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EMERGENCE PHENOLOGY OF THE GIANT SALMONFLY AND RESPONSES BY BIRDS
IN IDAHO RIVER NETWORKS

By

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To the Graduate faculty:

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EMERGENCE PHENOLOGY OF THE GIANT SALMONFLY AND RESPONSES BY BIRDS
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Thesis Abstract – Idaho State University (2019)

Emergence of adult aquatic insects depends on water temperature and its timing influences this ephemeral but often critical resource for terrestrial insectivores. Spatial heterogeneity in timing of emergence and its consequences for terrestrial insectivores are poorly understood. We investigated the emergence phenology of the giant salmonfly (*Pteronarcys californica*) at three different scales in two Idaho river networks, and we studied the influence of tributary confluences on this timing, along with associated bird responses. At the basin-scale, salmonfly emergence timing was patchy, whereas at the scale of a sub-drainage, emergence followed a downstream-to-upstream pattern. At the scale of reaches thermal discontinuities created by tributary confluences created asynchrony in salmonfly emergence. Many bird species consumed salmonflies and some captured large numbers of them. Emergence asynchrony created by tributaries was associated with shifts in bird abundance and distribution as they apparently tracked the availability of this pulsed prey resource.

Key Words

stream invertebrate, food webs, *Pteronarcys*, salmonfly, birds, tributary confluences, resource subsidies, resource waves

INTRODUCTION

Aquatic and terrestrial ecosystems are connected across spatial boundaries (Hynes, 1975; Wallace et al., 1997) and are characterized by strong reciprocal linkages (Baxter et al., 2005). Through exchanges of materials and organisms from one habitat to another, referred to as “resource subsidies,” population and community dynamics of the two habitats are connected (Polis et al., 2004; Schindler and Smits, 2017). Resource subsidies vary over space and time, and can take several forms, including nutrients, detritus, or organisms (Polis et al., 1997). For example, a study conducted by Nakano and Murakami (2001) found that across-habitat fluxes of stream and forest invertebrate prey subsidized both birds and fishes, accounting for 26% and 44% of the annual total energy budget of the bird and fish assemblages, respectively. Such reciprocal linkages within food webs are based strongly on exchanges of organisms and detritus, and can represent crucial resource fluxes both seasonally and annually.

Emergence of aquatic insects, specifically from rivers, lakes and streams, is a common and widespread example of a biologically mediated transfer from water to land (Jackson and Fisher, 1986; Baxter et al., 2005). Studies have shown the importance of the flux of emerging adult aquatic insects to terrestrial organisms and food webs (Iwata et al., 2003; Paetzold et al., 2005; Power et al., 2004). Emerging adult aquatic insects can act as prey for variety of consumers, and the exoskeleton left behind during emergence can provide nutrients to terrestrial soils (Dreyer et al., 2015). Aquatic insects are an important food for a suite of terrestrial insectivores including spiders, lizards, and birds (Nakano and Murakami, 2001; Sabo et al., 2002; Marczak et al., 2008), and a synthesis by Baxter et al. (2005) illustrated that emergent adult aquatic insects can contribute 25-100% of the energy used by populations of a suite of

terrestrial organisms. Gaining access to emergent aquatic insect can have profound effects on recipient consumer populations.

Due to the seasonality of the emergence of many aquatic insects, time may be a limiting constraint on responses by insectivores. Resources may appear abundant when averaged across time, yet due to temporal variation in availability, prove to be limiting (Sinclair, 1975). For example, food availability can be pulsed with strong seasonal variation, resulting in times of scarcity, interspersed with superabundance (Yang et al., 2008). Several studies have explored how trophic interactions are mediated by the timing of prey life histories relative to those of consumers (Visser et al., 1998; Winder and Schindler, 2004), as well as how variation and asynchrony in resource phenology may mediate trophic interactions by causing temporary constraint of consumers via satiation (Ims, 1990). Studies of the timing of resource fluxes have shown that the temporal characteristics of their availability can strongly affect consumer responses (Yang et al., 2008). However, the influence of aquatic insect emergence patterns and timing on insectivore responses remains largely unknown.

Resource pulses, defined as "...episodes of increased resource availability that combine low frequency (rarity), large magnitude (intensity), and short duration (brevity)" (Yang et al., 2008), provide mobile consumers food resources that are ephemerally available (Armstrong et al., 2016). Ephemeral fluxes, such as the emergence of adult aquatic insects, are a good example of this phenomenon. Spatial heterogeneity in phenology of prey organisms can cause asynchronous development, resulting in prey life-stages that are profitable for the consumer being reached at different times in different places (Armstrong et al., 2016). Such heterogeneity may produce pulsed foraging opportunities for consumers (Werner and Gilliam 1984; Wilmshurst et al., 1999; Yang et al., 2008). Due to insect life cycles being partially dependent on

water temperature, which can be heterogeneous over a variety of spatial scales, emergence may exhibit asynchronous peaks in quantity, quality and accessibility driven by combinations of environmental heterogeneity and variation in species life histories. In turn, this could mediate responses by terrestrial insectivores, such as birds. It is unknown if asynchronous pulses in aquatic insect emergence cause an associated shift in bird abundance at different times in different places.

Foraging opportunities for a consumer may not occur in response to a single synchronized resource pulse alone, but may track an asynchronous series of pulses that propagate across space and time, which Armstrong et al. (2016) refers to as a “resource wave.” Such pulses may be important when a prey species is only available to a given consumer during a specific developmental stage (Deacy et al., 2016). Several studies have illustrated how spatial variation in the phenology of resources can enhance the seasonal energy consumption for a variety of consumers who may track and exploit the asynchronicity of resource pulses across a landscape at various scales. For example, ungulates track spring vegetation to higher altitudes (Bischof et al., 2012); both glaucous-winged gulls and coastal brown bears track the migrations of spawning anadromous fishes upstream (Schindler et al., 2013); surf scoters swim northbound parallel to the herring migration and consume their energy-rich eggs as they spawn at increasingly northern latitudes (Lok et al., 2012; Armstrong et al., 2016). Such mobile consumers are able to protract their foraging opportunities by tracking a resource as it occurs across different habitats through space and time. Emergence of aquatic insects has not been studied in this context, though it may occur as asynchronous pulses across the landscape or in river networks, allowing consumers, such as birds, extended foraging access.

Habitat variation in rivers can influence aquatic insect community composition and timing of life histories, with potential consequences for emergence timing that could create heterogeneity in resources for terrestrial insectivores. Physical conditions of a river such as discharge, channel form and temperature have long been studied in relation to river ecology, for example, the “River Continuum Concept” (Vannote et al., 1980) hypothesizes that a continuous gradient of physical conditions should result in a continuum on river biota. However, scientists have challenged the simple RCC predictions, illustrating that tributary confluences can create discontinuities in physical habitats, resulting in ecological patchiness (Montgomery, 1999; Poole, 2002; Benda et al., 2004). Tributary confluences can alter environmental conditions of the mainstem such as temperature and discharge (Rice et al., 2008), which are important to stream biota and may elicit biological responses from organisms such as aquatic insects (Bruns et al., 1984; Rice et al., 2001). Moreover, as conceptualized by Benda et al (2004) in their “Network Dynamics Hypothesis,” tributary confluences are locations in networks at which influences of explains disturbances propagate and create important ecological heterogeneity (Benda et al., 2004). In this context, confluences are not viewed as aberrations along a continuum, but as important to the heterogeneity and dynamics of the broader ecosystem, which may include offsetting synchrony in organism phenology and increasing life-history diversity of riverine organisms (Moore et al., 2015). Such spatial discontinuities can affect the flow of ecologically important materials (Kiffney et al., 2006), but the effect of thermal heterogeneity created by tributary confluences on the emergence patterns of aquatic insects has not been studied.

Phenological variation in the life histories and emergence timing of aquatic insects created by habitat heterogeneity may affect consumer behavior. Investigation of this possibility, however, has primarily been conducted at scales of a reach or smaller. For example, small-scale

spatial heterogeneity in stream water temperature desynchronized the emergence timing of a mayfly, leading to their increased availability to and influence on riparian spiders (Uno 2016). Similarly, stream meanders influence the flux of aquatic insects into the riparian forests, which caused an increase in insectivorous bird abundance (Iwata et al. 2003). Thus, response of aquatic insect emergence to habitat heterogeneity at larger scales has not been the focus of investigation, nor has the potential consequence of such variation for predators that may be mobile at such scales. Additionally, tributary confluences as mediators of aquatic insect emergence timing have not been studied, nor has their potential importance in prolonging birds' access to these prey.

Giant salmonflies, *Pteronarcys californica* (Order Plecoptera), are large-bodied aquatic insects whose emergence is an iconic character of wild rivers of the western U.S. Salmonflies have distinct characteristics, the most obvious being their size; nymphs can reach 35 to 50 mm in length prior to emerging (Kauwe et al., 2004). Additionally, as adults, they have a bright orange band behind their head and on the underside of their abdomen, and have broad, flat wings that are darkly veined. The duration of their nymphal stage is 2-4 years (Stewart and Stark, 1993), with their rate of development influenced by water temperature (Baumann et. al., 1977; Poole, 1981). For salmonfly nymphs to attain maturity, a cumulative regimen of development is required (customarily measured in degree-days), as is common among aquatic insects (Sweeney, 1984). Thus, their emergence appears to be water temperature dependent and under warmer thermal regimes, it typically occurs sooner (Gregory et al., 2000). Additionally, the carbon flux associated with salmonfly emergence can be very large, in some rivers contributing up to 250% of the predicted annual carbon flux of the rest of the insect assemblage combined (Walters et al., 2018). Annually, salmonfly emergence at a given location is a highly synchronized event, occurring over two weeks in early summer, such that at different spatial and temporal scales, it

may be a pulsed event (Walters et al., 2018). Because the timing of emergence is associated with water temperature, salmonflies are an interesting case for investigating the effect of thermal discontinuities created by tributary confluences, which may be expressed as asynchrony in their emergence timing.

Timing of giant salmonfly emergence may have consequences for insectivores, such as birds, whose typical breeding seasons may span the weeks of salmonfly emergence. Iwata et al. (2003), through direct observation, found that aquatic insects composed up to 82.3% of the diet of birds such as flycatchers, and up to 66.7% of the diet of gleaners. Although it is known that birds feed on aquatic insects, there have been no published investigations of the relationship between birds and salmonflies. Due to the importance of aquatic insects in a bird's diet, it is possible that these highly mobile consumers may take advantage of pulses of salmonfly emergence created by thermal discontinuities, and could track the prolonged availability of salmonflies at different scales within a watershed. Relationships between the asynchronous emergence of salmonflies driven by thermal discontinuities created by tributary confluences and the response of birds to the asynchrony remain unknown.

Here we investigated the emergence patterns of the giant salmonfly across time and space at three different scales within the thermally heterogeneous Salmon River Basin. We also investigated the temporal asynchrony in salmonfly emergence associated with tributary confluences, and the behavioral responses of birds above and below confluences at the scale of reaches in the Salmon River Basin, as well as in the Henry's Fork of the Snake River watershed. With this combined approach, we addressed the following questions:

- 1) How does emergence of giant salmonflies vary across space and time at different scales within a river network?

- 2) Is asynchrony in emergence timing associated with thermal discontinuities created by tributary confluences?
- 3) Is bird abundance and species richness associated with the presence of salmonflies?

METHODS

Study areas

We conducted this study in the Salmon River Basin (11T 678863 4851692) in central Idaho, and within the Henry's Fork of the Snake River watershed (12T 422893 4844861) in southeastern Idaho. We chose these basins for several reasons, including the presence of robust populations of salmonflies. The Salmon River Basin has an overall network topology contributing to a series of mid-sized rivers joining each other at major confluences. Additionally, the Salmon River is free-flowing and drains a mixture of elevations, which combined with topographic complexity, contributes to thermal heterogeneity (Tang et al., 2012), potentially influencing the timing of salmonfly emergence.

Because we wanted to expand the scope of inference associated with our observations, we also conducted investigations at a pair of confluences in the Henry's Fork of the Snake River watershed. The Henry's Fork has strong thermal discontinuities associated with major spring water influences (Gregory et al., 2000), which could contribute to differences in emergence timing. Additionally, salmonfly emergence generally occurs weeks earlier than in the Salmon River Basin, which from a logistical standpoint allowed us to conduct measurements in both settings. Bird communities differ somewhat between the two study areas. For example, Lewis's woodpeckers (*Melanerpes lewis*) are abundant and (as we report below) forage on salmonflies in the Salmon River Drainage, whereas American Robins (*Turdus migratorius*) are abundant and forage on salmonflies in the Henry's Fork watershed. However, we judged that any similar

patterns in the change of bird abundance and species richness in response to salmonfly presence across sites in the two watersheds reasonably could be combined in terms of ecological trophic effects.

Study Design

To evaluate the questions described above, we investigated the spatial and temporal variation in emergence of giant salmonflies at three different scales: the basin, the sub-drainage and the reach. At the scale of the reach, we also investigated the behavioral response of birds to the temporal asynchrony of salmonfly emergence associated with thermal discontinuities created by tributary confluences. Due to seasonality in salmonfly emergence, field investigation was conducted across several weeks (May – June) in 2018.

We used a nested, hierarchical approach. First, we stratified the tributary confluences by the presence of salmonflies. Second, we stratified the tributary confluences within the Salmon River Basin by major sub-drainages, or forks of the river (e.g., mainstem, South Fork and Middle Fork). Third, in both the Salmon River Basin and Henry's Fork watershed, we further stratified confluences by identifying those whose tributary was large enough (i.e., by discharge) relative to the size of the mainstem that it would be potentially sufficient to create an ecologically meaningful thermal discontinuity (Benda et al., 2004). We then selected confluences across an elevation gradient, from the headwaters high in the basin, to the mainstem lower in the basin, encompassing hundreds of kilometers of river. Thus, all of the chosen confluences included a tributary within two orders of their mainstem, ranging from first to eighth-order, but were generally larger streams and mid-sized rivers (5th to 8th order), with the exception of those in the Henry's Fork of the Snake River basin. Warm River is a first-order stream, but is a large, spring-fed stream and contributes 15.6% of the average May discharge of the mainstem Henry's Fork.

Robinson Creek is a second-order stream, but contributes 18.6% of the average May discharge to the mainstem Henry's Fork. In addition, we chose confluences that were not in urban areas or in areas of high land-use, because we wanted to avoid human impacts on salmonflies (Elder and Gaufin, 1973) or birds in riparian areas. Finally, because of the logistical challenges of visiting a large number of sites in a short time period, we were not able to survey the highly remote locations (which would have required many days of backcountry travel), but chose sites that were relatively accessible (i.e., within one day of travel). Overall, between the two river basins, we identified 10 confluences that captured a range of stream size, gradient, aspect, and thermal heterogeneity.

Timing of emergence

To assess the timing of emergence of salmonflies, we conducted repeated counts of the shed exoskeletons of emergent nymphs (exuviae) along 20m of the riverbank at from a series of sites across the basin. This technique is effective to calculate the salmonfly emergence in terms of total carbon flux ($\text{g C} * [\text{m bank}]^{-1}$) from individual sites (Walters et al., 2018), and we used it to assess the relationship between total C flux and bird response. At the basin scale, we conducted repeated counts of exuviae at 22 different sites throughout the Salmon River Basin, using up to three crews of observers due to some overlap in emergence timing. At this scale, we used the NorWeST Stream Temperature model (Issak et al., 2016), which draws on an integrated collection of temperature logger data from sites in the Salmon River Basin to generate spatially continuous thermal maps for the basin, as a relative index of temperature, and we made the assumption that the thermal patterns described in the NorWeST map would be representative of relative differences in river temperature at the basin scale. We used simple linear regression to

evaluate if the general sequence of emergence was associated with the overall pattern of modeled stream temperatures.

At the reach scale, we surveyed 1 km reaches above and below each confluence (n=20). Within each reach, we conducted randomized 20m repeated counts of exuviae within every 200m, stratified by habitat (riffle and pool), and we selected areas along riffles with clean, clear cobbles and gravels, which are prime salmonfly habitat (Elder and Gaufin, 1973; Bryce et al., 2010; Relyea et al., 2012). Along each 1 km transect, we also conducted continuous walking surveys of all live adult salmonflies, recording numbers every 200m. We were interested in short-term patterns that might occur between temperature and emergence, for which we deployed HOBO Stowaway temperature loggers. The goal of collecting these data was to measure relative differences in temperatures above versus below each confluence during the period encompassing emergence, not to estimate the seasonal or annual thermal conditions of each habitat, for which more temperature data would have been needed. Water temperature was measured above and below the confluence during the emergence process using temperature loggers positioned in locations representative of temperatures that might be associated with emergence timing (i.e. in riffles, and far enough downstream from the confluence that the tributary water had likely mixed, ~1km).

We conducted a binomial test to evaluate the likelihood that the thermal difference of a tributary relative to its mainstem was associated with the directionality of emergence timing compared to the pattern that might be expected by chance alone. The unit of replication for this analysis was a confluence pair. Due to some overlap in the actual timing of the emergence at different sites, we were unable to collect temperature and emergence data at each site, creating variation in which sites were included in each analysis.

Focal bird observations

To evaluate the extent to which birds were capturing adult salmonflies, we conducted avian foraging observations during all bird surveys. When salmonflies were actively emerging, we conducted several focal bird surveys (n = 105) at opportunistic locations. The duration of the focal surveys ranged from 30 seconds to 20 minutes, and each focused on an individual bird. Time started once the focal bird was identified, and was stopped after the bird could no longer be seen, or after two minutes of inactivity. We recorded the species of bird, the total number of salmonflies captured and the total elapsed time. All salmonfly-consuming species observed were assigned habitat associations based on Sullivan and Vierling (2009).

Bird Count Surveys

At the reach scale, we assessed whether changes in bird distribution were associated with the presence of adult salmonflies. We conducted repeated point counts every 200m along each 1 km transect, above and below each confluence when salmonflies were present and when salmonflies were absent, but within a week of peak emergence. We positioned points at 200 m intervals to ensure that the distance between each point was enough such that it minimized the double counting of birds (Reynolds et al., 1980). During each point count, the number of individuals of all bird species detected was recorded within a 50m radius surrounding the observer. We recorded bird presence immediately upon arrival at each point for a duration of 10 min (Hutto et al., 1986).

Point surveys of birds were supplemented by repeated walking transect surveys which were conducted continuously along the 1 km segment above and below each tributary, when salmonflies were absent, and when salmonflies were actively emerging. Birds were not surveyed on days that were affected by rain or strong winds. A single observer conducted the point counts,

as well as the line transects, and all birds that were seen within the established area were recorded (Iwata et al., 2003). To accomplish the continuous walking transect within each 1 km reach, we established 200m sub-transects corresponding to those used for salmonfly surveys. Observers walked steadily along each transect at a pace of approximately 10 m/min (Ralph et al., 1993), consistently spending at least 10 minutes along all five survey transects.

We were unable to determine if the birds at each reach within a confluence pair were the same birds, and in this sense the reaches were not spatially independent of one another. The confluence pairs, however, were assumed to be spatially independent of other confluence pairs due to the distance between confluences (ranging from 1 km to 100s of kms). Regardless, we were interested in the overall change in abundance and species richness of birds associated with the presence of adult salmonflies. We conducted binomial tests to evaluate whether the presence of adult salmonflies was associated with an increase in the numbers of individual birds or species richness. Because P-values are influenced by small sample sizes (Gelman, 2013), we considered P-values <0.05 significant and those between 0.05 and 0.1 as marginally significant, according to statistical convention (Gerstman, 2014), and because of their potential ecological meaning giving the small sample size and low statistical power of this study (Gerstman, 2014).

RESULTS

Timing of emergence

The pattern of salmonfly emergence varied greatly across space and time at different scales within the Salmon River Basin. At the largest scale, emergence occurred in discrete patches at varied locations throughout the basin (Fig. 2). For example, emergence occurred at roughly the same time on the mainstem Salmon River below the Middle Fork confluence, on the Middle Fork above the Big Creek confluence (approx. 50 river km away), and at the Lower Stanley river

access site near Stanley, ID (approx. 300 river km away). Typically, emergence happened earlier in the year at warmer sites (in 17 of the 22 observed sites, Table 2). On the other hand, at the scale of a sub-drainage pathway (above confluences only), emergence generally proceeded from downstream to upstream (Fig. 3). For example, along the Middle Fork sub-drainage, emergence occurred over a period of approximately eight days, starting at the confluence with the mainstem Salmon River and continuing upstream to the headwater confluence of Bear Valley and Marsh Creek (total distance: approximately 108 river km). However, along the Middle Fork/Big Creek sub-drainage pathway, which is only ~50km in length, emergence occurred over a period of approximately three days to the confluence of Rush Creek and Big Creek (total distance: approximately 50 km). At the sub-drainage scale, regression analysis showed an association ($R^2=0.67$) between the relative thermal patterns derived from the NorWeST temperature model map and the general timing of peak emergence of salmonflies at both the basin and sub-drainage scales (Fig. 4).

At the scale of reaches bracketing confluences, we included data gathered in the Salmon River Basin, as well as in the Henry's Fork of the Snake River. At this scale, thermal differences created by tributary confluences were associated with temporal asynchrony in emergence timing across all confluence pairs (P-value = 0.002), which ranged from 1 to 6 days. That is, at the four confluences at which tributaries were colder relative to their mainstem, emergence occurred first above the confluence, whereas the opposite occurred at the remaining five confluences with warmer tributaries (Fig. 5). The timing of the actual emergence event was associated with local temperature, in that we observed a minimum threshold of 8.4 °C across all sites (Fig. 6), below which peak emergence did not occur.

Focal bird observations

We observed 10 bird species feeding on salmonflies across the 10 confluence pairs (Table 3), which we henceforth refer to as “salmonfly-consuming birds.” We found that 50% of the number of bird species feeding on salmonflies were species associated in the literature with upland habitats (Sullivan and Vierling, 2009), 40% were associated with riparian habitats, and 10% were waterbirds. Ten species of birds fed on salmonflies, and some of these species fed heavily on salmonflies. Observed capture rates of salmonflies by birds varied among the ten species of salmonfly-consuming birds, with the most observations (n= 44) of Lewis’s woodpeckers (*Melanerpes lewis*) and the fewest observations (n=3) of Black-billed magpies (*Pica hudsonia*). Additionally, we observed that some birds captured salmonflies to feed their nestlings, based on observing the birds feeding salmonflies to young, as well as repeatedly transporting captured salmonflies into typical nesting habitats (e.g., cavities). For example, on the Warm River above the confluence with Robinson Creek, we observed a pair of American dippers (*Cinclus mexicanus*) capturing salmonflies, killing them and feeding them to their three nestlings. Between the two dippers, they captured four salmonflies in 10 minutes. Numerically, peak capture rate slightly preceded peak emergence. For example, below the confluence of the Middle Fork and mainstem Salmon River, we observed an average rate of salmonfly capture by Lewis’s woodpeckers of 3.9 salmonflies/10min on the day before peak emergence, and 3.0 salmonflies/10min on the date of peak emergence, though this was not consistent across all sites.

Bird Count Surveys

The presence of emerging adult salmonflies was also associated with an increase in the local species richness of salmonfly-consuming birds. The number of salmonfly-consuming bird species observed was greater when salmonflies were present than when not present, and increased with salmonfly presence at 10 of the 14 reaches (P-value=0.0898) (Fig. 7). Though the

differences in these 10 reaches were only marginally significant, in the remaining 4 reaches, species richness remained constant (i.e., it never decreased). The number of species ranged from 0 to 4 species, and the average percent change in bird species richness was 114%, ranging from 0% to 400%. The increase in the average number of individuals and species was comprised of different species compositions at different sites. For example, Lewis's woodpeckers were primarily exploiting salmonflies at the sites in the lower Salmon River drainage, whereas American Robins were primarily exploiting the salmonflies in the Henry's Fork drainage.

The average number of individual salmonfly-consuming birds observed was greater at 14 of the 14 reaches analyzed when salmonflies were present vs. when they were not (P-value < 0.0001) (Fig. 8). Across all reaches analyzed, the difference in the average number of salmonfly-consuming birds observed increased (P-value = <0.0001) when salmonflies were present, and this increase ranged from 1 to 7 birds. The average percent change in bird abundance was 148%, and ranged from 6% to 333% (Mainstem/Yankee Fork below and South Fork/Secesh below, respectively).

Although we observed increases in both the number of individual birds and species richness when salmonflies were present, differences in the average number of individual salmonfly-consuming birds observed when salmonflies were present was not associated with the magnitude of salmonfly flux, nor with the total number of live adult salmonflies observed present (Fig. 9). For example, we observed the beginning of the emergence on the Henry's Fork and we counted only six salmonflies, all of which were eaten within ten minutes by four American robins. On the other hand, at the same site during the peak of the emergence, with hundreds of salmonflies present, we observed little bird feeding activity. This pattern principally occurred at sites in the Henry's Fork watershed where the magnitude of emergence was larger

(average of 552 adult salmonflies on peak emergence day) than the magnitude at sites in the Salmon River Basin (average of 110 adult salmonflies on peak emergence day).

DISCUSSION

We found that variation in timing of the emergence of giant salmonflies was associated with spatial variation in river temperature, and the patterns of their emergence varied at different spatial scales. At the scale of a basin, the overall pattern of emergence occurred in patches throughout the river network. This large-scale patchiness could have been driven by many factors, but thermal heterogeneity appeared to explain most of the patterns we observed. The NorWeST Stream Temperature model provided mean August temperatures, and not June (the month of emergence) temperatures which would have been more meaningful. Regardless, the relative thermal patterns from that model revealed an association of temperature and emergence timing at the basin scale. Some variation around this overall pattern is understandable. Not only might June temperature patterns have differed, but we did not do a mechanistic evaluation of drivers of salmonfly development, and it is likely that factors such as accumulated degree-days, food resources available for salmonflies, or other factors may have influenced emergence timing at this scale. Although future work is necessary to evaluate the mechanisms responsible for such large-scale patchiness, at the scale of a sub-drainage pathway within a river network, the overall emergence pattern (above confluences only) occurred sequentially from downstream to upstream, as might be expected based upon changes in river habitat, as conceptualized by The River Continuum Concept (Vannote et al., 1980). The RCC has been used to generate expectations that various phenomena in rivers change along a longitudinal gradient, which may be the case for with the phenology of salmonfly emergence at this scale.

At the scale of reaches within river segments, our results indicate that the thermal discontinuities created by tributary confluences resulted in temporal asynchrony of 1-6 days in emergence timing above and below confluences. What we observed at this scale is conceptually consistent with the river as a series of discontinuities (Poole, 2002), as influenced by tributary junctions that introduce dynamics, such as thermal heterogeneity, into networks (Benda et al., 2004; Rice et al., 2008). Temperature is important for aquatic insect maturation (Sweeney, 1984), and can affect the synchrony of aquatic insect life history events (Sniegula et al., 2015). Moreover, spatial and temporal variation in geomorphic processes at this scale can contribute to patchiness in aquatic habitats, influencing aquatic organisms and ecosystems (Montgomery, 1999). We found tributary confluences to reflect this concept, modifying the life-history timing of salmonfly emergence via thermal heterogeneity at the reach scale. By studying this phenomenon at different scales, we were able to detect a thermal pattern related to emergence, but likely driven by different mechanisms at different scales. The scale-driven patchiness of salmonfly emergence results in ephemeral, disjunct pulses of a potentially valuable trophic resource within the river system rather than a wave of resource availability moving progressively and systematically through the river system each year. Importantly, had we only conducted our investigation at one of these scales, we would have missed the relationships at the other scales. This is a lesson that has been repeatedly demonstrated in the study of riverine ecology in recent decades (Fausch et al., 2002).

Our results indicate that there may be a minimum temperature threshold that is associated with the timing of salmonfly emergence. The minimum water temperature recorded on the date of peak emergence was 8.4°C. Such a minimum temperature threshold may be an important cue to salmonflies that reduces mortality upon emergence resulting from low air temperatures

(Rockwell & Newell, 2009). However, males typically emerge up to 3 days before females begin to emerge (Sheldon, 1999), which increases their chances of mortality due to cold temperatures and predation. Additionally, our qualitative observations suggest that salmonflies that emerged earlier were male, which suggests that females, especially those with eggs, may be more sensitive to colder conditions, requiring certain temperatures for oviposition and for their flight over the river to deposit their egg mass into the water column. Future investigations are needed to determine if female salmonflies are more sensitive to colder temperatures for successful reproduction, or to evaluate other mechanisms that might be responsible for the pattern we observed.

Our findings are consistent with those of previous studies in the region that have demonstrated the temperature dependence of salmonfly emergence timing along thermally complex river reaches (Poole, 1981; Gregory et.al, 2000). However, this investigation is unique because of the varying scales at which we investigated the phenomenon. Although emergence timing at all scales was associated with variation in river temperature, it is also likely a function of accumulated degree-days, as is the case with growth rate and sexual maturation of many invertebrates (Vannote and Sweeney, 1980). Indeed, previous studies of salmonflies have pointed to this possibility, reporting that emergence timing has been observed to occur earlier in warmer waters and later in cooler waters (Poole, 1981; Flannagan and Cobb, 1984; Gregory et al., 2000). Though the number of accumulated degree-days likely plays a significant role in the duration of development, our temperature data were not extensive enough to draw cause-effect inferences, or inferences regarding the potential role of degree-days accumulation over long periods of time leading up to the emergence. Several factors could influence the development

and survival of the giant salmonfly, affecting different life stages that, in turn, may also provide insectivores with high-quality foraging opportunities.

In the thermally heterogeneous river networks we studied, salmonfly emergence did not occur as a single synchronized pulse, but instead occurred as an asynchronous series of pulses which emerged at different locations across space and time. This pattern potentially enhances the seasonal energy consumption opportunities for any consumers that track and exploit salmonflies, as has been described for other resources and their consumers (Bischof et al., 2012; Lok et al., 2012; Schindler et al., 2013). For example, if emergence were perfectly synchronous across a basin, birds would have only a few days to locate and exploit the salmonflies. However, spatial variation in the phenology of emergence may allow mobile consumers to extend their foraging opportunities by foraging sequentially at local pulses.

Our results can be used to modify and expand on the somewhat one-dimensional concept of a resource wave moving through the landscape in a progressive, predictable, continuous fashion. We show that scale and geomorphic complexity results in disjunct pulses of a valuable resource that can be accessed by mobile foragers such as birds. We identify a new level of complexity that builds on previous consumer-resource subsidy investigations. Specifically, our results indicated that a diverse array of bird species forage on salmonflies and apparently shift their spatial distributions to exploit the temporal asynchrony in salmonfly emergence created by thermal heterogeneity above and below confluences. Across all sites, the average number of individual salmonfly-consuming birds and the species richness increased or remained constant during the salmonfly emergence event. We infer that birds were responding to the presence of salmonflies above and below a given confluence as indicated by the 148% average increase in bird abundance in relation to emergence. Admittedly, we did not track individual birds meaning

our results partially may be a function of detectability which might have increased when salmonflies were present if birds increased their foraging activities or focused their foraging effort on salmonflies. Regardless, because salmonflies are an ephemeral resource at any single location, individual birds that can shift their distributions across a watershed to track this phenological variation may extend their access to the resource.

Phenological diversity may be just as important as abundance in determining energy flow to upper trophic levels of food webs in seasonally dynamic ecosystems (Armstrong et al, 2016). Our results are consistent with this idea; for instance, we observed that the magnitude of the bird response was not associated with total salmonfly C flux, nor with the total number of adult salmonflies present in the reach, but was instead more closely linked to timing of prey occurrence. This observation was somewhat surprising because we had expected that a large flux of salmonflies would elicit a stronger avian response. However, observations made in the field suggested that the ratio of salmonflies to birds plays an important role in the feeding and capturing rate exhibited by birds. This may be a result of the evolutionary strategy of predator swamping, which is the hypothesis that individuals of prey species can improve their fitness by synchronizing various aspects of their life history, such as emergence (Tucker et al., 2007). Furthermore, as described by Sweeney and Vannote (1982), predator satiation may also occur when the quantity of emerging aquatic insects outnumber the potential number that can be captured by predators like birds, allowing remaining insects to survive and reproduce. This phenological diversity in timing of emergence may be more important to the foraging efforts made by birds than overall abundance of salmonflies.

Our findings take on additional importance when we consider due to warming trends, or other unknown factors, salmonfly populations are declining, or altogether disappearing, from

many rivers of the western U.S. (Nehring, 2011; Walters et al., 2018). This is of serious concern for both ecological and socio-economic reasons, as this emergence, referred to by anglers as a “hatch,” is among the most famous and anticipated in the country for trout anglers, and is therefore important for many local economies (Nehring, 2011). Moreover, as global temperatures increase, salmonfly emergence is occurring earlier in the year in locations like the Henry’s Fork of the Snake River (Gregory et al., 2000; R. Van Kirk, Henry’s Fork Foundation, personal communication), which may affect the overlap in timing between emergence and the timing of bird life histories, including the arrival of migratory neo-tropical birds. This could be of serious ecological concern if salmonflies represent a key resource to migratory birds. For instance, the western tanager is a neotropical migrant that arrives in Idaho during the timeframe of salmonfly emergence, that we repeatedly observed feeding on salmonfly adults, and that was an important contributor to the patterns we observed. Even subtle changes in salmonfly emergence timing (e.g., on the order of days) could mean that this prey resource would be unavailable to these birds upon their arrival in the region, especially if salmonfly emergence timing also became more synchronized by forms of habitat homogenization. Climate change and habitat homogenization, driven by flow regulation, channelization, and vegetation homogenization threatens the physical mechanisms underlying spatial variation in phenology by changing the characteristics of river thermalscapes. In the future, investigations should focus on understanding how phenological diversity like that we found for salmonflies may contribute to the maintenance of biodiversity, and understanding the consequences of climate change and river management policies not only for individual species, but for webs of interacting species associated with rivers.

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FIGURES

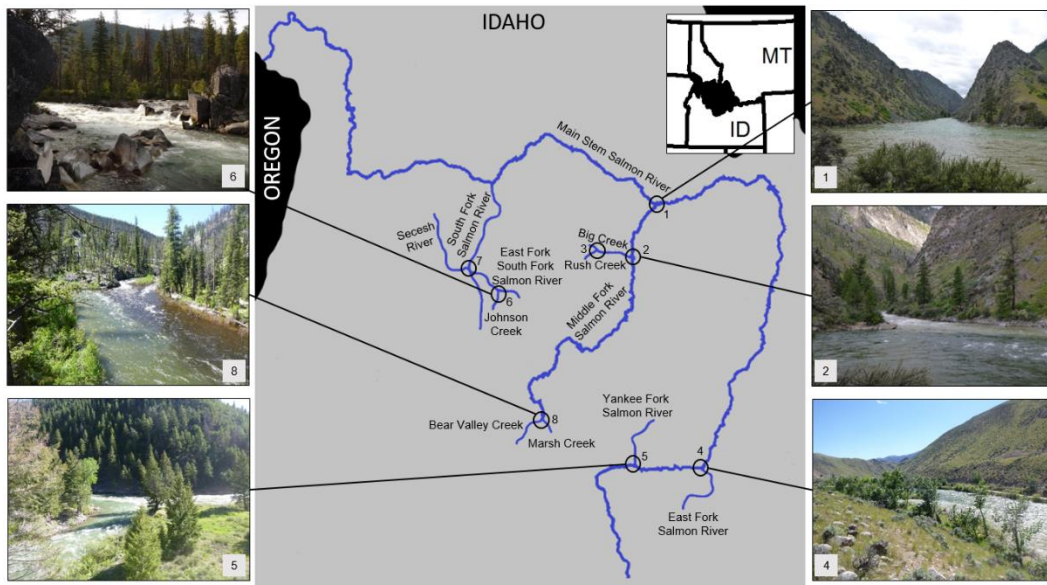


Figure 1a. Map of the study confluences (indicated by number 1-8) in the Salmon River Basin, Idaho, USA, which were surveyed in summer 2018.

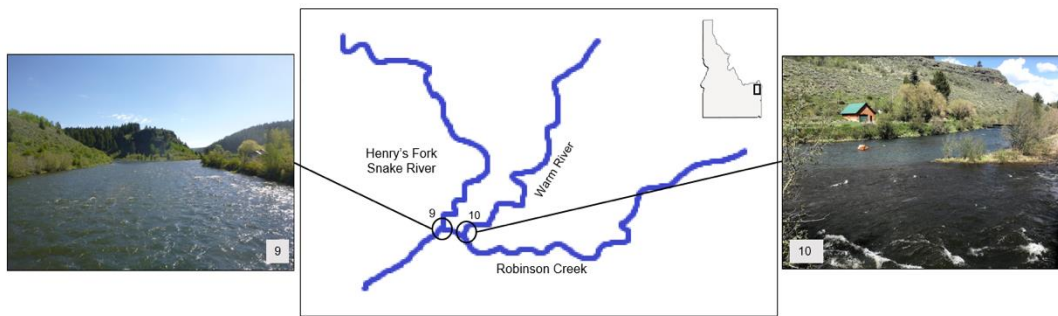
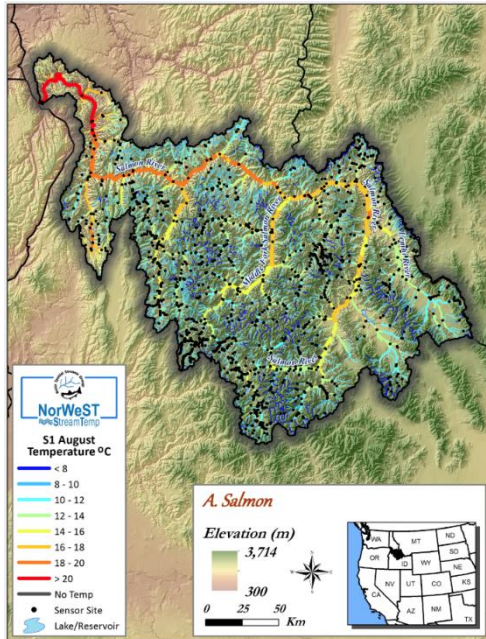


Figure 1b. Map of the study confluences (indicated by number 9-10) in the Henry's Fork of the Snake River, Idaho, USA which were surveyed in summer 2018.

A)



B)

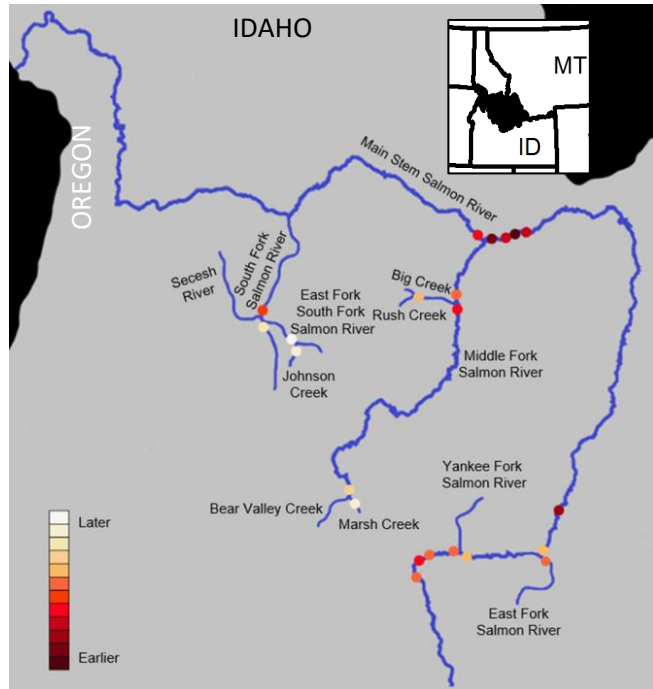


Figure 2. A) Map of thermal heterogeneity in the Salmon River Basin, Idaho, USA, based on mean August temperatures from 1993-2011 (NorWeST temperature model (Isaak et al. 2016)). B) Diagram of salmonfly emergence across space and time in the Salmon River Drainage, Idaho, USA in June 2018. The color scale indicates the occurrence of emergence from earlier to later in the year.

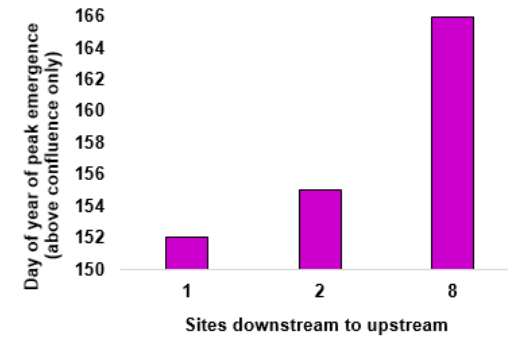
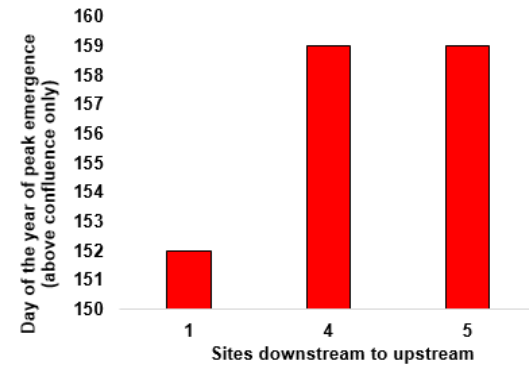
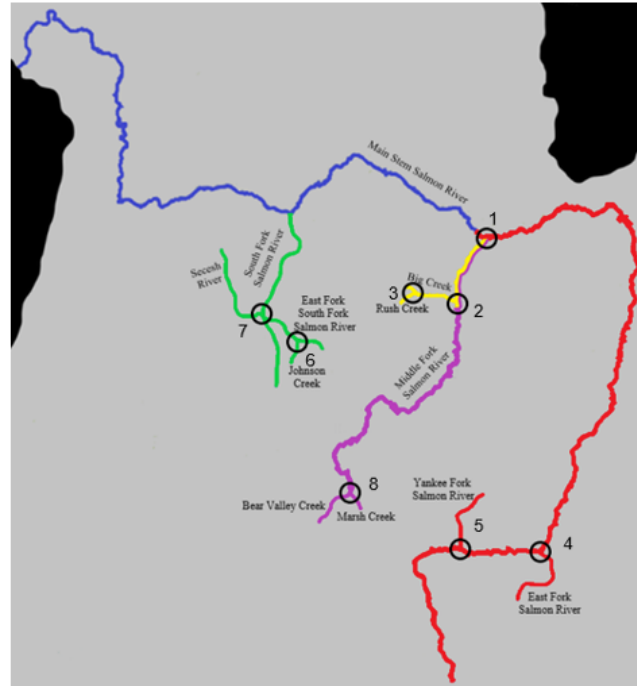
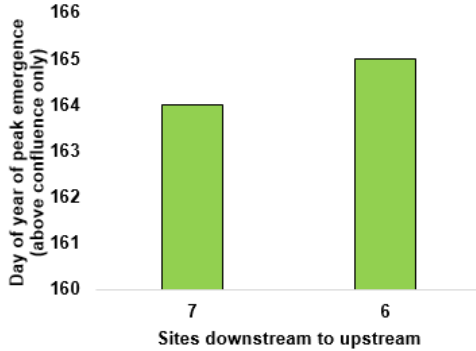
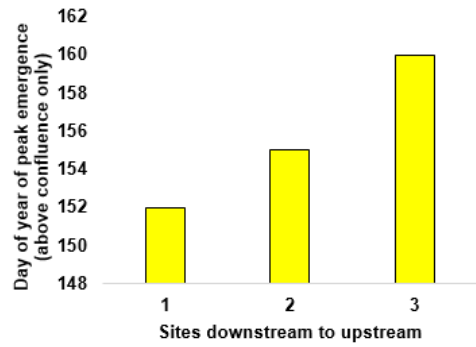


Figure 3. Timing of salmonfly emergence in the Salmon River sub-drainages, Idaho, USA in June 2018, above confluences only. Numbers indicate confluences as labeled in Figure 1. Letters indicate river sub-drainages.

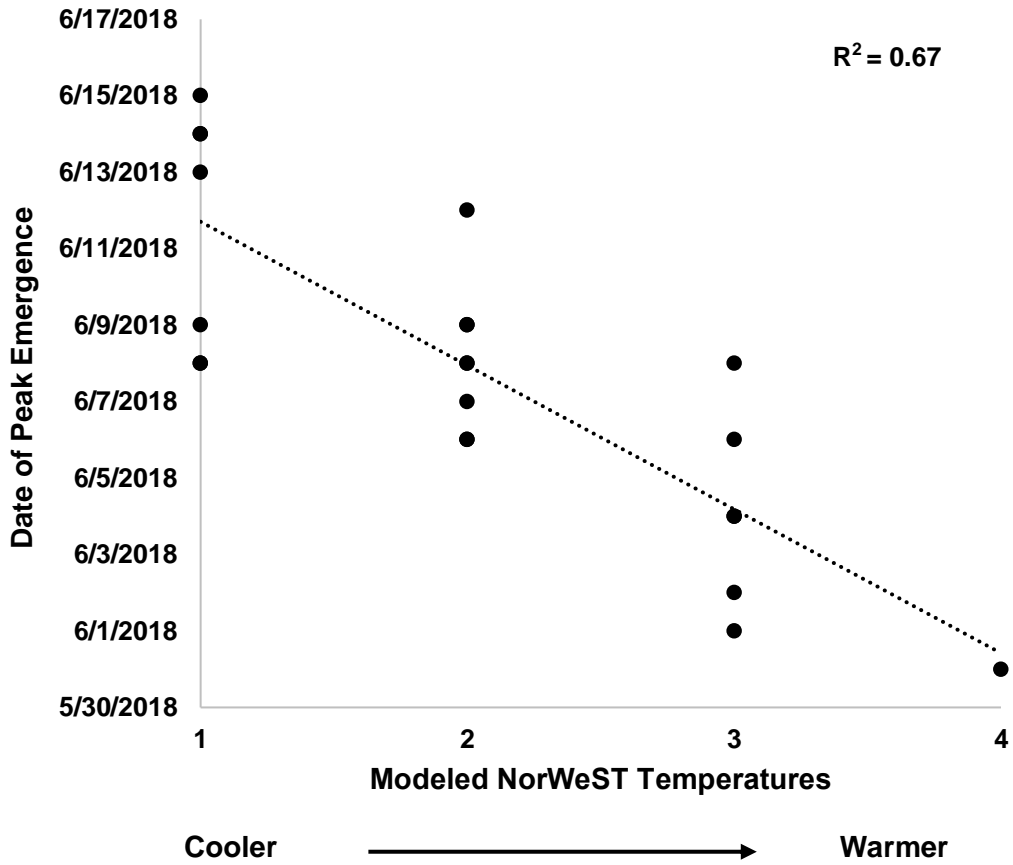
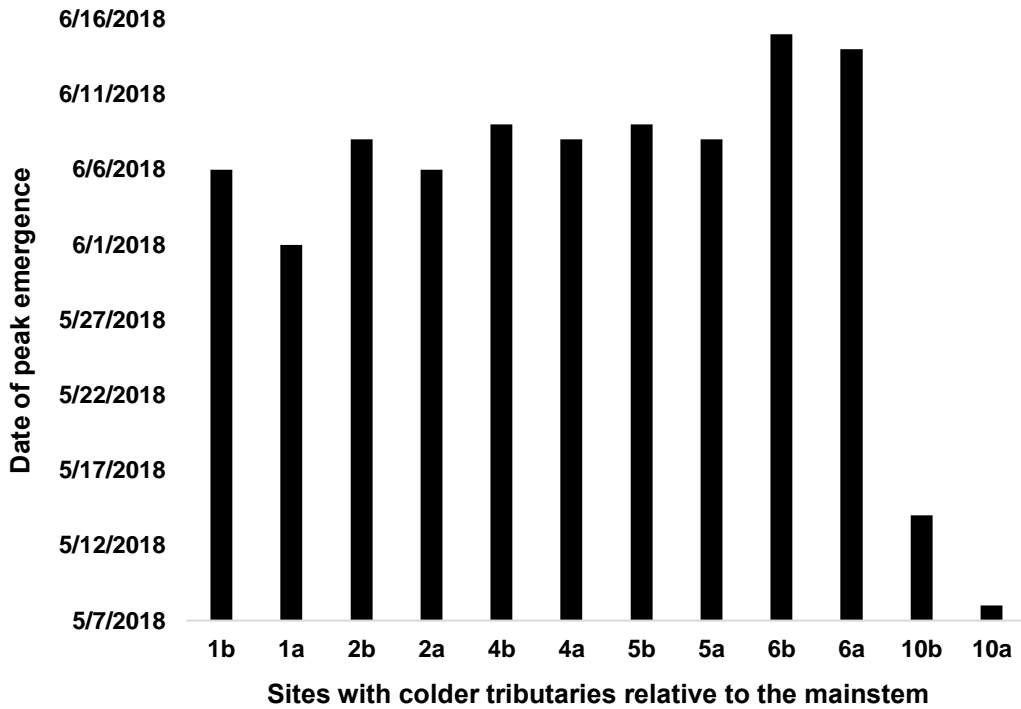


Figure 4. Date of peak emergence across 22 sites in the Salmon River Basin as a function of modeled NorWeST temperatures (°C). Temperatures are categorized based on color categorizations from the modeled map: 1= 12-14, 2=14-16, 3=16-18, 4=18-20, and range from cooler to warmer.

A)



B)

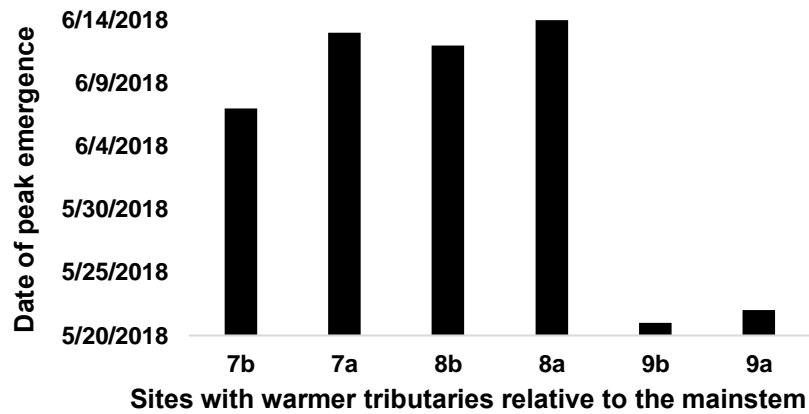


Figure 5. Timing of salmonfly emergence at the scale of a river segment in the Salmon River sub-drainages, Idaho, USA in June 2018. Thermal discontinuities created by tributary confluences create temporal asynchrony in emergence timing. *P*-value (binomial test) = 0.0020. a=above, b=below confluence. A) Sites with colder tributaries relative to the mainstem. Emergence occurred above the confluence first then below. B) Sites with warmer tributaries relative to the mainstem. Emergence occurred below the confluence first, then above. Temperature is based on measurements taken within a few days of peak emergence. Site 3 was excluded due to lack of sufficient temperature data required to assess whether the waters above or below the confluence were warmer on the date of peak emergence.

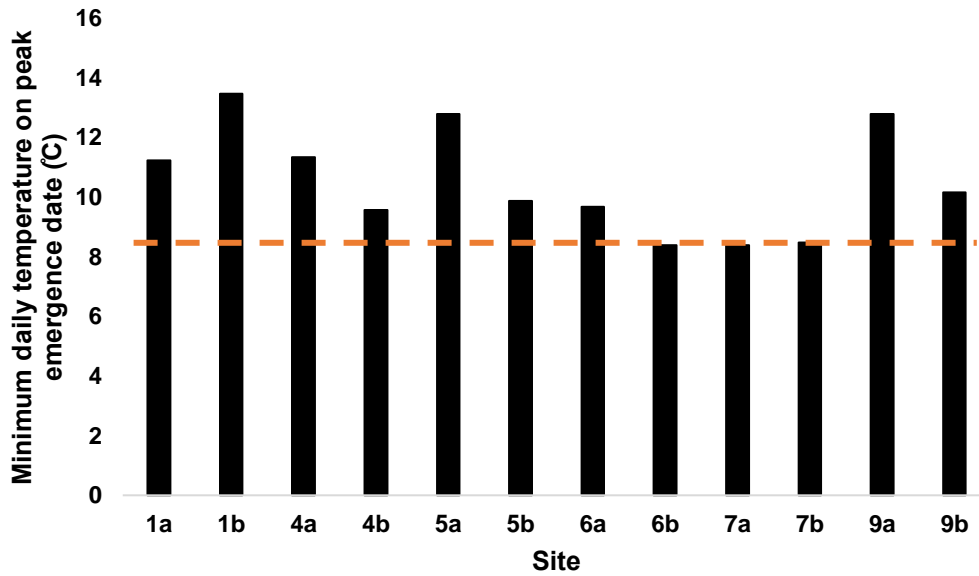


Figure 6. Minimum temperature threshold associated with timing of salmonfly emergence at each site in the Salmon River Drainage and Henry’s Fork of the Snake River Drainage, Idaho, USA in May-June 2018. Across these sites, peak emergence never occurred if water temperatures were below 8.4 °C. Sites 2,3,8,10 were excluded due to lack of temperature data on peak emergence date.

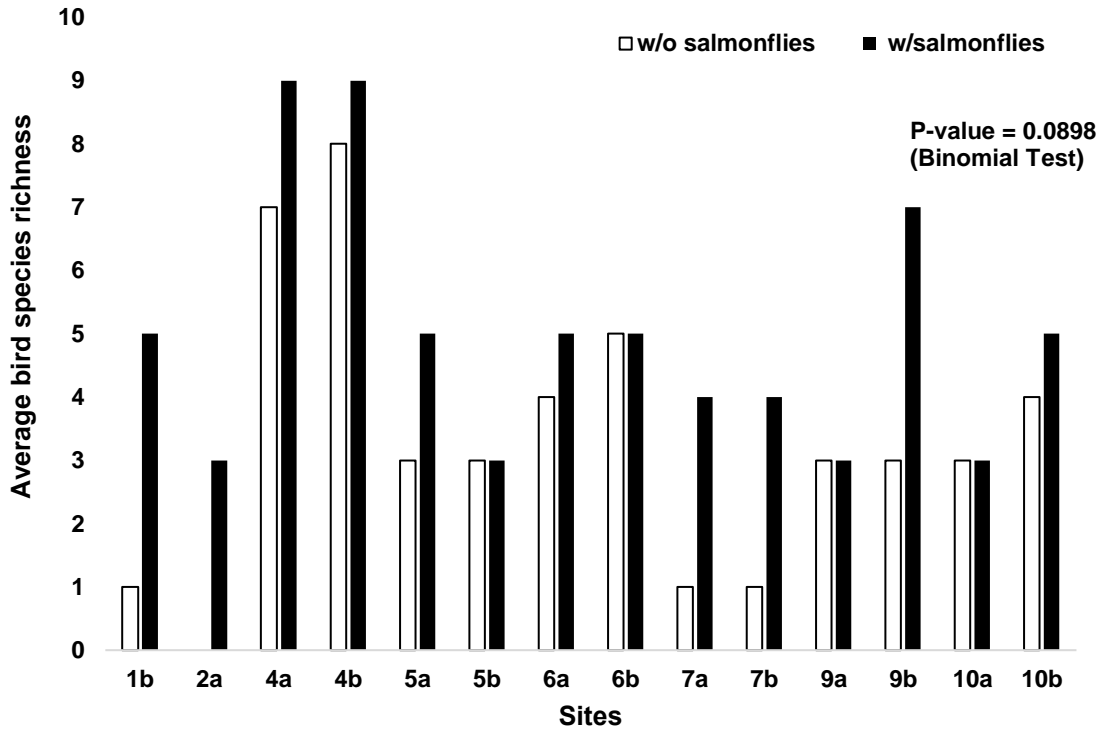


Figure 7. Associated shifts in the average number of bird species richness (for the 10 species of birds observed feeding on salmonflies) at each reach above and below the confluence when adult salmonflies were present vs absent. *P*-value (binomial test) = 0.0898 when salmonflies were present in the Salmon River Drainage and Henry's Fork of the Snake River Drainage, Idaho, USA in May-June 2018.

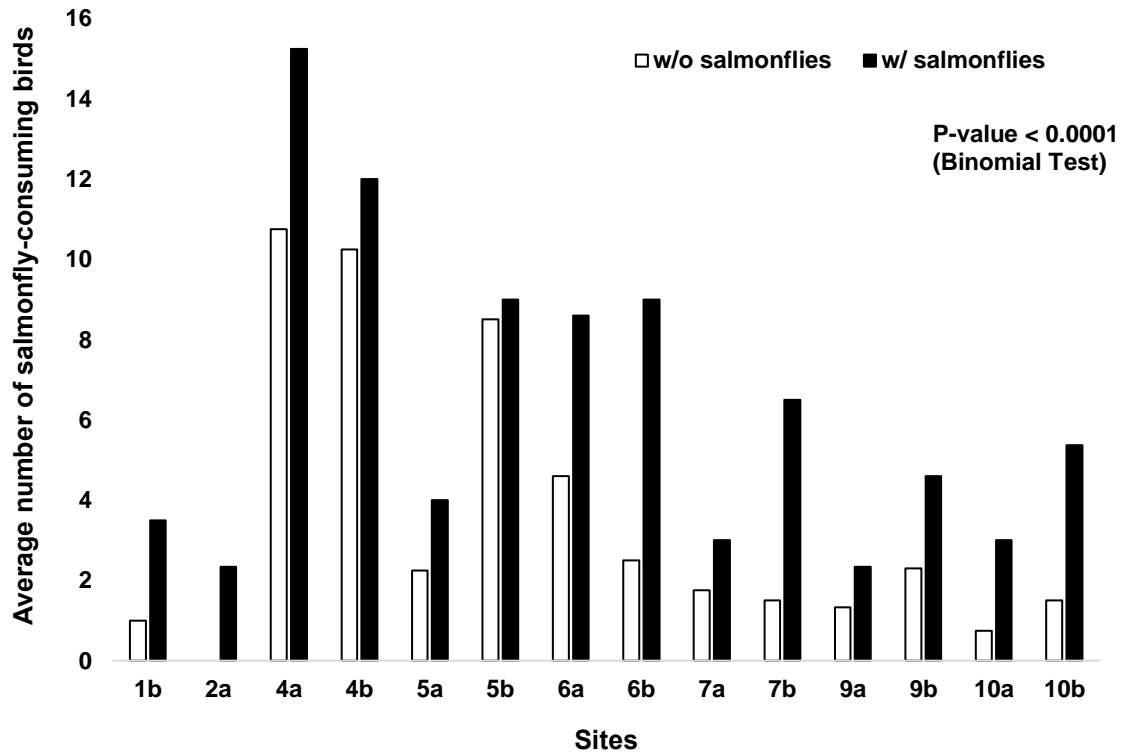
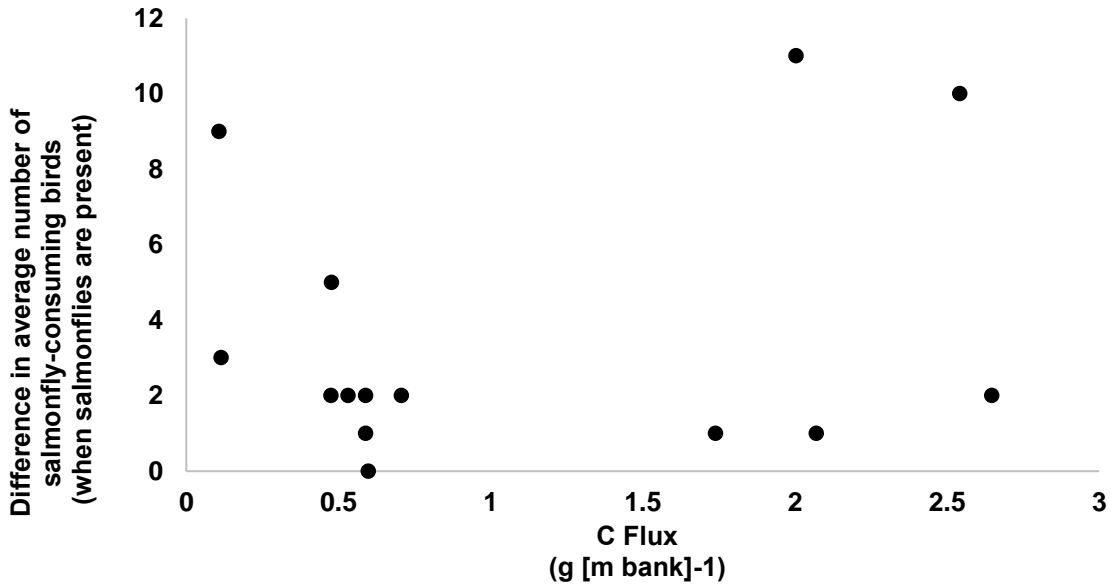


Figure 8. Associated shifts in the average number of individual salmonfly-consuming birds (for the 10 species of birds observed feeding on salmonflies) at each reach above and below the confluence when adult salmonflies were present vs absent. P-value (binomial test) <0.001 when salmonflies were present in the Salmon River Drainage and Henry’s Fork of the Snake River Drainage, Idaho, USA in May-June 2018.

A)



B)

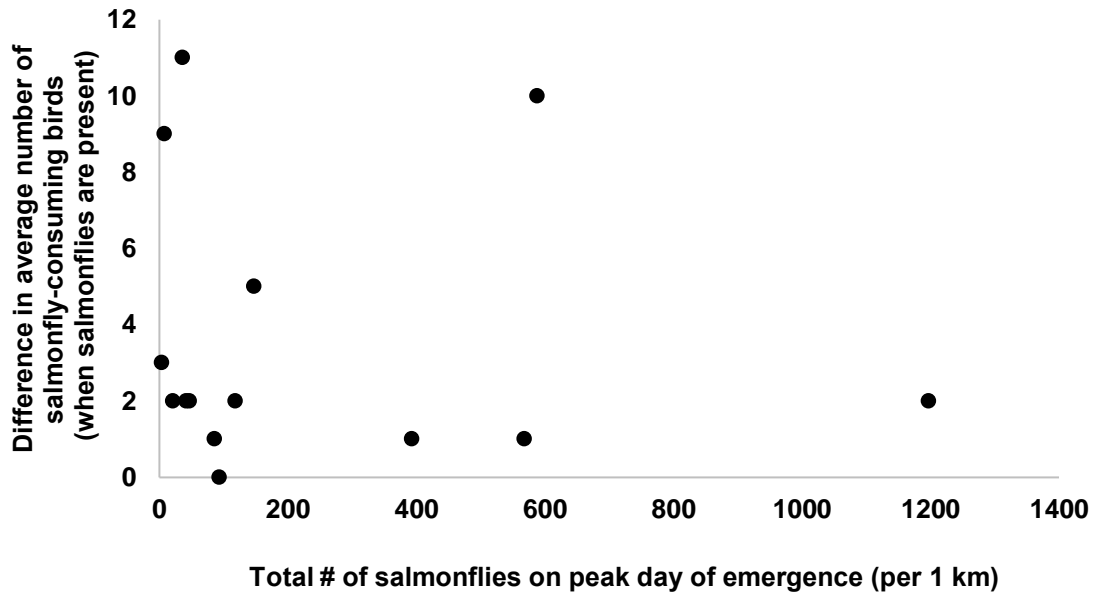


Figure 9. A) The change in the average number of salmonfly-consuming birds present when adult salmonflies were present was not associated with the magnitude of the salmonfly emergence C flux B) The change in the average number of salmonfly-consuming birds present when adult salmonflies were present was not associated with the total number of live salmonfly adults present in the Salmon River Drainage and Henry's Fork of the Snake, Idaho, USA in May-June 2018.

TABLES

Table 1. Physical descriptions and locations for study sites in the Salmon River Basin and Henry’s Fork of the Snake River, Idaho, USA. Relative temperatures based on temperature loggers measured within a week of date of peak emergence of salmonflies.

Confluence (mainstem/tributary)	Latitude, Longitude	Stream Order (mainstem/trib.)	Peak emergence date	Relative temperature (mainstem/trib.)
Main Salmon/ Middle Fork Salmon	45°17'51.46"N, 114°35'35.78"W	8 th order/7 th order	Above: 6/1/18 Below: 6/6/18	Warmer/cooler
Middle Fork Salmon/ Big Creek	45° 5'41.62"N, 114°44'0.19"W	7 th order/5 th order	Above: 6/6/18 Below: 6/8/18	Warmer/cooler
Big Creek/ Rush Creek	45° 6'17.40"N, 114°51'38.63"W	5 th order/4 th order	Above: 6/9/18 Below: 6/9/18	Warmer/cooler
Main Salmon/ East Fork Salmon	44°16'7.38"N, 114°19'37.82"W	8 th order/7 th order	Above: 6/8/18 Below: 6/9/18	Warmer/cooler
Main Salmon/ Yankee Fork Salmon	44°16'10.59"N, 114°44'4.52"W	8 th order/6 th order	Above: 6/8/18 Below: 6/9/18	Warmer/cooler
East Fork South Fork/ Johnson Creek	44°57'45.18"N, 115°30'9.55"W	6 th order/5 th order	Above: 6/14/18 Below: 6/15/18	Warmer/cooler
Secesh River/ South Fork Salmon	45° 1'29.87"N, 115°42'25.44"W	5 th order/7 th order	Above: 6/13/18 Below: 6/7/18	Cooler/warmer
Marsh Creek/ Bear Valley Creek	44°26'57.1"N, 115°13'51.5"W	5 th order/4 th order	Above: 6/14/18 Below: 6/12/18	Cooler/warmer
Henry’s Fork Snake/ Warm River	44° 6'41.29"N, 111°20'2.08"W	4 th order/2 nd order	Above: 5/22/18 Below: 5/21/18	Cooler/warmer
Warm River/ Robinson Creek	44° 6'52.39"N, 111°19'30.06"W	1 st order/2 nd order	Above: 5/8/18 Below: 5/14/18	Warmer/cooler

Table 2. Modeled NorWeST August temperatures and the date of peak emergence of salmonflies for each site throughout the Salmon River Drainage, Idaho, USA.

Peak Emergence Date	Site	Latitude, Longitude	NorWeST Modeled Mean August Temps (°C)
5/31/2018	Above Main Salmon/ Panther Creek	45°18'55.5"N 114°24'18.1"W	18-20
6/1/2018	Above Main Salmon/ Middle Fork	45°17'49.9"N 114°35'31.4"W	16-18
6/2/2018	Cottonwood	44°40'06.6"N 114°04'50.9"W	16-18
6/4/2018	Below Main Salmon/ Pine Creek	45°21'48.4"N 114°18'02.9"W	16-18
6/4/2018	Cove Creek	45°19'33.7"N 114°25'42.8"W	16-18
6/6/2018	Lower Stanley River Access	44°14'06.3"N 114°54'53.5"W	14-16
6/6/2018	Below Main Salmon/ Middle Fork	45°17'55.8"N 114°35'43.9"W	14-16
6/6/2018	Above Middle Fork/ Big Creek	45°05'39.7"N 114°43'58.2"W	16-18
6/7/2018	Below South Fork/ Secesh River	45°01'27.4"N 115°42'30.4"W	14-16
6/8/2018	Casino Creek	44°15'16.6"N 114°51'23.8"W	12-14
6/8/2018	Below Main Salmon/ Valley Creek	44°13'30.8"N 114°55'41.6"W	12-14
6/8/2018	Above Main Salmon/ East Fork	44°16'01.2"N 114°19'30.4"W	14-16
6/8/2018	Below Middle Fork /Big Creek	45°05'42.3"N 114°43'58.2"W	16-18
6/8/2018	Above Main Salmon/ Yankee Fork	44°16'14.7"N 114°44'11.0"W	14-16
6/9/2018	Below Big Creek/ Rush Creek	45°06'18.4"N 114°51'40.7"W	14-16
6/9/2018	Below Main Salmon/ East Fork	44°16'13.9"N 114°19'34.2"W	12-14
6/9/2018	Below Main Salmon/ Yankee Fork	44°16'10.1"N 114°44'03.6"W	14-16
6/12/2018	Below Marsh Creek/ Bear Valley Creek	44°26'58.1"N 115°13'50.4"W	14-16
6/13/2018	Above East Fork South Fork/South Fork	45°00'51.2"N 115°42'50.8"W	12-14
6/14/2018	Above East Fork South Fork/Johnson Creek	44°57'42.7"N 115°30'01.5"W	12-14
6/14/2018	Above Marsh Creek/ Bear Valley Creek	44°26'55.6"N 115°13'49.6"W	12-14
6/15/2018	Below East Fork South Fork/Johnson Creek	44°57'45.5"N 115°30'10.9"W	12-14

Table 3. Species observed capturing and feeding on adult giant salmonflies in the Salmon River Basin and Henry's Fork of the Snake River, Idaho, USA in May-June 2018. Habitat associations based on common use (as designated by Sullivan and Vierling, 2009).

Common Name	Scientific Name	Sites observed	Habitat
American dipper	<i>Cinclus mexicanus</i>	1-10	Waterbird
American kestrel	<i>Falco sparverius</i>	1	Upland
American robin	<i>Turdus migratorius</i>	1-10	Upland
Black-billed magpie	<i>Pica hudsonia</i>	1-10	Upland
Bullock's oriole	<i>Icterus bullockii</i>	7, 9-10	Riparian
Lewis's woodpecker	<i>Melanerpes lewis</i>	1-8	Riparian
Northern flicker	<i>Colaptes auratus</i>	2	Riparian
Red-tailed hawk	<i>Buteo jamaicensis</i>	10	Upland
Red-winged blackbird	<i>Agelaius phoeniceus</i>	4	Riparian
Western tanager	<i>Piranga ludoviciana</i>	1-10	Upland

APPENDIX 1

Complete Bird, Exuviae, and Live Adult Count Table

Appendix 1. Location and date of bird point counts, exuviae counts and live adult counts. Bird names are in Alpha Code (as designated by the American Ornithological Union).

Site	Date	WETA	LEWO	AMRO	BBMA	RTHA	AMDI	RWBL	NOFL	AMKE	BUOR	Total # live sflies (per 1 km)	total exuvia (20m*5)
1A	6/1/2018	0	4	0	1	0	0	0	0	2	0	310	367
1A	6/1/2018	1	4	0	0	0	0	0	0	1	0	--	--
1A	6/5/2018	0	7	0	1	0	0	0	3	0	0	19	392
1A	6/6/2018	0	0	0	2	0	0	0	0	0	0	4	--
1B	6/1/2018	0	0	0	0	0	0	0	0	0	0	1	36
1B	6/2/2018	0	0	2	3	0	0	0	0	0	0	1	45
1B	6/4/2018	0	0	0	3	0	1	0	0	1	0	17	175
1B	6/5/2018	0	0	0	1	0	0	0	0	1	0	110	197
1B	6/6/2018	0	8	0	5	0	1	0	0	0	0	86	342
1B	6/12/2018	0	0	0	1	0	0	0	0	0	0	0	6
2A	6/6/2018	0	0	1	2	0	3	0	0	0	0	93	114
2A	6/7/2018	0	0	1	0	0	0	0	0	0	0	18	88
2A	6/8/2018	0	0	0	0	0	0	0	0	0	0	54	67
2B	6/6/2018	0	3	0	0	0	0	0	0	0	0	0	161
3A	6/9/2018	0	2	0	3	0	0	0	2	1	0	5	14
3A	6/11/2018	1	1	0	2	0	0	0	0	0	0	2	0
3B	6/9/2018	0	1	0	4	0	0	0	0	0	1	20	14
3B	6/10/2018	0	0	1	3	0	0	0	1	0	3	2	2
3B	6/11/2018	0	0	0	2	0	0	0	0	0	1	0	0
4A	6/7/2018	7	0	10	0	0	0	4	2	0	2	0	36
4A	6/8/2018	2	5	6	3	0	0	1	1	2	1	36	931
4A	6/9/2018	3	2	16	0	0	0	12	1	0	6	26	354
4A	6/16/2018	1	1	8	0	0	3	0	1	0	4	0	--
4B	6/7/2018	0	1	5	0	2	0	11	0	0	1	1	37
4B	6/8/2018	2	3	0	5	2	0	1	3	2	1	141	67

4B	6/9/2018	2	2	1	1	2	0	15	1	0	5	588	420
4B	6/16/2018	12	2	5	1	0	1	0	0	0	0	0	--
5A	6/8/2018	0	0	1	0	1	1	0	0	0	0	118	189
5A	6/9/2018	2	0	4	0	0	0	0	1	0	0	101	22
5A	6/12/2018	3	0	3	0	0	0	0	0	0	0	2	84
5A	6/16/2018	0	0	1	0	2	0	0	0	0	0	0	--
5B	6/8/2018	0	0	3	0	0	1	2	0	0	0	0	11
5B	6/9/2018	0	0	1	0	0	0	0	0	0	0	8	18
5B	6/12/2018	15	0	6	0	0	1	0	0	0	0	0	6
5B	6/16/2018	3	0	1	0	0	2	0	0	0	0	0	--
6A	6/8/2018	0	0	3	0	0	1	0	2	0	0	0	0
6A	6/13/2018	7	2	5	0	0	1	0	0	0	0	20	--
6A	6/13/2018	0	4	7	0	0	2	0	2	0	0	--	--
6A	6/14/2018	10	0	3	0	0	0	0	0	0	0	147	79
6A	6/15/2018	12	0	5	0	0	0	0	0	0	0	0	--
6B	6/7/2018	0	1	2	0	0	2	0	1	0	0	0	0
6B	6/14/2018	2	1	3	0	0	1	0	1	0	0	16	15
6B	6/15/2018	20	0	8	0	0	0	0	0	0	0	4	19
6B	6/15/2018	4	0	0	0	0	0	0	0	0	0	0	11
7A	6/7/2018	0	0	3	0	0	0	0	0	0	0	2	6
7A	6/8/2018	0	0	2	0	0	0	0	0	0	0	3	5
7A	6/13/2018	0	2	6	0	0	1	0	1	0	0	42	88
7A	6/15/2018	0	0	4	0	0	0	0	0	0	0	0	--
7B	6/7/2018	3	2	6	0	0	2	0	0	0	0	21	117
7B	6/12/2018	0	0	3	0	0	0	0	0	0	0	0	116
9A	5/9/2018	0	0	0	0	0	0	0	0	0	0	0	0
9A	5/9/2018	0	0	0	0	0	0	0	0	0	0	0	0
9A	5/9/2018	0	0	2	0	2	0	0	0	0	0	0	0
9A	5/9/2018	0	0	0	0	3	1	0	0	0	0	0	0

9A	5/22/2018	0	0	7	0	0	1	0	0	0	1	568	230
9A	6/3/2018	0	0	5	0	0	0	0	0	0	0	--	20
9B	5/9/2018	0	0	6	0	0	0	0	0	0	0	0	0
9B	5/9/2018	0	0	2	0	2	1	0	0	0	0	0	0
9B	5/9/2018	0	0	6	0	0	1	0	0	0	0	0	0
9B	5/9/2018	0	0	2	0	1	2	0	0	0	0	0	0
9B	5/18/2018	0	0	5	0	0	1	0	0	0	0	--	9
9B	5/19/2018	0	0	5	0	1	2	1	0	0	0	--	18
9B	5/21/2018	0	0	7	0	0	1	0	0	0	0	1197	350
9B	5/26/2018	1	0	6	0	0	0	0	0	0	0	--	--
9B	5/26/2018	0	0	0	0	0	0	0	0	0	0	--	--
9B	6/3/2018	2	0	9	0	1	2	0	1	0	1	--	45
10A	5/10/2018	0	0	6	0	0	0	0	0	0	0	393	78
10A	5/10/2018	0	0	5	0	1	0	0	0	0	0	239	--
10A	5/11/2018	0	0	1	0	0	0	0	0	0	0	--	--
10A	5/11/2018	0	0	10	0	0	0	0	0	0	0	--	--
10A	5/13/2018	0	0	1	0	0	0	0	0	0	0	--	--
10A	5/13/2018	0	0	0	0	0	0	0	0	0	0	--	--
10A	5/16/2018	0	0	0	0	0	0	0	0	0	0	--	--
10A	5/16/2018	2	0	2	0	0	2	0	0	0	0	--	--
10B	5/13/2018	0	0	1	0	0	0	0	0	0	0	--	27
10B	5/13/2018	0	0	8	0	0	3	0	0	0	0	--	--
10B	5/14/2018	0	0	7	1	1	1	0	0	0	1	47	51
10B	5/16/2018	0	0	7	0	0	0	0	0	0	0	--	44
10B	5/16/2018	0	0	7	0	0	0	0	0	0	0	--	45
10B	5/17/2018	0	0	6	0	0	0	0	0	0	0	--	--
10B	5/17/2018	0	0	3	0	2	0	1	0	0	0	--	--
10B	5/18/2018	0	0	5	0	0	1	0	0	0	0	--	5