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Spawning salmon and the phenology of emergence in stream insects

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Phenological dynamics are controlled by environmental factors, disturbance regimes and species interactions that alter growth or mortality risk. Ecosystem engineers can be a key source of disturbance, yet their effects on the phenologies of co-occurring organisms are virtually unexplored. We investigated how the abundance of a dominant ecosystem engineer, spawning sockeye salmon (*Oncorhynchus nerka*), alters the emergence phenology of stream insects. In streams with high densities of salmon, peak insect emergence occurred in early July, immediately prior to salmon spawning. By contrast, peak insect emergence in streams with low densities of salmon was weeks later and more protracted. The emergence of specific taxa was also significantly related to salmon density. A common rearing experiment revealed that differences in emergence timing are maintained in the absence of spawning salmon. We hypothesize that these patterns are probably driven by predictable and severe disturbance from nest-digging salmon driving local adaptation and being a trait filter of insect emergence. Thus, salmon regulate the timing and duration of aquatic insect emergence, a cross-ecosystem flux from streams to riparian systems.

Keywords: ecosystem engineer; disturbance regime; bioturbation; marine-derived nutrients

1. INTRODUCTION

Seasonal dynamics of communities are controlled by a combination of ecological and evolutionary forces (e.g. Van Noordwijk *et al.* 1995). The phenology of an organism can consist of plastic responses to cues (e.g. Laurila *et al.* 1998) or be a locally adapted trait (e.g. Van Noordwijk *et al.* 1995). According to theory, the evolution of phenology is controlled by the conflict between advantages of further growth versus the risk of mortality (Ludwig & Rowe 1990; Iwasa & Levin 1995). Thus, organisms can mediate growth potential of other species; for example, shrimp populations have evolved so that their offspring will hatch during the spring phytoplankton bloom (Koeller *et al.* 2009). Alternatively, ecosystem engineers that change abiotic drivers can indirectly influence phenology; for example, beaver dams warm wetlands, altering the emergence phenology of an amphibian (Skelly & Freidenburg 2000). Furthermore, organisms that cause mortality through predation or disturbance would directly modify risk. Although there are many examples of predation driving phenology; for example, fish predation pressure causes earlier maturity of their zooplankton prey (e.g. Stibor 1992), the evolutionary effects of biotic sources of disturbance are virtually unexplored. We would anticipate that organisms which strongly alter either growth resources or mortality risk have the potential to strongly influence the phenology of co-occurring organisms.

Anadromous and semelparous Pacific salmon (*Oncorhynchus* spp.) are a critical structuring component of coastal freshwater ecosystems through cumulative effects as sources of nutrients and energy, and as a source of physical disturbance to spawning habitats (Schindler *et al.* 2003; Moore 2006; Janetski *et al.* 2008). Pacific salmon grow large through foraging in the marine ecosystem, and then migrate to relatively confined freshwaters where they cease feeding, spawn and die (Quinn 2005). Their carcasses and excreta can fertilize food webs (e.g. Chaloner *et al.* 2004; Tiegs *et al.* 2008), and their nest-digging can disturb benthic communities (Peterson & Foote 2000; Moore *et al.* 2004; Lessard & Merritt 2006; Moore & Schindler 2008; Honea & Gara 2009; Monaghan & Milner 2009). These previous studies have focused on how salmon impact the populations or growth of stream organisms. For example, previously we found that salmon nest-digging is strongly negatively associated with aquatic invertebrate seasonal abundance in spawning streams; in fact many lotic insects were virtually absent during salmon spawning seasons in streams with high salmon densities (Moore & Schindler 2008). Given that spawning salmon strongly alter resources for growth and mortality risk in a seasonally predictable fashion; they may be a likely driver of the phenology of stream organisms. To our knowledge, there has only been one study that has explicitly examined how spawning salmon impact the phenology of coastal organisms—Ben-David (1997) found that lactation timing in mink corresponded tightly to the seasonality of salmon carcass availability, upon which they feed.

We investigated how the phenology and abundance of an ecosystem engineer alters the phenology of a suite of co-occurring species. Specifically, we examined the relationship between spawning salmon and the emergence phenology of benthic stream insects. We tested the hypothesis that aquatic insects emerge into terrestrial

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adults prior to salmon spawning, minimizing their risk from this predictable and severe disturbance. We observed that high densities of spawning sockeye salmon (*Oncorhynchus nerka*) strongly alter the timing of aquatic insect emergence, thereby changing the seasonality of aquatic-terrestrial coupling.

2. MATERIAL AND METHODS

(a) *Study system*

We examined the relationship between spawning sockeye salmon and the phenology of benthic insects in streams of the Wood River system of southwestern Alaska, USA (59°24′ N, 158°53′ W). This 2600 km^2 river system is a spawning and nursery habitat for anadromous sockeye salmon (*O. nerka*). Sockeye represent more than 99 per cent of the spawning salmon in the study streams. An average of 1.1 million sockeye spawn in the streams, rivers and beaches of this system every year (Baker *et al.* 2006). This watershed has no logging, agriculture, roads or other major direct sources of human land-use change.

In the many streams of this system, salmon enter to spawn in mass in mid-July, peaking in August and finishing in September. Salmon generally start spawning within 2 days of entering streams. The phenology of this spawning varies among streams, but is consistent among years for a given stream. For example, the average standard deviation of entry dates for streams in this area is approximately 2 days (*n* = 5, University of Washington Alaska Salmon Program 2009, unpublished data). Spawning sockeye dig large nests (approx. 2 m^2 and 20 cm deep), and previous studies in this system have shown that this nest-digging can disturb large proportions (up to 100%) of spawning habitats (Moore 2006) impacting benthic communities (Moore & Schindler 2008). In this study we focus on aquatic insects. Their life cycle starts as an egg, frequently deposited in off-channel habitats (with fewer salmon), which lasts from several hours to several months, after which they hatch into a small larvae or nymph (Merritt & Cummins 1996). It is likely that these early phases are more resistant than later (and larger) stages to disturbance, such as that from nest-digging salmon, because of their small size and ability to persist in the interstices of stream substrates. For example, previous studies have found small-sized benthic invertebrates to be more resistant to disturbance from flooding in streams (e.g. Townsend *et al.* 1997).

We focused our study on 10 streams that flow into lakes Nerka and Aleknagik. Streams were selected to span a natural gradient in salmon density, influenced by environmental factors such as access (e.g. shallow reaches at the entrance of streams) and spawning habitat (e.g. substrate size and stream gradient). Streams are fed by a combination of groundwater, snow-melt and rain. Linear intersite distances between streams ranged from approximately 1 to 43 km. We quantified water temperatures in the study streams using a combination of Hobo data loggers (Onset Co.) and i-buttons (Thermochron). To control for seasonal differences in temperature monitoring across streams, we focused on temperatures during July and August. To verify that this index of stream temperature is indicative of the annual temperature regime that would be experienced by stream invertebrates; we collected stream temperatures over an entire annual cycle in five of our study streams using Hobo data loggers (Onset Co.) (September 2007–September 2008) and estimated cumulative degree-days. Annual cumulative degree-day was strongly and positively correlated with average July and August temperature (r^2 = 0.74).

(b) *Benthic insect phenology*

We monitored insect emergence phenology from June to September, which represents the bulk of the ice-free period. Aquatic life stages of insects were collected every 11.3 $\pm$ 4.3 days (mean $\pm$ 1 s.d.) from June to September using a Surber sampler (0.5 mm mesh; sampling to a depth of 10 cm). We collected 4.8 $\pm$ 1.3 Surber samples at each stream at each sampling event for a total of 1063 samples, distributed over four summers from 2002 to 2005. Each sample was taken from a different sampling location in the stream. Samples were preserved in 70 per cent ethanol. Invertebrates were sorted and identified to the taxonomic resolution shown in the electronic supplementary material, table S1 (Merritt & Cummins 1996). For each taxa in each sample, the body length of 5–10 random individuals was measured using an ocular micrometer. We also noted the life stage of each individual (e.g. pupal stages and dark wing pads (dwp) indicating late instars). These data were used to estimate emergence timing using three different approaches, as outlined below.

We also directly quantified emergence timing in two of the study streams (N-4, low salmon; Pick, high salmon) using traps that captured insects as they emerged into their terrestrial stages (Francis *et al.* 2006). We monitored emergence continuously from 24 June to 10 September in 2004. Emergence traps were boxes (0.5 × 0.5 × 0.2 m; length × width × height) made of hardware cloth, secured above the stream bed with rebar, and covered with 1 mm mesh mosquito netting. These traps were secured flush with the water surface, and were open on the bottom side, allowing insects emerging from the stream to enter the trap. A suspended translucent plastic plate (345 cm^2) coated with Tangle-trap Insect Trap Coating was attached to the underside of the roof of the emergence trap to catch the emerged insects. Emergence was generally quantified over 48 h periods.

(c) *Common rearing experiment*

We used a common rearing experiment to examine if observed *in situ* differences in emergence phenology among streams persisted in the absence of nest-digging salmon. We collected live insects with a Surber sampler from three source streams, N-4 (low salmon), Pick (high salmon) and Hansen (high salmon) and allowed them to grow and emerge in mesocosms. We focused this experiment on chloroperlidae stoneflies and *Cinygmula* spp. mayflies given their abundance across the different study streams. A subsample of 15 insects per taxa were stocked in each mesocosm. Insects were collected prior to salmon entering the streams to spawn. The resultant insect densities were on the lower end of densities observed in streams. Starting sizes were significantly different across the different streams for *Cinygmula* spp. (mean $\pm$ 1 s.d. of length was 6.06 $\pm$ 1.5 for Hansen and 4.4 $\pm$ 0.9 for N-4; two-sample *t*-test, t_{178} = 8.07, $p < 0.001$) but not for chloroperlidae (mean $\pm$ 1 s.d. of length was 6.24 $\pm$ 1.3 for Hansen and 5.84 $\pm$ 1.4 for N-4; two-sample *t*-test, t_{29} = 0.73, p = 0.47).

Mesocosms were plastic totes (68 l; 61 × 40 × 41.9 cm) with a bottom layer of rinsed cobble from the adjacent lake to provide substrate. These mesocosms were covered with 1 mm mesh mosquito netting to retain emerging insects. Mesocosms were fed with water that was a mixture from

Lake Aleknagik and a groundwater spring. Water temperature in each tote was measured every several days with a hand-held thermometer, temperatures ranged from 6 to 14°C and showed no variation among mesocosms. Mesocosms were placed on the beach of Lake Aleknagik, thus subjected to ambient air temperatures and light regimes, and different source populations were randomly assigned among totes. There were six replicates for each of three source streams, for a total of 18 mesocosms. A grizzly bear destroyed three of the mesocosms during the early phases of the experiment (two from Pick Creek and one from N-4). This loss of replication for Pick Creek compromised statistical power. Thus, analyses were constrained to insects from N-4 and Hansen Creek. This experiment was run from 19 June to 24 August, 2004, and the mesocosms were checked every 2–4 days for emerging insects.

(d) Statistical analyses

We estimated *in situ* emergence timing based on benthic samples via three techniques. When possible, we estimated the mean and standard deviation of emergence timing for each taxa for each stream using all of these three indices. However, there were cases where sample sizes were insufficient to estimate one or more of these indices of emergence for a given taxon. Normal distributions were used to describe the emergence patterns of insects, fit to the observed data by using the nonlinear function fitting in SYSTAT (v. 12.0). Data from all years of the study were pooled in the analyses.

(i) Size trajectories

We used size trajectories of benthic insects as an index of emergence timing. Average emergence timing was estimated as the day when the average-sized individual reached the estimated size of emergence. We estimated size of emergence as the average body length of observed pupae (or dark wing pad individuals) for that taxon and stream. When we did not observe individuals that exhibited signs of metamorphosing, we used the strong relationship between maximum size observed and pupae size to extrapolate size at emergence. We estimated the average date of emergence as the intersection between the average size of emergence (as described above) and the linear regression between date and body length of benthic individuals. The linear regression on date and body length was restricted to individuals from dates prior to when individuals started to reach the size of emergence threshold, and excluded smaller individuals from the next generation. In order to estimate variance around the estimated average date of emergence, we ran the regression 500 times on bootstrapped data for each taxa and stream, estimating average emergence for each bootstrap. The lowest 5 per cent bootstrap value was used as a lower confidence interval of emergence timing.

(ii) Abundance of upcoming metamorphosis

We fit normal distributions of emergence timing based on cumulative observations of pupation or observations of individuals in the last instar (e.g. dwp for *Baetis*) for each stream. In this index, peak emergence represents the date when the number of emerging individuals from a given taxa is the highest.

(iii) Proportion of upcoming metamorphosis

We fit normal distributions of emergence timing based on cumulative proportions of pupation or observations of individuals in the last instar (e.g. dwp). In this index, peak

emergence represents the date when 50 per cent of individuals of a population have emerged.

The three indices of emergence timing were strongly related across all taxa and streams (emergence$_{number}$ = $0.57 \times$ emergence$_{size}$ + 4.3, r^2 = 0.73; emergence$_{number}$ = $0.70 \times$ emergence$_{proportion}$ + 9.1, r^2 = 0.66). Using the regression parameters, we converted all estimates from methods 1 and 3 above to be equivalent to the second (i.e. based on abundance of emerging individuals). The emergence timing from all indices were averaged for each taxa and stream. For each stream, we estimated the seasonal flux of aquatic insects by summing the distributions of estimated emergence for all taxa in a stream, with taxa being weighted by their biomass. We used these distributions to calculate the date of 5 and 95 per cent emergence for each stream.

We used general linear models (GLM; SYSTAT 12.0) to assess potential factors influencing emergence timing for the entire community and for each specific taxon (estimated as described above). Factors included stream temperature, stream total phosphorus (TP) concentration during spring (Moore *et al.* 2007), salmon density and taxa. Akaike's Information Criterion, corrected for small sample sizes (AICc), was used to assess model parsimony (Burnham & Anderson 1998). Akaike importance weights for parameters (ω) were also calculated, an index of the relative importance of individual parameters (Burnham & Anderson 1998). Salmon densities were estimated based on the annual surveys of total count of spawning sockeye (live and dead; Rogers & Schindler 2008) from 2001 to 2005 and spawning area estimates from Marriott (1964).

The data from the direct measurement of insect flux and the common rearing experiment were analysed by fitting cumulative normal distributions to the cumulative proportion emerged for each mesocosm using the nonlinear function fitting (SYSTAT 12.0).

3. RESULTS

(a) Community patterns

Study streams varied widely in salmon density, with a 5-year average density ranging from 0.81 to less than 0.01 salmon m^{-2}. Patterns of insect emergence varied dramatically among these streams (figure 1). The average emergence timing across all taxa in the five streams with high densities of salmon was in early July (6–9 July). By contrast, peak insect emergence in streams with lower densities of salmon was weeks later (23 July–7 August). Furthermore, in streams with high densities of salmon, all abundant taxa emerged in the narrow window of early- to mid-July, where 90 per cent of the emerging biomass of insects occurred over a 40-day period (figure 2). This emergence window corresponded to the period immediately prior to the entry of spawning salmon to these streams (figure 1). By contrast, in streams with low densities of salmon, emergence of different taxa was spread across the summer period, ranging from early July to late August, where 90 per cent of emerging insect biomass occurred over a 70-day window (figure 2). Specifically, the date of 5 per cent emergence was not significantly related to salmon density ($p > 0.15$), but the date of 95 per cent of emergence was significantly negatively related to salmon density (r^2 = 0.47, n = 10, p = 0.03).
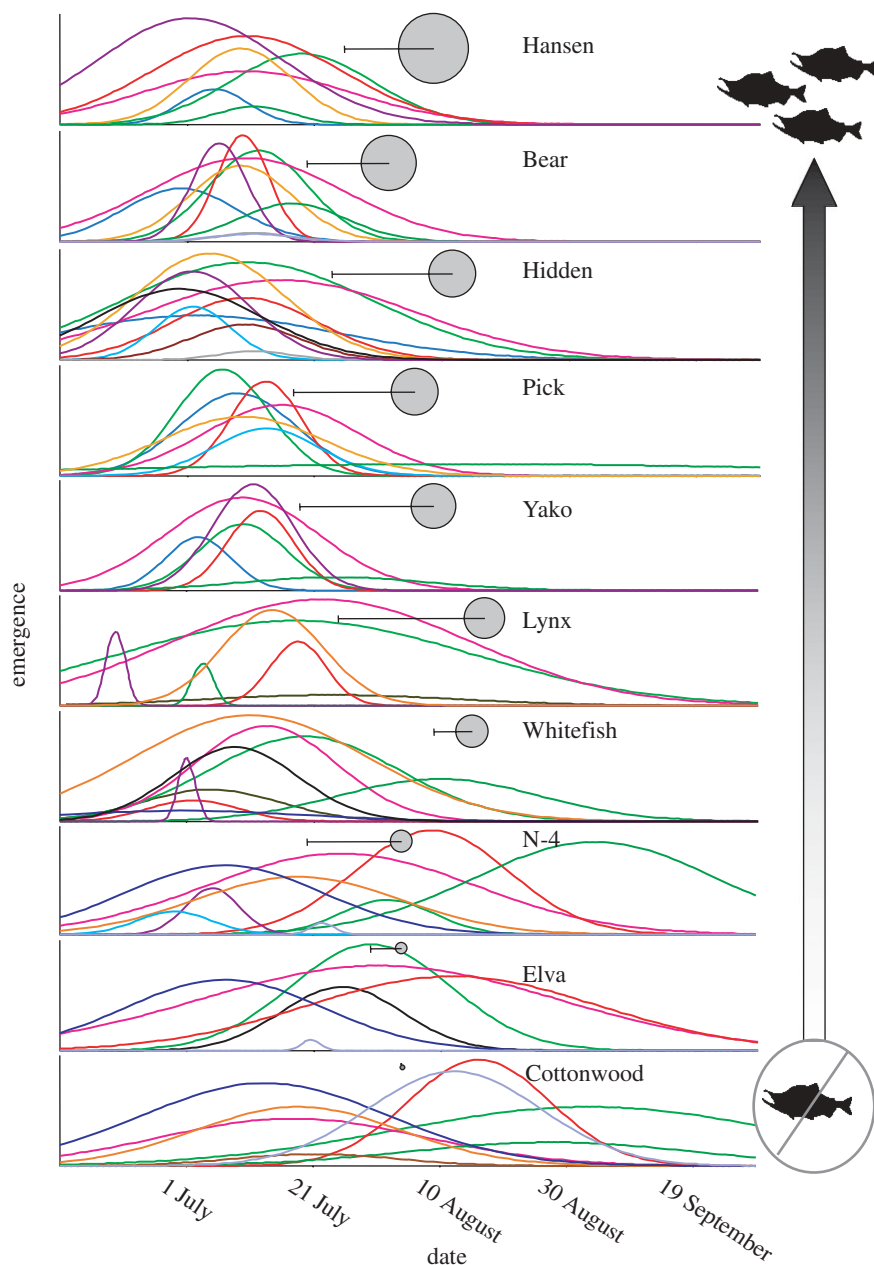
Figure 1. Seasonal patterns of aquatic insect emergence in 10 streams spanning a gradient in salmon density. Streams are ordered from top to bottom by descending spawning salmon densities. Each curve represents the estimated emergence timing of an insect taxon. Curves were normalized such that the height of each curve was relative to the rank abundance of the taxa for each stream. Different coloured curves represent different taxa (Plecopterans: bright green = Chloroperlidae, dark green = *Zapada* spp., aqua blue = *Isoperla* spp.; Dipterans: pink = Chironomidae, Trichopterans: orange = all Trichopterans; Ephemeropterans: black = *Ephemerella inermis*, royal blue = *Baetis bicaudatus*, red = *Cinygmula* spp., purple = *Drunella doddsi*, brown = *Acentrella turbidae*, grey = *Ameletus* spp., lavender = *Epeorus grandis*; see electronic supplementary material, table S1). Grey circles represent timing and magnitude of spawning sockeye salmon. The diameter of the circle is proportional to the average density of spawning salmon, and the centre of the circle is the median date of peak salmon density. The left error bar portrays the median date of entry of spawning salmon.

A combination of factors explained variation in the community-wide patterns of emergence across streams (electronic supplementary material, table S2). First, insect emergence was significantly earlier in streams with higher salmon density ($n = 74$, salmon, $r^2 = 0.21$, $p < 0.0001$). In addition, insect emergence was significantly earlier in streams that were warmer ($n = 74$, temperature, $r^2 = 0.07$, $p = 0.021$). Furthermore, different taxa had significantly different emergence timing ($n = 74$, taxa, $r^2 = 0.37$, $p = 0.001$). In addition, insect emergence was significantly earlier in streams with higher phosphorus levels ($n = 74$, TP, $r^2 = 0.10$, $p = 0.004$). When these different factors were combined in a GLM, the most parsimonious model was one that included all four of these factors ($n = 74$, salmon density, stream temperature, TP and taxa; AICc = 578.6, ΔAICc = 0); together, these three factors explained 64 per cent of the variance in insect emergence timing. The other model that received substantial empirical support (ΔAICc = 1.7) included the factors of salmon density, TP and taxa ($r^2 = 0.61$). We note that all predictor variables were weakly correlated with each other (all
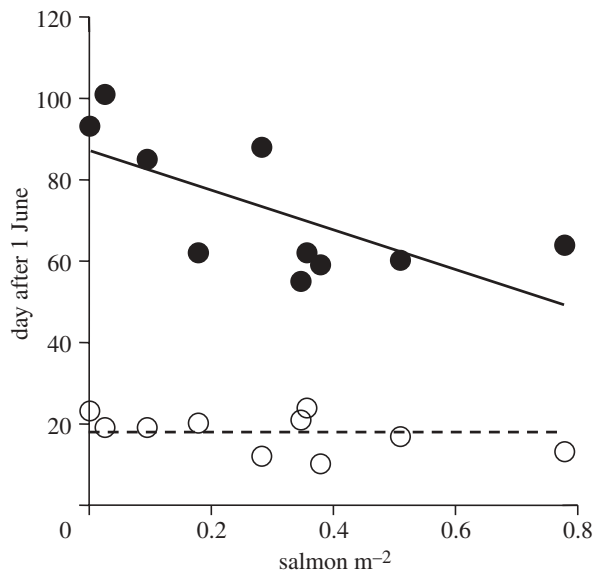
Figure 2. Relationship between salmon density and timing of total insect emergence. Open circles represent the date at which 5 per cent of the insect biomass had emerged and closed circles indicate the date when 95 per cent of insect biomass had emerged. The solid line shows the significant negative relationship between stream salmon density and date of 95 per cent emergence. The dashed line indicates the average date of 5 per cent emergence, as this slope was not significant.

pairwise comparisons $r^2 < 0.05$). Models that included interaction terms between the factors were substantially less parsimonious (electronic supplementary material, table S2). Inclusion of all parameters received substantial support from the data, but salmon was the most important parameter according to Akaike importance weights (ω; electronic supplementary material, table S2).

(b) Taxon-specific patterns

Patterns of emergence for specific taxa were also strongly but differently influenced by salmon density (figure 1). Taxa that emerged early in streams with few salmon tended not to exhibit temporal shifts in emergence timing in streams with higher densities of salmon. For example, both *Baetis bicaudatus* and *Drunella doddsi* emerged in late June and early July across all streams where it was found (figure 1). By contrast, taxa that emerged late in streams with few salmon either exhibited phenological shifts in streams with many salmon (e.g. *Cingymula* spp.) or were found in exceedingly low densities in streams with many salmon (e.g. *Nemouridae* spp.; figure 1). We could estimate emergence timing for three taxonomic groups that were common to all 10 study streams: *Cinygmula* spp. mayflies, chloroperlidae stoneflies and chironomids.

Cingymula spp. mayflies emerged significantly earlier in streams with higher densities of salmon and higher concentrations of TP (figure 3a), and the models that received substantial empirical support were those that included salmon and TP ($n = 10$, $\Delta AICc = 0$, $r^2 = 0.74$) or only salmon ($n = 10$, $\Delta AICc = 0.48$, $r^2 = 0.50$). These mayflies emerged roughly a month earlier in streams with high salmon densities. Stream temperature explained only 17.4 per cent of the observed variance in *Cingymula* spp.
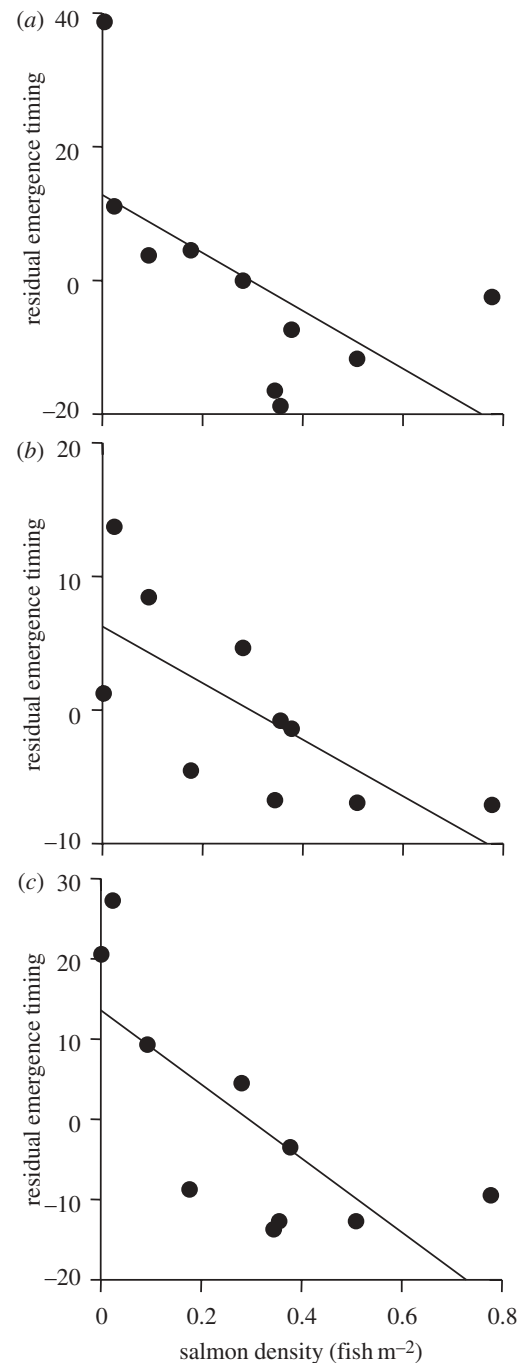

Figure 3. Relationships between salmon density and emergence phenology of three insect groups. Each point represents the estimated average emergence timing for a stream. The *y*-axis is the residual emergence timing after regressing emergence timing with stream temperature (i.e. larger number indicate later emergence). (*a*) Chloroperlidae; (*b*) Chironomidae; (*c*) *Cinygmula*.

emergence timing and was not a significant explanatory factor alone or in concert with other factors (electronic supplementary material, table S2). According to Akaike's ω for parameters, salmon was 5.4 times more plausible than temperature and 1.4 times more plausible than TP in explaining emergence timing of these taxa (electronic supplementary material, table S2).

Peak emergence of chironomids was also earlier in streams with higher densities of salmon; the only model with substantial empirical support was one with only salmon ($n = 10$, $\Delta AICc = 0.0$, $r^2 = 0.50$). Models that

included temperature and TP received considerably less empirical support ($n = 10$, ΔAICc > 4.9 for all; electronic supplementary material, table S2). As a predictor parameter, salmon was 12.3 times more plausible than temperature and 6.8 times more plausible than TP based on Akaike's ω (electronic supplementary material, table S2).

Chloroperlidae also emerged earlier in streams with higher densities of salmon, the only model with substantial empirical support only included salmon as a factor ($n = 9$, ΔAICc = 0, $r^2 = 0.39$). TP alone exhibited some empirical support ($n = 9$, ΔAICc = 2.1, $r^2 = 0.24$), and other models including temperature received considerably less support (electronic supplementary material, table S2). Salmon was 5.4 times more plausible than temperature and 2.3 times more plausible than TP based on Akaike's ω (electronic supplementary material, table S2).

(c) *Direct measurement of insect flux from two focal streams*

Emergence traps that directly measured the flux of emerging insects also revealed differences in emergence phenology between a stream with high density (Pick Creek) and a stream with low density (N-4 Creek) of salmon (electronic supplementary material, figure S1 and table S3). Specifically, mayfly emergence rates were highest in early July in Pick Creek (high salmon), while rates were highest in late August in N-4 (low salmon). Dipteran (predominantly chironomids) emergence was dispersed across the season in Pick Creek, and peaked in late August in N-4. Patterns of caddisfly emergence were more similar across the two streams; however, peak emergence of caddisflies in Pick Creek was in late June, while the peak was around two weeks later in N-4 (early- to mid-July). Stonefly emergence was highest in early- to mid-July in Pick Creek, while their emergence was low and dispersed across the season in N-4. Insects emerged statistically earlier in the stream with many salmon when compared with the stream with few salmon, as confidence intervals for mean emergence date did not overlap across streams (electronic supplementary material, table S3). These emergence patterns also confirmed the patterns we observed using indirect methods, there was a strong positive relationship between the estimated emergence using direct (emergence traps) and indirect methods (size trajectories and pupation) ($r^2 = 0.69$, $p = 0.01$).

(d) *Common rearing experiment*

A common rearing experiment revealed that differences in emergence timing among streams were maintained in the absence of spawning salmon (figure 4; electronic supplementary material, table S4). In the common rearing experiment, *Cinygmula* spp. mayflies from Hansen Creek (high salmon) emerged on 18 July on average, more than two weeks earlier than those from N-4 (low salmon). The direction of this pattern is consistent with that observed *in situ* from stream populations, where Hansen *Cinygmula* spp. emerged on 9 July and N-4 *Cinygmula* spp. emerged on 9 August. In the common rearing experiment, chloroperlidae from the two streams emerged at fairly similar timing, with N-4 chloroperlidae
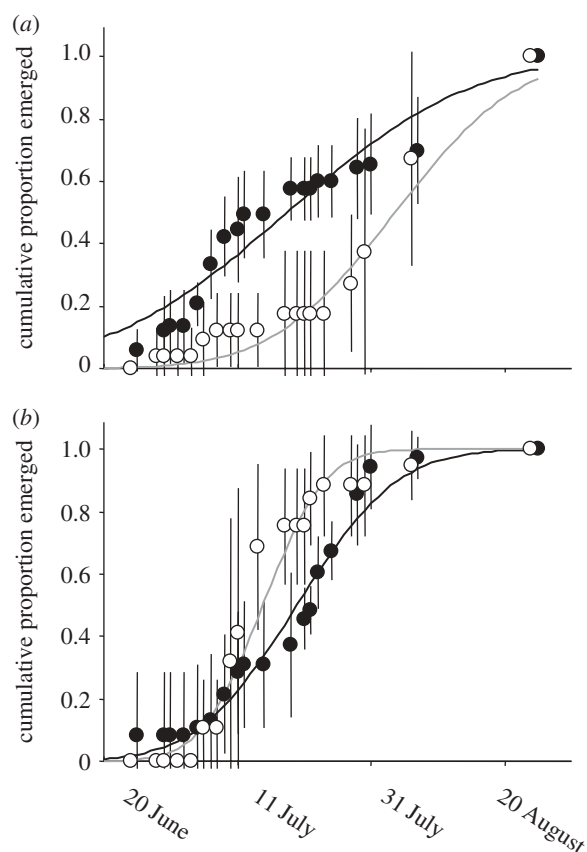
Figure 4. Emergence timing from the common rearing experiment. Shown are the cumulative proportion emerged of (*a*) *Cinygmula* spp. and (*b*) chloroperlidae, averaged across replicates, ± 1 s.d. The curves represent the best-fit cumulative normal distributions. Open circles, N-4 (low salmon); closed circles, Hansen (high salmon).

emerging slightly before Hansen chloroperlidae (5 days). Patterns of *in situ* emergence of chloroperlidae were also fairly similar between N-4 and Hansen (figure 1); after correcting for differences in stream temperature, *in situ* emergence of Hansen chloroperlidae was 6 days later than those in N-4.

4. DISCUSSION

The phenology of organisms is controlled by a combination of abiotic and biotic factors. The most likely abiotic driver of stream insect emergence phenology is water temperature—previous studies have demonstrated that warmer water leads to earlier emergence (e.g. Harper & Peckarsky 2006). In this study, temperature did explain some of the variation in emergence timing, with warmer streams having earlier emergence for most taxa (electronic supplementary material, table S2). Total phosphorus also explained some of the variation in emergence timing, with more nutrient-rich streams having earlier emergence for most taxa (electronic supplementary material, table S2).

Across all analyses, salmon density was a factor in all of the top models and had the highest Akaike importance weight in every aspect of this study (electronic supplementary material, table S2). In streams with high densities of salmon, insects emerged in early July, leaving the stream immediately prior to the onset of salmon

spawning (figure 1). By contrast, peak insect emergence in streams with low densities of salmon was weeks later, in late July to early August. The duration of insect emergence was truncated in streams with high densities of salmon, the period that contained 90 per cent of emerging insect biomass was approximately 30 days shorter in streams with high salmon densities (figure 2). Salmon density was significantly related to large shifts in phenology for the entire community, for coarse taxonomic groups such as chironomids, and for single taxa (*Cinygmula* spp.; figures 1 and 3). These strong relationships between salmon density and aquatic insect emergence raises the question: what is the mechanism of relationship between salmon density and aquatic insect emergence (figure 1)? Below, we discuss several possible mechanisms.

(i) Given the large body of research on the importance of predation in controlling phenology (e.g. Laurila *et al.* 1998), it may be tempting to hypothesize that the observed patterns are driven by predation by adult salmon. However, salmon do not feed as spawning adults (Quinn 2005), so predation by adult sockeye cannot be driving insect phenology.

(ii) Salmon could induce changes in insect phenology because of their effects on stream productivity and growth rates of insects. Spawning salmon can increase concentrations of key limiting nutrients such as phosphorus through excretion and decomposition, and much research has investigated how these nutrients fertilize stream food webs (Janetski *et al.* 2008). This bottom-up fertilization could increase insect growth and, consequently, advance insect phenology. However, during salmon spawning (when nutrient concentrations are elevated), we previously found that bioturbation from salmon nest-digging decreased algal abundance, thereby decreasing available food for grazing benthic insects (Moore & Schindler 2008). After salmon spawning, nutrient concentrations decrease to background levels (Moore *et al.* 2007)—salmon density explained little of the observed stream-to-stream variance in spring TP concentrations ($n = 10$, $r^2 = 0.05$, $p = 0.52$). TP was present in some of the top models (but never replaced salmon density) for analyses on the total community and for *Cinygmula*, but not for other taxa (electronic supplementary material, table S2). While some invertebrate taxa feed directly on salmon carcasses (e.g. Winder *et al.* 2005), the vast majority of insects were not observed in these streams with high densities of salmon when carcasses were available, during or after salmon spawning (Moore & Schindler 2008). For these reasons, it seems unlikely that fertilization from salmon is the primary mechanism by which salmon influence insect phenology.

(iii) Emergence may be a plastic response to increased risk (e.g. Peckarsky *et al.* 2002), perhaps insects are responding to cues from salmon. Given that insects predominantly emerge prior to salmon entering the stream to spawn (figure 1), the cue would need to be from the previous year of spawners. If this were the case, interannual variation in salmon density could translate into interannual variation in emergence timing. The most extreme interannual variation in salmon densities was in N-4, with peak annual salmon densities that ranged from 0.002 salmon m^{-2} during 2003 to 0.16 salmon m^{-2} during 2004. Despite this change, insects did not exhibit interannual variation in emergence timing (electronic supplementary material, figure S2); evidence against emergence plasticity.

(iv) Direct mortality from salmon nest-digging could drive earlier emergence if late emerging individuals are killed by salmon nest-digging. Salmon nest-digging dislodges and kills benthic invertebrates (Peterson & Foote 2000; Monaghan & Milner 2009) and may make them more vulnerable to predation by stream-dwelling fishes (Scheuerell *et al.* 2007). This nest-digging can directly control insect abundance; in a previous study that was performed in the subset of the same streams (Moore *et al.* 2004), we found that excluding salmon from small plots in spawning areas led to a three times increase in densities of Chironomidae relative to reference plots. However, these exclusions did not alter the densities of other insect taxa such as mayflies, which disappeared from streams prior to salmon spawning (even in locations where salmon were excluded from spawning), indicating that seasonal mortality from salmon nest-digging does not directly drive emergence timing for many taxa. Furthermore, phenological differences across salmon densities persisted even when data analyses were restricted to size trajectory-based estimates of emergence; this method of estimating emergence would not be influenced by direct mortality from salmon spawning. In addition, the common rearing experiment indicated that the observed differences in emergence timing for specific taxa (*Cingymula* spp.) persisted in the absence of direct disturbance from nest-digging salmon (figure 4). Therefore, direct mortality by nest-digging salmon probably contributes to observed differences in phenology across streams in some (i.e. Chironomidae), but not most taxa.

(v) Salmon nest-digging could cause selection for earlier emergence timing of aquatic insects. Predictable, severe and frequent disturbances are strong selective agents on life histories (Lytle 2002; Lytle & Poff 2004) and high densities of spawning salmon fit all three of those categories (Moore 2006). Insects that emerge prior to salmon spawning would avoid this potentially dangerous period, with their eggs or young persisting through this disturbance. Our data support the notion that eggs and the smaller larval instars are less vulnerable to salmon disturbance, as has been previously observed for flood disturbance (e.g. Townsend *et al.* 1997). We hypothesize that high densities of spawning salmon drives local adaptation of insect emergence phenology, and if insect species cannot adapt, this biotic disturbance acts as a trait filter (Poff 1997) that excludes late-emerging taxa. Consistent with this

hypothesis, insect taxa that emerged late in streams with few salmon either exhibited a shift in emergence timing (i.e. local adaptation in phenology) or were absent from streams with high densities of salmon (i.e. trait filter). Taxa that emerged early in streams with few salmon did not exhibit these shifts in phenology (figure 1). These results build upon several previous studies suggesting that the life histories of benthic invertebrates may mediate the impact of nest-digging; stream invertebrates with rapid life cycles (such as chironomids) can recover rapidly following salmon disturbance (e.g. Chaloner *et al.* 2004; Lessard & Merritt 2006).

Our data strongly suggest that salmon nest-digging drives insect phenology. However, local adaptation of insect phenology to salmon is predicated on two conditions. First, emergence timing needs to be controlled by variable and heritable traits. This assumption is supported by previous research on insects (e.g. Mousseau & Roff 1989). Second, gene flow between populations must be relatively low so that local adaptation is not swamped. Although this depends on species (and their dispersal abilities), many stream insects do exhibit fine-scale genetic structure associated with limited gene flow (Bohonak & Jenkins 2003). Furthermore, we acknowledge that the taxonomic resolution of insects that exhibited a phenological shift was not to the species level. For example, the *Cinygmula* genus is poorly described, and the specimens we collected did not allow for identification by taxonomic experts. Thus, we cannot be certain that phenological shifts are occurring within a single species. Finally, our common rearing experiment provided evidence that phenological differences persisted in the absence of spawning salmon. However, this experiment does not control for maternal effects or other differences across source populations that were manifested during the earlier phases of the insects' lives. For example, starting sizes of *Cinygmula* from Hansen were larger than N-4, thus these taxa were already on different life-history trajectories.

If nest-digging salmon are indeed driving the evolution of aquatic insect life histories, then our study represents an example of how an ecosystem engineer can drive life-history evolution. There are few examples of how ecosystem engineers, through changing abiotic conditions, drive evolution of other species. For example, Stinchcombe & Schmitt (2006) showed that oak tree leaf litter, through modifying soil microclimate, impacts evolution of an understory annual plant. Our study represents an alternative pathway, how bioturbation by an ecosystem engineer drives evolution of life histories. Ecosystem engineers do not only modify their own evolutionary trajectory (e.g. Odling-Smee *et al.* 1996), but also other species they impact (e.g. Thayer 1979).

Through influencing aquatic insect phenology, salmon modify the timing and duration of resource fluxes from streams to riparian ecosystems (figure 2). While this resource subsidy is shorter in duration in streams with many salmon, it was concentrated during the period prior to salmon spawning when salmon resources are not readily available for riparian consumers. Emerging aquatic insects can be an important source of prey for a variety of riparian consumers, such as bats, spiders, lizards and birds (Baxter *et al.* 2005). Thus, salmon, through changing insect phenology, may indirectly alter the behaviour, distributions and populations of riparian consumers. In this and many coastal ecosystems; salmon migrate, spawn and die in a pulse that is concentrated in time—our study shows that these regular migrations set the rhythms of stream communities. While there is growing concern that climate change can disrupt coupling of organisms' phenologies (e.g. Winder & Schindler 2004), our study suggests that human activities that decrease the abundance of dominant species could also have cascading phenological consequences.

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