Mainstem-tributary linkages by mayfly migration help sustain salmonids in a warming river network

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LETTER

Mainstem-tributary linkages by mayfly migration help sustain salmonids in a warming river network

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Abstract

Animal migrations can link ecosystems across space. We discovered an aquatic insect that migrates between a river mainstem and its tributaries, and provides an important trophic subsidy for tributary predators. A mayfly, *Ephemerella maculata*, rears in a warm, sunlit productive river mainstem, then migrates as adults to cool, shaded unproductive tributaries where they oviposit and die. This migration tripled insect flux into a tributary for 1 month in summer. A manipulative field experiment showed that this *E. maculata* subsidy nearly tripled the growth of the young of the year steelhead trout (*Oncorhynchus mykiss*) in the recipient tributary over the summer months, and was more important than terrestrial invertebrate subsidies, which have been considered the primary food source for predators in small, forested creeks. By delivering food subsidies from productive but warming river mainstems to cool but food-limited tributaries, aquatic insect migrations could enhance resilience to cool-water predators in warming river networks.

Keywords

Aquatic insect, ecological resilience, food web, landscape, migration, river network, salmonid, spatial connectivity, subsidy, warming.

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INTRODUCTION

Animal migrations can link distinct ecosystems over large landscape scales (e.g. salmon from the ocean to rivers (Wipfli *et al*. 1998), continental migrations of snow geese (Jefferies *et al*. 2004) or monarch butterflies (Calvert *et al*. 1979)). Seasonal or life history migrations can concentrate many individual migrants into specific habitats, with large impacts on local communities, either as consumers (e.g. snow geese that migrate continentally, Jefferies *et al*. 2004), vectors of resources (e.g. salmon carcasses from the ocean to rivers, Wipfli *et al*. 1998) or diseases (Altizer *et al*. 2011). Habitat coupling by migratory animals may destabilize ecosystems (Jefferies *et al*. 2004), or enhance their resilience (Lundberg & Moberg 2003). Effective conservation and land management requires understanding natural migratory patterns of animals and their ecological significance (Bauer & Hoye 2014).

Fluxes of adult aquatic insects from productive rivers to riparian predators have attracted the attention of ecologists (Gray 1993; Nakano & Murakami 2001; Sabo & Power 2002). River to forest subsidies primarily occur near land-water margins, with fluxes declining exponentially with distance from the shore (Power *et al*. 2004; Muehlbauer *et al*. 2014), as adult aquatic insects stay near water for oviposition (Huryn & Wallace 2000). Adult aquatic insects, in fact, often actively fly along river corridors to aquatic oviposition sites. Müller (1982) hypothesised a ‘colonization cycle’ for riverine insects, in which upstream flight of adults compensated for downstream drift and active movement of larvae. Movement of adult aquatic insects along river corridors has been well documented (Williams & Williams 1993; Macneale *et al*. 2005). However, the effect of their longitudinal movements along channels on food webs is less well studied.

In river networks, many small tributary streams flow into larger mainstem channels. Large mainstem channels are generally wide, sunlit and warm, and typically have high biological productivity. Smaller tributaries are narrow, shaded and cool and typically have low productivity (Vannote *et al*. 1980). While small tributaries have received less public and political attention and protection, they make up a large part of the river network, and provide distinct habitats and ecological functions (Benda *et al*. 2004). Many cold-adapted stenothermic animals like juvenile salmonids and salamanders live in small shaded headwater tributaries that remain relatively cool through summer. However, shading by riparian vegetation often lowers productivity, so predators in tributaries are often food-limited, and rely largely on the allochthonous resource input such as terrestrial invertebrates and organic matter for food (Nakano & Murakami 2001; Baxter *et al*. 2005; Atlas *et al*. 2013).

At confluences where small shaded tributaries meet mainstems, the adjacency of contrasting environments enable some animals to exploit favorable habitats that may change for a given season, diel time period or life stage. For example, some amphibians (Kupferberg 1996; Wheeler *et al*. 2008) and fish (Fausch *et al*. 2002) are known to migrate across confluences between mainstems and tributaries in river networks. Movements of such species link mainstems and tributary communities. Similar migrations by aquatic insects (but see Hayden & Clifford 1974), which play critical roles in stream and riparian food webs, are poorly known. Here we document a previously unknown migratory pattern in the life history of the riverine mayfly (Fig. 1), *Ephemerella maculata* (Ephemerellidae), which is widely distributed across California (Allen 1968; Meyer & McCafferty 2008).

We hypothesised that adult migration of this mayfly, from productive mainstems to unproductive tributaries, could support consumers in tributaries. Recipient consumers include juvenile salmonids, which are increasingly thermally restricted to these cool refugia as mainstem habitats are warm due to factors like drought, water withdrawals and deforestation. This biological backflow could therefore prolong the persistence of salmonids and other cold-adapted stenothermic predators in warming river networks.

MATERIALS AND METHODS

Study system

We studied mayfly life history and its ecological consequences in the upper basin of the South Fork Eel River, in and around the Angelo Coast Range Reserve in Mendocino County, California (39°44′17.7″ N, 123°37′48.8″ W). Under Mediterranean seasonality, the South Fork Eel River watershed typically has wet winters and dry summers. Wide mainstem reaches of the South Fork Eel River (that drain > 80 km^2) are sunlit, and in summer, water column temperatures warm to 25°C (Fig. 2a and c). In contrast, smaller tributaries of the South Fork Eel River are shaded by riparian forest, and remain cool (Fig. 2b and c). Mainstems support productive blooms of attached algae (Power *et al.* 2008), which in turn support abundant aquatic insect larvae that feed not only aquatic predators (Finlay *et al.* 2002), but also on terrestrial insectivores (spiders, lizards, and bats) via emergence (Sabo & Power 2002; Power *et al.* 2004). In contrast, in small tributaries of the South Fork Eel, where primary productivity is light-limited (Finlay *et al.* 2011), algal accrual is limited and almost entirely suppressed by armoured grazers (*Glossosoma spp.*), which are largely avoided as prey by the dominant predators (McNeely *et al.* 2007). Therefore the predators in the small tributaries largely depend on allochthonous subsidies (Atlas *et al.* 2013) for their food.

The South Fork Eel River joins the Eel River, which flows into the Pacific Ocean. Anadromous steelhead trout (*Oncorhynchus mykiss*) spawn in the mainstem and tributaries of the South Fork Eel River. Juvenile steelhead rear in the river for 2 years before they migrate to the ocean. *O. mykiss* is the only fish found in small tributaries, co-occurring there with the Pacific giant salamander (*Dicamptodon tenebrosus*). The density of juvenile steelhead varies from year to year, with estimates for Fox Creek ranging from 0.17 to 1.5 individuals m^{-2}. In the South Fork mainstem, in contrast, the juvenile steelhead species are less dense, and outnumbered by other fishes, such as California roach (*Lavinia (Hesperoleucus) symmetricus*), three-spined stickleback (*Gasterosteus aculeatus*), and Sacramento pikeminnow (*Ptychocheilus grandis*) (Fig. 2d).

In this study, we investigated the distribution of adult and nymphal *Ephemerella maculata* in a 25-kilometer reach of the South Fork Eel River mainstem and ten tributaries (Fig. 3). We observed and quantified the mayfly subsidy flux and conducted a field experiment to evaluate its impact on consumers in Fox Creek, a tributary of the South Fork Eel River. Fox Creek drains 2.6 km^2, and during summer base flow is 0.5–2 m wide with pool depths ranging from 25 to 60 cm.

Life history description of *Ephemerella maculata*

In Fox Creek, floating accumulations of dead adult mayflies that cover large portions of pool surfaces have been observed by researchers during early summer for over 20 years. Mayflies were identified as *Ephemerella maculata* (Ephemerellidae) (Allen 1968) in 2010. To investigate how the life history of *E. maculata* led to massive accumulations of dead adult females in unproductive tributaries, we carried out intensive visual field observations in the South Fork Eel River and ten of its tributaries, including Fox Creek from 2012 to 2014.

Predator density and subsidy flux estimation

Areal rates of input of terrestrial and adult aquatic insects into Fox Creek were measured with pan traps and drift

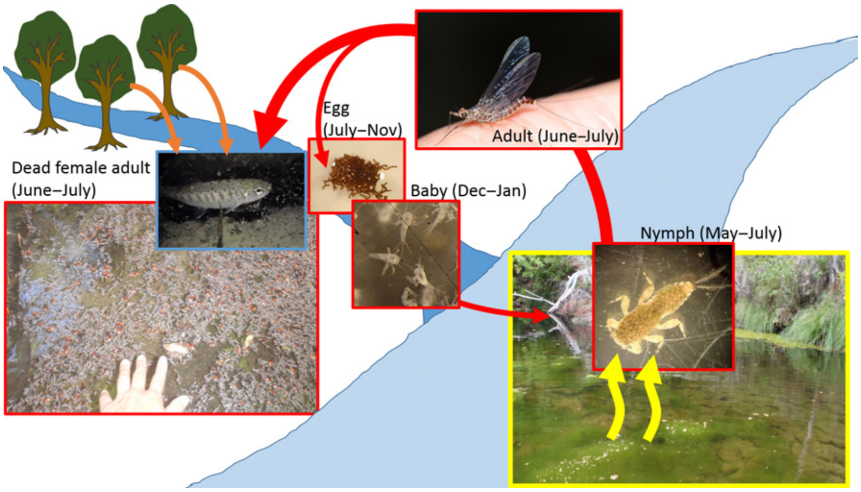

Figure 1 Life cycle of *Ephemerella maculata* and associated energy flow. *E. maculata* nymphs feed on algae in productive mainstem, then emerge as adults and mate. Female then fly into small tributaries, oviposit and die. The dead female adults subsidize predators rearing in cool unproductive tributaries including juvenile steelhead.

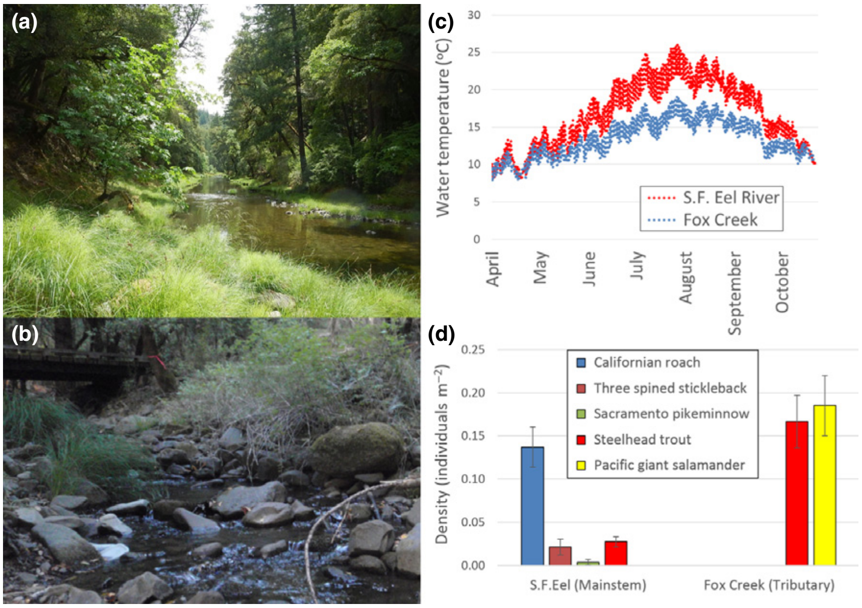

Figure 2 Environment and predator distributions in mainstem and tributary. (a) Mainstem of the South Fork Eel River. (b) Fox Creek, a tributary of the South Fork Eel River. (c) Water temperature in the South Fork Eel River and Fox Creek. (d) Major vertebrate predator densities in the South Fork Eel River and Fox Creek in 2013. Error bars show mean ± SE.

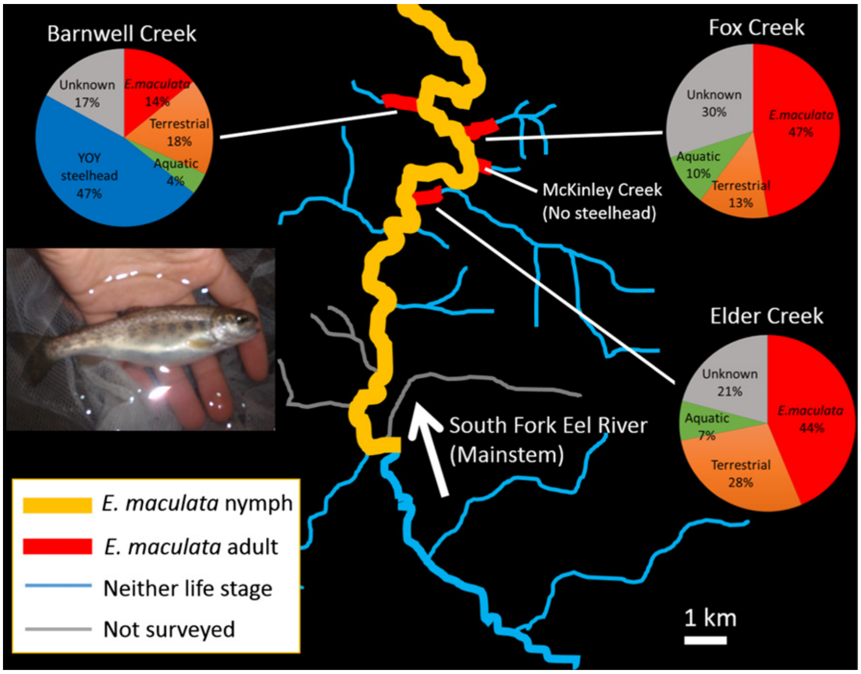

Figure 3 Migratory pattern of *E. maculata* in the headwater South Fork Eel River, and juvenile steelhead gut contents in *E. maculata* recipient tributaries. Red lines indicate reaches *E. maculata* adults but no nymphs were found; yellow lines indicate reaches where *E. maculata* nymphs but no adults were found; blue lines are reaches where neither adults nor nymphs *E. maculata* were found; grey lines are non-surveyed reaches. The pie graphs show the proportion of gut contents in 1 + steelhead trout in three creeks in June and July 2014. Inset, lower left: typical 1 + steelhead in Fox Creek with its stomach distended with *E. maculata* adults.

nets. To measure terrestrial insect subsidies, five transparent circular pan traps (30 cm diameter) were set on the water surface of Fox Creek for 24 or 48 h on five occasions from June through July 2012. Because *E. maculata* adults and many other adult aquatic insects selectively oviposit and get drawn into stepped riffles, their flux was not measurable with pan traps. Therefore, we set drift nets across the channel downstream of riffles, and measured mayfly input to each riffle, corrected for the capture efficiency of drift nets (Fig. S1). In June and July 2014, six drift nets were set out 9 times at

3–7 days intervals for 1–2 h periods at dusk, when most of adult aquatic insects, including *E. maculata* plunge into the water. Colour-marked Douglas fir katkins (floating tree flowers similar in size and buoyancy to spent adult *E. maculata*) were used to estimate capture efficiency of drift nets in each riffle where the subsidy was measured. We distributed 50 colour-marked katkins evenly over the riffle just upstream of the driftnet, and in the next two riffles upstream, with a distinct colour for each riffle. After 1–2 h, we counted how many of the released katkins were captured in the drift net. Very few katkins released into two most upstream riffles were captured in drift nets, so only inputs to the adjacent upstream riffle were considered as a source to the drift nets. The capture efficiency from the nearest riffle varied from 34–92% among riffles. Biomass of *E. maculata* and adult aquatic insects captured in drift nets was divided into the capture efficiency estimated for the given riffle to estimate total input to the riffle, which was then divided by the area of the riffle to estimate area-specific input. Finally, the estimated mayfly input per riffle area was converted into the biomass per channel area by multiplying the input per riffle by the proportion of the total wetted channel area made up of riffles (46%) over the surveyed reach.

The densities of fish and salamanders in Fox Creek and the South Fork Eel River were estimated by visual counts from the banks at night and snorkeling surveys in July 2013 following the methods described in Hankin & Reeves (1988). In Fox Creek, 24 riffles and pools over a 300 m reach were mapped, surveyed and all the fish and salamanders were counted. In 2013, Fox Creek steelhead fell almost entirely into two age classes: young-of-the-year (age 0, hereafter YOY) and juveniles of more than 1 year of age (hereafter 1 +). In the South Fork Eel River, 7 riffles and 7 pools in an 1130-m reach near the Fox Creek confluence were surveyed and all the fish and salamanders were counted. Densities were estimated as counts per water surface area.

Gut contents analysis

Juvenile (1 +) steelhead diet composition was quantified in three creeks (Fox Creek, Elder Creek, Barnwell Creek: Fig. 3) where *E. maculata* adults oviposit. Sixty-eight juvenile steelheads (47 in Fox Creek, 11 in Elder Creek, and 10 in Barnwell Creek) were captured by night-time dip-netting in each creek over 1 or 2 days. We used non-lethal gastric lavage, which limited our diet samples to larger (1 +) individuals. The sampled 1 + steelhead were 105.9 ± 2.5 mm standard length, and 14.4 ± 1.1 g live weight. The gut contents of each individual were filtered through 0.3 mm mesh nylon netting in the field, and frozen within 3 h. Fish gut contents were separated into categories (i.e. *E. maculata*, other aquatic insects, terrestrial insects, fish and other unknown species) under a dissecting microscope. Each category of food from each individual fish was separately oven dried at 60°C for 24 h and weighed. The proportion of the gut contents in each creek was calculated by summing each category of gut contents weight of all individual fish in the creek, and dividing by the total gut contents weight of all individual fish in the creek.

Field manipulative experiment

A manipulative field experiment was conducted in Fox Creek to evaluate the impact of the *E. maculata* subsidy relative to that from other terrestrial insects on growth of YOY steelhead in Fox Creek, we manipulated both subsidies experimentally. After 4 weeks, we compared the growth of YOY steelhead trout among treatments: with and without terrestrial subsidy, and with and without the *E. maculata* subsidy (Fig. 4).

Sixteen reaches of Fox Creek, each containing one upstream riffle and one downstream pool, were fenced with 5 mm mesh Vexar® plastic fence to enclose YOY steelhead for the experiment. The sixteen reaches spanned 300 m of Fox Creek, and were spaced more than 2 m apart. The area of the enclosed reaches ranged from 5.1 to 22.9 m^2, and the maximum depth varied from 25–60 cm. The 16 reaches were divided into four blocks of four reaches from upstream to downstream, and within a block, each experimental reach was randomly assigned one of four treatments: each combination of *E. maculata* subsidy and terrestrial subsidy presence or absence in a crossed design. (Fig. 4b).

We used past field estimates to determine our experimental stocking densities. Juvenile steelhead densities in Fox Creek varied from year to year. In 2013, juvenile steelhead species were present at densities of 0.071 individuals m^{-2} (YOY) and 0.096 individuals m^{-2} (1 +). In 2009, densities of YOY and 1 + steelhead were 1.25 individuals m^{-2} and 0.26 individuals m^{-2}, respectively. We chose an average of these YOY estimates for our experimental stocking density of 0.6 individuals m^{-2} of YOY. 1 + and larger steelhead trout were removed from the enclosures to avoid the risk of predation on YOY steelhead, as *O. mykiss* is threatened in California. All YOY steelhead species for the experiment were collected from the experimental reaches of Fox Creek, and randomly assigned and redistributed to enclosures 1 week prior to the beginning of the experiment. We standardised the density and size of YOY steelhead species among all four treatments, so that at the onset of the experiment, there were no statistical differences in initial size among treatments (Table S1).

To control the migratory subsidy, we used driftnets and dipnets to remove *E. maculata* adults floating on Fox Creek after oviposition every day from early to late June during their flight period. These mayflies were frozen. We began the enclosure experiment as soon as their flight period ended in early July by adding defrosted *E. maculata* to mainstem subsidy-present treatments every dusk until the experiment ended in early August. We standardised this input of the *E. maculata* at average levels measured during their flight period, adjusting *E. maculata* input to juvenile steelhead density, so that each individual received 1.5 g in wet mass, equivalent to 0.23 g in dry mass of *E. maculata* adults per day for 1 month. Based on the previous estimate, the mean *E. maculata* adult flux into Fox Creek was 0.152 g $m^{-2}d^{-1}$. As the density of fish in the creek is 0.6 individuals m^{-2} on average, the *E. maculata* adult subsidy that each fish received was estimated to be 0.25 g d^{-1} (0.152 g $m^{-2}d^{-1}$ divided by 0.6 individuals m^{-2}). Therefore, the amount added in the experiment was slightly less than the

Figure 4 Design of the field experiment. (a) experimental manipulation of mayfly subsidy and terrestrial subsidy (b) The distribution of field sites in Fox Creek. The thin lines are 1 m contour lines, and the thick lines are 5 m contour lines. The bold line shows the border of Fox creek watershed.

natural input of *E. maculata* adults into the creek available per capita to rearing steelhead. The terrestrial subsidy was excluded from terrestrial-free treatments with roofs of transparent plastic and screen (Fig. 4a) after the method of Atlas *et al.* (2013). Roofs had no effect on temperature, water flow, or chlorophyll-a in benthic algae in enclosed pools (Table. S2 and S3).

All steelhead were individually tagged (Fig. S2) and their body sizes (wet mass and standard length) measured at the beginning and the end of the experiment. Visible Implant Elastomer Tags (Northwest Marine Technology, Inc.) were injected under the skin of all YOY steelhead, and individuals were distinguished with distinct combinations of colour and position on the body. Initial average standard length and body weight of YOY steelhead used in the experiment was 46.0 ± 1.3 mm and 1.96 ± 0.14 g.

To examine indirect effects of subsidies to predators on the other community members, we measured chlorophyll-a and the benthic invertebrate density in each site before and after the experiment (Table S2). Algae were sampled from three cobbles in each enclosed pool: 25 cm^2 of the cobble surface was scrubbed to collect algae and biofilm, and acetone extraction and fluorometry were used to estimate the mean chlorophyll-a per area on each sampled area. All benthic invertebrates > 1 mm long were counted on three randomly selected benthic cobbles 10–20 cm in median diameter.

Changes in standard length and weight of the YOY steelhead in each site were analysed, using a two-way randomised block design ANOVA, with longitudinal (upstream-downstream) block treated as a random factor. The analyses were performed on average growth values of the individual fish in length (mm) and weight (g) within each enclosed pool. Cochran's tests confirmed that variances were homogeneous among treatments, so the analyses were conducted on untransformed data. Preliminary tests found no evidence of interactions between the two treatments and blocks ($P > 0.8$ in all cases), so sums-of-squares for these interactions were pooled into the error mean square prior to testing the main effects.

Seasonality of growth of free-swimming fish

The standard length of YOY steelhead trout was measured five times throughout the year from 2013 to 2014 (Fig. S1). In each sampling event, ten or more YOY steelhead trout species were captured, measured, and released outside the enclosures in the same reach of Fox Creek where *E. maculata* subsidies occur.

RESULTS

Life cycle of *Ephemerella maculata*

Intensive field observations (2012–2014) in the upper South Fork Eel River revealed that different life stages of the mayfly *E. maculata* occupy different habitats, suggesting a migratory life cycle. Large (5 –10 mm) late-stage nymphs occur only in sunlit rivers from May to July, where they sometimes dominate benthic invertebrate assemblages. Ovipositing adult female *E. maculata* were only found flying above small tributaries (in four of ten surveyed, Fig. 3), up to 1 km upstream the confluences with mainstem reaches where *E. maculata* nymphs occurred. Adult females emerge from the mainstem reaches, mate, then fly into tributaries every evening for about 30 min at dusk for a month between June and July. Ovipositing females plunge into white water in riffles, drop their egg masses, and die on the water surface, to float downstream and collect in pools occupied by juvenile steelhead. *E. maculata* eggs sink and stick to the riverbed, remaining in the tributaries in a resting state until December, when they hatch and the small first instar nymphs drift down tributaries into the mainstem (Fig. 1). The timing of the life cycles varies across rivers, years, and locations: dates of observations of *E. maculata* nymphs in rivers throughout California have ranged from March to August (Meyer & McCafferty 2008).

Resource subsidy to tributary predators

In Fox Creek where *E. maculata* adults were observed from early June until early July in 2014, the estimated input of *E. maculata* from the confluence with the mainstem to 1 km upstream was 0.15 ± 0.06 SE g dry mass $m^{-2}d^{-1}$ (86.2 individuals $m^{-2}d^{-1}$). In contrast, the average input of terrestrial insects and other adult aquatic insects into Fox Creek during this same period was 0.075 ± 0.031 g dry mass $m^{-2}d^{-1}$ and 0.0015 ± 0.0007 g dry mass $m^{-2}d,^{-1}$ respectively.

Stomachs of juvenile steelhead in recipient tributaries were distended during the mayfly flight period, and gastric lavage showed that their stomachs were full of dead *E. maculata* adults (Fig. 3). In the creeks where *E. maculata* migrated, adult mayflies were the dominant food item in the guts of 1 + steelhead trout, making up 14–47% (average proportion) of gut contents. Few gut contents of YOY steelhead trout were examined, as they were generally too small for non-lethal gastric lavage. We observed, however, that YOY steelhead trout also foraged on *E. maculata* adults. We also observed active foraging on adult *E. maculata* by other predators in tributaries: pacific giant salamanders (*Dicamptodon tenebrosus*), foothill yellow-legged frogs (*Rana boylii*), water striders (*Gerris remigis*), spiders (*e.g. Tetragnatha spp.*) and bats (*Myotis spp.*)

Effect of the subsidy on YOY steelhead growth

In enclosed segments of the creek where YOY steelhead received the *E. maculata* subsidy, they grew nearly three times more than without the *E. maculata* subsidy, while exclusion of the terrestrial subsidy had no significant effect (Fig. 5, Table S1). YOY steelhead that received the *E. maculata* subsidy grew 6.6 ± 0.7 mm (14.3%) in length, and gained 0.68 ± 0.07 g (34.7%) in live weight over the month-long experiment, while the steelhead without the *E. maculata* subsidy grew 2.8 ± 0.7 mm (6.1%) and had little or no weight change (-0.08 ± 0.11 g; −4.1%). During this 1-month period (which this year was after the flight period for mayflies), the *E. maculata* subsidy increased YOY steelhead growth threefold over the average growth in length and weight [1.5 ± 0.5 mm (3.3%) and 0.42 ± 0.09 g (21.4%)] of free-swimming YOY steelhead in the same creek reaches outside the enclosures. Potential indirect impacts of subsidies on algae and benthic invertebrates were also examined, but no effects were detected (Table S2).

Seasonal growth patterns of YOY steelhead trout in Fox Creek showed that free-swimming YOY steelhead trout grow very rapidly when *E. maculata* migrate into tributaries (Fig. 6). The eggs of steelhead trout are laid in February and March, and the YOY fly (20–30 mm standard length) emerge from the stream bed in late May. They grow rapidly until August, with little growth over the subsequent winter.

DISCUSSION

This newly discovered adult mayfly migration represents a cryptic but potentially important trophic pathway that can support food-limited predators in headwaters and small tributaries. Our observations and experiment show that the *E. maculata* subsidy can support and enhance growth of YOY steelhead trout rearing in small tributaries during a critical growth period. While terrestrial subsidies have been considered the primary food source for juvenile salmonids rearing in small creeks, the effects of terrestrial insects on YOY steelhead growth were insignificant in our experiment. Mainstem-to-tributary subsidies should be further considered, in addition to subsidies from watersheds and from the ocean, as potential trophic linkages that can fuel food webs and add resilience to river networks.

The *E. maculata* subsidy lasts for only 1 month, but it occurs in summer when the tributary water temperatures result in high rates of YOY steelhead growth. YOY steelhead trout in Fox Creek grew rapidly when the *E. maculata* subsidy occurred, but added little length over the rest of the season (Fig. 6). At favourable temperatures, the food demand of juvenile salmonids increases, along with their growth rates if food levels are sufficient (McCullough *et al.* 2009). Our experiment showed that summer growth of YOY steelhead is food-limited without the *E. maculata* subsidy. The *E. maculata* subsidy is also likely stored as lipid to fuel annual growth, as has been shown for other salmonids exploiting resource pulses (Armstrong & Schindler 2011; Armstrong & Bond 2013). Increased summer growth and lipid stores should also increase overwinter survivorship (Biro *et al.* 2004). Although the terrestrial subsidy flux measured in this study (0.075 g $m^{-2}d^{-1}$) is similar to the flux of terrestrial subsidy Nakano and Murakami (2001) reported in summer in Japan (0.050–0.130 g $m^{-2}d^{-1}$) as being a significant food source for aquatic predators, its contribution to YOY steelhead growth was small when compared to the *E. maculata* subsidy, and not statistically detectable in our month-long experiment. Lower-level but more prolonged terrestrial subsidies likely contribute to fish production over the rest of the year, but the *E. maculata* subsidy is more important for the summer growth of YOY steelhead in our system.

Synchrony of the subsidy both in time of the day (~30 min at dusk) and season of the year (1 month from June to July) distinguishes the *E. maculata* subsidy from other subsidies in the nature. *E. maculata* adults accumulated in pools or stranded along shores are indicative of predator satiation or handling time limitation. The stomach parts of many (both YOY and 1 +) steelhead were distended and full of *E. maculata* adults when subsidised. The pulsed nature of the subsidy appeared to reduce or eliminate agonistic interactions of juvenile steelhead in Fox Creek, within and across cohorts. At very high levels of food abundance, agonistic behaviours to defend food resources is often abandoned, as there is little benefit from interference when all foragers are satiated (Davies & Houston 1984). In the experiment, we only used YOY steelhead trout to avoid the risk of cannibalism. However, we believe the benefit to YOY from the *E. maculata* subsidy would not change in the presence of 1 + steelhead trout,

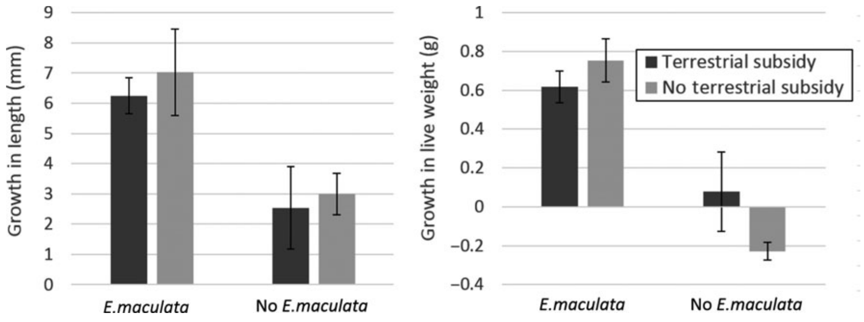

Figure 5 Growth of juvenile steelhead in standard length (a) and live weight (b).The *E. maculata* subsidy significantly increased the growth of the juvenile steelhead (standard length: $F_{1,9} = 12.5$, $P = 0.006$, weight: $F_{1,9} = 41.7$, $P = 0.0012$), while the terrestrial subsidy did not (standard length: $F_{1,9} = 0.32$, $P = 0.6$, weight: $F_{1,9} = 0.55$, $P = 0.5$). The interaction of the treatments were not significant (standard length: $F_{1,9} = 0.03$, $P = 0.88$, weight: $F_{1,9} = 3.5$, $P = 0.095$). Error bars show mean ± SE.

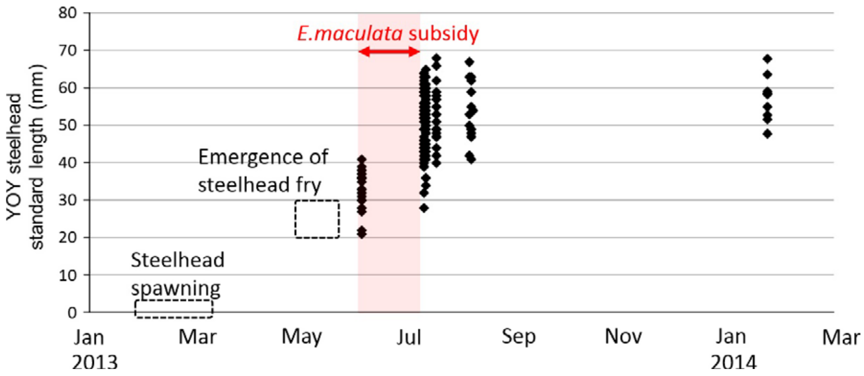

Figure 6 Annual growth of YOY steelhead in Fox Creek. The eggs of steelhead trout were deposited between February and March 2013, and the first steelhead fry (20–30 mm standard length) emerged from the nest to the water column on May 14th in 2013. The juvenile steelhead grow rapidly until mid-August, then maintain their body size until the next spring.

given that the 1 + steelhead trout would also be satiated by the *E. maculata* subsidy. Although not examined in this study, it seems likely that the *E. maculata* subsidy would decrease predation by 1 + steelhead on YOY, and therefore increase YOY survivorship.

A trophic subsidy to shaded cool tributaries would be particularly important for cold-adapted stenothermic predators like salmonid juveniles, which are concentrated in these thermal refugia in warming rivers (Fig. 1d). As summer river temperatures warm above 20°C, juvenile salmonids become increasingly physiologically stressed (Richter & Kolmes 2005; McCullough *et al.* 2009), and also more susceptible to parasites and diseases (Marcogliese 2001; McCullough *et al.* 2009), as well as competition or predation from invasive warm-water fishes (Reese & Harvey 2002). Therefore, small tributaries that sustain cooler water over summer would be critical refuges to stenothermic predators like juvenile salmonids and many salamanders. The density of juvenile steelhead in Fox Creek was five times higher than in the river mainstem (Fig. 2d). The *E. maculata* subsidy occurred only in the downstream reaches of tributaries; however, these locations are particularly an important habitat for anadromous salmonid juveniles whose distribution is limited by adult upstream migration. In Fox Creek in 2012, steelhead in the *E. maculata* subsidy recipient reach were twice as abundant as those occupying reaches more than 1 km upstream of the confluence (0.32 ± 0.09 individuals m^{-2} compared to 0.17 ± 0.08 individuals m^{-2}). By redistributing resources from the productive but stressfully warm mainstems river to cool, but food-limited tributaries, the *E. maculata* migration could help sustain cold-adapted stenothermic predators in river networks.

Prey movements that support stenothermic predators may be of increasing importance in warming rivers and other habitats. With deforestation, water withdrawals and climate warming, temperatures of river mainstems are increasing (Webb *et al.* 2008). Shaded tributaries that remain cool through the summer rearing period are increasingly important thermal refugia for juvenile steelhead and other cold-water native species. California is at the southern limit of the geographic range of coho salmon (*Oncorhynchus kisutch*), chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout. The *E. maculata* migration that delivers food resources from productive warm mainstem rivers to adjacent cool, otherwise food-limited tributaries, could help rearing salmonids persist in warming river networks in California.

Migrations of adult aquatic insects from mainstems to tributaries, though not yet well-known, may be widespread. Another mayfly *Leptophlebia cupida* (Hayden & Clifford 1974) also migrates between mainstem and tributaries, but the nymphs migrate from mainstems to tributaries, in the opposite direction to *E. maculata*. Longitudinal flights of adult aquatic insects have been widely observed (Müller 1982; Williams & Williams 1993; Macneale *et al*. 2005), but the extent to which these flights traverse confluences is not yet known. Movements of adult aquatic insects are cryptic. It is far more difficult to observe aerial adult aquatic insects than the movements of their larvae in water (Macneale *et al*. 2004). Flight and mating activity can occur high above the ground, and in many species, including *E. maculata*, reproductive migrations are tightly synchronised within narrow seasonal and diel time windows. The lack of taxonomic expertise to associate adult and juvenile life stages of potential migrants may also challenge field biologists attempting to study whole life cycles of aquatic insects. More collaborative research on life histories of aquatic insects by field biologists and taxonomists, along with new technologies such as isotope analysis (Macneale *et al*. 2005) and genetic tools (Valentini *et al*. 2008) may help reveal whether similar migrations in other insect taxa convey undetected subsidies from productive mainstems to predators in tributaries.

The importance of trophic subsidies across habitat boundaries has long been recognised by ecologists (Summerhayes & Elton 1923, Polis *et al*. 1997). Subsidies delivered by directed migrations of small organisms, however, are more difficult to detect than chronic cross-habitat fluxes of multiple resource species over relatively short distance (e.g. seaweed stranded on the coast (Polis & Hurd 1995), or aquatic insects dispersing into forests (Power *et al*. 2004)). While animal migration can transport massive amounts of resource over long distances, the short duration of these synchronised population life history events may make them harder to observe. Long-distance movements of migrants from their source to recipient habitats may also make it harder to recognize the subsidy fluxes they contribute. While migrations are commonly known for large animals like mammals, birds and fish, migratory patterns of small animals like insects are understudied, except for a few species like locust, monarch butterflies or milkweed bugs (Dingle 2014). Further study of insect migrations may reveal additional cryptic trophic linkages over landscapes with large potential ecosystem impacts. In river networks, the importance of habitat connectivity for migratory fish, especially for salmonids, is well known. Much remains to be learned, however, about how salmonid persistence in freshwater rearing habitat is influenced by migrations of their food organisms, and the habitat features required by these invertebrate river migrants. Given the strong impact of a single migratory species, *E. maculata,* in tributaries where it was detected, we suggest that occurrence and impacts of other such migrations in river drainages be further examined, so that the environmental features and types of connectivity that support such services can be maintained in watersheds.

Rivers and many other natural environments exhibit surprising degrees of thermal heterogeneity at small to large scales (Nielsen *et al*. 1994; Helmuth & Hofmann 2001). With global warming, habitat shifts of cold-adapted stenothermic animals to cooler local habitats could allow their survival and persistence (Kearney *et al*. 2009; Moritz & Agudo 2013; Scheffers *et al*. 2014), but if productivity in cool refugia is light- or temperature-limited, taking refuge may come at the cost of lowering their energy intake. Migration-mediated subsidies and other fluxes of prey or food resources from warm, productive habitats to cool refugia could help sustain cold-adapted consumers in a warming world. Conservation of environmental features that connect habitats is needed, not only for consumers, but also, in some cases, for their important mobile prey.

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AUTHORSHIP

HU and MEP designed the study, HU performed the research and both HU and MEP wrote the manuscript.

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