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Holy flux: spatial and temporal variation in massive pulses of emerging insect biomass from western U.S. rivers

The river stonefly, *Pteronarcys californica* (aka salmonfly), is an iconic insect in rivers of western North America due to its large size and its support of economically important species like wild trout (Nehring et al. 2011). Their emergence generates a large economic subsidy to local communities, as anglers from around the world travel to western rivers to fish the salmonfly "hatch" (e.g., Willoughby 2013). Salmonflies, which have a 4-yr lifespan in the central Rocky Mountains (Nehring et al. 2011), emerge *en masse* during 1 week in late spring (Sheldon 1999), and more than 20 terrestrial species, including humans, are known to eat adult salmonflies (Muttkowski 1925, Sutton 1985, Rockwell et al. 2009). How they influence populations of insectivores or the broader river-riparian ecosystem is unknown; this itself is an issue because salmonflies are disappearing from some rivers (Nehring et al. 2011).

We observed massive synoptic emergence of salmonflies from some western rivers, but not others (Fig. 1), and wondered how large and temporally variable these fluxes might be, which could have implications for local riparian consumer populations. We quantified salmonfly emergence and carbon (C) flux over 5 yr from 21 river reaches within 5 major rivers in Colorado and Wyoming (Appendix S2: Tables S1–S3, Figs. S1–S4). We then compared our direct estimates of salmonfly C flux (i.e., an aquatic resource subsidy) to modeled estimates of total yearly emergent insect production using a global model based on stream size (Gratton et al. 2009).

Emerging aquatic insects represent a globally important subsidy from freshwater habitats to terrestrial consumers (Baxter et al. 2005). For example, an estimated 6,800 t C·yr^{-1} are moved from water to land in the state of Wisconsin by emerging aquatic insects (USA, Bartrons et al. 2013). While aquatic-to-terrestrial and other resource subsidies are ubiquitous, their effects have largely been measured by experimentally manipulating subsidy presence or absence, an approach that assumes that the time-averaged amount of the subsidy is the primary factor limiting consumer abundance (Hastings 2012).

Fig. 1. (A) Salmonfly larvae crawl to land to complete metamorphosis, and we estimated their population size by counting their abandoned exuvia. Here, exuvia litter the bank along the Colorado River in 2013 during the largest salmonfly emergence that we observed during this study (558 salmonflies per meter of stream bank). (B) Male salmonflies emerge for several days before females emerge. After females emerge, adults form large breeding conglomerations on streamside vegetation. Females return to the river shortly after mating to lay their eggs and then die. Males can linger in streamside vegetation for several days before eventually entering riparian consumer or detrital food webs. (Photos: D. A. Kowalski).

Yet in nature resource subsidies can appear along a gradient from relatively constant (press subsidy) to rare pulses of superabundant resources (pulse subsidy; Yang et al. 2010). The spatiotemporal variation in the press-pulse phenology of subsidies is not well-described, particularly at large scales or for aquatic insects.

Our most striking result is that 1 week of salmonfly C flux at some river reaches represents up to 250% of the entire yearly emerging insect C flux predicted using the Gratton and Vander Zanden (2009) model (Fig. 2). This estimate ranges widely among individual reaches (0–258%) and among whole rivers (mean 0–60%, Fig. 1). Importantly, at sites with high salmonfly emergence ("Pump", Fig. 2), salmonfly larvae also comprise up to 95% of benthic macroinvertebrates biomass (Nehring et al. 2011), indicating that salmonflies, where abundant, are likely to be the dominant emerging insect species. Variation in the relative abundance of this single species thus creates an enormous potential gradient in the duration and timing of C subsidies from freshwater to terrestrial ecosystems, with the annual export of insect-based river carbon in salmonfly-dominated reaches occurring almost entirely during a single week. This observation runs counter to the prevailing view that aquatic systems provide a more or less steady supply of insect prey to riparian consumers over the warmer parts of the year. For instance, much of the existing research on aquatic insect subsidies has been conducted in temperate ecosystems where insect emergence is typically largest in late spring and early summer and is sustained for several months (e.g., press subsidy) by different cohorts of insect species (Nakano et al. 2001, Wesner 2010).

Our data suggest that large variation in the timing of C-flux (i.e., subsidy) from western rivers to riparian

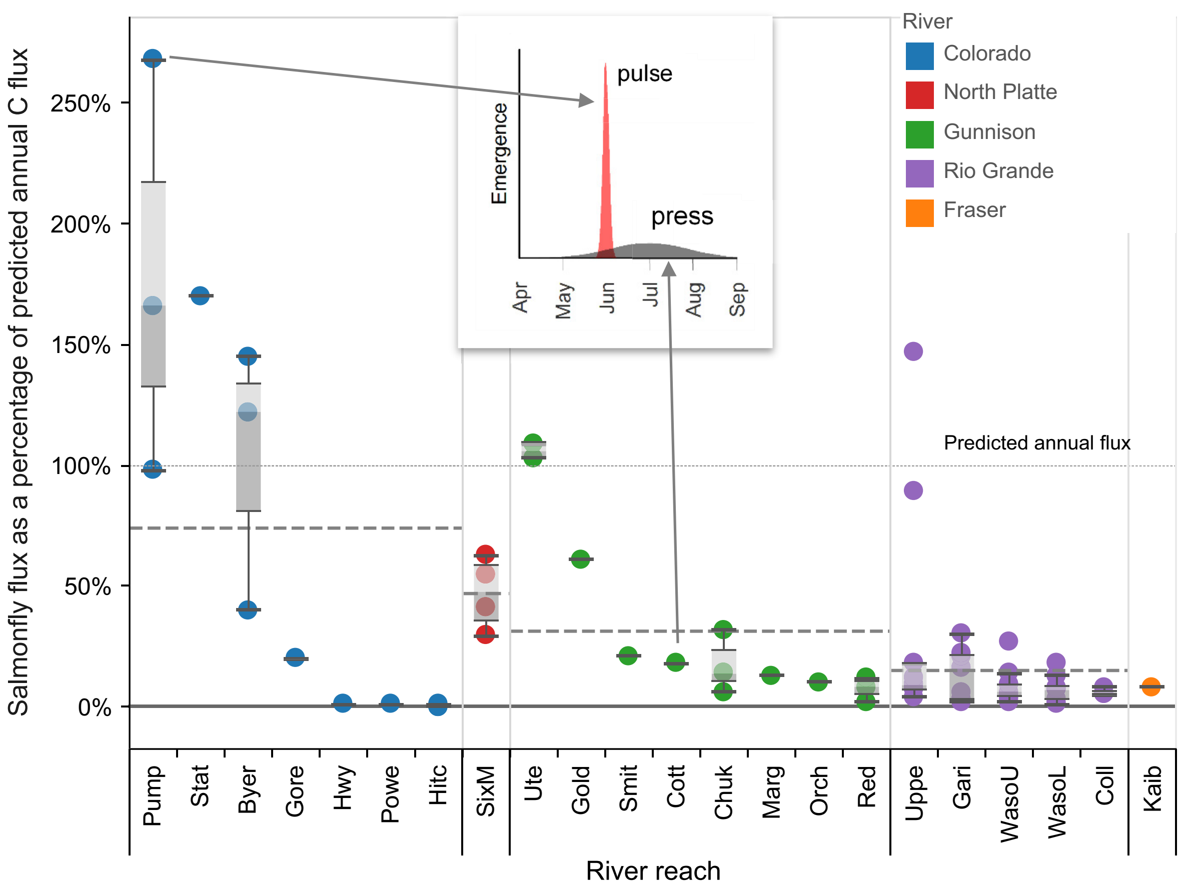

FIG. 2. Salmonfly C flux (g C·[m bank] $^{-1}$·yr^{-1} derived from exuvia counts) as a percentage of predicted annual emerging insect C flux in different river reaches (*n* = 71 observations, raw values are shown in Appendix S2: Fig. S4). The horizontal dotted line is predicted annual flux of the entire insect community based on river width (Gratton and Vander Zanden 2009). The horizontal dashed lines represent the means for each river, averaged over all data points. Multiple points within sites represent different sampling years or multiple riffles for a single reach. Box plots show the median, upper and lower quartiles, and maximum and minimum values for each site. The inset shows a hypothetical emergence phenology (press vs. pulse) in reaches with large (red) and small (grey) salmonfly populations. Salmonflies were formerly abundant at Colorado River reaches *Hwy, Powe, and Hitc*, but have since been extirpated from these reaches. Additional reach information is provided in Appendix S2: Table S1, Fig. S1.

zones is tied to variable production and emergence of salmonflies. This variation is likely to dramatically alter the press-pulse phenology of subsidies within and among river-riparian ecosystems (Fig. 2). Ecological theory predicts that variation in the pulse-press phenology of subsidies, as well as variation in their location and timing, can alter the ability of recipient consumers to respond to them (Yang et al. 2010, Hastings 2012). For example, we hypothesize that the density of sedentary riparian predators such as spiders would be lower at “pulsed” sites because these predators are unable to efficiently convert rapidly pulsed prey to seasonally-accumulated predator biomass (Yang et al. 2010). In contrast, we would expect highly mobile predators such as birds and reptiles, to exploit this wave of pulsed resources across the landscape (Schindler et al. 2013).

An additional effect of pulsed insect resources is delivery of nutrients such as N and P to riparian zones (Gratton et al. 2009). Converting salmonfly C flux rates to P and N fluxes (mean C:P and C:N $\approx$ 124 and 6.3 for aquatic insect herbivores, respectively; Elser et al. 2000), indicates that salmonflies at pulsed sites (“Pump”, Fig. 2; Appendix S2: Fig. S4) transport substantial quantities of P (0.25 [0.15–0.40] g P·[m bank] $^{-1}$·yr^{-1}) and N (4.8 [2.9–7.8] g P·m^{-1}·yr^{-1}) to riparian forests. The large variation in total C flux, C flux duration, and C pulse magnitude (along with associated fluxes of other nutrients) represents a unique opportunity to test ecological theory related to the consequences of resource subsidies for consumers and nutrient cycling at landscape scales. The ecological effects of pulsed nutrients may be particularly strong for less productive terrestrial habitats like those in the semi-arid southwest (Gratton et al. 2009). Here, these rivers act as ribbons of productivity flowing through otherwise unproductive landscapes.

The life histories of species within benthic communities clearly matter to the flux of nutrients in linked aquatic-terrestrial systems. The magnitudes and possible fates of these nutrient pulses associated with salmonfly emergence are further influenced by life history difference between males and females. Females are 2.2× larger than males on average across rivers (Appendix S2: Table S3, Fig. S3), and so carry a correspondingly large amount of nutrients to riparian zones. Males typically emerge for up to 3 d before females begin emerging (Sheldon 1999 and observations from this study), and their prolonged emergence increases their likelihood of predation by riparian animals. Likewise, nutrients in male salmonflies may be more likely to enter terrestrial food webs (either directly to consumers or into the detrital pool) than females, many of whom drown and/or are eaten by fish during egg deposition.

There is increasing concern that salmonfly populations are declining. Salmonflies have been extirpated from ~560 river km in Montana (Stagliano 2010) and from some Colorado River reaches (e.g., *Hwy*/*Powe*/*Hitc*, Fig. 2) where they formerly dominated benthic biomass (Nehring et al. 2011). These losses have the potential to dramatically alter fluxes of aquatic insect C and other nutrients from water to land across large parts of western North America, but the consequences of this change to riparian communities and ecosystem processes remain unknown.

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