

Just add water: sources of chironomid drift in a large river floodplain

Gina M. Benigno · Ted R. Sommer

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Abstract Although seasonal floodplains represent one of the most dynamic and productive of aquatic ecosystems, the sources of this productivity are poorly understood. We examined composition and sources of chironomid drift in the Yolo Bypass, the primary floodplain of the Sacramento River. We found that invertebrate drift during winter floodplain inundation is dominated by a single species, the newly identified chironomid *Hydrobaenus saetheri* (Diptera: Chironomidae). In order to determine sources of chironomids in the Yolo Bypass, invertebrates were sampled from several potential sources prior to and during initial floodplain inundation. Rehydration of dried floodplain sediments from several locations showed that *H. saetheri* dominated insect emergence from this colonization pathway. By contrast, *H. saetheri* was not a substantial component of inundated floodplain ponds or of tributary inputs to the floodplain. We conclude that the initial pulse of invertebrate abundance in Yolo Bypass floodwaters is

dominated by chironomid emergence from sediments in multiple regions of the floodplain.

Keywords Floodplain · Chironomidae · *Hydrobaenus saetheri* · Invertebrate colonization · Sacramento River · Yolo Bypass

Introduction

Seasonal floodplains are dynamic and productive components of freshwater ecosystems (Junk et al., 1989). During flood events, secondary production of seasonally inundated habitats can often exceed that of adjoining perennial water sources (Bayley, 1991; Sparks, 1995; Tockner & Stanford, 2002). Moreover, aquatic invertebrate abundance in seasonal floodplains is often substantially greater than in main channels (Gladden & Smock, 1990; Sommer et al., 2004; Grosholz & Gallo, 2006). In temporary aquatic systems such as floodplains, larvae of the dipteran family Chironomidae can be the most abundant invertebrate (Wiggins et al., 1980; Taylor et al., 1999; Sommer et al., 2004). While invertebrate colonization and species succession are well-studied in seasonal ponds (e.g., Jenkins & Boulton, 1998; Hillman & Quinn, 2002; Batzer et al., 1999), fluvial floodplain invertebrate populations have received little attention (Steinhart, 2000a).

Methods of floodwater colonization by invertebrates include aerial colonization by adults

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G. M. Benigno · T. R. Sommer
California Department of Water Resources, Sacramento,
CA 95816, USA

G. M. Benigno (✉)
Department of Biology, California State University Chico,
Chico, CA 95929, USA
e-mail: gbenigno@water.ca.gov

originating from nearby aquatic habitat, passive drift with inflowing floodwaters, dispersal from newly connected wetlands, and emergence from drought resistant life stages (Wiggins et al., 1980). All of these colonization pathways have been demonstrated to occur for floodplain invertebrate communities (e.g., Smock, 1999), and specifically among Chironomidae. Certain chironomid species exploit temporary water sources with several different life history strategies, including desiccation-resistant eggs (Tronstead et al., 2005) and larvae (Cantrell & McLachlan, 1982), drought resistant cocoon formation and diapause (Grodhaus, 1980; Steinhart, 2000a, b), and rapid colonization by ovipositing females (Clement et al., 1977). Although several of these potential floodplain colonization pathways have been examined for zooplankton (Jenkins & Boulton, 2003), we are not aware of similar work on the colonization of floodplain waters by aquatic insects.

In the present study, we focus on chironomid larvae because they are ubiquitous in seasonally aquatic habitats (Williams, 1996). Chironomid larvae are especially important as a significant food source in winter food webs because of the scarcity of other food sources during this time (Euliss & Grodhaus, 1987; Sommer et al., 2001a). Our focus was on the first flood pulse of the season in order to track colonization pathways of the initial dominant taxa. We identified three potential sources of chironomid larvae: dry floodplain sediments, inundated floodplain ponds, and tributary input. In order to evaluate the relative contribution of each, we compared invertebrate samples collected from each source with floodplain drift invertebrates collected during the first flood pulse of the season. Our study objectives were to identify sources of the abundant chironomid taxa of floodplain waters, and to gain insight into the colonization pathways and life history strategies of dominant floodplain Chironomidae.

Study site

Our study site is the Yolo Bypass, the main floodplain of the Sacramento River (Sommer et al., 2001b; Fig. 1). Soon after inundation, chironomid larvae become the most abundant invertebrate in Yolo Bypass floodwaters (Sommer et al., 2004). The seasonally inundated 24,000 ha leveed floodplain

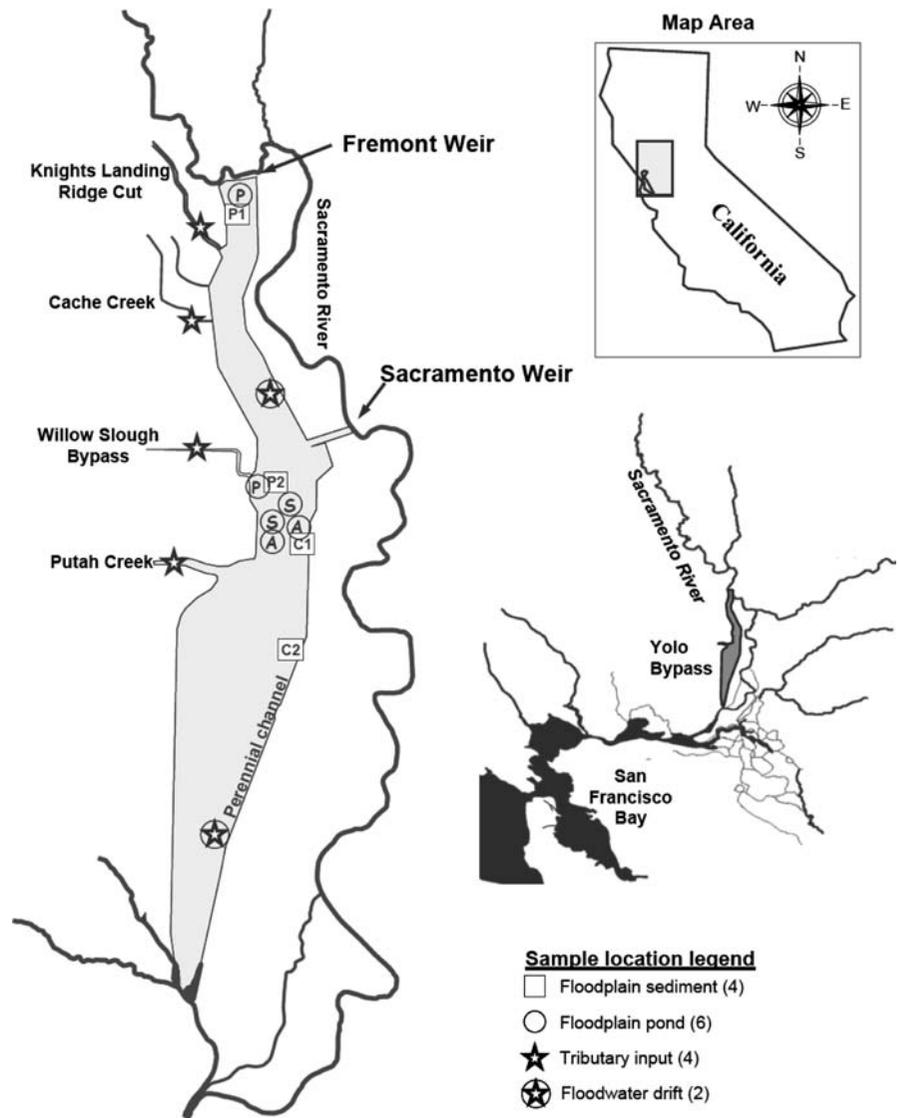
conveys floodwaters diverted from the Sacramento River at the Fremont and Sacramento Weirs, and receives input from four tributaries—Knights Landing Ridgecut, Cache Creek, Willow Slough, and Putah Creek—which enter the west side of the floodplain. Sacramento River water spills into the floodplain during winter and spring high-flow events in approximately 2 out of 3 years, causing extensive flooding throughout the Bypass. During the wet season, tributary input is substantial and causes localized flooding at times when Sacramento River water is not spilling into the system. At the southern end of the Bypass, floodwaters drain into the Sacramento River Delta. Typically, the Yolo Bypass is partially to fully inundated January–March. Perennial ponds and a tidally influenced perennial channel remain after floodwaters recede. During the dry season, land in the Yolo Bypass is managed for agriculture and wildlife. Summer agriculture use includes rice, row crops, and livestock grazing. Much of the land is managed as natural grasslands for wildlife habitat. In order to provide habitat for migratory waterbirds, seasonal wetland ponds within the Yolo Bypass are flooded during late fall, prior to natural inundation events.

Methods

Flow data for the Yolo Bypass and Cache Creek were obtained from gauging stations reported by California Data Exchange Center (<http://www.cdec.water.ca.gov>). Stream flow data for Putah Creek were obtained from Solano County Water Agency. Willow Slough and Knights Landing Ridgecut were not gauged, so approximate flow values were calculated using relationships based on available interdam runoff data for a known area of neighboring watershed with similar landscape characteristics, scaled by watershed size (California Department of Water Resources, unpublished analyses). Water temperatures averaged 8.7°C in the main channel of the floodplain during the study period.

Dry floodplain sediment samples were collected to assess the presence of desiccation-resistant taxa over summering in the dry floodplain. In November 2004, prior to the wet season, dry floodplain sediments were collected adjacent to two types of perennial water sources: pond and channel (Fig. 1). At each sample

Fig. 1 The Yolo Bypass floodplain in relation to San Francisco Bay, and invertebrate sampling locations within the floodplain: Dry floodplain sediment samples were collected at riparian and inland habitats from perennial pond (P1 and P2) and perennial channel (C1 and C2) locations; floodplain pond samples were collected at 2 perennial pond (P), 2 seasonal wetland (S), and 2 agricultural wetland (A) locations; invertebrate drift samples were collected at inflowing tributaries and at two floodplain channel locations



site, riparian samples were collected within 2 m of the water's edge, and inland samples were taken 50 m inland from the water source. Three replicates each of riparian and inland sediment samples were taken at four sample sites. Sediment samples were approximately 45 × 30 cm in area, and 10 cm deep. Standing live vegetation was clipped and removed, and care was taken to keep the sediment intact as each sample was placed in an individual plastic bin (45 × 30 × 30 cm). Sediment bins were taken to indoor animal holding facilities at the nearby UC Davis Center for Aquatic Biology and Aquaculture where they were flooded to a minimum depth of

10 cm, and covered with 1-mm-mesh lids to prevent contamination and retain any emerging adult insects. Water depth was maintained and samples were exposed to ambient daylight and temperature for the duration of the study. Invertebrates emerging from rehydrated sediments were collected 4, 7, 11, and 14 days after flooding by sweeping a 100- μ m hand net twice through the flooded area of each bin. Net contents were preserved in 70% ethanol. The small mesh size was used in order to collect small early instar larvae as they first emerged from the sediments.

Inundated floodplain ponds were sampled in November and December, prior to floodplain

inundation, to determine if these waterbodies were a source of floodwater Chironomidae. We collected samples from three types of floodplain ponds: perennial pond, seasonal pond, and agricultural water (Fig. 1). Perennial ponds occur naturally on the floodplain. Seasonal ponds are managed wetlands flooded early to provide water bird habitat. Agricultural water sampled includes irrigation canals and flooded fields. Two sampling sites were selected for each standing water type. A 500- μm , 12-in-diameter D-ring dip net was used to collect samples at each of the six sample sites. Samples were collected by scraping the flat edge of the net across 2 m² of substrate, and preserved in 70% ethanol.

Tributary input to the floodplain was sampled to detect chironomid larvae entering the floodplain with inflowing water (Fig. 1). Five samples were collected between December 30 and January 20. Samples were collected at each location by placing a drift net (45 \times 30 cm mouth, 1 m length, 500- μm mesh) into the surface flow for 10 min during mid-morning. A larger mesh size (500- μm) was used for the pond and drift samples than for the hand net sampling due to the large amount of organic debris in these types of samples, which would have quickly clogged smaller mesh. Although the larger mesh size was likely less efficient at collecting smaller taxa and early instars, they were not entirely excluded from the drift nets because the high organic matter load created a finer effective mesh. Invertebrate drift generally exhibits diel abundance patterns (Brittain & Eikeland, 1988); by consistently collecting during the same mid-morning time period, we hoped to minimize variability due to these patterns. Drift nets were fitted with a General Oceanics flow meter to measure volume of water sampled. Because of high organic matter content, drift samples were first fixed in 10% formalin and then transferred to 70% ethanol for preservation.

Floodplain invertebrate drift ("floodplain drift" samples) was sampled from the perennial floodplain channel at two locations (Fig. 1). At each location, six samples were collected between December 29 and January 26 using the methods described for tributary sampling. All specimens were identified to family using Merritt & Cummins (1996). Chironomid larvae and pupae were identified to genus using keys in Merritt & Cummins (1996) and an unpublished key for chironomid larvae (Peter Cranston, UC Davis,

unpublished document). Adult Chironomidae were identified only to family due to difficulty of identification (Peter Cranston, pers. comm.). When possible, emerging adults with pupal exuviae still attached were identified to genus. Larval instar stages were determined based on mandible length relationships.

Total chironomid emergence from sediments over the 2-week sample period following rehydration was compared using a two-way ANOVA. Statistical analysis was conducted on the dominant chironomid, *Hydrobaenus saetheri* (see below) because it was the only species collected in substantial numbers in each sample. Densities of chironomids in the three different floodplain pond types were compared using a one-way ANOVA. Several components used different sampling gear and effort, so we did not analyze quantitative differences among the possible chironomid sources. Instead, we looked for major qualitative differences in the relative abundance of the primary types of chironomids.

Results

Initial floodplain inundation in winter 2004 was entirely due to tributary inflow, with no direct Sacramento River inputs. Localized shallow flooding was limited to the northern half of the floodplain where tributaries enter the system. Each of the four tributaries showed a single major flow pulse during the study period, although the magnitude of the flow pulse was greatest for the two northernmost tributaries (Fig. 2). Based on the historical record, the peak flow in the floodplain during the sampling period was approximately a 1.5-year recurrence event.

Chironomid larvae were collected from the three potential sources sampled. From the floodplain sediment samples, 227 individuals representing five genera were collected; 153 individuals from 13 different genera were collected from floodplain ponds; and 70 individuals from 14 genera were collected from tributaries entering the floodplain. Relative abundance of chironomid genera for the different sample types is summarized in Table 1.

Chironomid larvae collected from rehydrated sediment samples were dominated by a single species, *Hydrobaenus saetheri* (Fig. 3). *Hydrobaenus saetheri* was present in sediments collected from all sample

Fig. 2 Flow data (m³/s) for the Yolo Bypass and inflowing tributaries during the study period with sample collection dates indicated. Sediment collection and standing water sample dates are indicated with symbols. The tributary and floodplain drift collection period is indicated by shading

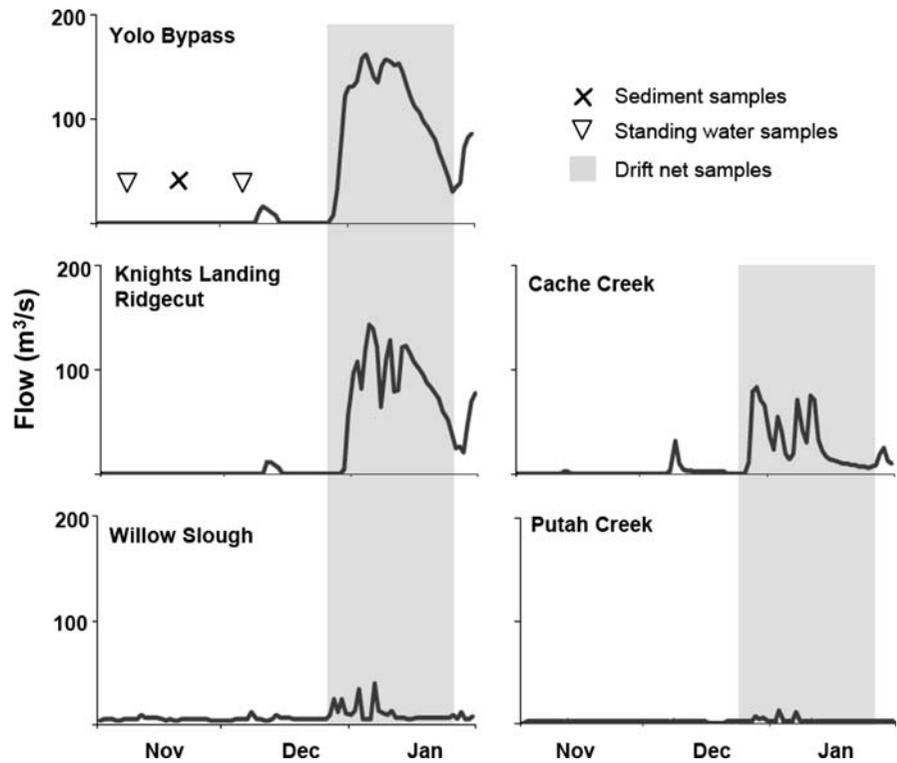


Table 1 Relative abundance of all chironomid genera comprising greater than 1% of the total collection for each habitat type sampled

Habitat type	Floodplain sediment	Floodplain ponds	Tributary input	Floodwater drift
<i>Chironomus</i> sp.	–	3.3	14.9	–
<i>Cladopelma</i> sp.	–	3.3	–	–
<i>Corynoneura</i> sp.	–	20.3	–	–
<i>Cricotopus</i> sp.	–	3.3	13.5	–
<i>Dicrotendipes</i> sp.	–	–	6.8	–
<i>Glyptotendipes</i> sp.	–	–	8.1	–
<i>Goeldichironomus</i> sp.	2.6	–	–	–
<i>Hydrobaenus</i> sp.	74.0	2.0	8.1	99.2
<i>Limmophyes</i> sp.	9.3	47.7	–	–
<i>Nimbocera</i> sp.	–	7.8	–	–
<i>Orthocladus</i> sp.	–	–	16.2	–
<i>Paratanytarsus</i> sp.	13.2	7.2	5.4	–
<i>Procladius</i> sp.	–	1.3	16.2	–
<i>Tanytarsus</i> sp.	–	1.3	–	–
<i>Thienemanniella</i> sp.	–	–	2.7	–

locations, and accounted for 74% of the total chironomid larvae collected from rehydrated sediments. Although pond and channel locations were not paired, differences were seen in chironomid emergence adjacent to the two water source types. Sediments collected

close to floodplain channels were a significantly greater source of *H. satheri* larvae than sediments collected near floodplain ponds (Table 2; *P* = 0.014). While more larvae appeared to be collected from riparian sediments than from inland sediments,

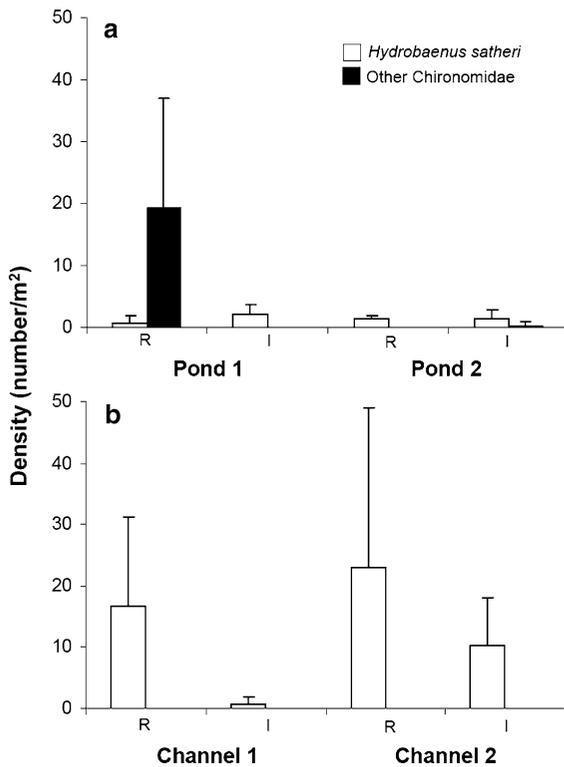


Fig. 3 Average density (number/m²) and standard deviation of chironomid larvae collected from rehydrated riparian (R) and inland (I) sediments collected near perennial ponds (a) and channels (b)

this difference was not statistically significant ($P = 0.089$). Early (2nd and 3rd) instar *H. saetheri* larvae were collected 4 days after rewetting of dried floodplain sediments; 4th instar larvae were present in collections after 7 days, and by 2 weeks after rewetting all larvae collected were 4th instar or pupae. Lengths of *H. saetheri* larvae collected from rehydrated sediments increased from 2.4 ± 0.5 mm (mean \pm SD) 4 days after rewetting, to 7.0 ± 0.6 mm after 2 weeks.

Overall abundance of chironomid larvae collected in floodplain pond samples varied between sites (Fig. 4). *Hydrobaenus saetheri* was uncommon in

these samples. Rather, *Limnophyes* sp. and *Corynoneura* sp. dominated collections from pre-inundation floodplain wetlands (48% and 20% of total chironomid larvae, respectively). Chironomid abundance was highest at the perennial pond sites, and lowest at the agricultural wetland sites, although the results were not statistically significant (One-Way ANOVA; $P = 0.216$). Our small sample size ($n = 2$ of each pond type) may have limited our ability to reliably detect statistically significant differences.

Chironomid drift abundance was higher in floodplain channels than in the tributaries (Fig. 5). While *H. saetheri* was rare in tributary drift, it accounted for 99% of the Chironomidae collected in floodplain drift. Most of the chironomid drift in floodplain channels was incompletely emerged adult *H. saetheri* with pupal exuviae still attached. Drift densities of *H. saetheri* peaked at 550/m³ 2 weeks after floodplain inundation. Chironomids collected from tributary drift were primarily mature adults which were identified only to family.

Discussion

Like seasonal floodplain habitats in other regions (Gladden & Smock, 1990; Grosholz & Gallo, 2006), invertebrate drift in floodwaters of the Yolo Bypass is significantly greater than invertebrate drift in the main channel of the Sacramento River (Sommer et al., 2001a, 2004). In the Yolo Bypass, the enhanced abundance is largely due to abundant chironomid larvae. This seasonally abundant food source supports wildlife populations during critical winter breeding and rearing periods; chironomid larvae are major winter dietary components of migratory waterfowl (de Szalay et al., 1999) and juvenile Chinook salmon (Sommer et al., 2001a).

We found that the initial peak in abundance of floodwater invertebrate drift in the Yolo Bypass is

Table 2 ANOVA results comparing *Hydrobaenus* sp. emergence from floodplain sediment sample types (Two-way ANOVA: *Hydrobaenus* versus Water, Habitat)

Source	DF	SS	MS	F	P
Water type: (Pond vs. channel)	1	771	771	7.29	0.014
Habitat: (Riparian vs. inland)	1	280	280	2.65	0.119
Interaction	1	338	338	3.19	0.089
Error	20	2114	106		
Total	23	3502			

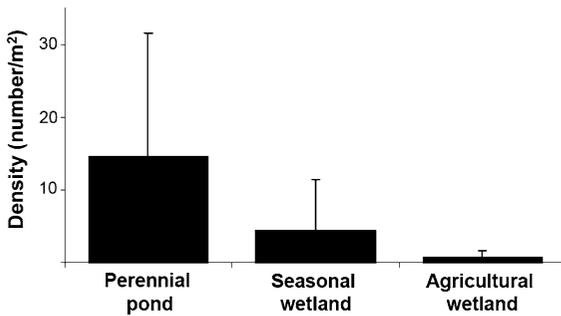


Fig. 4 Average density (number/m²) and standard deviation of chironomid larvae collected from perennial ponds, seasonal ponds, and agricultural water within the floodplain

dominated by a single species, *H. saetheri*, a species that has been described based on material collected from this study (Cranston et al., 2007). Our first study objective was to identify sources of the abundant chironomid taxa of floodplain waters. Based on our results, it appears that *H. saetheri* initially colonizes floodwaters primarily by emergence from floodplain sediments. A key observation was that *H. saetheri* was the numerically dominant chironomid that emerged from experimentally rehydrated floodplain sediments, while chironomid species common in floodplain ponds were not a substantial component of floodwater drift. Tributary drift samples contained a fairly diverse range of chironomid larvae, but the genera collected also were not a major component of floodwater drift. The presence of adult Chironomidae in surface floodwater drift indicates that aerial oviposition is a possible colonization pathway for floodwater chironomid larvae. However, minimum maturation time required to complete larval development can range from weeks to years (Merritt & Cummins, 1996). The immediate presence of late aquatic stages of *H. saetheri* in both rehydrated sediments and in floodwater drift indicates that emergence from sediments is the main colonization pathway.

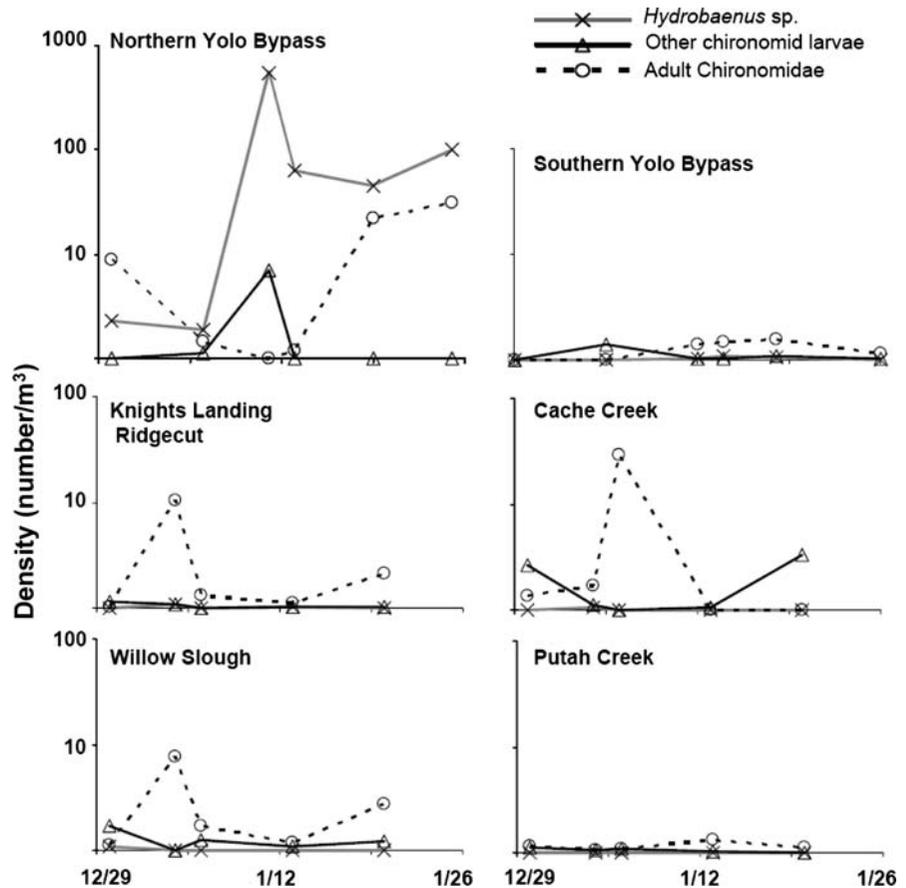
A second objective of our study was to gain insight into the life history strategies of Chironomidae in floodwater drift. It appears that early instar *H. saetheri* can overwinter in dried floodplain sediments and rapidly commence development once sediments are rehydrated. This life history strategy is consistent with other floodplain specialist species of the genus *Hydrobaenus* (e.g., *H. kondoi* in Japan, Kondo, 1996; *H. lugubris* in Germany, Steinhart, 2000a, b). These

species form cocoons and enter an obligatory diapause period as 2nd or 3rd instar larvae, allowing them to overwinter in dried floodplain sediments. Upon rehydration, active larvae emerge in large numbers. The winter-dominant Yolo Bypass chironomid, *H. saetheri*, likely follows this same cocoon formation and winter emergence pattern, which leads to extraordinary abundance in floodplain waters soon after floodplain inundation.

Our study results are most relevant to the initial period of winter flooding. They do not necessarily reflect diel, intra- or interannual trends. It is likely that the dominant chironomid taxa change over time, as floodplain invertebrate taxa shift from lotic to lentic assemblages following floodplain inundation (Grosholz & Gallo, 2006). Year to year variation in hydrology is also likely to be important; Sommer et al. (2004) found lower densities of Diptera (primarily Chironomidae) in Yolo Bypass drift in a dry year compared with two wet years. This may help to explain why patterns for the two-floodplain drift sampling locations yielded very different results (Fig. 5). The modest flood event during our study inundated habitat adjacent to the northern drift sampling station, but habitat at the southern site did not flood. Consistent with our hypothesis that *H. saetheri* colonize floodwaters by emerging from inundated sediments, our northern floodwater sampling station showed much higher densities of chironomid drift than the southern sampling station where flooding did not occur. Much higher drift densities have been observed at the southern sampling station in wetter years (Sommer et al., 2004).

This study has demonstrated the ecological importance of floodplain sediment as an important source of the initial peak of chironomid abundance in floodwater drift in the main floodplain of the Sacramento River. The immediate presence, rapid growth, and high abundance observed after floodplain inundation indicate that these larvae are a readily available food source for fish and wildlife utilizing floodwater habitat. These findings provide useful insights for the management of floodplains for invertebrates and higher trophic levels including fish and wildlife. While artificial maintenance of managed wetland ponds can be important for waterfowl (Euliss & Grodhaus, 1987; de Szalay et al., 1999), our study suggests that fallow dry periods may be particularly important to maintain aquatic food webs. In addition,

Fig. 5 Density (number/ m^3) of chironomids in drift samples collected from the Yolo Bypass floodplain and four inflowing tributaries



it appears that the spatial distribution and hydroperiod of seasonal habitats could affect chironomid abundance. Greater emergence of *H. saetheri* larvae occurred from sediments collected near the perennial floodplain drainage channel. This is consistent with findings of greater invertebrate emergence from floodplain sediments with more frequent inundation (Boulton & Lloyd, 1992) and longer hydroperiod (Gladden & Smock, 1990; Dietz-Brantley et al., 2002). Land use and other anthropogenic factors can also influence the productivity due to sediment emergence (Angeler & Garcia, 2005). Information about these and other aspects of the ecology of floodplain sediments is therefore critical to maintaining the high productivity and diversity of seasonal habitats.

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