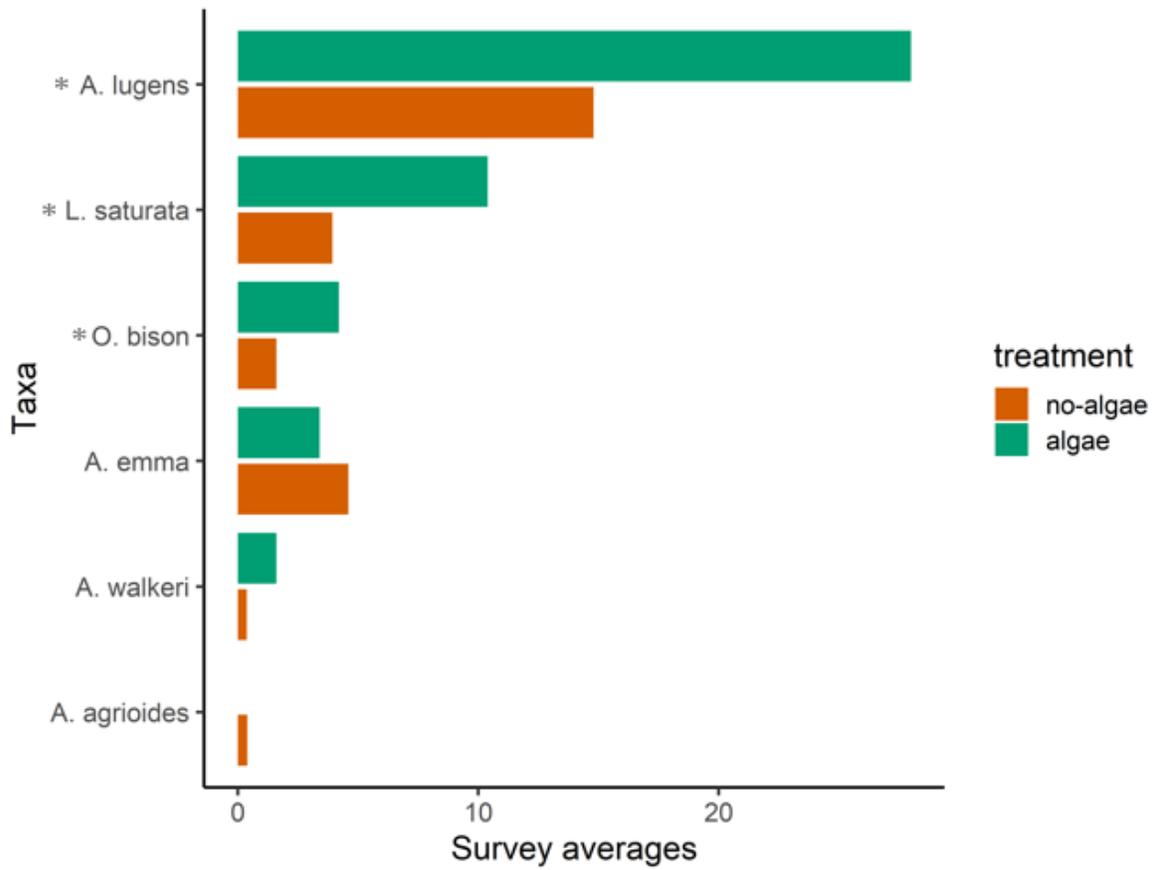


**Figure C1. The sum of scan averages for odonate surveys by taxa per treatment.** Asterisk indicates that species displayed a small trend towards higher individual average in algae plot than no-algae plot.