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Aerial insect responses to non-native Chinook salmon spawning in a Great Lakes tributary

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ABSTRACT

We investigated whether spawning by non-native Chinook salmon influenced aerial insect abundance in the riparian zone of Thompson Creek, a tributary of Lake Michigan, located in Michigan, USA. Specifically, we evaluated whether decades of salmon disturbance affected patterns of aquatic insect emergence, and how both live salmon and salmon carcasses influenced the abundance of terrestrial carrion flies. Retaining wall timbers from a low-head dam on Thompson Creek were removed, providing a unique opportunity to compare stream reaches that were exposed to the immediate ecological impacts of salmon (i.e., disturbance, subsidy effects) with reaches experiencing decades of spawning activity. Using sticky traps to collect aerial insects, we observed fewer adult aquatic insects in downstream reaches conditioned to decades of salmon disturbance in comparison to naïve upstream reaches. Reduced abundance in downstream reaches was primarily driven by taxa more susceptible to disturbance in the larval life stage (e.g., Diptera: Simuliidae, Ephemeroptera). A greater abundance of adult Chironomidae midges were detected in upstream reaches with higher numbers of spawning salmon and carcasses. Though abundance of adults differed between upstream and downstream reaches, we observed no evidence of early emergence. In addition, carrion fly abundance was greatest at reaches with more live and dead salmon. Evidence from our study suggests that non-native salmon have the potential to influence patterns of aerial insect abundance in riparian zones. Our findings suggest that non-native Chinook salmon can affect aerial insect assemblages; however, the propagating effects of these changes through riparian food webs warrant further investigation.

Introduction

The ecological impacts of salmon in freshwater ecosystems are complex due to their modification of benthic habitats during spawning and because their nutrient and organic matter contributions influence multiple food web pathways (Naiman et al., 2002; Janetski et al., 2009; Collins and Baxter, 2014; Collins et al., 2015). For instance, disturbance by live salmon alters benthic stream characteristics including sediment and flocculent transport (Kondolf and Wolman, 1993; Rex and Petticrew, 2008), standing crops of periphyton and insects (Peterson and Foote, 2000; Moore et al., 2007), and ecosystem metabolism (Holtgrieve and Schindler, 2011; Levi et al., 2012). Salmon alter nutrient dynamics via excretion, re-suspension of adsorbed nutrients, and released nutrients through decomposition of carcasses (Groot et al., 1995; Tiegs et al., 2011). Many aquatic and terrestrial organisms also directly consume salmon tissue and eggs (Gende et al., 2002; Naiman et al., 2002). Ecological responses to disturbance and subsidy effects are also driven by differences in the size of salmon runs and environmental conditions of receiving habitats (Janetski et al., 2009, 2014; Verspoor et al., 2010; Collins and Baxter, 2014).

Though living salmon are constrained to the aquatic environment, their direct and indirect effects extend across ecosystem boundaries through several food web pathways (Collins et al., 2015). Emergence of aquatic insects provides an important linkage to terrestrial food webs (Baxter et al., 2005). In streams receiving salmon subsidies, emerging aquatic insects transport these nutrients to the surrounding terrestrial environment (Francis et al., 2006). Strong engineering effects by salmon have also been linked to the timing of aquatic insect emergence (Moore and Schindler, 2010), suggesting that strong disturbance impacts by salmon may impact the magnitude and timing of emergence. Salmon carcasses are also frequently transported to adjacent riparian and forest habitats by wildlife (Quinn et al., 2009), and subsequently attracting terrestrially-derived insects such as carrion flies (Hocking and Reimchen, 2006; Collins and Baxter, 2014). These flies provide a food resource for insectivores, while also fulfilling other non-consumptive ecological roles including the pollination of riparian plants (Lisi and Schindler 2011). The combined ecological impacts of salmon on aquatic insect communities via disturbance and subsidy effects, coupled with terrestrial insect responses, may greatly influence local abundance of aerial insects in riparian habitats.

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Pacific salmon (*Oncorhynchus* spp.) were introduced into the Great Lakes to establish a new top predator and to control non-native alewife (*Alosa pseudoharengus*) populations in the early 1960s (Mills et al., 1994). Since their introduction, Pacific salmon have exhibited life history patterns consistent to those observed within their native range. These salmon reside, grow, and mature in the open waters of the Great Lakes, then migrate into nearby tributaries to spawn (Ricciardi, 2001). Migrations of non-native salmon into Great Lakes tributaries have been occurring for less than a century, a relatively short period of time when considering that this cycle has occurred in their native range for millennia.

The ecological impacts of these non-native spawning migrations on the structure and function of stream tributaries of the Great Lakes are less understood relative to their native range; however, several studies have explored their impacts. Consistent with the effects in their native range, spawning salmon migrations in Great Lakes tributaries elevate stream nutrient concentrations above ambient levels (Schuldt and Hershey, 1995; Collins et al., 2011). Likewise, spawning can greatly reduce standing crop biomass of stream biofilms and invertebrates during redd construction (Denison and Meier, 1979; Collins et al., 2011; Levi et al., 2012; Janetski et al., 2014).

Non-native fishes can reduce aquatic insect emergence through the direct consumption of insects or indirectly by altering the behaviors of other native fishes (Baxter et al., 2004; Pope et al., 2009; Epanchin et al., 2010; Benjamin et al., 2011). There are uncertainties as to whether decades of spawning by non-native Pacific salmon in Great Lakes tributaries can similarly influence the emergence of aquatic insects. The timing of emergence may shift earlier in the season to avoid mortalities associated with salmon spawning, similar to patterns in their native range (Moore and Schindler, 2010). Alterations to emergence may have additional impacts in terrestrial environments, as adult aquatic insects are an important food resource for many terrestrial organisms (Baxter et al., 2005). Decomposing salmon carcasses also attract terrestrial carrion flies toward the riparian zone (Hocking and Reimchen, 2006; Collins and Baxter, 2014), though this process has not been explored outside salmon's native range. Nevertheless, if these mechanisms are consistent across native and introduced ranges, then the impacts of non-native salmon may extend beyond the confines of the stream and lake environments in the Great Lakes ecosystem.

We investigated how a spawning migration of Chinook salmon (*Oncorhynchus tshawytscha*) influenced the local abundance of aerial insects in stream reaches of a Great Lakes tributary that were either naïve (i.e., first exposure to a spawning event) or conditioned to decades of Chinook salmon spawning. We sought to determine whether decades of spawning by non-native Chinook salmon resulted in earlier emergence by aquatic insects between upstream reaches naïve to salmon and downstream reaches experiencing decades of disturbance. We predicted that decades of spawning would result in reduced abundance of aquatic insects sensitive to disturbance (e.g., Ephemeroptera, Trichoptera), and have no effect on taxa tolerant of disturbance (e.g., Diptera), in the weeks prior to Chinook salmon spawning. Upon the arrival of spawning Chinook, we further predicted increased numbers of short-lived midges (e.g., Chironomidae) in response to subsidies of nutrients and organic matter. Finally, we evaluated whether the number of spawners within reaches influenced the local abundance of terrestrially-derived dipterans. We predicted increased numbers of carrion flies in reaches with the greatest numbers of Chinook salmon.

Methods

Study site and design

Our study was conducted at Thompson Creek, Michigan, USA, a third-order tributary (mean width = 5.3 m) of Lake Michigan, which has been studied extensively due to its high densities (0.14–0.54 m^2) of spawning Chinook salmon (Collins et al., 2011; Janetski et al., 2012; Levi et al., 2012). Chinook salmon spawning typically occurs in late summer or early fall within Thompson Creek. A low-head dam blocked the passage of Chinook salmon into upstream reaches since the 1940s. Consequently, upstream reaches have not been exposed to Chinook salmon and their ecological effects, but downstream reaches have for over a half-century. The Thompson Creek's low-head dam was decommissioned in spring of 2010. Although the dam structure remains intact, the retaining wall timbers were removed, thus allowing non-native Chinook salmon to access upstream habitats. The removal of the retaining timbers provided a unique opportunity to compare reaches that were exposed to the ecological impacts of salmon; however the timescales of exposure varied drastically. For this opportunistic study, the reaches were the experimental unit, and used the upstream vs. downstream dichotomy to describe effects. Upstream reaches ($n = 3$) were naïve to any ecological effects of salmon whereas downstream reaches ($n = 3$) had experienced such effects for decades. The unique circumstances of our study involving dam removal and a sizable salmon migration precluded replication across multiple streams, thus this design is constrained by the inability to completely differentiate effects of Chinook salmon from location (Hurlbert, 1984; Underwood, 1994). These limitations prevented interspersion of treatments; thus, reaches are considered pseudo-replicates (Hurlbert, 1984). Nevertheless, similar approaches have been applied previously for dam removal studies, acknowledging these limitations (e.g., Bushaw-Newton et al., 2002; Orr et al., 2008). We used knowledge of the natural history of the organisms in concert with ecological effects of Chinook salmon to aid in interpretation of patterns between locations. The upstream reference reaches, well above the influence of the dam, were chosen because there were no suitable streams with low-head dams in the area that received runs of spawning salmon. The closest upstream and downstream reaches were spaced approximately 800 m apart. Within the respective upstream and downstream groupings, each reach was spaced 50–150 m apart. At each reach, six cylindrical sticky traps (subsamples) were deployed. Sticky traps were deployed for two-week intervals and then replaced to provide a continuous estimation of aerial insect abundance within the wetted margins of the stream surveyed from August to November of 2010.

Spawner surveys

Visual counts of live Chinook salmon and carcasses were conducted in conjunction with bi-weekly sticky trap sampling. One hundred meter survey transects were conducted upstream and downstream of the dam on Thompson Creek. Surveys were conducted every 2 weeks from August to November of 2010.

Sediment characterization

To determine whether the removal of the retaining wall timbers influenced average substrate size, the pebble counts from upstream and downstream reaches were compared. Data from other studies conducted at Thompson Creek were used to make the pre and post comparison. In 2009, prior to the dam decommissioning, pebble counts ($n = 50$ per subreach) were conducted across three transects in three 100-m subreaches upstream and downstream. In 2013, the pebble counts ($n = 30$) were conducted across three transects in one 100-m reach upstream and downstream. All sampling was conducted using the Wolman pebble count method (Wolman 1954), where random particles were measured using a gravelometer. A step-toe procedure was used to randomly select particles along each transect.

Aerial insect abundance

Temporal responses of aerial insect abundance were measured in Thompson Creek, bi-weekly from September to November 2010. Sticky traps were suspended from stakes 1.2 m above the surface of the water.

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