Brigham Young University
BYU ScholarsArchive

Theses and Dissertations

2011-07-11

An Invasive Species Reduces Aquatic Insect Flux to Terrestrial Food Webs

Steven S. Merkley
Brigham Young University - Provo

Follow this and additional works at: https://scholarsarchive.byu.edu/etd

Part of the Biology Commons

BYU ScholarsArchive Citation
Merkley, Steven S., "An Invasive Species Reduces Aquatic Insect Flux to Terrestrial Food Webs" (2011). *Theses and Dissertations*. 2806.
https://scholarsarchive.byu.edu/etd/2806

This Thesis is brought to you for free and open access by BYU ScholarsArchive. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of BYU ScholarsArchive. For more information, please contact scholarsarchive@byu.edu, ellen_amatangelo@byu.edu.

An Invasive Species Reduces Aquatic Insect Flux
to Terrestrial Food Webs

Steven Merkley

A thesis submitted to the faculty of
Brigham Young University
in partial fulfillment of the requirements for the degree of

Master of Science

Russell Rader, chair
Mark Belk
Jerry Johnson

Department of Biology

Brigham Young University

August 2011

Copyright © 2011 Steven Merkley

All Rights Reserved

ABSTRACT

An Invasive Species Reduces Aquatic Insect Flux to Terrestrial Food Webs

Steven Merkley
Department of Biology, BYU
Master of Science

Although it is well documented how introduced species can negatively affect native species, we only poorly understand how they may alter ecosystem functions. We investigated how an invasive fish affected the flux of aquatic insects to terrestrial food webs using mesocosms in a desert spring ecosystem. We compared aquatic insect emergence between alternative community states with monocultures and polycultures of two native species of fish, least chub (*Iotichthys phlegethontis*) and Utah chub (*Gila atraria*) plus, introduced western mosquitofish (*Gambusia affinis*). We tested three hypotheses: (1) aquatic insect biomass will be greater than terrestrial insect biomass and thus, constitute a vital source of energy for terrestrial consumers (2) invasive mosquitofish will negatively impact the biomass of emerging aquatic insects, and (3) terrestrial consumers will negatively respond to decreased emerging aquatic insect biomass. Aquatic insects represented 79% of the flying insect community, and treatments with mosquitofish significantly reduced emergent aquatic insect biomass by 60% relative to the control without mosquitofish. Behavioral traits of invasive species are important, because mosquitofish most heavily affected insects that emerged during the day. Also, spiders that build horizontal webs were negatively correlated with decreasing aquatic insect biomass. Invasive mosquitofish can achieve very dense populations because of their high intrinsic rate of population increase, which can significantly disrupt the flow of energy between aquatic and terrestrial ecosystems, thereby reducing the energy available for terrestrial consumers.

Keywords: invasive species, ecosystem function, aquatic-terrestrial linkages, insect emergence, desert springs, *Gambusia affinis*

ACKNOWLEDGEMENTS

I'd like to thank my funding sources: BYU department of biology, BYU graduate studies, and the Charles Redd Center for Western studies for providing money for materials, stipend, and transportation to and from Fish Springs. I'd also like to thank all the following people for the time, energy, and resources they put into this project: Brian Allen, Jay Banta, and all the staff at Fish Springs National Wildlife Refuge, US Fish and Wildlife Service, Utah Division of Wildlife Resources, Dr. Jerry Johnson, Dr. Mark Belk, Josh Moody, Rachel Connell, Chris Busath, Marci Nelson, Leilani Williams, Frans Lamsbrechtsen, Karsten Busby, Nick Davis, and Jeff Moore. I'd like to give a special acknowledgement to Jeff Wesner for helping develop some ideas and helping me edit my manuscript.

I am also very appreciative to my friends and family who have showed me support and love as I have pursued my graduate education at BYU and worked hard to put together a successful project. I'd like to thank my wonderful wife, Elizabeth, for being patient and loving. I'd especially like to thank my grandfather, Wayne Merkley, a biology professor for over 30 years at Drake University, who passed away during the start of my graduate studies in August 2009. He was a wonderful example of a successful professor and dedicated father and grandfather.

Table of Contents

Table of Figures

Introduction

Aquatic food webs are often subsidized by allocthonous plant and animal material from terrestrial food webs (e.g. Nakano et al. 1999). These subsidies provide essential nutrients and energy; especially in systems where autochonous primary productivity is low, such as heavily shaded headwater streams (Vannote et al. 1980). Many terrestrial food webs also depend on the energy subsidies flowing from aquatic systems, usually in the form of emerging adult aquatic insects (Nakano and Murakami 2001, Wesner 2010). Introduced aquatic species that prey on emerging aquatic insects may have a negative impact on the flow of energy between aquatic and terrestrial food webs by reducing energy available for terrestrial consumers (e.g. spiders, birds, bats). Several studies have shown that there are numerous terrestrial species that depend on the flux of energy from emerging aquatic insects (e.g. Sabo and Power 2002, Fukui et al. 2006). However, only a few studies have examined the effect of introduced species on the flow of energy from aquatic to terrestrial food webs (Baxter et al. 2004, Epanchin et al. 2010, Benjamin et al. in press). This is an important issue because invasive species are one of the main drivers of change in aquatic environments (Mills et al. 2004, Crowl et al. 2008) and energy flow between aquatic and terrestrial environments is a critical subsidy for both systems.

Mosquitofish, from the genus *Gambusia* (particularly *G. affinis* and *G. holbrooki),* are the most widely distributed species of freshwater fish on earth having been introduced as a mosquito control agent to every continent except Antarctica (Pyke 2005). Mosquitofish are one of eight fish species listed as the world’s worst 100 invasive species (Lowe et al. 2000). Western mosquitofish (*Gambusia affinis*) are particularly detrimental because they have physiological, ecological, and behavioral traits that allow them to rapidly reproduce, achieve high population densities, and thrive in a wide range of habitats (Bay 1972, Haynes 1993, Pyke 2008). Thus, mosquitofish are one of the most important introduced species in the world. Despite the potential importance of this species in altering natural ecosystems, most studies have examined effects on single species with little regard to ecosystem or community effects, especially when such effects pertain to aquatic-terrestrial linkages.

We examined the effects of introduced mosquitofish on aquatic-terrestrial linkages in desert artesian springs in the Bonneville Basin of the Great Basin Province. Artesian springs are an excellent model ecosystem to detect the general effects of mosquitofish applicable to a variety of freshwater environments because desert terrestrial food webs appear highly dependent on aquatic subsidies and mosquitofish can reach their maximum population growth potential in this habitat. Desert springs have previously shown a high level of asymmetry in insect production between aquatic and terrestrial food webs (e.g. Jackson and Fisher 1986). This asymmetry leads to extreme sensitivity and dependence of the terrestrial food web on aquatic production. Also, biotic and abiotic conditions are ideal for the growth and reproduction of mosquitofish. For example, temperatures are very constant and usually warm (25° C and 30° C), providing excellent thermal conditions for this sub-tropical species (Pyke 2005). Also, there is little predation or competition from other species because of a depauperate fish fauna (Courtenay and Meffe 1989). Historically, native fish in springs of the Bonneville Basin consisted primarily of Utah chub (*Gila atraria*) and least chub (*Iotichthys phlegethontis*). Neither native species appear to negatively influence mosquitofish. Thus, desert artesian springs are ideal systems to rapidly detect the effects of mosquitofish on aquatic-terrestrial linkages.

The objective of this study was to determine the how invasive western mosquitofish (*G. affinis*) disrupt the linkage between aquatic and terrestrial food webs in spring ecosystems. We hypothesized that mosquitofish would interrupt the flow of energy from aquatic to terrestrial food webs and cause a reduction in food available for terrestrial consumers. We predicted that: (1) the biomass of aquatic insects would greatly exceed terrestrial insect biomass, (2) invasive mosquitofish would negatively impact the biomass of emerging aquatic insects, and (3) terrestrial consumers that depend on aquatic subsidies would respond negatively to a potential decrease in emerging aquatic insects.

Methods

Study site

We examined the effects of introduced western mosquitofish on energy flow between aquatic and terrestrial food webs at Fish Springs National Wildlife Refuge (FSNWR), Juab County, Utah (N 39.841799° W 113.393130°). Fish Springs NWR is the largest spring complex in the Great Basin Province at over 40 km^2 (Ayala et al. 2007). It is composed of numerous spring wells and large, shallow marshes connected by flowing channels. All of these spring wells are geothermally heated (approximately 25 °C year-round). Numerous terrestrial species depend on this system for water and energy. For example, from May 2008 to Jan 2011, four hundred and forty-seven species of birds were surveyed in FSNWR. The total abundance of birds reached well over 8,000 in some months (unpublished data provided by Fish Springs NWR).

Two fish species are currently found within this spring complex: Utah chub and introduced western mosquitofish. Introductions of native least chub, a threatened cyprinid, have been unsuccessful due to competition and predation with introduced mosquitofish (Mills et al. 2004, Ayala et al. 2007, Priddis et al. 2009).

Although mosquitofish preferentially feed at the water's surface (Hurlbert et al. 1972, Garcia-Berthou 1999), all three species are capable of feeding throughout the water column on a variety of protein rich resources (insects, amphipods, zooplankton) as well as some plant material (Graham 1961, Billman et al. 2007, personal obervations). Animal resources, including aquatic insects are an important part of the diet of mosquitofish and least chub throughout their life cycle. However, Utah chub feed primarily on animal resources as juveniles and switch to plant material as adults (John 1959). Both mosquitofish and least chub mature at approximately 30 mm (Mills et al. 2004), but Utah chub does not reach maturity until around 90 mm (Gaufin 1964). Thus, we only used juvenile Utah chub (30 mm to 60 mm) in this study because their size and diet was similar to adult least chub and mosquitofish.

Aquatic Contribution to the Terrestrial Environment (Hypothesis 1)

We used sticky traps in four springs to capture flying insects at the water's edge, 30 m away from the water's edge, and between 125-390 m into the desert along 2 to 6 transects per spring to determine the importance of aquatic insects to the terrestrial food web. Sticky traps consisted of a transparent sheet (21.6 x 28 cm) wrapped around a clear 2-liter plastic bottle placed at 1.25 m off the ground on the top of rebar. We sprayed the transparencies with Tanglefoot®, a non-drying adhesive spray. Sticky traps were left out for periods of 2 weeks in

May and July, 2010. We subsampled six out of thirty-six 2.5 cm^2 squares on each sheet. All insects were classified as either aquatic or terrestrial.

Effects of an Introduced Predator on Aquatic Insects (Hypothesis 2)

In May 2010, we partially submerged 36 hard plastic mesocosms (circular Rubbermaid tanks; 1.83 m diameter, 0.75 m deep, 1100 liters) throughout a 100-meter section of Middle Spring at The Fish Springs National Wildlife Refuge and filled them with 0.6 meters of natural spring water. Each mesocosm had a circular meshed opening (2.5 cm diameter) near the bottom that allowed for the exchange of but prevented the movement of fish. We also replenished each mesocosm with approximately 110 liters of fresh spring water on a weekly basis to avoid stagnation and to replenish nutrients. In order to standardize the number of benthic aquatic insects at the beginning of our study, we added a 20-liter bucket of *Chara* sp., a dominant submerged macrophyte, and two 20-liter buckets of silty substrate, which formed an even layer 2 cm thick in each replicate mesocosm. Adding spring water, substrate, and macrophytes effectively inoculated each mesocosm with a variety of aquatic invertebrates. We found no significant difference in the starting densities of benthic invertebrates after randomly sampling half of mesocosms before establishing fish density treatments ($F_{1.51, 17}$; P=0.1457). Egg-laying adult insects were able to colonize each mesocosm throughout the study including two weeks before fish were added. Mesocosms balance the tradeoff between experimental manipulations of fish abundance while reproducing the natural spring ecosystem (e.g. Downing and Leibold 2002).

We used seven different experimental treatments representing natural alternative community states to measure fish effects on aquatic insect emergence (Table 1). Each alternative community state was replicated at least 5 times, and randomly assigned a position throughout our study section. Each mesocosm contained thirty total fish between 30-60 mm, with the exception of the control with no fish. We did not include a least chub/mosquitofish treatment, because all evidence suggests that mosquitofish will drive least chub to extinction at local scales (Bailey et al. 2005, Priddis et al. 2009). Thus, this is not a stable interaction that can be found over the long term in a natural spring. We replaced the few fish that died with healthy fish throughout the study.

We covered 15% of the surface of each mesocosm with a floating trap (0.34 m^2), to sample emerging aquatic insects once a week for 8 weeks between June 29 and August 24, 2010 (Figure 1). Insects from each sample were preserved in 70% ethanol, identified to the family level, dried at 50° C for 24 hours, and weighed to the nearest milligram to determine the dry weight biomass of each family.

Effects of an Introduced Predator on a Terrestrial Consumer (Hypothesis 3)

Every week for the duration of this study, we counted the number of occupied spider webs associated with each mesocosm to determine if a terrestrial consumer would respond to potential differences in aquatic insect emergence. We chose spiders because they show rapid behavioral responses (web building) to altered food availability that are easier to detect than other taxa also dependent on aquatic resources (e.g. birds and bats). We classified occupied spider webs as either vertical or horizontal. Spiders that build horizontal webs are more likely to respond to changes in insect emergence than spiders that build vertical webs (Kato et al. 2003, Wesner in press).

Data analysis

We ran a mixed model (PROC MIXED) with repeated measures on total aquatic insect biomass in SAS 9.2 to determine differences between treatments/alternative community states to test hypothesis 2. We also ran the same mixed model analysis on the four most common taxa: baetid mayflies, chironomid midges, libellulid dragonflies, and lestid damselflies. We used a sequential bonferroni correction to adjust for a Type 1 error (Holm 1979, Rice 1989).

We ran a linear regression (PROC REG) in SAS 9.2 to compare the number of occupied spider webs (both vertical and horizontal) versus the biomass of aquatic insects in each mesocosm replicate. We performed a square root transformation on the count data to meet conditions of normality.

Results

Aquatic Contribution to the Terrestrial Environment (Hypothesis 1)

Aquatic insects represented 79% of the flying insect biomass averaged over all transects, and represented 65% of the flying community even in traps located over 350 m from the water's edge (Figure 2). These results support our first hypothesis. That is, the proportion of flying aquatic insects was far greater than the proportion of flying terrestrial insects in this desert spring ecosystem.

Effects of an Introduced Predator on Aquatic Insects (Hypothesis 2)

Mosquitofish numbers increased from ten to 30 individuals at the beginning of this study to between 70-200 individuals over the course of 8 weeks. By contrast, least chub experienced very low recruitment over the course of this study and only in monocultures. Juvenile Utah chub grew larger but did not reproduce.

The average biomass of insect emergence from our mesocosms tended to peak at the end of July and decreased throughout August (Figure 3). The lowest emergent biomass was during the last week of our study. The strongest fish effects were during the end of July and beginning of August.

Only treatments/alternative fish community states containing mosquitofish significantly reduced the aquatic insect flux: mosquitofish only ($F_{6,29}$; P=0.042), mosquitofish/Utah chub ($F_{6,29}$; P=0.042) and mosquitofish/least chub/Utah chub ($F_{6,29}$; P=0.042). Mosquitofish reduced the biomass of emergent insects by an average of 60% relative to the control (Figure 4). Thus, these results support our second hypothesis. Invasive mosquitofish reduced the amount of aquatic insect biomass for terrestrial consumers. Baetid mayflies and lestid damselflies were particularly susceptible to mosquitofish predation and fish predation in general. Baetid mayfly emergence was significantly lower than the control in all experimental treatments ($F_{6,29}$; P=.0001; Figure 5), whereas lestid damselflies were most susceptible to mosquitofish and Utah chub ($F_{6,29}$; P=.048; Figure 6). Although chironomid midges and libellulid dragonflies (*Libellula saturata*) represented 78% of the total aquatic insect emergence, fish treatments did not significantly reduce their emergent biomass (Figure 7).

Effects of an Introduced Predator on a Terrestrial Consumer (Hypothesis 3)

Occupied horizontal spider webs were positively correlated with total aquatic insect biomass (Figure 8), whereas occupied vertical spider webs showed no significant correlation (Figure 9). Spiders that build horizontal webs responded negatively to a decrease in emergent aquatic insect biomass.

Discussion

Can introduced predators disrupt the linkage between aquatic and terrestrial ecosystems? Western mosquitofish significantly disrupted the flow of energy from aquatic to terrestrial food webs, becoming a sink for insect biomass that terrestrial consumers depend upon. Treatments with mosquitofish reduced the emergence of aquatic insects by 60% compared to control treatments without fish. Similarly, introduced brook trout (*Salvelinus fontinalis*) reduce the emergence of aquatic insects by 70% in alpine lakes (Epanchin et al. 2010). Both ecosystems have a narrow band of low-lying riparian vegetation. By contrast, introduced rainbow trout (*Oncorhynchus mykiss*) in a montane stream with an extensive zone of riparian vegetation only reduced the emergence of aquatic insects by 35% (Baxter et al. 2004). Thus, introduced fish predators in systems with dense riparian zones have a reduced dependence on aquatic prey, which tends to reduce their negative impact on the flow of energy to the terrestrial environment (Baxter et al. 2005). The reciprocal transfer of energy between aquatic and terrestrial ecosystems in desert environments and alpine lakes is out of balance and introduced predators are primarily dependent on aquatic resources. Thus, introduced fish predators will exert their greatest influence on aquatic-terrestrial linkages when they are restricted to feeding primarily on aquatic prey. This relationship is intensified when environmental conditions are suited to the maximal growth and survival of the introduced species.

When do introduced species have a harmful effect?

When introduced species have an overall net negative effect on ecosystem function, they are considered invasive. However, introduced species may exert a positive impact on ecosystem function, especially when they provide nutrients to and facilitate the growth and/or survival of native species (Schlaepfer et al. 2011). Under certain conditions, invasive species have a greater tendency to exert direct and indirect negative impacts on native species.

We suggest that introduced species are most harmful when: (1) there is a depauperate fauna, (2) favorable environmental conditions for the survival and population growth of the invader, and (3) strong asymmetry between aquatic and terrestrial food webs, leading to a higher dependence of terrestrial consumers on aquatic emergence. Introduced species may be more likely to invade and establish populations where there is a depauperate species pool (e.g. Elton 1958, Robinson and Dickerson 1984, Tilman 1997). When the invader is a superior competitor, it can drive the native competitor to local extirpation (e.g. Mills et al. 2004). Introduced species are also more likely to be invasive and experience population explosions when environmental conditions are ideal for their growth and survival (Davis 2009). Terrestrial consumers are indirectly affected by aquatic invasive species by indirect effects via predation on vital subsidies flowing to the terrestrial food web (e.g. Epanchin et al. 2010). In Fish Springs NWR and other highly asymmetric systems, these effects may be even greater due to the increased dependence of terrestrial consumers on aquatic subsidies.

At Fish Springs NWR, mosquitofish meet all three of these conditions. Because of the constant warm temperature, high primary and secondary productivity, and lack of predators, mosquitofish have no constraints to their survival and population growth and may only be limited by intraspecific competition. Environmental conditions allow the already prolific mosquitofish to grow even faster and store more biomass (Pyke 2005).

Why didn't mosquitofish reduce the emergence of all aquatic insect taxa? Mosquitofish had a strong effect on the emergence of mayflies and damselflies, whereas the emergence of midges and large dragonflies was not significantly affected. There are at least three potential explanations for why mosquitofish only seemed to target certain taxa: 1) prey may grow too large to handle, 2) some prey may overwhelm the predator's functional response by swamping the environment with a mass emergence of individuals, and 3) some prey may have a temporal or spatial refuge from fish predation. Personal observations suggest that libellulid dragonflies can outgrow the gape-width of mosquitofish and thus, reduce the effects of predation with only minimal disturbance during emergence. Also, the mass emergence of thousands of midges may satiate fish predators and overwhelm their functional response (Solomon 1949). In addition, western mosquitofish are active during the day and become sedentary and inactive at night (Ayala et al. 2007), whereas many species of chironomid midges in temperate regions generally emerge at night (Oliver 1971). The nocturnal behavior of chironomid emergence appears to create a temporal refuge from daytime predators. Finally, many chironomids may have a spatial refuge from mosquitofish predation because they burrow in soft substrate or dwell in tubes, whereas mayflies and damselflies are active during the day and crawl on or swim among aquatic vegetation. Thus, the most susceptible prey to mosquitofish are aquatic insects that actively emerge during the day and lack a spatial refuge.

What terrestrial consumers may be negatively impacted by mosquitofish? Because the majority of flying insects (79%) are comprised of aquatic insects in desert spring ecosystems, terrestrial consumers should be highly dependent on aquatic sources of energy. Mosquitofish significantly reduced the flux of aquatic biomass to the terrestrial food web. For example, mosquitofish reduced baetid mayfly emergence by 89% compared to the control without mosquitofish. However, mosquitofish may not reduce aquatic subsidies to all terrestrial consumers. Behavioral traits should be important in determining which terrestrial consumers are most susceptible to mosquitofish invasion. Diurnal terrestrial predators (e.g. birds) should experience a greater reduction in food subsidies compared to nocturnal terrestrial predators (e.g. bats) because nocturnal aquatic prey (e.g. midges) were not reduced by mosquitofish predation. In general, terrestrial predators with traits most similar to the aquatic invader will be most negatively impacted, whereas terrestrial consumers with different traits than the aquatic invader may not be negatively affected. Interestingly, our study showed that terrestrial spiders had a significant but weak negative correlation to a decrease in emergent biomass. Spiders are neither nocturnal nor diurnal and thus, will respond to the overall reduction in aquatic insect biomass. Thus, they show that terrestrial consumers with traits that only partially overlap with mosquitofish can still be negatively affected but the most susceptible terrestrial predators will show the greatest temporal niche overlap with the invader.

Introduced species will have greatest effects on aquatic-terrestrial linkages and energy flow where there are few constraints to their rapid population growth (e.g. open niche, enemy-free space, and favorable abiotic conditions) and when there is a strong asymmetry in resources where the recipient food web is strongly dependent on the donor food web. In systems with sparse riparian vegetation, both aquatic and terrestrial predators are more dependent on aquatic prey. The most susceptible species in both aquatic and terrestrial food webs have the greatest overlap in niche requirements with the introduced species. Here we show that an invasive predator (*G. affinis*) significantly disrupts the energy flux from aquatic food webs to terrestrial food webs in a desert spring ecosystem under alternative fish community states. Our study provides more evidence that not only can invasive species impact ecosystem function; they can impact the flow of energy between aquatic and terrestrial food webs.

Literature Cited

Ayala, J. R., R. B. Rader, M. C. Belk, and G. B. Schaalje. 2007. Ground-truthing the impact of invasive species: spatio-temporal overlap between native least chub and introduced western mosquitofish. Biological Invasions **9**:857-869.

Bailey, C. L., K. W. Wilson, M. E. Andersen, and Utah. Division of Wildlife Resources. 2005. Conservation agreement and strategy for least chub (*Iotichthys phlegethontis*) in the state of Utah. Utah Division of Wildlife Resources, Salt Lake City, Utah.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology **85**:2656-2663.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology **50**:201-220.

Bay, E. C. 1972. Mosquitofish: a controversial friend to mosquito control. Pest Control **40**:32-33.

Benjamin, J., K. Fausch, and C. Baxter. 2011. Species replacement by a nonnative salmonid alters ecosystem function by reducing prey subsidies that support riparian spiders. Oecologia. In Press.

Billman, E. J., E. J. Wagner, and R. E. Arndt. 2007. A comparison of mosquito consumption and prey selection between least chub (*Iotichthys phlegethontis*) and western mosquitofish (*Gambusia affinis*). Western North American Naturalist **67**:71-78.

Courtenay, W. R. and G. K. Meffe. 1989. Small fishes in strange places: a review of introduced poeciliids. Pages 319-331 *in* G. K. Meffe and F. F. Snelson Jr., editors. Ecology and evolution of livebearing fishes (Poeciliidae). Prentice Hall, Englewood Cliffs, New Jersey.

Crowl, T. A., T. O. Crist, R. R. Parmenter, G. Belovsky, and A. E. Lugo. 2008. The spread of invasive species and infectious disease as drivers of ecosystem change. Frontiers in Ecology and the Environment **6**:238-246.

Davis, M. A. 2009. Invasion biology. Oxford University Press, Oxford ; New York.

Downing, A. L. and M. A. Leibold. 2002. Ecosystem consequences of species richness and composition in pond food webs. Nature **416**:837-841.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London.

Epanchin, P. N., R. A. Knapp, and S. P. Lawler. 2010. Nonnative trout impact an alpine-nesting bird by altering aquatic-insect subsidies. Ecology **91**:2406-2415.

Fukui, D., M. Murakami, S. Nakano, and T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. Journal of Animal Ecology **75**:1252-1258.

Garcia-Berthou, E. 1999. Food of introduced mosquitofish: ontogenetic diet shift and prey selection. Journal of Fish Biology **55**:135-147.

Gaufin, R. F. 1964. Ecology of the Utah chub in Fish Lake, Utah. University of Utah, Salt Lake City, UT.

Graham, R. J. 1961. Biology of the Utah chub in Hebgen Lake, Montana. Transactions of the American Fisheries Society **90**:269 - 276.

Haynes, J. L. 1993. Annual reestablishment of mosquitofish populations in Nebraska. Copeia **1993**:232-235.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scandinavian Journal of Statistics **6**:65-70.

Hurlbert, S. H., J. Zedler, and Fairbank.D. 1972. Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. Science **175**:639-641.

John, K. R. 1959. Ecology of the chub, *Gila atraria*, with special emphasis on vertebral curvatures, in Two Ocean Lake, Teton National Park, Wyoming. Ecology **40**:564-571.

Kato, C., T. Iwata, S. Nakano, and D. Kishi. 2003. Dynamics of aquatic insect flux affects distribution of riparian web-building spiders. Oikos **103**:113-120.

Lowe, S., M. Browne, S. Boudejlas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species: A selection from the global invasive species database, Auckland, New Zealand.

Mills, M. D., R. B. Rader, and M. C. Belk. 2004. Complex interactions between native and invasive fish: the simultaneous effects of multiple negative interactions. Oecologia **141**:713-721.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: Riparian arthropod inputs alter trophic cascades in a stream food web. Ecology **80**:2435-2441.

Nakano, S. and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America **98**:166-170.

Oliver, D. R. 1971. Life history of the Chironomidae. Annual Review of Entomology **16**:211-230.

Priddis, E., R. Rader, M. Belk, B. Schaalje, and S. Merkley. 2009. Can separation along the temperature niche axis promote coexistence between native and invasive species? Diversity and Distributions **15**:682-691.

Pyke, G. H. 2005. A review of the biology of *Gambusia affinis* and *G-holbrooki*. Reviews in Fish Biology and Fisheries **15**:339-365.

Pyke, G. H. 2008. Plague minnow or mosquito fish? A review of the biology and impacts of introduced *Gambusia* species. Annual Review of Ecology Evolution and Systematics **39**:171-191.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution **43**:223-225.

Robinson, J. V. and J. E. Dickerson, Jr. 1984. Testing the invulnerability of laboratory island communities to invasion. Oecologia **61**:169-174.

Sabo, J. L. and M. E. Power. 2002. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. Ecology **83**:3023-3036.

Schlaepfer, M. A., D. F. Sax, and J. D. Olden. 2011. The potential conservation value of non-native species. Conservation Biology **25**:428-437.

Solomon, M. E. 1949. The natural control of animal populations. Journal of Animal Ecology **18**:1-35.

Sousa, R., P. Morais, E. Dias, and C. Antunes. 2011. Biological invasions and ecosystem functioning: time to merge. Biological Invasions **13**:1055-1058.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. Ecology **78**:81-92.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. River continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130-137.

Wesner, J. S. 2010. Seasonal variation in the trophic structure of a spatial prey subsidy linking aquatic and terrestrial food webs: adult aquatic insects. Oikos **119**:170-178.

Wesner, J. S. 2011. Predator diversity effects cascade across an ecosystem boundary. Oikos. In Press.

Table 1. Alternative community states

Treatment	**Species**	**Individuals**
Single Species	*G. affinis*	30
Single Species	*I. phlegethontis*	30
Single Species	*G. atraria*	30
Natural community	*I. phlegethontis* *G. atraria*	15 15
Invaded community	*G. affinis* *G. atraria*	15 15
Three species combined	*G. affinis* *G. atraria* *I. phlegethontis*	10 10 10
Control	No fish	0


Figure 1. Floating aquatic emergence trap inside hard plastic mesocosm.

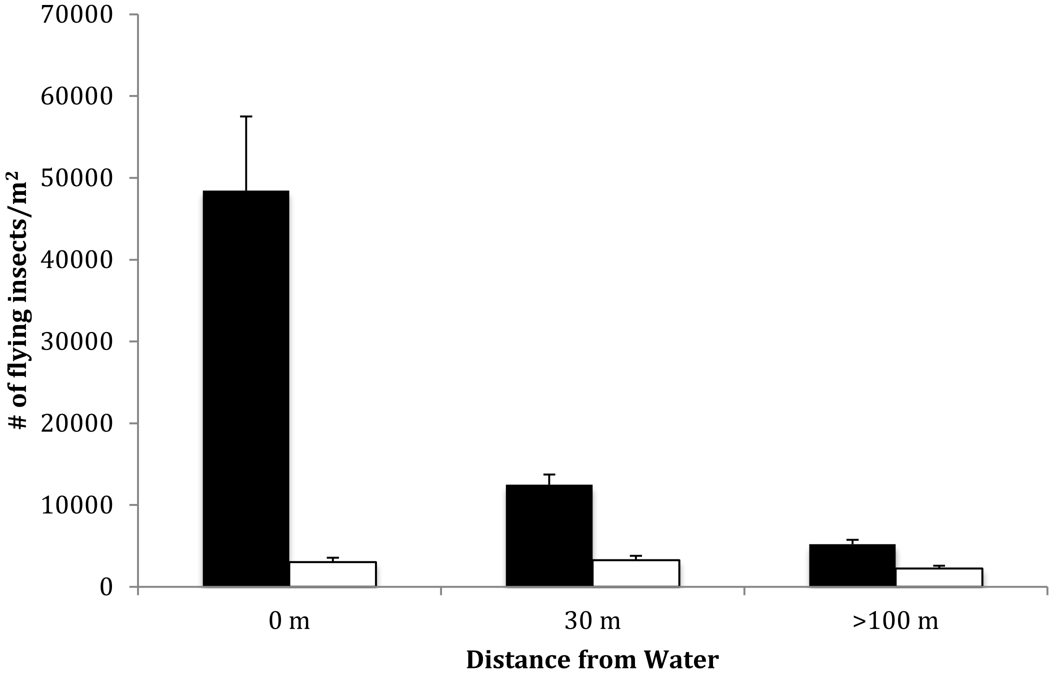

Figure 2. Density of emergent aquatic insects per m^2 (closed bars) compared to density of terrestrial insects per m^2 (open bars) from four springs in Fish Springs NWR during 2-week periods in May and July 2010.

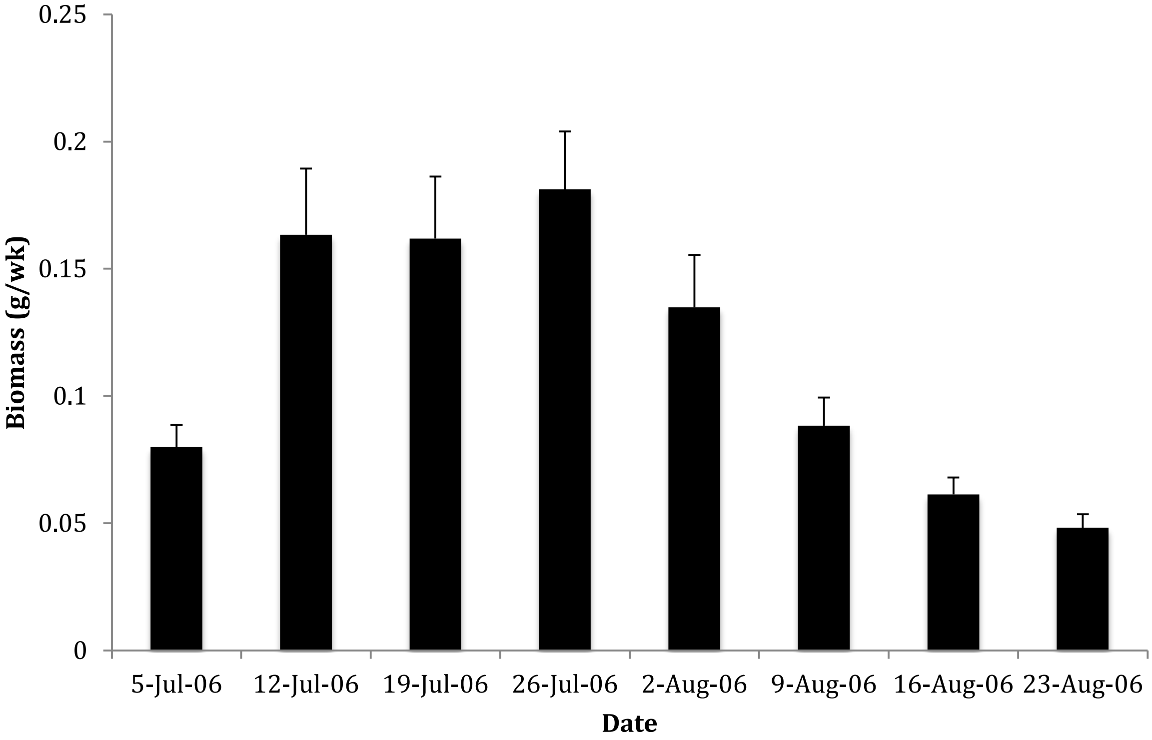

Figure 3. Total emergent aquatic insect biomass by date in grams per week from experimental mesocosms.

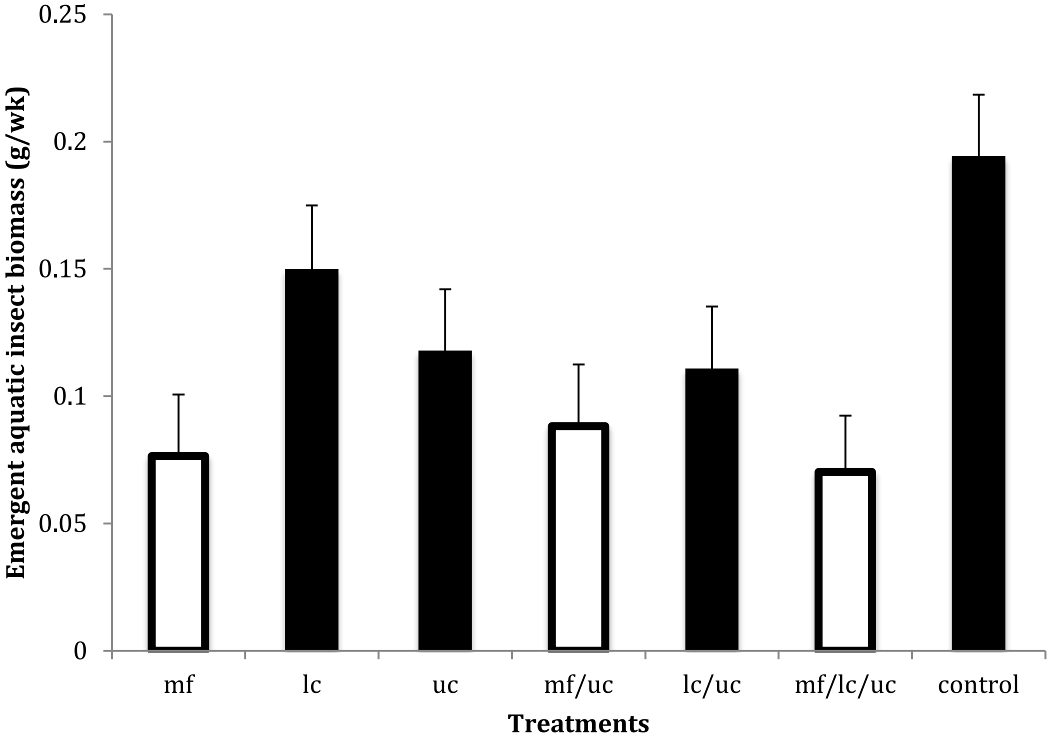

Figure 4. Emergent aquatic insect biomass in grams per week for each treatment. Open bars are significantly lower than the control ($P<0.05$). mf=mosquitofish; lc=least chub; and uc=Utah chub.

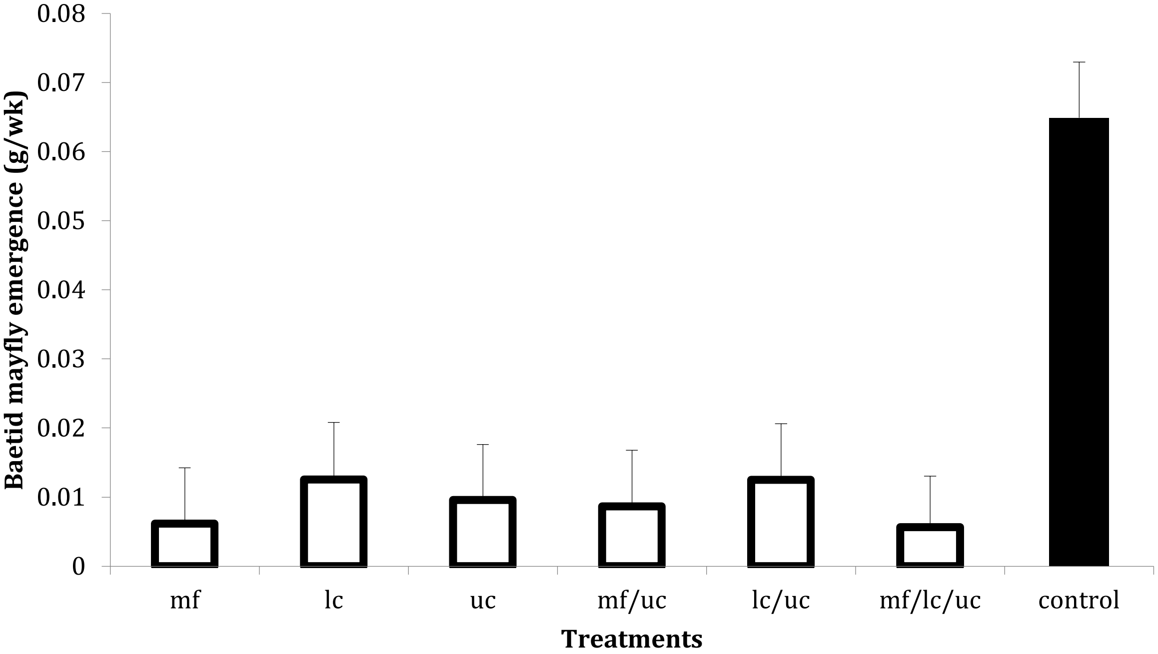

Figure 5. Baetid mayfly emergence in grams per week for each treatment. Open bars are significantly lower than the control (P<0.05). mf=mosquitofish; lc=least chub; and uc=Utah chub.

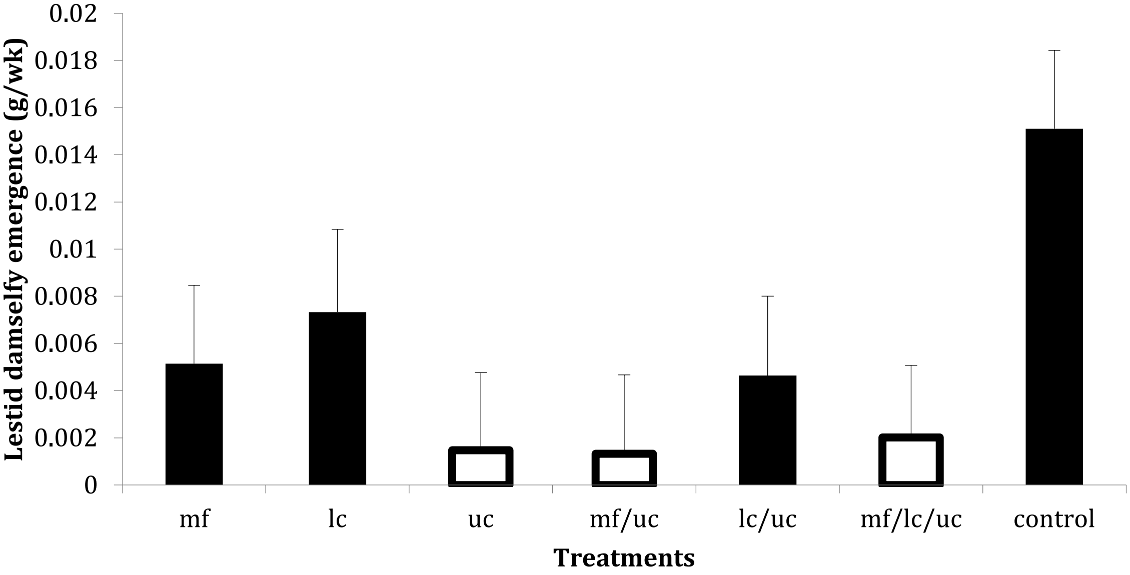

Figure 6. Lestid damselfly emergence in grams per week for each treatment. Open bars are significantly lower than the control ($P<0.05$). mf=mosquitofish; lc=least chub; and uc=Utah chub.

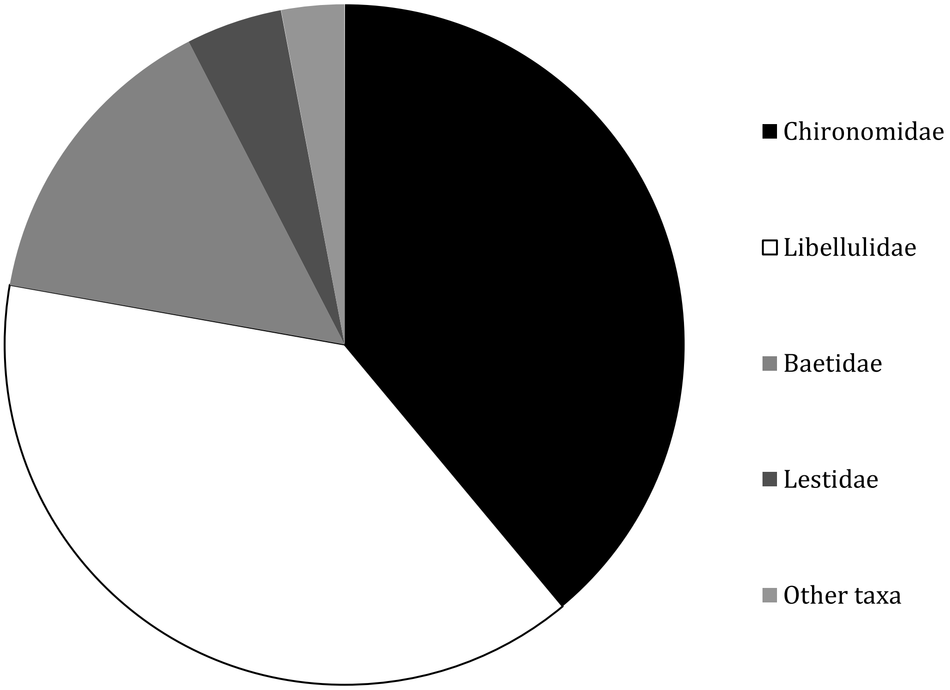

Figure 7. Average proportion of emergent biomass of taxonomic groups throughout the course of the 8-week study.

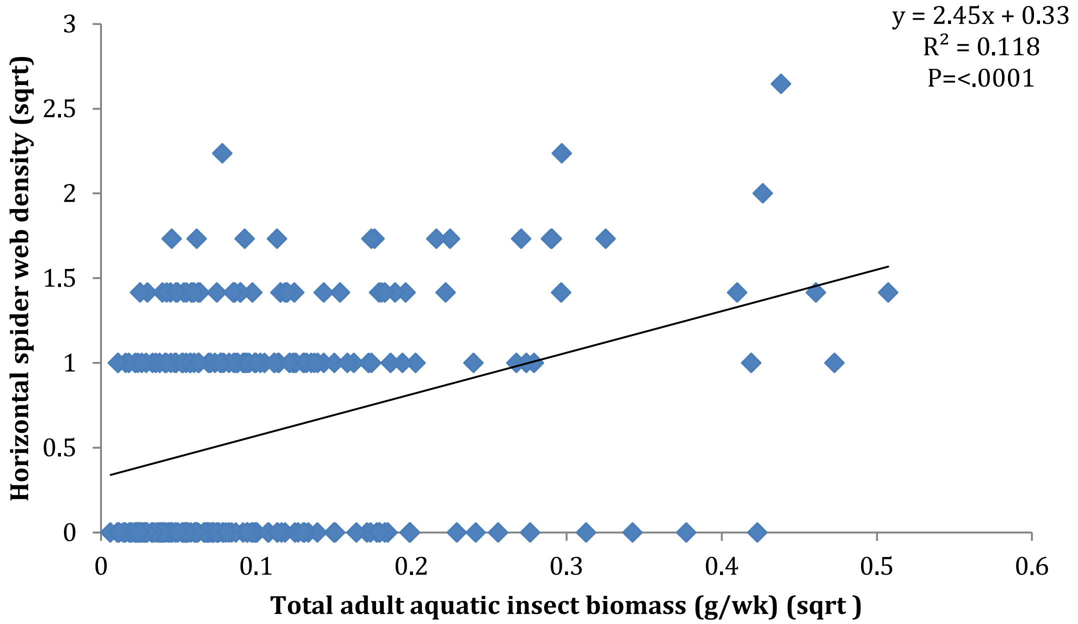

Figure 8. Horizontal spider web density per microcosm related to total biomass (sqrt) transformed with a linear regression.

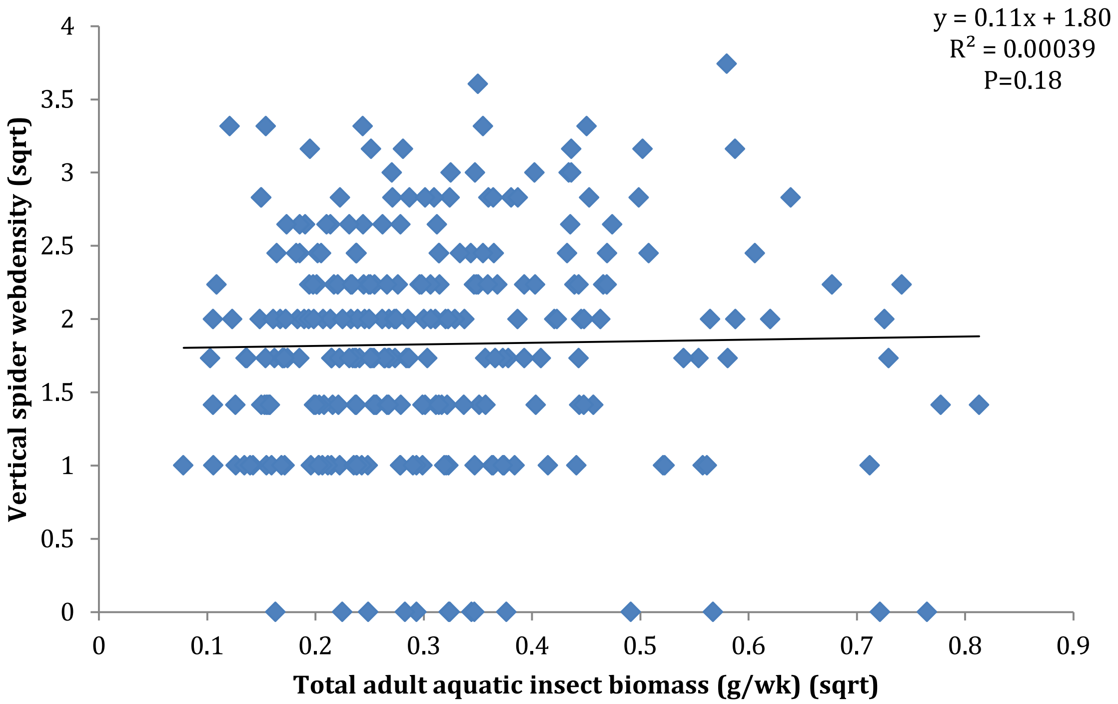

Figure 9. Vertical spider web density per mesocosm related to total biomass (sqrt) transformed with a linear regression.